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Invited Review

Resurrecting the ghost of green revolutions past: The brown planthopper as a recurring threat to high-yielding rice production in tropical Asia

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ABSTRACT

The brown planthopper (BPH), *Nilaparvata lugens* (Stål), which periodically erupted in tropical Asian rice before the 1960s, became a major threat after farmers adopted green revolution technologies in the 1960s. Management and policy changes in the 1980s and 1990s emphasized non-insecticidal tactics to avert BPH outbreaks. However, insecticides have resurfaced as the primary means for controlling rice insect pests and tropical Asian countries have recently experienced planthopper outbreaks in record numbers. Our review of factors that have contributed to the outbreaks points to insecticides as the most tangible outbreak factor primarily because of their harmful effects on natural enemies. BPH resistance to insecticides and especially imidacloprid has increased the probability of outbreaks as farmers have applied increasing quantities of insecticide in an attempt to combat resistant populations. Similarly, heavy use of nitrogen fertilizer, especially on hybrid rice, has increased the potential for outbreaks. Other factors triggering outbreaks are less documented, but we discuss the possibility that the high outbreak synchrony in geographically separated populations of BPH may suggest a “Moran effect” such as climate that promotes an environment favoring above-average increases in BPH populations. Also, we hypothesize that BPH functions as a metapopulation and, as such, periodic outbreaks could be a natural phenomenon requiring resupply of planthoppers into vacant areas to ensure genetic linkage among subpopulations. We conclude with a series of recommendations for research and policy changes aimed at better understanding the cause of BPH outbreaks and for developing sustainable management practices to prevent future outbreaks.

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Background to problem

Green revolution transforms Asian rice

Beginning in the 1960s, the production of rice (*Oryza sativa* L.) in tropical Asia evolved from a low-yielding traditional system that used rice landraces developed by farmers and produced with nominal artificial inputs to a high-yielding scheme founded on genetically improved cultivars, synthetic fertilizers, and synthetic pesticides. IR8 developed by the International Rice Research Institute (IRRI) and introduced into the Philippines in 1966 was the first high-yielding rice cultivar for tropical farmers. In favorable growing environments, IR8 produced $\approx 10 \text{ t ha}^{-1}$ (harvested grain) compared to $\approx 1 \text{ t ha}^{-1}$ for traditional rice (De Datta et al., 1968). IR8 quickly spread throughout tropical Asia and contributed significantly in elevating rice production in areas that faced rice shortages (Conway and Toenniessen, 1999).

“Green revolution” technologies (IR8 and later improved cultivars, controlled irrigation, synthetic fertilizers, and pesticides) quickly displaced traditional rice farming methods in many areas (Jennings, 1974). In the Philippines, >40% of the riceland was planted with improved cultivars within 3 years after the release of IR8 in 1966 (Huke and Huke, 1990). Philippine rice production attributable to the new technologies increased an average of 12.4% annually from 1967–1968 to 1971–1972 (Jennings, 1974). The new rice cultivars reached harvest maturity relatively quickly (105–110 days for later improved varieties from the Philippines, Bangladesh, and India) compared to the traditional cultivars (160–200 days) (De Datta, 1981). This meant that farmers with irrigation systems could yearly harvest two and sometimes three crops from the same rice paddy. Monocultures of the new high-yielding cultivars appeared year round in many irrigated areas. Artificial fertilizers and insecticides became trademark features of the high-yielding system. Without fertilizers, the genetically improved cultivars yielded no better than the traditional cultivars (De Datta et al., 1968). Farmers perceived chemical insecticides as insurance to protect investments in fertilizers and other inputs. Insecticide use spiraled in the high-yielding production systems as illustrated in several Philippine provinces. In the decade before the availability of IR8 in 1966, about 60% of Philippine farmers were using some insecticides; by the late 1970s, nearly 70% of farmers planting high-yielding rice cultivars routinely applied insecticidal

treatments to the rice (Kenmore et al., 1987). In the Philippine province of Nueva Ecija, a major irrigated rice area of Southeast Asia, Litsinger (2008) found that farmers treated high-yielding rice (seedbeds and main crop) 1–10 times (average of 1.4–3.2) per crop using 40 different insecticides (comprising 64 distinct brands). National agricultural research and education systems (NARES) and chemical companies inspired by the green revolution recommended insecticides to rice farmers as a means to boost crop yield and avert catastrophic pest losses. Insect epidemics, which, ironically, the insecticides often triggered, reinforced the farmers’ fear of insect pests and the need to apply the chemicals (Heong et al., 1994; Bandong et al., 2002; Litsinger, 2008). The farmers continued to treat the rice routinely even after breeders had incorporated insect resistance into the high-yielding cultivars (Heinrichs, 1992; Litsinger, 2009). Some governments provided insecticides at low costs to ensure that farmers would regularly treat their rice crops (Kenmore, 1991; Gallagher et al., 2009). In Indonesia, for example, 1986 government subsidies for pesticides amounted to \$179 million (1995 U.S. dollars), which was about 0.17% of the country’s GDP and 0.8% of the total government expenditure (World Bank data cited in Gallagher et al., 2009). From 1976 to 1987, Indonesian government expenditure on pesticides totaled nearly \$1.5 billion (1995 U.S. dollars) (World Bank data cited in Gallagher et al., 2009). Yet, few farmers were trained to use insecticides properly. Rice farmers in the Philippines surveyed by Heong et al. (1995a) applied some 80% of the insecticide sprays at the wrong pest or when pests were not a problem. Because of poor application equipment, >75% of an insecticide’s active ingredient ended up in the rice fields’ water instead of the intended target area (Heong et al., 1995a). Despite the farmers’ belief that insecticides were essential to protect rice yield, numerous evaluations showed that the insecticides were rarely necessary for profitable rice farming (Waibel, 1986; Pingali and Roger, 1995; Matteson, 2000).

BPH impedes the green revolution

An unanticipated problem arising with the rice green revolution was the recurring outbreaks of the brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae). This insect develops on cultivated rice, several species of wild *Oryza* (Pathak and Heinrichs, 1982;

Claridge et al., 1985; Romena and Heinrichs, 1989), and the weed *Leersia hexandra* Swartz (Heinrichs and Medrano, 1984; Claridge et al., 1985). Diagnostic markers and genetic distance analysis using RAPD-PCR revealed the possibility of sibling species in the BPH complex between rice-caught and *Leersia*-caught populations (Latif et al., 2008). BPH feeds by inserting its stylets into the vascular tissue of plant leaf blades and leaf sheaths and ingesting the sap (Sōgawa, 1982). Populations concentrate at the base of the plant and reach maximum density after canopy closure (Reissig et al., 1986). Heavy infestations can cause the complete drying and wilting of rice plants, a condition known as “hopperburn” (Bae and Pathak, 1970). The pest also transmits the plant pathogens ragged stunt virus and grassy stunt virus (Ling, 1972; IRRI, 1983; Hibino et al., 1985; Cabauatan et al., 2009). BPH may complete some 12 generations per year in the tropics (Dyck et al., 1979) but only ≤ 3 generations in temperate areas (Kuno, 1979; Perfect and Cook, 1994). The northern geographical limit of winter breeding for the species is around the Red River Delta of Vietnam (Kisimoto, 1976). It occurs throughout the year in the Asian tropics and subtropics and expands its range northward when rice becomes available in temperate areas of China, India, Japan, and Korea (Perfect and Cook, 1994). Migration aided by weather frontal systems ensures that some members of a migrating population will reach distances of several hundred kilometers (Kisimoto, 1976, 1979; Kisimoto and Rosenberg, 1994; Turner et al., 1999; Zhu et al., 2000b; Otuka, 2009). However, BPH does not survive the winter in temperate areas. Infestations of BPH in the temperate environments originate from yearly migrations from tropical Asia and China (Cheng et al., 1979; Kisimoto, 1979; Kisimoto and Rosenberg, 1994; Perfect and Cook, 1994; Zhu et al., 2000b; Otuka, 2009; Watanabe et al., 2009). During autumn, return migrations (north-to-south) of BPH populations have been studied over China and India (Riley et al., 1991, 1995). Such return migrations may help explain how long-distance migrants are maintained in southern overwintering populations.

According to references cited by Dyck and Thomas (1979), Heinrichs (1994), and Mochida and Okada (1979), planthopper outbreaks occurred in rice hundreds of years before the green revolution started in the 1960s. Outbreaks reputedly occurred in Korea around AD 18 (Paik and Paik, 1977; Dyck and Thomas, 1979) and in Japan as early as AD 697 or 701 (Miyashita, 1963; Grist and Lever, 1969; Konishi and Ito, 1973; Dyck and Thomas, 1979). After the discovery of whale oil as an insecticide in 1670, followed by the use of slaked lime and bitter (Konishi and Ito, 1973), leafhoppers (Hemiptera: Cicadellidae) and planthoppers reputedly surged in Japan (Miyashita, 1963). Confirming such early reports as BPH outbreaks presents taxonomic problems, as the species *N. lugens* was not described until 1854 (Dupo and Barrion, 2009). However, Fiji, Japan, Korea, Solomon Islands, Taiwan, and perhaps other countries had confirmed BPH outbreaks before 1966, the year that IR8 was introduced (Dyck and Thomas, 1979; Kenmore, 1980). Before the green revolution, the most notable outbreaks were in temperate areas, notably Japan and Korea. Outbreaks in the tropics were generally localized and occurred infrequently (Dyck and Thomas, 1979; Kenmore, 1980).

In 1977, in response to the threat that BPH outbreaks presented to the new high-yielding tropical rice, IRRI (1979) convened an international conference to review the problem and to identify priority research and education programs leading toward better management of the pest. The conferees concluded that Intensification of rice cropping and its associated technologies had brought significant changes to the rice landscape, which encouraged BPH outbreaks, especially in irrigated areas where farmers planted 2 or 3 rice crops per year. The continuous succession of monocultures over large areas provided abundant BPH habitat that enabled the populations to reproduce nearly year round, and the heavy use of nitrogen fertilizer likely increased the pest's reproductive potential (Dyck et al., 1979). Frequent use of insecticides exacerbated the problem by killing natural enemies that regulated BPH's populations. The conferees emphasized the importance of developing rice cultivars with genetic resistance

to BPH while acknowledging that the pest had the capacity to adapt to the resistant cultivars (IRRI, 1979). IR26, the first high-yielding rice cultivar with BPH resistance released by IRRI in 1974, was successful only for ≤ 3 years. In the laboratory, Pathak and Heinrichs (1982) discovered that BPH populations could adapt to IR-26 in 7–10 generations.

IPM heralded as the solution

The IRRI (1979) conferees highlighted integrated pest management (IPM) as a management strategy to help prevent BPH outbreaks. A term introduced by the Council on Environmental Quality (CEQ, 1972) from the earlier term integrated pest control (Stern et al., 1959), IPM uses different methods to prevent pest populations from reaching damaging levels. Rather than relying on a single method of pest control, IPM combines pest-resistant cultivars, fertilizer management, agronomic practices that conserve and increase the effects of predators and other naturally occurring biological control agents, and, when needed, prudent use of pesticides based on need rather than prophylactic treatment.

In 1980, with technical assistance from the Food and Agriculture Organization of the United Nations (FAO), countries of tropical Asia launched a major rice IPM program to increase economically and environmentally sound pest management practices (Gallagher et al., 1994, 2009; Matteson et al., 1994; Pontius et al., 2001). From 1980 to 1989, the program emphasized pest surveillance, host-plant resistance, judicious use of pesticides, natural enemies of pests, and field demonstrations that gave farmers first-hand experience with IPM practices and ecological concepts. Each component had a working group led by designated NARES. The governments of India, the Philippines, and Indonesia declared national IPM policies in the mid-1980s. Indonesian officials banned 57 pesticides known to cause BPH outbreaks and also stopped pesticide subsidies. The policy shift to curb pesticides saved the Indonesian government more than \$100 million per year (1995 U.S. dollars) and reduced pesticide imports by two-thirds (World Bank data cited in Gallagher et al., 2009). The approximate cost of the FAO program in Indonesia between 1985 and 1988 was US\$650,000 (P.E. Kenmore, personal communication 31 Jan. 2011).

The FAO-IPM program emphasized intense on-farm training in farmer field schools (FFS) to make rice farmers proficient at implementing IPM with minimal technical assistance. From 1980 to 2002, the IPM program trained farmers in 13 countries (Bangladesh, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, the Philippines, Sri Lanka, Thailand, and Vietnam). Data from Malaysia and Myanmar are not available, but >2 million rice farmers in the other 11 countries were FFS-trained from 1989 to 2000 (Pontius et al., 2001). According to van den Berg and Jiggins (2007), the number of FFS-trained farmers represented only 1–5% of all farmer households in those countries. Six of the countries that participated in the FAO program (Bangladesh, China, India, Indonesia, the Philippines, and Vietnam) accounted for more than 90% of all FFS graduates (van den Berg and Jiggins, 2007). Farmers trained in IPM reduced insecticide use by 50–80% while sustaining or increasing rice yield (Matteson, 2000). The greatest impact was in Indonesia, where some 1.5 million farmers received IPM training (Oka, 2003). The IPM training combined with the pesticide policies led to a 75% reduction in insecticide use on rice of the IPM-trained farmers in the province of Java (Gallagher et al., 1994).

In 1991, IRRI launched a complementary pesticide-reduction program called farmer participatory research (FPR) to resolve the farmers' misperceptions about the need to control leafhoppers (Lepidoptera: Pyralidae). Studies at IRRI indicated that leafhoppers rarely reduce rice yield if left untreated (Graf et al., 1992; De Kraker, 1996); yet rice farmers perceived that these insects would cause heavy yield losses if not controlled (Heong et al., 1994; Heong and

Escalada, 1997). Surveys indicated that most insecticide applications during the first 30–40 days of rice planting were aimed at leaffolders (Heong and Escalada, 1997). In FPR experiments, during the first 30–40 days after planting, participating farmers applied insecticidal sprays as they normally would have (usually 1–3 times) to most of their crop but they left a portion ($\approx 100 \text{ m}^2$) of each field untreated. At harvest, the farmer determined yields from both portions of the field and then compared results with neighboring farmers who had conducted similar experiments. Participating farmers often quickly realized economic benefits when stopping the early treatments and became ambassadors in spreading the "no-spray" message to other farmers. In some areas, government agencies initiated complementary media campaigns using radio, TV, printed materials, and other methods of communication to encourage more farmers to stop early-season use of rice insecticides. The FPR programs in several locations of Southeast Asia eliminated 50–80% of the insecticide use on rice without yield loss (Heong and Escalada, 1997). The greatest impact was in the Mekong Delta of Vietnam. Surveys showed that from 1992 to 1997, Delta farmers reduced the average number of insecticide sprays per rice crop from 3.1 to 1.0 (Huan et al., 1999). Throughout the Delta, the FPR programs decreased insecticide use by $\approx 50\%$ on some 2 million rice farms (Escalada et al., 1999).

The BPH problem resurfaces

The FAO-IPM and IRRI-FPR programs and complementary efforts of the participating Asian countries, various national and multinational donor agencies, and nongovernmental organizations contributed significantly in promoting natural biological control and other non-chemical methods, reducing insecticides, and lessening risks of planthopper outbreaks (Kenmore, 1991; Gallagher et al., 1994, 2009; Heong and Escalada, 1997; Matteson, 2000; Heong and Hardy, 2009). However, the efforts were not sustainable. This was the conclusion reached at a major international conference on rice planthoppers at IRRI in 2008 (Heong and Hardy, 2009). The conferees reported that chemical control had resurfaced as a primary tactic for controlling rice insects and since 2003 Asian countries have seen planthopper outbreaks equal to or worse than those of the 1970s (Heong and Hardy, 2009). The resurrection of chemical control is illustrated by data from Vietnam's Mekong Delta (Escalada et al., 2009). The FAO-FFS, initiated in 1992, had trained an estimated 410,000 Mekong Delta farmers by 1997. Delta rice farmers neither trained in the FFS nor exposed to the IRRI-FPR media campaign to reduce insecticides applied insecticide sprays about 2.1 times per rice crop. Farmers exposed to the media campaign alone sprayed about 1.2 times and those exposed to both the media campaign and FFS training sprayed about 0.5 times. However, starting in 2005, insecticide use intensified and by 2007 the level of use had surpassed the level that preceded the FFS and FPR-media campaigns (Escalada et al., 2009). The chemical industry now conducts major mass media campaigns to promote insecticidal control in rice throughout Vietnam's Mekong Delta.

Bangladesh, Cambodia, China, India, Indonesia, Japan, Korea, Laos, Malaysia, the Philippines, Thailand, and Vietnam have recorded major BPH outbreaks in recent years (Heong and Hardy, 2009). Reports of difficulty controlling BPH because of insecticide resistance are increasingly common (Gorman et al., 2008; Wang et al., 2008b; Matsumura et al., 2009; Heong et al., 2011; IRRI-ADB, 2011). BPH outbreaks in China in 2005–2007, which affected 6.6–9.4 million ha of rice (Catindig et al., 2009), exceeded those ever recorded (Cheng, 2009). The outbreak area of 2005–2007 amounted to $\approx 23\text{--}30\%$ of China's ≈ 29.2 million ha of rice (IRRI, 2011b). By comparison, BPH outbreaks in 1998–2000 affected only 2.2–3.5 million ha of rice (Catindig et al., 2009) or $\approx 7\text{--}11\%$ of China's total rice area (≈ 31.2 million ha) (IRRI, 2011b).

Aims of review

A widely shared view of rice insect management specialists is that the BPH poses a significant threat to tropical rice only after its natural enemies have been disrupted by insecticidal treatments. In other words, the BPH will remain at non-damaging levels unless insecticides unleash it from natural control. That was the prevailing view in 1977 when IRRI (1979) held the first major international conference on planthoppers. The same view persisted three decades later when IRRI held the second major international conference on planthoppers in 2008 (Heong and Hardy, 2009). We will critically examine the rationale and limitations to the "insecticide-induced outbreak paradigm," which advocates that BPH outbreaks are triggered by insecticides. Then we will assess other factors that might contribute to BPH outbreaks. Our review of the extensive literature on this topic includes papers, books, and book chapters published through early 2011.

Although our assessment is restricted to outbreaks of the BPH, outbreaks of two other species of rice planthoppers, the whitebacked planthopper (WBPH), *Sogatella furcifera* (Horváth), and the small brown planthopper (SBPH), *Laodelphax striatellus* (Fallén), have also intensified in many areas of Asia in recent years (Heong and Hardy, 2009). BPH and the two other delphacids occur sympatrically in some areas (Dupo and Barrion, 2009) and may co-occur in the same rice field in a given cropping season. Like BPH, WBPH and SBPH have periodically reached outbreak levels in rice for decades, but recurring outbreaks became increasingly common in the past decade. In some areas of China, all three species have caused serious yield losses every year since the early 2000s (Cheng, 2009). SBPH and WBPH have primarily infested hybrid rice, SBPH and BPH have primarily infested Japonica rice (*O. sativa japonica*), and all three species have infested Indica rice (*O. sativa indica*) in China (Cheng, 2009). WBPH occurs widely in rice areas of Asia (Dupo and Barrion, 2009). As with the BPH, the northern limit of the winter breeding area for the WBPH is around the Red River Delta of Vietnam (Kisimoto, 1976). Like the BPH, the WBPH makes long migratory flights and annually colonizes in the temperate areas of Japan, Korea, and most areas of China (Kisimoto, 1976; Turner et al., 1999; Otuka, 2009). During the period 1998–2007, WBPH damaged more hectares of rice in China than the brown planthopper (Catindig et al., 2009). WBPH has become the most predominant insect pest in areas planted with Indica hybrid rice in China (Sōgawa et al., 2009). The SBPH, which attacks rice and also wheat (*Triticum* spp.) and sugarcane (*Saccharum officinarum* L.), occurs mainly in temperate rice areas (Dupo and Barrion, 2009). In China, this pest is becoming increasingly damaging and research has confirmed high levels of insecticidal resistance in its populations (e.g., Gao et al., 2008).

Besides directly damaging rice plants, WBPH and SBPH transmit rice diseases. WBPH vectors the southern rice black streak dwarf virus (SRBSDV) discovered in 2001 in Guangdong province, China and described by Zhou et al. (2008) and Zhang et al. (2008). Il-R. Choi reported that SRBSDV had also been found in Japan (Kyushu island) (Sept. 24, 2010 Ricehoppers, IRRI-ADB, 2011). SBPH vectors the virus diseases rice stripe virus (RSV) and rice black streaked dwarf virus (RBSDV). China has experienced serious RSV epidemics in recent years (Wang et al., 2008a). In western Japan, according to information by local plant protection offices (Otuka, 2009), the proportion of RSV viruliferous adults of *L. striatellus* has recently shown a gradual increase to 6–16%.

All three planthopper species are r-strategists with short life cycles, rapid reproductive rates, and high migratory potential (Cheng, 2009; Heong, 2009). They normally reside at low densities but their populations can exhibit explosive increases and cause devastating economic impacts. The prevailing view is that outbreaks of all three species are primarily triggered by insecticide use (Heong and Hardy, 2009). The blog Ricehoppers maintained by IRRI-ADB (2011) is a valuable source for information on the status of the three species in Asian rice.

The insecticide-induced outbreak paradigm

Impact on natural enemies

The seminal research of Kenmore (1980) and Kenmore et al. (1984) in the Philippines clearly demonstrated the ability of natural enemies to regulate the population density of BPH in tropical rice not treated with insecticides. Although BPH populations can reach relatively high densities even on BPH-resistant cultivars in low-pesticide (molluscicide only) fields when predators are abundant (e.g., Schoenly et al., 2010), predation primarily by spiders and the insects *Microvelia douglasi atrolineata* Bergroth (Hemiptera: Veliidae) and *Cyrtorhinus lividipennis* (Reuter) (Hemiptera: Miridae) appears to prevent BPH outbreaks in tropical rice (e.g., Kenmore, 1980; Heinrichs and Mochida, 1984; Kenmore et al., 1984; Nakasugi and Dyck, 1984; Sahu et al., 1996; Settle et al., 1996; Fagan et al., 1998; Sigsgaard, 2007; Dupo and Barrion, 2009). Less intensively studied is the role of parasitoids in regulating BPH density under field conditions, although significant levels of parasitism of BPH eggs have been observed (e.g., Chiu, 1979; Kenmore, 1980; Kenmore et al., 1984; Fowler et al., 1991; Claridge et al., 2001; Dupo and Barrion, 2009; Gurr et al., 2011). Parasitism by many of the BPH parasitoids is usually insufficient to cause significant BPH mortality (Greathead, 1983). However, habitat manipulation of non-rice vegetation seems to have potential in increasing the effects of some parasitoids, especially mymarid wasps (Gurr et al., 2011). Important egg parasitoids of BPH may include mymarid (e.g., *Anagrus* spp., *Gonatocerus* spp.), trichogrammatid (*Oligosita* spp. and *Paracentrobia* spp.), and eulophid (*Tetrastichus* spp.) wasps (Sahad, 1984; Fowler et al., 1991; Claridge et al., 2002; Dupo and Barrion, 2009; Gurr et al., 2011). A range of parasitoids, including strepsipterans, dryinid wasps, pipunculid flies, and other taxa (Claridge et al., 2002; Dupo and Barrion, 2009), attack BPH nymphs and adults.

Although insecticide applications to rice do not always trigger BPH outbreaks (e.g., Heinrichs et al., 1982a, 1982b), they often disrupt the actions of BPH's natural enemies either by direct killing action or by disrupting food chains (e.g., Chelliah and Heinrichs, 1980; Heinrichs et al., 1982a; Heinrichs et al., 1982b; Reissig et al., 1982; Heinrichs and Mochida, 1984; Song et al., 1984; Cohen et al., 1994; Schoenly et al., 1996; Cuong et al., 1997; Fagan et al., 1998; Heong and Schoenly, 1998). Wide-scale outbreaks of BPH in tropical Asian rice in the 1970s and 1980s (IRRI, 1979; Heinrichs et al., 1982a; Shepard et al., 1991) were attributed to the insecticidal destruction of natural enemies (Matteson, 2000). The BPH's ascendancy following insecticide use was commonly called "pest resurgence" (e.g., Chelliah and Heinrichs, 1980; Heinrichs et al., 1982a,b; Reissig et al., 1982; Heinrichs and Mochida, 1984). Smith and van den Bosch (1967) originally used the term pest resurgence to describe the rapid numerical rebound of a pest following use of an insecticide aimed at that specific pest. In many areas of Asia, farmers use insecticides specifically to control BPH even when its population density is low. More often, however, in the tropics except during BPH outbreaks insecticides are directed at leaffolders or other pests (Heong et al., 1994; Litsinger, 2008) and not BPH. Smith (1970) proposed the term "secondary pest outbreak" to describe the increase of a nontarget secondary pest from its normal sub-injurious level to pest status following insecticidal control of a target pest. Normally, a secondary pest does not attain injurious levels because of effective natural enemies or other regulatory factors; it erupts only when insecticides or other factors cause ecological disruption. Insecticides have caused both resurgence and secondary outbreaks of BPH.

Insecticide-induced hormesis

Insecticides not only increase the likelihood of pest outbreaks by disrupting the actions of natural enemies but also may promote pest

increase via hormesis (Hardin et al., 1995; Cohen, 2006; Dutcher, 2007). Chelliah et al. (1980) showed that sublethal doses of methyl parathion and decamethrin applied topically to 5th instar BPH nymphs increased reproduction in BPH adults that developed from the nymphs. Sublethal doses of some insecticides increase fecundity in BPH females by stimulating changes in rice plant nutrients (Wu et al., 2001, 2003; Yin et al., 2008). Yin et al. (2008) found that insecticide-induced reproductive stimulation varied among rice cultivars, insecticides, and the insecticides' application rates. Sublethal applications of the insecticide deltamethrin resulted in significantly more brachypterous (flightless) BPH adults when compared to sublethal applications of imidacloprid or triazophos. The highest BPH reproductive rate occurred on plants treated with triazophos. Treatments of all insecticides evaluated (deltamethrin, imidacloprid, triazophos, and a synthetic pyrethroid) on both BPH susceptible (TN1) and resistant (Xieyou 963) rice cultivars increased soluble sugar levels in 3rd- and 5th-instar nymphs and adults developing from nymphs that had fed on insecticide-treated rice plants. Also, adults developing from nymphs that fed on treated plants had significantly more crude fat than adults developing from nymphs that fed on untreated plants. Reproductive stimulation attributed to insecticide treatment was more pronounced on BPH-susceptible cultivars.

The results of Yin et al. (2008) indicate that sublethal insecticide applications could theoretically increase BPH's capacity for migration because the planthoppers would acquire more fat and sugar, which provide fuel for flight, when feeding on insecticide-treated rice plants than when feeding on untreated rice plants. Litsinger (2008) found that, to save time and money, Philippine rice farmers often apply insecticides in wide sweeps (wetting only a subset of leaves) and apply sprays at rates lower than recommended by insecticide manufacturers. Moreover, because BPH populations build up at the base of the rice plant over time, the closed canopy can shield them from spray droplets (Reissig et al., 1986). The results of Yin et al. (2008) suggest that farmer applications of sublethal rates of certain insecticides could enhance both BPH's reproductive and migratory capacity and theoretically increase the threat of BPH outbreaks even if the insecticides did not harm natural enemies.

Insecticide resistance magnifies the problem

Genetic resistance to the organochlorine compound BHC appeared in BPH populations in Japan in 1967 some 15 years after the insecticide was first used on the country's rice (Miyata, 1989). Researchers detected resistance to malathion and diazinon (organophosphorus compounds) in BPH populations on IRRI's experimental farm in the Philippines in the late-1960s and 1970s (Heinrichs, 1979, 1994) and resistance to organophosphorus and carbamate insecticides in Taiwan in the 1970s (Miyata, 1989). By the early 1990s, numerous Asian countries had reported BPH resistance to organochlorine, organophosphorus, carbamate, and pyrethroid insecticides (e.g., Nagata et al., 1979; Kilin et al., 1981; Miyata, 1989; Hirai, 1993; Heinrichs, 1994). Until recently, the reports of resistance in BPH populations were mostly from temperate areas. Wide-scale use of neonicotinyl compounds (mainly imidacloprid) has magnified the resistance problem in both tropical and temperate areas (Matsumura et al., 2009; Heong et al., 2011; IRRI-ADB, 2011). By 2008, laboratory assays had confirmed imidacloprid resistance in BPH populations in China, India, Japan, Indonesia, Malaysia, Taiwan, Thailand, and Vietnam (Gorman et al., 2008; Matsumura et al., 2009). Rice farmers in several countries have reported reduced efficacy using imidacloprid to control BPH (Gorman et al., 2008). BPH resistance to imidacloprid has created especially difficult problems for Chinese rice farmers (Cheng, 2009).

From 1996 to 2006, Wang et al. (2008b) assayed 42 field samples of BPH from eight Chinese provinces for resistance to imidacloprid. Most of the BPH populations remained susceptible to imidacloprid

from 1996 to 2003 except in Guilin (Guangxi Zhuang Autonomous Region) where minor resistance was detected in 1997. However, by 2005 high to extremely-high resistance levels appeared in BPH populations from numerous locations. Within only a 2-year period, a population from Nanning (Guangxi Zhuang Autonomous Region) increased in resistance by >200-fold. In other areas, especially in southeast China, BPH developed >800-fold resistance to imidacloprid. To control the imidacloprid-resistant populations, farmers increased the application rate of imidacloprid from 15 g (a.i.) ha⁻¹ to ≈60–120 g (a.i.) ha⁻¹. In many rice-growing areas, farmers sprayed during every BPH generation to prevent outbreaks of the pest (Wang et al., 2008b). Imidacloprid's long residual activity and high efficacy make it the preferred insecticide for controlling BPH in many areas (Denholm and Rowland, 1992; Wang et al., 2008b). Trends suggest that continued heavy use of the insecticide will exacerbate the problem of genetic resistance in BPH populations in China and other countries (Heong et al., 2011).

Because BPH migrates long distances, it seems that resistance to insecticides should be slowed by the regular influx of immigrants from areas of low insecticide use (Zhuang et al., 2004). However, in China imidacloprid has been used intensively on a large scale to control BPH in both the emigrating area and the immigrating area (Liu et al., 2003; Cheng, 2009). Imidacloprid has also been used intensively in southeastern Asian countries (Gorman et al., 2008; Wang et al., 2008b) where BPH populations develop on rice year round and are the major source for northbound migration to China in the following year (Kisimoto, 1979; Perfect and Cook, 1994; Matsumura et al., 2009). Therefore, once resistance to imidacloprid evolves, the resistant BPH migrants may quickly spread the imidacloprid-resistance alleles long distances (Wang et al., 2008b).

Insecticide resistance can aggravate the problem of resurgence and secondary outbreaks of BPH because farmers must use increasing quantities of insecticide to combat the resistant population. Furthermore, as discussed, Yin et al. (2008) showed that imidacloprid foliar applications to rice could increase lipids and soluble sugar in BPH nymphs and adults feeding on the plants. BPH populations that survived imidacloprid applications could theoretically migrate above-average distances and therefore serve as an especially important conduit in the spread of imidacloprid-resistance alleles into new areas.

Do insecticides speed up BPH's adaptation to resistant rice?

Gallagher et al. (1994) and Heinrichs (1992) proposed that insecticides could accelerate the rate at which BPH adapts to resistant rice cultivars. Their hypothesis assumed that insecticidal applications to BPH-resistant plants would significantly disrupt the regulatory effects of BPH's natural enemies. When natural enemies are abundant, insecticides would kill a significant portion of a BPH population and therefore reduce the population's exposure to the host-plant resistance mechanism. With fewer natural enemies following an insecticide application, the level of plant selection pressure on the BPH populations would theoretically increase, thereby speeding up BPH's adaptation to the resistant rice. The argument advanced by Gallagher et al. (1994) and Heinrichs (1992) makes intuitive sense but we are unaware if it has been tested in controlled field experiments.

Synthesis

Our review of the extensive literature suggests that insecticides are the single most tangible human-controlled input responsible for BPH outbreaks. The literature since the start of the green revolution in the 1960s, much of which we have cited, provides many persuasive examples of the insecticides' negative effects on BPH. The two largest international conferences on rice planthoppers to date (IRRI, 1979; Heong and Hardy, 2009) singled out heavy use of insecticide as the primary driving force behind BPH outbreaks. However, it is highly

unlikely that insecticides have been wholly responsible for outbreaks in the tropics, as we will discuss.

Does nitrogen fertilizer provoke BPH outbreaks?

Nitrogen is the most limiting nutrient for rice in tropical Asian soils (Bouldin, 1986; Kundu and Ladha, 1995). As a rule, 1 kg of nitrogen is required to produce 15–20 kg of grain. Naturally available nitrogen from biological fixation (e.g., Ladha et al., 1993) and mineralization of soil nitrogen (e.g., Bouldin, 1986; Kundu and Ladha, 1995) is sufficient to attain harvest yields of 2–3.5 t ha⁻¹. Farmers expecting a higher yield must apply additional nitrogen. Before the availability of IR8 and later high-yielding cultivars, tropical rice farmers did not regularly apply fertilizers because the traditional cultivars usually produced less than 2–3 t ha⁻¹. However, large amounts of fertilizer were necessary to achieve successful yield from the improved cultivars (De Datta et al., 1968; De Datta, 1981). In China, for example, the yield of rice increased from 4.13 to 6.26 t ha⁻¹ in the past 25 years (2006 data from China's ministry of agriculture, Cheng, 2009). During this same period, total chemical fertilizer and nitrogen use increased from 12.69 and 9.34 million tons to 47.66 and 22.29 million tons, respectively (Cheng, 2009). Farmers in China now apply an average of 180 kg N ha⁻¹ to rice (Lu et al., 2007), compared to ≥100 kg N ha⁻¹ that tropical farmers in Asia apply to high-yielding rice cultivars (Saleque et al., 2004).

Nitrogen-enriched plants can significantly enhance the size, performance, and abundance of herbivorous insects (Awmack and Leather, 2002). In 1970, Sōgawa showed that rice plants fertilized with high levels of nitrogen will attract more BPH than nitrogen-poor plants and also improve the insect's survival and reproduction. Since then, field studies have repeatedly demonstrated that BPH populations respond positively to nitrogen fertilization (e.g., Cheng, 1971; Dyck et al., 1979; Heinrichs and Medrano, 1985; Lu and Heong, 2009) and also have implicated nitrogen fertilizer as a cause for BPH outbreaks in high-yielding systems (Mochida and Dyck, 1977; Dyck et al., 1979; Kenmore, 1980; Lu et al., 2005; Lu and Heong, 2009). Increased plant nitrogen accelerates BPH feeding and honeydew-excretion (Sōgawa, 1970; Cheng, 1971), survival (Lu and Heong, 2009), fecundity (Visarto et al., 2001; Lu and Heong, 2009), and population growth (Cheng, 1971; Visarto et al., 2001; Lu and Heong, 2009) and the tendency for BPH outbreaks (Uhm et al., 1985; Lu and Heong, 2009). Although not substantiated in the field, laboratory results of Lu et al. (2005) suggested that BPH's tolerance to adverse environmental stresses increases when nitrogen is applied to rice. Survival of nymphs, fecundity, and egg hatchability were significantly higher in BPH populations on nitrogen-rich rice plants than nitrogen-poor rice plants. Also, feeding on the nitrogen-rich plants allowed female adults to survive longer in the absence of food.

Although nitrogen-rich rice plants can boost BPH's reproductive and growth capability, the populations often remain small in insecticide-free rice receiving high levels of nitrogen (Lu and Heong, 2009). On the other hand, Schoenly et al. (2010) recorded relatively high BPH densities in low-pesticide (molluscicide only) fields of BPH-resistant rice when high levels of nitrogen (120 kg ha⁻¹) were applied. Natural enemies, especially when combined with BPH-resistant cultivars (e.g., Cuong et al., 1997), seem to be essential in preventing BPH outbreaks in tropical rice heavily fertilized with nitrogen.

Concerns with fertilizer use on hybrid rice

Hybrid rice produced by crossing two inbred lines is occupying significantly more Asian riceland. Hybrid rice now accounts for ≈60% of the rice planted in China (IRRI, 2011c). Although hybrid seeds may cost two times more than non-hybrid seeds, farmer profits can be substantially higher because the hybrids yield 16–20% more than their inbred parents (IRRI, 2006). Larger planthopper populations and frequent outbreaks in farmers' fields have been reported for the hybrid rice (Mew et al., 1988; Sōgawa et al., 2003). The hybrids' dense canopy,

resulting from more vigorous vegetative growth, apparently makes them more attractive to migrating or dispersing insects (Cohen et al., 2003). The hybrid plants have greater nitrogen uptake and nitrogen use efficiency (defined as grain yield per unit nitrogen fertilizer applied) than their inbred parent lines (Virmani, 1994; Yang et al., 1999). The increased nitrogen uptake and use efficiency in the hybrids could result in more available nitrogen for BPH and other pests (Cohen et al., 2003). Furthermore, the hybrids' complete lack or low level of genetic resistance to planthoppers makes them more susceptible to the insects. The main hybrid rice cultivars in China are susceptible to WBPH, and only about 12% of the newly developed varieties showed any BPH resistance in field tests (Chen et al., 2005).

Impact of resistant cultivars on BPH

Developing improved rice cultivars with insect and disease resistance is an important objective of rice breeding (Khush, 1971, 1979, 1984; Bonman et al., 1992; Park et al., 2007; Jena and Mackill, 2008; Brar et al., 2009). High-yielding cultivars with resistance to BPH, other insects, and diseases (Brar et al., 2009) have contributed significantly in elevating rice yield throughout tropical Asia. IRRI is the world's primary rice breeding center and has supplied thousands of improved breeding lines to rice producing countries. An estimated 50% of the world rice area is planted to IRRI-bred varieties or their progenies (IRRI, 2011a).

IRRI started a program to breed rice for resistance to BPH soon after Pathak et al. (1969) identified sources of rice resistance to the insect in 1967. Many countries in Asia have started similar programs. The first two resistance genes were designated as *Bph1* and *bph2* (Athwal et al., 1971). Twenty-one genes for BPH resistance have now been identified from cultivated and wild species of *Oryza* (Park et al., 2007; Jena and Mackill, 2008; Brar et al., 2009). Producing rice with durable resistance to BPH is a major challenge because of the pest's history of adapting to resistant cultivars (Brar et al., 2009; Horgan, 2009). The pest adapted to IR26, the first high-yielding cultivar with BPH resistance (with *Bph1* gene), within 2 or 3 years after being released to farmers. Other BPH-resistant cultivars have remained viable for only a relatively short time (e.g., Heinrichs, 1988, 1992). Although some BPH-resistant cultivars and notably IR36 and IR64 have shown greater durability (e.g., Cohen et al., 1997; Alam and Cohen, 1998; Brar et al., 2009), BPH is still a nemesis of plant breeders.

Fifteen of the BPH-resistance genes have been mapped to chromosomal location and 8 have been linked with molecular markers (Brar et al., 2009). Resistance to BPH may be due either to major (qualitative) or minor (quantitative) traits. Recent advances in BPH genomics (Noda, 2009), marker-assisted selection (Jena and Mackill, 2008; Brar et al., 2009), genetics of host-plant resistance to BPH (Fujita et al., 2009), and rice genomics (Jena and Mackill, 2008; Brar et al., 2009) offer new opportunities for rice breeders. The breeders can now identify and map precisely the genes for BPH resistance (Gramene, 2011). Marker-assisted selection techniques can help breeders develop rice cultivars with two or more genes for resistance pyramided into a single plant, therefore theoretically achieving greater durability (Brar et al., 2009). Breeders can use DNA profiles and genetic linkage maps to evaluate the genomes of wild species for new and useful resistance genes (Tanksley and McCouch, 1997). Numerous species of wild *Oryza* are genetically resistant to BPH and other insects (e.g., Jung-Tsung et al., 1986; Romena and Heinrichs, 1989) and are a valuable resource for plant breeders seeking resistance sources for improved rice cultivars.

In addition to the natural sources of BPH resistance in *O. sativa* and its wild relatives, scientists have identified numerous BPH toxins from non-rice sources that have potential in transgenic rice plants engineered specifically to resist BPH. To our knowledge, no varieties of transgenic rice are currently grown commercially although several engineered varieties have been approved for commercialization.

Plant breeders are especially interested in transgenic rice plants expressing snowdrop lectin, *Galanthus nivalis agglutinin* (GNA), to control planthoppers. Transgenic plants with GNA have exhibited resistance to BPH (Nagadhara et al., 2003) and WBPH (Nagadhara et al., 2004) and also green leafhoppers (*Nephotettix* sp.) (Nagadhara et al., 2003). Of the available transgenic rice plants, GNA plants are the closest to commercialization (Malone et al., 2008).

Mechanisms of resistance

Researchers do not clearly understand what natural mechanisms in rice plants confer resistance to BPH and how these mechanisms relate to identified resistance genes (Chen, 2009; Horgan, 2009; Seo et al., 2009). How the major resistance genes or quantitative trait loci (QTLs) function is uncertain (e.g., Horgan, 2009). It has been generally accepted that host selection by planthoppers is due to phloem chemistry and likely involves the lack of particular feeding stimulants (Cook and Denno, 1994). Silicic and oxalic acids deter BPH feeding on resistant rice (Yoshihara et al., 1979a, 1979b, 1980). Phenolic acids in resistant varieties appear to be related to the inability of BPH to find and ingest phloem (Fisk, 1980). On the other hand, BPH is more likely to reject rice varieties with low levels of essential amino acids in the phloem (Sōgawa, 1982). Shigematsu et al. (1982) found that sterols acted as sucking inhibitors for BPH whereas asparagine stimulated sucking. However, the results of studies in Korea suggest that BPH can thrive on resistant rice with *Bph1* or *bph2* genes despite its difficulty ingesting the phloem sap of resistant plants (Seo et al., 2009). The results of Du et al. (2009) reveal that the BPH-resistance gene *Bph14* is a member of the CC-NB-LRR disease resistance gene family that mediates resistance through direct or indirect recognition of pathogen-associated molecular patterns or pathogen effectors (Jones and Dangl, 2006; Takken and Tameling, 2009). *Bph14* confers resistance to BPH at seedling and maturity stages of the rice plant. It carries a unique LRR domain that might function in recognizing the BPH invasion and activating the defense response. *Bph14* is predominantly expressed in vascular bundles, the site of BPH feeding. Expression of *Bph14* activates the salicylic acid signaling pathway and induces callose deposition in phloem cells and trypsin inhibitor production after planthopper infestation, thereby reducing the feeding, growth rate, and longevity of BPH.

Studies of inter-specific interactions suggest that BPH's response to rice and vice versa may be affected by the presence of other species of organisms. Cheng et al. (2001), for example, found that the level of resistance to BPH in a rice plant can decline if WBPH previously infested the plant, although the mechanisms were not determined. Several genes have been linked to induced defenses in rice. *OsBi1* is a BPH-inducible gene implicated in the resistance of rice plants to BPH (Wang et al., 2004). Whether other insects of rice also induce *OsBi1* is not known. *Bph14*, discussed above, mediates disease resistance through direct or indirect recognition of pathogen-associated molecular patterns or pathogen effectors (Jones and Dangl, 2006; Takken and Tameling, 2009). As noted, *OsBi1* is also a BPH-inducible gene that reduces the performance of BPH (Du et al., 2009). The interacting effects of BPH and plant diseases on rice with the *Bph14* gene are not known.

The presence of mutualistic yeast-like endosymbionts (YLS) may increase the complexity of the interactions between BPH and rice. The intracellular endosymbionts reside in BPH's fat bodies (Chen et al., 1981) and appear to play a role in providing protein through the recycling of uric acid stored in the fat bodies (Sasaki et al., 1996). Uric acid content in planthoppers decreases when nitrogen is unavailable (Sasaki et al., 1996). YLS also synthesize ergosterol-5,7,24 (28)-trienol, which is a precursor of cholesterol and the molting hormone ecdysone (Wetzel et al., 1992). If BPH depends on the YLS for securing essential amino acids as Lu et al. (2004) suggested, variation in YLS in the BPH populations might partially explain the variation in planthopper performance on different rice varieties (Chen, 2009).

Researchers have also detected bacterial endosymbionts in BPH. Tang et al. (2010) identified 18 operational taxonomic units of bacteria representing four phyla (*Proteobacteria*, *Firmicutes*, *Actinobacteria*, and *Bacteroidetes*) in BPH populations but did not determine their function. In other species of insects, the bacterial endosymbionts may function as obligate nutritional mutualists, facultative mutualists that protect against natural enemies or stress, and reproductive manipulators that enhance productivity of infected female lines (Moran et al., 2008). The discovery by Tang et al. (2010) that the frequencies of bacterial infections differed among the three populations investigated (designated as BPH biotypes 1, 2, and 3) raises more questions about how microbial endosymbionts may affect the intra- and inter-population variation in BPH's response to different rice cultivars.

Screening for BPH resistance

Breeders at IRRI and at other rice breeding centers in Asia have incorporated BPH-resistance sources in rice aimed at designated BPH biotypes (Brar et al., 2009). In the greenhouse, IRRI has screened as many as 44,335 accessions for biotype 1 (15.4% resistant); 10,553 for biotype 2 (1.9% resistant); and 13,021 for biotype 3 (1.8% resistant) (Jackson, 1997). [IRRI has also screened thousands of accessions for resistance to the WBPH, green leafhoppers, *Nephotettix* spp., yellow stem borer, *Scirpophaga incertulas* (Walker), and striped stem borer, *Chilo suppressalis* (Walker) (Jackson, 1997).] The screening methods use greenhouse populations of designated BPH biotypes that vary in their virulence to cultivars with different plant resistance genes (Gallagher et al., 1994). Biotype numbers correspond to the rice genes for resistance. Populations of a particular biotype are maintained in the greenhouse. For example, cultures of BPH maintained on the rice variety Mudgo with the *Bph1* gene and on the variety ASD7 with the *bph2* gene are designated respectively biotype 1 and biotype 2 (Pathak and Saxena, 1980). Biotype 1 is susceptible to all BPH-resistance genes. Biotype 2 is virulent to the *Bph1* gene but susceptible to the other genes, biotype 3 is virulent only to *bph2*, and biotype 4 is virulent to both *Bph1* and *bph2* but not *Bph3* or *Bph4* (Khush, 1984).

The conventional method for evaluating rice for BPH resistance is the standard seedbox-screening test (SSST) (Heinrichs et al., 1985; IRRI, 1996). Some rice breeding centers have modified the screening protocols slightly (e.g., Kaneda et al., 1981), but the fundamental procedures developed at IRRI in the 1970s (Heinrichs et al., 1985; IRRI, 1996) are still used to screen rice germplasm for resistance (Brar et al., 2009; Horgan, 2009). Test plants are sown in rows in a seedbox ($\approx 60 \times 40 \times 10$ cm). A susceptible check and resistant variety are also sown in rows in the same box. Seven days after sowing, seedlings are thinned to about 20 plants per row and infested with 2nd instar BPH nymphs (≈ 8 per seedling) of a designated biotype (Horgan, 2009). When susceptible checks are killed (usually after about 1 week), plants are rated for damage on a 0–9 scale, where 0–3 is classified as resistant, 4–6 as moderately resistant, and 7–9 as susceptible (Velusamy et al., 1986). The modified seedbox-screening test (MSST) has also been used at some rice breeding centers. Investigators using the MSST infest rice seedlings 20 days after sowing with four 2nd instar BPH nymphs per plant. Plants are evaluated when susceptible checks are killed, using the SSST rating scale to identify relative levels of BPH resistance. With the MSST, F₁ BPH nymphs cause mortality of the susceptible check as the original nymphs have had time to mature and reproduce in the seedboxes (Horgan, 2009).

The screening methods offer the planthoppers a choice among plants (the accession of unknown resistance, resistant check, and susceptible check) before initiating feeding (SSST and MSST) or oviposition (MSST) responses (Horgan, 2009). However, the SSST, which is more widely used, only evaluates nymphal feeding responses. The MSST improves on the SSST by allowing nymphs to develop to adults, when they can oviposit, presumably in response to cultivar suitability

for nymphal development (Horgan, 2009). When cultivars have different levels of resistance, nymphs will disperse between plants, the degree of movement (activity) being negatively correlated with feeding. Although movement between plants may appear to simulate field responses, it is largely governed by “push–pull” dynamics in the experimental seedboxes (Horgan, 2009). The outcome is influenced by peculiarity, combinations, and relative positions of the plants in a particular seedbox and would not be expected to remain constant between successive tests (Horgan, 2009).

Questions about the validity of the BPH biotype concept

Many have questioned the validity of the BPH biotype concept and have pointed to flaws in rice breeding objectives that target specific BPH regional biotypes (e.g., Claridge and Den Hollander, 1980, 1983; Sōgawa, 1981; Claridge et al., 1984; Denno and Roderick, 1990; Gallagher et al., 1994; Hare, 1994; Heinrichs, 1994; Roderick, 1994). Considerable evidence indicates that IRRI's biotype models do not mirror the genetic variation found in natural field populations of BPH. Individual populations of BPH are heavily influenced by and adapted to local host-plant associations. Within a 200-kilometer radius in Sri Lanka, for example, Claridge et al. (1982) detected substantial variation in response to resistant cultivars among BPH populations inhabiting traditional and modern rice cultivars and wild *Oryza* species. The BPH populations appear to contain abundant polygenic variation for host associated traits (Sezer and Butlin, 1998).

Claridge et al. (1984) showed that morphological and fecundity differences between BPH biotypes are largely lost after one generation on a common rice cultivar. The differences among designated biotypes appear to be mostly environmentally induced and may be because of nutritional differences across cultivars. Studies reviewed by Roderick (1994) indicate that there is minimal genetic difference among the BPH biotypes, and short periods of selection can alter their survival and performance. Furthermore, there is not a one-to-one correspondence between a single gene in a BPH biotype and any single gene for resistance in the rice host (Roderick, 1994).

On the other hand, the critics have yet to establish practical cost-effective alternatives that rice breeders can use when evaluating breeding lines for resistance that is best tailored for the genetic variation found in natural field populations of BPH. The breeders obviously want to release rice breeding lines and cultivars with BPH resistance that provides the best defenses against natural populations. Although they have relied on the seedbox-screening test, they recognize its limitations and in the future will likely rely increasingly on DNA markers for evaluating rice breeding material for BPH-resistance genes. Marker-assisted selection can be used to determine the presence or absence of BPH-resistance genes in plant breeding material (Jena and Mackill, 2008; Brar et al., 2009).

Achieving greater durability in BPH-resistant rice

Evolutionary models predict that the less a control tactic such as plant resistance challenges a pest, the longer it will take for the pest to adapt to the tactic (Gould, 1988, 1991). Management strategies that integrate natural enemies and other tactics alongside plant resistance would theoretically reduce the rate at which BPH adapts to resistant rice. Rotating different cultivars between planting seasons, planting multiple resistant lines within the same field, combining different resistance genes with the same cultivar, and other schemes used singularly or in combination may have potential in slowing BPH's adaptation to resistant rice (e.g., Hare, 1994). Breeding for moderate or polygenic resistance to BPH may be a better strategy for achieving durable resistance than a strategy that seeks high resistance from a single major gene (e.g., Heinrichs, 1986; Bosque-Pérez and Buddenhagen, 1992; Alam and Cohen, 1998; Xu et al., 2002). QTLs were found to confer durable BPH resistance in IR64 (Alam

and Cohen, 1998) and Teqing (Xu et al., 2002) and therefore would seem to offer considerable potential increasing the durability of resistant cultivars.

Plant pathologists have demonstrated that some diseases of small grains may be less severe in crop mixtures (multiline cultivars and cultivar mixtures) than in pure stands (e.g., Mundt, 2002). In field studies in China, rice blast disease caused by the fungus *Pyricularia oryzae* was 94% less severe in mixtures of rice than in pure stands (Zhu et al., 2000a). Disease-susceptible rice varieties planted in mixtures with resistant varieties had 89% greater yield than when planted alone. Mixing rice varieties may be an effective alternative to fungicides and may also reduce the dependence on high levels of plant disease resistance (Zhu et al., 2000a). As Mundt (2002) discussed, cultivar mixtures are more useful under some conditions than others, and experimental methodology (especially problems of scale) may be crucial in evaluating the potential efficacy of mixtures on disease.

Mixing a BPH-resistant cultivar with a susceptible cultivar may also have promise; mixing the two together would theoretically slow the rate at which the pest adapts to the resistant cultivar (Atsatt and O'Dowd, 1976; Gould, 1986). This is because in a homogenous planting of only resistant plants all members of a pest population will be exposed to the resistance factor. By contrast, in a random mixture of 50% resistant plants and 50% susceptible plants, only half of the pest population will be exposed to resistant plants. Of course, this assumes that equal numbers of pests initially colonize the resistant and susceptible cultivars, which may or may not be the case.

We did not find published information from field studies that compared the effects of random mixtures (two or more rice cultivars) versus pure stands (one rice cultivar) on BPH population development or plant damage. In greenhouse studies, Weerapat et al. (1977) found that BPH caused less damage to a susceptible variety (RD7) when it was mixed with a resistant variety (RD9). The researchers infested seedling plants (two leaf stage) with large numbers of 1st instar BPH nymphs and recorded plant damage 10 days later. When the two varieties were isolated from one another in homogeneous plantings, 100% of the RD7 plants were BPH damaged while none of the RD9 plants were damaged. In a mixture of 50% RD7 plants and 50% RD9 plants, only 18% of the RD7 plants were damaged. Weerapat et al. (1977) did not speculate why mixing the susceptible and resistant varieties provided protection to the susceptible variety. A number of factors could have contributed. In natural settings in the wild or in agricultural polycultures, neighboring plants sometimes act as natural pest repellents, mask the herbivores' preferred host plants, or reduce the time herbivores remain on their host plants (e.g., Pimentel, 1961; Tahvanainen and Root, 1972; Root, 1973; Andow, 1991; Barbosa et al., 2009).

The most urgent challenge in achieving durability is to convince farmers to stop using insecticides to control BPH on rice that is resistant to the pest. Breeding efforts aimed at boosting the rice's genetic defenses against the BPH are a poor investment if farmers continue to apply insecticides to the resistant plants (Gallagher et al., 1994). Chemical control of BPH on resistant rice is an unnecessary investment for farmers, is potentially harmful to humans and the environment, and, according to Gallagher et al. (1994) and Heinrichs (1992), could speed up BPH's adaptation to the resistant plants.

Integrating plant resistance and biological control

Even if natural enemies are protected from insecticides and cropping practices are favorable for their increase, they will not perform satisfactorily on inhospitable plants (e.g., Hare, 1992; Bottrell et al., 1998). Results of several studies indicate that different rice cultivars can differentially affect BPH's natural enemies (e.g., Kartohardjono and Heinrichs, 1984; Senguttuvan and Gopalan, 1990; Rapusas et al., 1996). One cultivar may discourage or even cancel the potentially beneficial effects of a natural enemy. On the other hand, a different

cultivar may enhance the beneficial effects. Sōgawa (1982) showed that rice cultivars resistant to the BPH reduce the insect's growth rate and stimulate increased probing and movement on plants. Both the reduced growth rate and increased activity may affect natural enemy response. By keeping the planthopper populations small, the resistant plants prevent some predators from exhibiting a strong numerical response in resistant rice (Stapely et al., 1979; Kenmore et al., 1984; Döbel and Denno, 1994). Simultaneously, the resistant plants increase BPH's risk of being eaten by visually responsive lycosid spiders that react to moving prey (Kenmore et al., 1984). Kartohardjono and Heinrichs (1984) found that lycosid spiders captured more prey on resistant than susceptible cultivars. Senguttuvan and Gopalan (1990) reported that the predator *C. lividipennis* is more effective against the BPH on resistant cultivars than susceptible cultivars, which they attributed to greater BPH activity on resistant plants.

In the Mekong Delta, Vietnam, Cuong et al. (1997) tallied the populations of BPH, whitebacked planthopper, green leafhoppers, hemipteran and spider predators, and rice yield on rice cultivars susceptible, moderately resistant, and highly resistant to the BPH under insecticide-treated and insecticide-free conditions. BPH outbreaks and hopperburned plants occurred only in plots of the insecticide-treated susceptible cultivars. Rice yield in insecticide-free plots was lower in the BPH-susceptible cultivars than in the resistant cultivars only in 1 of 4 seasons. In plots of a moderately resistant cultivar and a highly resistant cultivar, populations of the three pests and predators were generally similar. Furthermore, rice yield did not differ under either the insecticide-treated or insecticide-free conditions. In insecticide-free plots, predator–BPH ratios were generally higher on resistant cultivars than susceptible cultivars. The results of Cuong et al. (1997) suggest that susceptible cultivars left untreated will not necessarily incur BPH damage even if adjacent rice is experiencing BPH outbreaks. They also suggest that moderate and high levels of resistance were not incompatible with biological control of BPH, whitebacked planthopper, or green leafhopper. However, not all insect resistant cultivars are necessarily equally attractive or more attractive to natural enemies than non-resistant cultivars. Luo et al. (2006), for example, found that the BPH parasitoid *Anagrus nilaparvatae* (Pang et Wang) was less attracted to JA-treated resistant (IR26 and IR64) than JA-treated susceptible rice cultivars (TN1, B97-59, XS63) in laboratory and field tests.

To our knowledge, there have been no comprehensive field assessments to compare arthropod community structure in BPH-resistant and BPH-susceptible rice. Given that Philippine and Indonesian irrigated fields, for example, have more than 640 and 760 taxa of macroinvertebrates, respectively (Cohen et al., 1994; Settle et al., 1996), and that Indian irrigated rice supports at least 92 and 84 taxa of spiders and hymenopteran parasitoids, respectively (Beevi et al., 2000; Sebastian et al., 2005), the lack of community-level assessments is not surprising.

The ideal form of plant resistance may be when the resistant cultivars suppressed the pests and simultaneously benefited natural enemies. A high level of pest resistance may not be necessary, since the partial resistance would be potentiated by actions of natural enemies. Cultivars with partial resistance would put less selective pressure on the BPH and would theoretically delay its adaptation to the resistant rice. However, the simulation models of Gould et al. (1991) and Johnson and Gould (1992) suggest that natural enemies could actually accelerate the rate at which some insect pests adapt to resistant plants. Determining optimal strategies for combining plant resistance and biological control in BPH management requires much more research.

Effects of regional and local landscape patterns on BPH

Agricultural landscapes function as a mosaic patchwork of habitats that include the dominant crop, other crops, fallow fields, wild vegetation, and, often, aquatic systems. Both wild and cultivated plants

neighboring a crop field may affect pests and vectors, natural enemies, and other biological components of the agroecosystem (e.g., Bunce et al., 1993; Pickett and Bugg, 1998; Landis et al., 2000; New, 2005). In the Mekong Delta, Vietnam, Wilby et al. (2006) analyzed plant–arthropod relationships in a rice-dominated landscape along two 10-km long transects and found a complicated (and sometimes confounding) association between landscape heterogeneity (vegetation and crop richness, rice, and uncultivated cover) and arthropod diversity. In habitat-by-habitat comparisons, Wilby et al. (2006) found that maturing rice (near the flowering or ripening stages) supported greater arthropod diversity than rice in other stages (seedling, tillering, stubble, and ratoon). The maturing rice also supported greater arthropod diversity than other crop species (e.g., vegetables, flowers, and fruits), especially if the other crops received high pesticide inputs. Wilby et al. (2006) hypothesized that natural enemy diversity and effectiveness may be maintained even in regions of expanding rice monoculture if pesticide and fertilizer inputs are low and there is no large-scale synchronous fallow.

Synchronous or asynchronous planting?

The debate about which large-scale cropping pattern—synchronous or asynchronous planting—maintains lower pest densities year round in tropical rice landscapes has raged for decades (e.g., Dyck et al., 1979; Oka, 1988; Loevinsohn et al., 1993; Way and Heong, 1994; Settle et al., 1996; Ives and Settle, 1997; Schoenly et al., 2010). Historically, policy makers have recommended wide-scale synchronous planting to deprive rice pests food and refuges into which they could invade after planting. Synchronous cropping, which creates a rice-free fallow lasting 1–3 months (usually between the dry and wet seasons), is widespread due to the need to conserve water in the dry season; whereas, asynchronous cropping creates a heterogeneous mixture of cultivated and temporarily unused fields and is common where irrigation systems are less efficient or have slower water delivery rates (Litsinger, 2008). Fallowing reportedly disrupts insect pest life cycles (Dyck et al., 1979; Oka, 1988; Loevinsohn et al., 1993) and reduces leafhopper-transmitted disease (Wada and Nik, 1992; Cabunagan et al., 2001). Synchronous cropping allegedly promotes rapid population buildup of the BPH and green leafhopper *N. virescens* (Distant) in post-fallow, wet-season crops (Widiarta et al., 1990). Synchronous cropping may produce more frequent and intense pest outbreaks and smaller and less diverse predator populations than asynchronous crops (Sawada et al., 1992; Wada and Nik, 1992; Settle et al., 1996). Therefore, if the fallow between cropping seasons is prolonged and dry, it could deplete natural enemy populations and reduce their effectiveness in controlling pests in subsequent (post-fallow) crops.

Schoenly et al. (2010) tested the impact of small-scale, synchronous fallows on rice invertebrate faunas at two sites on Luzon Island, Philippines. Invertebrates were sampled in the same fields over two cropping seasons interrupted by a 6-week wet fallow at IRRI in Southern Luzon and a 12-week dry fallow at Zaragoza in Central Luzon. Except for significantly larger populations of green leafhoppers, *N. virescens* and *N. nigropictus* (Stål), in post-fallow crops, as Widiarta et al. (1990) recorded in wet-season crops, small-scale synchronous fallowing combined with molluscicide-only pesticide inputs and pest-resistant varieties did not induce pest outbreaks or notably diminish populations of natural enemies when embedded in asynchronous cropping on larger, regional scales (Schoenly et al., 2010).

It might appear that the original metapopulation model of Levins (1969) and later versions (e.g., Hanski, 1991) provide theoretical support for the synchronous rice cropping system. This is because the persistence of a metapopulation requires asynchronous dynamics of local genetically connected populations (Hanski, 1999). However, the Levins (1969) and subsequent metapopulation models ignored the role of natural enemies in mitigating pest outbreaks (Jervis, 1997). In their

metapopulation model that incorporated both natural enemy and pest population movements, Ives and Settle (1997) found that asynchronous crops with predators migrating between fields lowered pest densities more than synchronous crops without migrating predators. Moreover, they found that pest populations will be reduced if predators move into fields early and exploit alternate prey. In other human-managed ecosystems, heterogeneous landscapes are less prone to insect pest outbreaks than homogeneous landscapes (e.g., Su et al., 1996; Cappuccino et al., 1998; Jactel et al., 2002). Theoretical and empirical studies suggest that heterogeneous landscapes allow mobile generalists—characteristic of the arthropod predators and many insect parasitoids that frequent rice in tropical Asia—to increase rapidly in response to increasing pest abundance (i.e., “birdfeeder effect”) and play key roles in stabilizing food webs (Kondoh, 2003; McCann et al., 2005; Eveleigh et al., 2007). In agroecosystems, birdfeeder effects can be triggered by farmer interventions that encourage pest outbreaks. For example, in farmers’ fields at Zaragoza, Philippines, deltamethrin sprays triggered outbreaks in three delphacid planthoppers: BPH, WBPH, and *Tagosodes pusanus* (Distant). During the 21-day spray interval, predator populations plummeted, then rebounded in the sprayed plot, eventually outnumbering predators in the unsprayed plot (Schoenly et al., 1996). At this site, rice farmers have been forced to adopt the asynchronous planting system due to the uneven availability of irrigation water (Loevinsohn et al., 1993).

Asynchronous cropping offers the advantage of creating continuous refuges for migrating arthropods. However, its deployment over large areas results in less efficient use of irrigation water (Loevinsohn et al., 1993; Litsinger, 2008) and it may increase problems with rice rats, *Rattus argentiventer* (Robinson and Kloss), (Lam, 1983; Stenseth et al., 2003) and tungro virus (Wada and Nik, 1992; Cabunagan et al., 2001). Furthermore, the asynchronous system may increase certain mosquito-borne diseases (Mogi and Miyagi, 1990) by extending production of vector mosquitoes that prefer newly planted or harvested fields with short or sparse vegetation (Heathcote, 1970; Chandler and Highton, 1975).

Role of non-rice vegetation

To what degree wild habitats and non-rice crops affect the dynamics of BPH and its natural enemies in nearby rice fields is poorly understood at both the local spatial scale and across the broader landscape. In some landscapes, boundaries between habitat patches (i.e., ecotones) provide population refuges and optional routes for species movements and also buffer wind and water erosion (Wiens et al., 1985; Meffe and Carroll, 1994). The elevated earthen mounds (bunds or levees) that surround fields of irrigated and rainfed rice may be important habitat for both harmful species (e.g., weeds and rats) and beneficial organisms including natural enemies important in controlling BPH and other pests. In Sri Lanka, Bambaradeniya et al. (2004) recorded 82 species of weeds in rice field bunds; 36 species were exclusive to the bunds. Some arthropods concentrate on the bunds when rice is flooded and re-enter fields when irrigation ceases or the rice canopy closes. *Pardosa* spp. and *Atypena* (= *Callitrichia*) *formosana* (Oi), spiders that are dominant predators of BPH during the first 35 days after rice transplanting (Sahu et al., 1996; Sigsgaard et al., 1999), commonly transverse flooded rice fields. In the Philippines, colonies of the ant *Solenopsis geminata* (Fabricius) infest bunds of irrigated and rainfed fields in large numbers and prey on immature hemipterans (including planthoppers), lepidopterans, and the golden apple snail, *Pomacea canaliculata* (Lamarck) (Way et al., 1998; Way and Heong, 2009). Vegetation bordering rice fields (e.g., on bunds or levees, along irrigation canals or roadsides, in uncultivated fields, or in cultivated fields of crops other than rice) may provide important refugia for BPH’s natural enemies. For example, the egg parasitoids *Anagrus* spp. and *Oligosita* spp. of rice leafhoppers and planthoppers live in nearby *Echinochloa*- and *Leptochloa*-rich habitats, respectively, and move rapidly into newly planted rice (Yu et al.,

1996). Fallow fields harbor rice invertebrates that live in soil crevices and remain there or move to non-rice habitats (Arida and Heong, 1994). Nearby water sources (irrigation canals, drainage ditches, rivers, and streams) harbor aquatic taxa that recolonize rice fields and influence species richness (Roger, 1996) and also the management of disease vectors (Mogi and Miyagi, 1990) especially during the wet season. Although habitats surrounding rice potentially affect the rice field biota, it is not clear how and to what extent immigrants and especially predators and parasitoids from the non-rice habitats stabilize pest-natural enemy dynamics in rice fields. Understanding the link in the rice and non-rice habitats may be the key in pinpointing causes of BPH outbreaks at local and regional scales.

Isolating the rice crop in time may be highly effective in altering the dynamics of a pest population (Kiritani, 1979; Litsinger, 1994). For example, a rice cultivar that reaches harvest maturity in 100–130 days would provide much less time for a vegetative pest like BPH to develop than a cultivar that reaches harvest maturity in 180 days. Delaying the sowing and transplanting dates by 2 wks (May to June) in China's Yangtze Delta reduced densities of BPH immigrants by 70% and also reduced infection rates of rice stripe virus by 50% (Cheng, 2009). Similarly, planting rice at later dates in southern Japan reduced densities of SBPH, another vector of rice stripe virus (Okamoto et al., 1967). Although synchronous fallowing reportedly disrupts insect life cycles (Dyck et al., 1979; Oka, 1988; Loevinsohn et al., 1993), a prolonged and dry fallow may deplete natural enemy populations and allow pest populations to build up unchecked in the post-fallow crop. However, Schoenly et al. (2010) found that synchronous fallowing on small-scales (several adjacent fields) embedded within a larger asynchronously planted landscape did not disrupt the effectiveness of natural enemies. This was because the mixture of cultivated and temporarily unused fields ensured between-field and between-season exchanges of rice invertebrate populations. Low-pesticide (molluscicide only) inputs and pest-resistant rice varieties were compatible with this practice (Schoenly et al., 2010).

Intercropping (or polycropping) may also impact pest population dynamics. For example, in Fujian Province, China, Lin et al. (2011) recorded 49–55% fewer planthoppers (BPH, WBPH) in rice plots intercropped with chili pepper, *Capsicum* sp., ginger, *Zingiber officinale* Roscoe, sticky maize, *Zea mays* L., and peanut, *Arachis hypogaea* L., than in rice plots planted as monocultures. The authors hypothesized that the non-rice crops could have masked the chemical and visual cues planthoppers use to locate rice, reducing the crop's apparency to pests. The researchers did not determine how rice yield or natural enemies were affected by the intercropping.

Implications of the looming water crisis

Worldwide, irrigated lowland rice receives some 34–43% of the world's total irrigation water, or 24–30% of the world's total freshwater withdrawals (Bouman et al., 2007). Increasing water scarcity threatens the sustainability, production, and ecosystem services of rice fields and is forcing farmers and scientists to innovate more efficient water management practices. Conventional production of irrigated rice, which evolved centuries ago, involves continuous flooding of the paddies from planting to nearing harvest maturity. However, evidence has shown that periodic drainage of the rice fields may not reduce yield and in fact may bolster yield (Singh et al., 1996; Guerra et al., 1998). Moreover, some studies suggest that rice yield may decline in continuously flooded intensive rice monocultures because of reduced soil fertility (e.g., Dawe et al., 2000). Long-term experiments in Southeast Asia indicate that periodic drainage of rice fields can counter the detrimental effects of soil infertility (Dawe et al., 2000). In China, periodic drainage reduced the volume of irrigation water by 40–70% with no apparent loss in rice yield (Guerra et al., 1998) and also reduced larval mosquitoes (*Anopheles* and *Culex*

sp.) and human malaria (Pao-Ling, 1984; Roger and Bhuiyan, 1990). Because of the looming water crisis, periodic drying of irrigated rice fields may be increasingly necessary even in areas where some yield loss might be expected (Bouman, 2001; Bouman et al., 2007). Although the changes may reduce problems with certain mosquitoes, they could disrupt the natural control of BPH and other pests. The water of irrigated rice in tropical Asia is rich in species diversity and, as discussed, includes aquatic predators important in regulating BPH populations.

Are BPH outbreaks the ecological consequence of natural large-scale changes in the environment?

It is tempting to conclude that human-controlled inputs such as insecticides or insecticides in combination with nitrogen fertilizer, for example, have been totally responsible for the synchronous BPH outbreaks in tropical rice observed across many areas of Asia, shortly after the beginning of the green revolution and again more recently. However, less-tangible natural governing factors may have created an environment favoring an above-average increase in the pest's populations independent of the human inputs. The high overall outbreak synchrony in the geographically separated populations of BPH could indicate that a "Moran effect" (Moran, 1953) such as climate has played a role. Moran (1953) predicted that if population synchrony was driven by an environmental variable such as climate, autocorrelation in population fluctuations would equal the autocorrelation in environmental noise. His prediction assumed the same linear density regulation on a logarithmic scale in all of the affected populations and that the correlation in the fluctuations between two geographically separated populations would always be the same, irrespective of initial population sizes. Spatial correlations in ecological variables caused by, for instance, similar climates, were initially suggested to be synchronizing agents for the fluctuations in size of spatially segregated populations. The Moran effect can potentially play an important role in driving synchrony in a wide variety of ecological phenomena regardless of scale (Koenig, 2002). In such an environment conducive for more rapid BPH increases, natural enemies and BPH-resistant cultivars would be expected to have less effect in regulating the BPH's density, and natural enemy destructive insecticides would therefore be expected to have an above-average negative impact.

Climate change

Predictions are that climate change will have adverse impacts on rice production through the interactive and combined effects of high temperature and humidity, drought, salinity, and submergence (IPCC, 2007; Wassmann et al., 2009). How such abiotic stresses will affect BPH, other pest populations, and their natural enemies and alternate prey is uncertain although limited research has provided some insights. In laboratory studies, survivorship of BPH eggs and adults was lower at temperatures ≥ 35 °C than at 25–30 °C (Bae et al., 1987; Heong et al., 1995b). Moreover, higher temperatures affected BPH instars and populations differently (Heong et al., 1995b), perhaps due to differential mortality rates of their intracellular symbiotes (Bae, 1995). In the past half-century in Japan, the major rice pest fauna has shifted from stem borers (1945–1965), to delphacids and cicadellids (1965–1995), and, more recently, to rice bugs (various species of the families Miridae, Coreidae, Alydidae, and Pentatomidae) and migrant populations of delphacids including BPH and WBPH (Kiritani, 2006). From 1961 to 2000, the mean surface temperature rose by 1.0 °C in Japan. Kiritani (2006) predicted that global warming could favor natural enemies (except for spiders) by increasing the number of generations more than it would their prey species. However, other studies have suggested that species-specific responses to rising temperatures could trigger range dissociations between pest and natural enemy populations by shifting their

phenologies, distributional ranges, or migration patterns (Peters, 1991; Heong et al., 1995b; Song et al., 1995; Song and Heong, 1997; Kiritani, 2006).

Evaluating the responses to large-scale effects such as climate requires insights into the spatial scaling of effects on local population dynamics. Testing the hypothesis that climate may have produced a Moran effect on BPH populations in recent years is difficult due to the sketchy published database on historical outbreaks in the tropics. Data systematically recorded at representative locations for long periods of time is necessary. Shu et al. (2011) studied the relationship between ENSO events (La Niña and El Niño) and outbreaks of BPH in the middle and lower reaches of Yangtze River during the period of 1957–2009. They found no apparent relationship in La Niña years and outbreaks. However, BPH outbreaks occurred mainly in El Niño years and 3 years after an El Niño year. More analyses similar to those in the Shu et al. (2011) study are needed before conclusions can be drawn about the impact of large-scale events such as ENSO phenomena.

Could sunspot-related UV-radiation produce a Moran effect?

Long-term variation in the activity of sunspots has been correlated with population fluctuations of some herbivores. Paik and Paik (1977) reported that five major outbreaks of BPH and WBPH between 1912 and 1976 in Korea correlated closely with low sunspot activity. They concluded that in years of low numbers of sunspots, outbreaks of the planthoppers would be expected. However, they did not speculate on the cause and effect relations. On the other hand, Shu et al. (2011), in the study in the middle and lower reaches of Yangtze River discussed above, detected no apparent relationship in sunspot activity and BPH outbreaks although their study spanned a shorter time interval than the Paik and Paik (1977) study.

Low sunspot activity leads to a thinner ozone layer and thus higher surface ultraviolet-B radiation (UV-B). UV-B is a potent elicitor of a variety of changes in the chemistry, morphology, and physiology of plants and animals. Common signals, such as jasmonic acid play important roles in the mechanisms by which plants respond to UV-B and to damage by herbivores. Foggo et al. (2007) found that the effects of UV-B may mediate the trophic links between cabbage, *Brassica oleracea* L., its diamondback moth pest, *Plutella xylostella* L., and the pest's parasitoid *Cotesia plutellae* Kurdjumov (Foggo et al., 2007). We do not suggest that sunspot-related UV-radiation would elicit a similar tritrophic interaction in rice, and we recognize that the correlation in sunspots and planthopper outbreaks reported by Paik and Paik (1977) may have been coincidental. However, analyses of sunspot-related factors similar to those of Paik and Paik (1977) and Shu et al. (2011) in different Asian countries might prove instructive.

Discussion, conclusions, and recommendations

The insecticide-induced outbreak paradigm

A compelling argument can be made to support the paradigm that BPH outbreaks are primarily and regularly insecticidally induced on high-yielding rice cultivars in the tropics. Insecticides do not always trigger BPH outbreaks in the treated fields, but frequent applications increase the likelihood because of their harmful effects on natural enemies. BPH resistance to insecticides intensifies the probability of outbreaks; once significant levels of resistance emerge, farmers must apply increasing quantities of insecticide to combat the resistant population. The wide-scale use of imidacloprid and related compounds since the early 1990s has magnified the problem of insecticide resistance in BPH populations in both tropical and temperate areas (Matsumura et al., 2009; Heong et al., 2011). Rice farmers in several countries have reported reduced efficacy using imidacloprid to control BPH. Furthermore, the results of Yin et al. (2008) suggest that sublethal applications of the insecticide could increase BPH's capacity

for migration. This is because the survivors seem to secure more energy and become heavier when feeding on the imidacloprid-treated plants. Planthopper populations that survive imidacloprid treatment could theoretically migrate above-average distances and therefore serve as an especially important conduit in spreading imidacloprid-resistance alleles into new areas.

Although insecticides appear to be the most predictable driving force behind BPH outbreaks, it is doubtful that they are solely responsible for outbreaks. A major gap in the insecticide-induced paradigm relates to the periodic outbreaks recorded in temperate and tropical areas before the start of the green revolution. BPH outbreaks that purportedly occurred in Korea as far back as AD 18 (Paik and Paik, 1977; Dyck and Thomas, 1979) and in Japan as early as AD 697 or 701 (Miyashita, 1963; Grist and Lever, 1969; Konishi and Ito, 1973; Dyck and Thomas, 1979) are taxonomically contestable because the BPH was not described as a separate species until 1854 (Dupo and Barrion, 2009). Insecticides derived from naturally occurring ingredients (e.g., whale oil, slaked lime) were used on some Asian rice long before the green revolution (Kenmore, 1980). Nevertheless, before the 1960s the BPH was considered a major rice pest only in Japan and Korea (Paik and Paik, 1977; Dyck and Thomas, 1979; Kenmore, 1980; Heinrichs, 1994). For certain, BPH populations regularly made long-distance migratory flights from tropical Asia northward before modern insecticides were widely used on tropical rice. The recurring pre-1960s migrations of BPH into Japan and Korea suggest that significant numbers of macropters (migratory forms) developed from more southerly tropical sources. Because of the infrequent pre-1960s use of insecticides in the tropics, factors other than insecticides likely triggered the movement of northerly-bound macropterous populations.

Recommendation

Collaborators from both tropical and temperate areas should design and implement large-scale coordinated experiments in representative areas to determine if outbreaks and major migrations of BPH (and also WBPH and SBPH) are exclusively insecticide-induced. The possibility of a Moran effect (Moran, 1953) related to climate events or sunspots needs to be considered alongside the effects of insecticides. The overarching need is to determine if the complete withdrawal of insecticides from tropical rice would be sufficient by itself to eliminate significant outbreaks and reduce production of macropters making migratory flights.

Fertilizer inputs

Beginning with the green revolution of the 1960s, the continuous succession of genetically improved rice monocultures in tropical Asia enabled BPH populations to reproduce nearly year round. Heavy use of nitrogen fertilizer has increased the pest's reproductive potential in rice. Planthoppers often remain at low densities in rice receiving high levels of nitrogen if insecticides are not applied (e.g., Lu and Heong, 2009). Although abundant nitrogen may push populations to relatively high densities even in fields of BPH-resistant rice not treated with insecticides (Schoenly et al., 2010), natural enemies, especially when combined with BPH-resistant cultivars (Cuong et al., 1997), usually keep the populations below outbreak numbers in nitrogen-rich, non-hybrid rice. However, the nitrogen-rich hybrid rice plants seem to create favorable conditions for BPH outbreaks in areas with large plantings of the hybrids (e.g., Cheng, 2009). The complete lack or low level of genetic resistance to planthoppers increases their susceptibility to outbreaks (Chen et al., 2005).

Studies in many areas indicate that rice farmers apply nitrogen fertilizer at rates higher than recommended. Although nitrogen fertilizer is necessary for high yield, overuse increases the likelihood of planthopper problems, contaminates the environment, and wastes money. In the face of increasing rice fertilizer prices, the need to focus on careful nutrient management is greater than ever (Fischer, 1998).

Recommendation

Planthopper specialists should collaborate with fertilizer specialists (and other relevant disciplines) in deriving optimal nutrient management practices to recommend to farmers who use high nitrogen inputs to grow hybrid and non-hybrid rice. The goal should be to develop practices that minimize nitrogen inputs while simultaneously sustaining profitable yield.

BPH migratory cycles and metapopulation dynamics

At any given time, a significant fraction of a BPH population may be flightless brachypters (Kisimoto, 1965). The production of (migratory) macropters seems to be positively density dependent, and crowding forces individuals into microhabitats that would not otherwise be occupied under low-density conditions (Denno and Roderick, 1990; Denno et al., 1994). Applications of insecticides that unleashed BPH populations from their natural enemies would be expected to provoke such a density dependent response. Under insecticide-induced outbreaks, large numbers of BPH would be expected to emigrate, some reaching long distances. As discussed, the factors that triggered outbreaks before the green revolution are unclear. Were the outbreaks due to extreme weather events such as abnormally dry or wet periods that favored the BPH but depressed its natural enemies? Another relevant issue is the frequency and duration of the outbreaks. Periodic outbreaks that lasted for short periods might indicate that the BPH was reacting to extreme weather or that these are merely natural phenomena triggered by overcrowding, etc. Sustained synchronous outbreaks in different geographical areas might point to a Moran effect as discussed. Unfortunately, gaps in historical BPH population records since the 1960s would probably preclude a reliable assessment except in certain locations.

Another question concerning pre-1960s BPH dynamics pertains to the migration of populations into the temperate areas of Asia. Did the pre-1960s migrants originate only from outbreak sources (cultivated *O. sativa* or wild *Oryza* host plants) in the tropics or were small persistent pulses of immigrants from non-outbreak tropical sources sufficient to fuel the BPH problem in temperate areas? Scientists have a good understanding of the intercountry migratory flight patterns of BPH (Turner et al., 1999; Otuka, 2009; Watanabe et al., 2009), although the specific conditions that produce macropters in the populations and activate migrations are not well understood. As discussed, the production of migratory forms seems to be positively density dependent, and crowding forces individuals into microhabitats that they would not otherwise occupy under low-density conditions. Unfortunately, factors other than insecticides that may trigger density dependent responses that lead up to crowding and migration have not been well documented.

The northern limit of the winter breeding area for BPH populations is around the Red River Delta of Vietnam (Kisimoto, 1976). The genetic analysis by Mun et al. (1999) indicated that populations south of the Red River Delta experienced regular mixing but were distinct from populations to the north, which contribute to yearly migrations to temperate areas of Japan, Korea, and most areas of China (Kisimoto, 1976; Otuka, 2009). The genetic connectivity within subpopulations of each of the two geographical populations suggests that BPH functions as a larger metapopulation. The theoretical pest model of Ives and Settle (1997) assumed that the insect functions in this manner. In the metapopulation scenario as originally described by Levins (1969), a group of genetically connected subpopulations will occupy spatially discrete areas. One subpopulation may go extinct but other subpopulations will remain to supply individuals that disperse and repopulate empty patches. How long a subpopulation survives in a given area depends on the relationship in the rate of extinction and the rate in which immigrants repopulate it. Hanski (1991) showed that persistence of a metapopulation in a variable environment requires asynchronous dynamics of local populations, dispersal among them, and an optimal density at the local population

level. If BPH exists as a metapopulation, then migrations would be expected to repopulate areas that have experienced extinction. This being the case, periodic outbreaks in source areas might be a necessary natural phenomenon to ensure that sufficient numbers of planthoppers enter migratory flights.

Recommendation

A comprehensive Asian-wide multidisciplinary, multi-institutional coordinated effort should be launched to determine the specific triggers leading up to planthopper migration, the resources in the habitat and climatic effects that govern these events, and the spatial scale dynamics and genetic interrelations of different subpopulations.

Resistant cultivars and BPH biotypes

A high percentage of the improved rice cultivars in Asia now contain genes for BPH resistance, and rice breeders continue to develop breeding lines and cultivars with resistance (Brar et al., 2009). As discussed, the natural mechanisms that make the plants resistant to BPH are not well understood. Clarifying how the mechanisms that confer BPH resistance are related to major genes or QTLs would benefit future breeding and plant resistance deployment strategies and also provide a better understanding of inter-population and inter-specific interactions on rice plants (Chen, 2009; Horgan, 2009; Seo et al., 2009). Studies of inter-specific interactions suggest that BPH's response to rice and vice versa may be affected by the presence of other species of organisms. As discussed, Cheng et al. (2001) found that the level of resistance to BPH in a rice plant can decline if WBPH previously infested the plant, although the mechanisms are unknown. As also discussed, *OsBi1* is an inducible gene implicated in the resistance to BPH (Wang et al., 2004). Whether other species of rice insects also induce *OsBi1* is not known. The BPH-resistant gene *Bph14*, as discussed, mediates disease resistance through direct or indirect recognition of pathogen-associated molecular patterns or pathogen effectors (Jones and Dangl, 2006; Takken and Tameling, 2009). The interacting effects of BPH and plant diseases on rice with the *Bph14* gene are not known.

The presence of mutualistic yeast-like endosymbionts may further increase the complexity of the interactions between BPH and rice. The YLS appear to play a role in providing protein through the recycling of uric acid stored in the fat bodies (Sasaki et al., 1996) and synthesizing ergosterol-5,7,24 (28)-triene, which is a precursor of cholesterol and the molting hormone ecdysone (Wetzel et al., 1992). Variation in YLS in the BPH populations might partially explain the variation in planthopper performance on different rice varieties (Chen, 2009). The discovery by Tang et al. (2010) that the frequencies of bacterial infections differed among the three populations investigated (designated as BPH biotypes 1, 2, and 3) raises more questions about how microbial endosymbionts may affect the intra- and inter-population variation in BPH's response to different rice cultivars.

Devising deployment strategies that extend the life of the resistant cultivars offers many untried opportunities. Pyramiding two or more BPH-resistance genes into a single plant (Brar et al., 2009), planting multiple resistant lines within the same field, mixing pest-resistant cultivars with pest-susceptible cultivars, ecological engineering strategies that increase and conserve natural enemies (e.g., Gurr et al., 2004; Gurr, 2009), seeking more "natural enemy" friendly rice varieties, and other deployment strategies might reduce BPH pressure on rice and prolong the life of resistant cultivars. However, any of these efforts are a poor investment if farmers continue to apply insecticides to the resistant plants. Any deployment strategy aimed at extending the life of resistant cultivars must have a companion effort to stop unnecessary insecticide use on rice.

An important need is the development of new evaluation methods and conceptual guidelines that plant breeders can use when evaluating rice for BPH resistance and releasing breeding lines and new cultivars tailored for the genetic variation found in natural populations

of BPH. Breeders will likely rely increasingly on DNA markers to evaluate rice for BPH resistance (Jena and Mackill, 2008; Brar et al., 2009). Evaluating novel resistance mechanisms such as natural enemy attractiveness will require entirely new methods. It is important that entomologists and breeders find common ground to resolve their differences on the concept of BPH biotypes. Beginning with the seminal discovery of Claridge et al. (1984), evidence suggests that the differences between BPH biotypes are to a great extent environmentally induced perhaps because of nutritional differences between the rice cultivars on which they develop. Considerable evidence has shown that IRRRI's biotype models do not mirror the genetic variation found in field populations of BPH.

Recommendation

Entomologists and breeders need to collaborate in establishing concepts and evaluation methods to ensure that rice breeding lines and cultivars are released in new areas only after they have been evaluated for resistance that reflects the genetic variation in the natural BPH populations targeted. They also need to collaborate in devising evaluation and deployment strategies explicitly aimed at extending the longevity of BPH-resistant cultivars.

Asian landscapes and climate change

Climate change, diminished water resources, loss of wild habitat, and other changes in the future could have profound effects on the Asian landscape. Future research will need to address a number of issues regarding how best to manage rice in the background of these changes. How climate change will affect planthoppers and other rice pests is not clear. Because individual pest species do not experience climate change in isolation from other species, whole community studies over multiple years will be necessary to understand the effects of changing climate in different Asian environments. Shrinking irrigation water will certainly force farmers in many areas to adopt irrigation practices that include periodic drying of the irrigated rice fields. As discussed, in tropical irrigated rice of Asia, a number of predators that attack BPH and other rice pests are aquatic (e.g., Kenmore, 1980; Kenmore et al., 1984; Nakasuji and Dyck, 1984; Reissig et al., 1986; Almazan and Heong, 1992; Settle et al., 1996; Schoenly et al., 1998; Dupo and Barrion, 2009). Therefore, research is needed to examine how changes in irrigation contribute to planthopper outbreaks and what measures might be available to mitigate the negative effects. Shrinking water sources will also force farmers that now practice asynchronous cropping in many areas to shift to more water-efficient synchronous cropping. Research is needed to determine how this change in planting scheme and how different intercropping manipulations (e.g., rice with maize, ginger, peanut, chili pepper, etc.) will affect planthoppers. Additional research is required to determine the link in rice and nearby wild habitat. Wild vegetation surrounding rice fields may harbor certain pests such as rats that negatively affect the rice crop or provide breeding habitat for arthropod vectors of human disease. On the other hand, wild vegetation may provide important caches for many species of natural enemies including those critical in controlling BPH and other rice pests.

Recommendation

Collaborators of the relevant disciplines should reassess pest management practices at both local and regional levels to deal with the new combinations of stresses that changes in climate and other factors will impose, especially in irrigated rice where water supplies are becoming increasingly scarce. Future assessments of rice pest management need to be coordinated with human disease and vector management practices (Service, 1989; Roger and Bhuiyan, 1990) to determine how such overlapping deployments affect planthopper dynamics.

An Asian-wide multidisciplinary, multi-agency approach

The seminal work of Kenmore (1980) and Kenmore et al. (1984) clearly showed that BPH in the Asian tropics normally resides at low densities but always has the potential to erupt into outbreak numbers. Once the outbreaks start, little can be done to stop them. Past efforts to avert outbreaks have not been sustainable. The current unilateral use of insecticides to remedy the situation is futile and will only perpetuate recurring outbreaks—that much is clear. Other factors contributing to the outbreaks are less clear.

The planthopper problem is so complex and so widespread geographically that no one institution can begin to understand the totality of factors leading up to outbreaks and migrations or to devise a management strategy for all situations. Considerable research is needed, ranging from the basic molecular level to the international landscape level, and new and coordinated surveillance and forecasting methods will be required to understand and predict outbreaks and migrations between countries.

The most important immediate need is for all of the affected countries to take coordinated actions on large spatial scales to reverse the pesticide-use treadmill. Unless this is done, the chemical industry will continue to dictate crop protection practices to farmers, unnecessary insecticide use will proliferate, and planthopper outbreaks will recur. Educational programs to increase the farmers' awareness of the futility of the unilateral chemical control are needed to counter the chemical companies' influence. However, deriving the best approach to farmer training and participation in the future poses some complex questions. For example, why did farmers that had profited from the IPM training or FPR participation resume their former insecticide-use patterns? Was the chemical industry's marketing campaign solely responsible for the change? Would the farmers have resumed their former insecticide-use patterns even if not influenced by the chemical marketing campaigns perhaps because they perceived that the crops eventually deteriorated when not treated? Or did the lack of resources in the affected countries prevent national plant protection services and pesticide regulatory agencies from sustaining the IPM and FPR efforts initiated in the 1980s and 1990s?

Recommendation

A comprehensive Asian-wide multidisciplinary, multi-institutional coordinated effort is necessary to develop a planthopper management strategy that achieves long-term sustainability. The management strategy should evolve under an umbrella of cooperative efforts between the affected tropical and temperate countries and all relevant disciplines and agencies. The strategy obviously must include provisions for addressing the prevailing pesticide problem and implementing educational programs and legislation to stop unnecessary and environmentally unsound use of insecticides on rice.

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