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Pesticide-Induced Planthopper Population Resurgence in Rice Cropping Systems

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Abstract

Planthoppers are serious rice pests in Asia. Their population resurgence was first reported in the early 1960s, caused mainly by insecticides that indiscriminately killed beneficial arthropods and target pests. The subsequent resurgence involved two mechanisms, the loss of beneficial insects and insecticide-enhanced planthopper reproduction. In this review, we identify two forms of resurgence, acute and chronic. Acute resurgence is caused by traditional insecticides with rapid resurgence in the F₁ generation. Chronic resurgence follows application of modern pesticides, including fungicides and herbicides, with low natural enemy toxicity, coupled with stimulated planthopper reproduction. The chemical-driven syndrome of changes leads to later resurgence in the F₂ or later generations. Chronic resurgence poses new threats to global rice production. We review findings on the physiological and molecular mechanisms of chronic planthopper resurgence and suggest research directions that may help manage these new threats.

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1. INTRODUCTION

1.1. A Conceptual Framework of Pest Resurgence

The term pest resurgence first appeared in the literature during the 1960s (4). Hardin et al. (44) listed 21 definitions. We do not discuss all concepts of resurgence, on the understanding that most of them are related to broad-spectrum insecticides killing natural enemies, thereby releasing pests from natural biological control services. Early occurrences of pest resurgence in planthoppers, especially the brown planthopper (BPH) (for a list of abbreviations, see **Table 1**), *Nilaparvata lugens* Stål (Hemiptera: Delphacidae), were induced by insecticide applications (1, 7–9, 26, 28, 45–47, 51, 69, 84, 85, 106). The definitions of resurgence emphasize insecticide-driven mortality of natural enemies because pest resurgence followed application of traditional (pre-1980s) insecticides, such as organochlorines, organophosphates, carbamates, and pyrethroids, and because it occurred in the F₁ generations. Simultaneously, at sublethal doses, most insecticides stimulated planthopper reproduction through a variety of physiological and molecular mechanisms. These two forces created an unusual ecological space that was ideal for pest population resurgence. Beginning in the 1980s, the traditional insecticides were replaced by modern chemicals with improved human and environmental safety profiles (42), lower toxicity, and reduced threat to natural enemies. Buprofezin in the early 1990s and, later, imidacloprid were released and widely used to control BPH in China (98, 136). These insecticides mitigated resurgence due to low toxicity to most natural enemies and reduced stimulation of pest reproduction. Resurgence, however, can still occur in chemical application scenarios because the modern insecticides are often applied in the presence of certain herbicides and fungicides. These chemicals, which do kill target insects, can stimulate pest reproduction without threatening natural enemies. The herbicides butachlor, metolachlor, and bentazone and the fungicides jinggangmycin (JGM) and carbendazim (CBM) lead to enhanced reproduction of BPH; white-backed planthoppers (WBPH), *Sogatella furcifera*; and small brown planthoppers (SBPH), *Laodelphax striatellus* (111, 114, 115, 117, 133)

Table 1 Abbreviations in text and corresponding full names

Abbreviation	Full name
ACC	Acetyl-CoA carboxylase
BPH	Brown planthopper
CBM	Carbendazim
EST-1	Carboxylesterase precursor
FAS	Fatty acid synthase
GST	Glutathione-S-transferase
HSP	Heat-shock protein
IGR	Insect growth regulator
IRRI	International Rice Research Institute
JGM	Jinggangmycin
JH	Juvenile hormone
OA	Oxalic acid
PIS	Pesticide-induced susceptibility
SBPH	Small brown planthopper
TEM	Transmission electron microscopy
TZP	Triazophos
WBPH	White-backed planthopper
ZR	Zeatin riboside

Table 2 Effect of pesticides on reproduction in the rice pest planthopper guild

Pesticide variety	BPH	WBPH	SBPH
Abamectin	+	×	×
Acetochlor	+	×	×
Bensulfuron-methyl	+	×	×
Bentazone	+	×	×
β-hexachlorocyclohexane	+	×	×
Bisultap	+	×	×
Buprofezin	o	o	o
Butachlorebtazone	+	×	×
Carbamate	+	×	×
Carbendazim	+	×	+
Carbofuran	+	×	×
Carbaryl	+	×	×
Chloraniliprol	o	o	o
Chlorpyrifos	+	×	×
Chlordimeform	+	×	×
Cinmethylin	+	×	×
Cyclosulfamuron	+	×	×
Diazinon	+	×	×
Deltamethrin	+	×	×
Imidacloprid	o	×	×
Jinggangmycin	+	+	—
Methanidophos	+	+	+
Nitenpyram	o	×	×
Oxyfluofen	o	×	×
Oxadiazon Pretilachlor	+	×	×
Pymetrozine	×	×	×
Quinclorac	o	×	×
Triazophos	+	×	×

A plus sign (+) represents stimulation of reproduction, a minus sign (−) represents suppression of reproduction, 0 represents no effect, and a multiplication sign (×) represents unclear results. Abbreviations: BPH, brown planthopper (*Nilaparvata lugens*); SBPH, small brown planthopper (*Laodelphax striatellus*); WBPH, white-backed planthopper (*Sogatella furcifera*).

(see **Table 2**). The resurgence may be induced via alterations of resistant or nutritious substances in treated host plants, possibly including allelochemicals (27, 111, 112, 114, 115), due to alterations in crop plant physiology. Pesticide-induced rice susceptibility may benefit BPH feeding, survival, and reproduction (114, 115).

In this review, we define resurgence as pest insect populations exceeding natural, untreated population sizes following pesticide applications. Based on time-related processes, we classify resurgence into two types, acute and chronic (**Figure 1**). The former is seen as a rapid resurgence in the F₁ generation, driven by the traditional insecticides. The key features are high mortality of natural enemies coupled with stimulation of pest reproduction. BPH resurgence in tropical rice fields is usually acute. Chronic resurgence is a relatively recent phenomenon associated with modern pesticides (including fungicides) that are far less harmful to natural enemies but induce pest resurgence through physiological mechanisms that promote increased reproduction. This resurgence has relatively longer latency (F₂ or later generations) following applications of agricultural

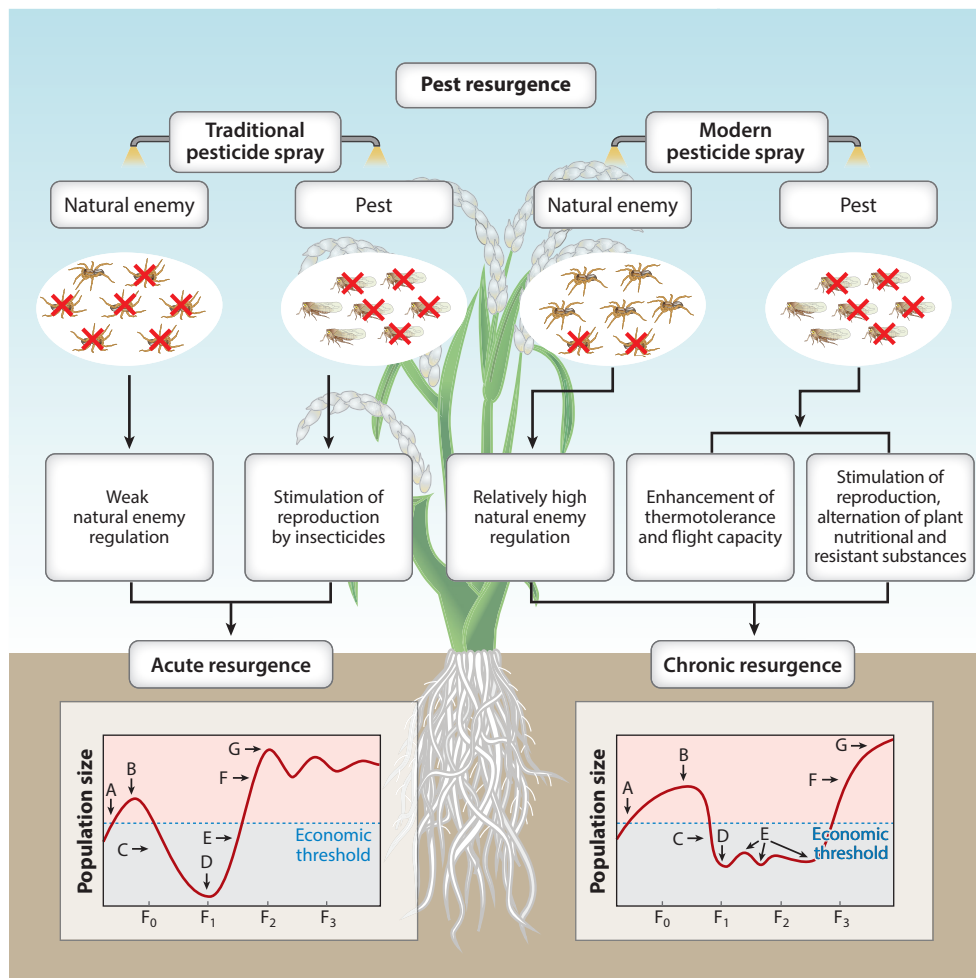


Figure 1

Conceptual framework of acute and chronic planthopper resurgence. Acute resurgence is linked to rapid planthopper population growth in the absence or weakening of natural enemies following traditional insecticide applications. Chronic resurgence after application of modern pesticides is characterized by delayed population growth due to the presence of natural enemies. At point A, the population exceeds the economic threshold; at point B, pesticide is applied; at point C, there is rapid population decline due to pesticides; at point D, the lowest population level before reproduction starts; at point E, reproduction leads to population growth, which is unchecked in acute resurgence but limited by natural enemies in chronic resurgence; at point F, there are large resurgence populations; and at point G, severe economic losses occur.

chemicals. We avoid terms such as physiological and ecological resurgence because they focus on proximate mechanisms without an historical perspective on pesticide technologies.

The definition we set forth differs from traditional ones (72, 87) by recognizing the distinctions among the influences of agricultural practices in different time periods and by recognizing physiological and molecular mechanisms underlying the process. As we suggest below, this definition enriches the connotation of the term resurgence in a pest management context.

The fungicides JGM and CBM promote planthopper resurgence. BPH populations exceeded untreated control population sizes by up to 99% following JGM foliar sprays (132). CBM

similarly stimulated SBPH reproduction (117). As fungicides, JGM and CBM stimulate planthopper reproduction, rather than killing natural enemies. We view this effect in the context of a chemical-driven syndrome with a range of symptoms, including enhanced flight capacity (134), increased thermotolerance (34, 126, 128), and increased body weight and valvula length (117), that lead to increased reproduction.

Pest resurgence is a real-world phenomenon with substantial potential for crop loss and reduced food and nutritional security. Our definition and conceptualization of resurgence is not a semantic argument. Rather, our goal is to create a broader understanding of the topic in ways that lead to effective models, predictors, and management plans that will minimize potentials for resurgence-driven agricultural disasters. In the following sections, we review case studies that illustrate chemically mediated pest resurgence.

1.2. Case Study: Planthopper Resurgence

The planthopper guild consists of three species, BPH, WBPH, and SBPH, that feed on rice and cause major problems throughout Asia (2, 5, 13, 14, 16, 24, 29, 43, 52, 59, 61, 68, 76, 77, 86, 90–94, 96, 97, 103, 107, 108, 119, 135) (**Figure 2**). The systematics of small insects is complicated in many ways, and there may be guild members that remain unrecognized. BPH and WBPH outbreak frequency in tropical Asian countries is lower compared to subtropical and temperate regions, possibly due to strong regulation by natural enemies (19, 50, 120). Natural enemy bio-control services in tropical Asian countries are higher compared to subtropical rice agroecosystems (54).

BPH emerged as a major pest soon after insecticides were used to control rice stemborers in 1962 (91), with resistance to diazinon confirmed in 1969 (91). The first sign of insecticide-induced

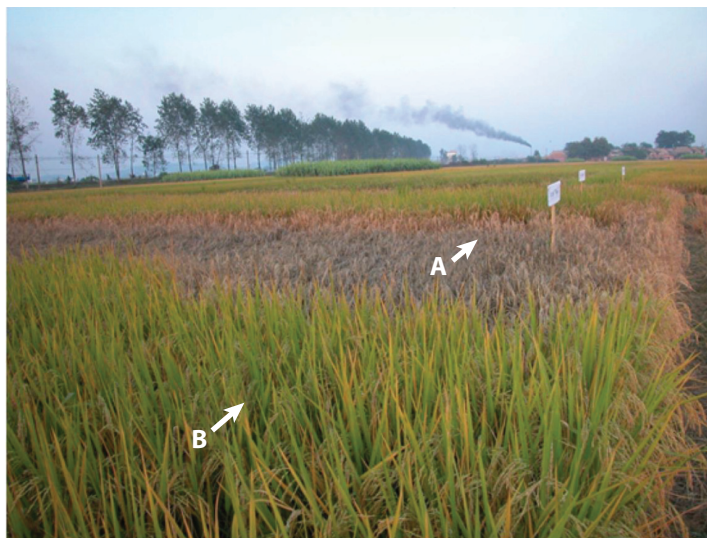


Figure 2

Hopperburn in a plot treated with pyrethroid insecticides to control rice leaffolder *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae). A indicates one segment of a field treated with insecticides. The brown shades indicate hopperburn. B indicates a small section of a control field without insecticide application. The hopperburn is a visible outcome of insecticide-induced brown planthopper resurgence, which occurred in 2005. The photo was provided by Professor Xiwu Gao, China Agricultural University.

BPH resurgence was recorded as increased reproduction and hopperburn in the diazinon-treated fields (91). Subsequently, BPH resurgence in International Rice Research Institute farms occurred following applications of almost all organophosphorus, carbamate, and pyrethroid insecticides (8, 9, 45, 47, 85, 86). In China, chemical control of rice pests (mainly stemborers and leaffolders) began in the mid-1960s, using organochlorine, organophosphorus, and carbamate insecticides as they became available. All of these products killed beneficial arthropods as well as the pests, and BPH resurgence occurred soon after insecticide applications (55, 79). Inexplicably, the literature on BPH resurgence in China did not appear until the mid-1980s (28, 41, 69), and this may help explain the previous lack of urgency in resurgence research. Apart from insecticides, some herbicides, such as butachlor and metolachlor, and some fungicides, such as JGM and CBM, also stimulate planthopper reproduction (56, 114, 115, 132, 137). Although chronic resurgence is associated with fewer planthopper outbreaks, chemically stimulated reproduction, coupled with favorable environmental conditions, can lead to resurgence (100, 101).

2. RESURGENCE WITHIN THE PLANTHOPPER GUILD

2.1. Impacts of Pesticide Application on Natural Enemies

Rice agroecosystems are complex, composed of predators, parasites, parasitoids, herbivores, and detritivores. Many of these animals provide valuable ecological services. Predators and parasitoids, in particular, are natural enemies of herbivorous pest insects. These natural enemies parasitize and consume pest insects in their ordinary life cycles and via those processes generate very valuable biological control services that contribute to rice agriculture. Agricultural chemicals challenge natural enemies in two ways, by killing some individuals and, in surviving individuals, by sharply reducing their abilities to search for and locate pest eggs, larvae, pupae, and adults. In this section, we discuss specific case studies that document the severe loss of biological control services due to pesticide application.

2.1.1. Pesticides kill natural enemies. The underlying, constant theme of planthopper resurgence is that insecticides are lethal to natural enemies that can provide valuable biological control services. We selected the planthopper egg parasitoid, *Anagrus* spp., as a case study. Carbofuran, carbaryl, and chlordimeform, but not β -hexachlorocyclohexane or bisultap, are highly toxic to *Anagrus* spp. (74). We take *Anagrus nilaparvatae* as one example of insecticide toxicity to parasitoids generally. Wang et al. (104) reported on acute and residual toxicity of fourteen insecticides to *A. nilaparvatae*, including insect growth regulators (IGRs). Imidacloprid was the most persistent insecticide, with 80% mortality of planthoppers feeding on rice leaves up to 7 days. Triazophos and deltamethrin, but not chlorantraniliprole and pymetrozine, are lethal to *A. nilaparvatae* (65). Oral IGR treatments affected longevity, fecundity, and offspring emergence, although contact and residual toxicity was low. Many scientists have contributed to the literature on insecticidal lethality to parasitoids in rice fields, much of which reports findings similar to the *A. nilaparvatae* case (60, 99).

Pesticides are also lethal to predators. Triazophos and deltamethrin, but not chlorantraniliprole and pymetrozine, are lethal to the BPH egg predator *Cyrtorhinus lividipennis* (109, 131), with deltamethrin causing 100% mortality (81, 82). In addition to predatory insects, spiders are effective predators. Many insecticides kill spiders, leading to spider population declines and serious loss of spider-driven biocontrol services (7–9, 10, 45, 47, 78, 79, 85, 123, 138, 139). Chen et al. (10) tested toxicities of seven insecticides commonly used in rice fields on *Pardosa pseudoannulata* in laboratory experiments and reported that chlorpyrifos and abamectin are toxic to *P. pseudoannulata*.

Many contributors in this area have developed a broad literature to support the generalization that agricultural chemicals are harmful, to various extents, to predatory arthropods (84, 122).

Agricultural chemicals other than insecticides can be harmful to beneficial arthropods. Some herbicides, such as pretilachlor and butachlor, and the fungicide disopropyl S-benzyl phosphorothiolate are lethal to *Cyrtorhinus lividipennis* and *Microvelia borvathi* (15). Butachlor, oxyfluorfen, oxadiazon, and metolachlor are very toxic to *Pirata subpiraticus* (62). We speculate that some other herbicides and fungicides may be deleterious to parasitoids, although these chemicals have not yet been appropriately tested.

These losses of the biocontrol services provided by natural enemies cannot be easily replaced or compensated for by other procedures, particularly in managing small insect pests such as planthoppers and aphids, which have the capacity for explosive population growth (16, 116, 118).

2.1.2. Reduction of natural enemy services due to pesticide exposure. In addition to mortality, biocontrol services of surviving natural enemies decline substantially after exposure to agricultural chemicals. The mean prey consumption by *C. lividipennis* treated with sublethal concentrations of triazophos and, separately, deltamethrin decreased approximately 18–35% compared to controls (113, 123). Wolf spiders (*P. subpiraticus*) that survived separate exposures to bisultap (shachongshuang), methanidophos, and buprofezin consumed fewer BPH. Bisultap treatments were not lethal to spiders but could reduce the spiders' functional response to prey by over 60%. (Functional response can mean several things. In this review, we use functional response to mean prey consumed over time.) Methanidophos and buprofezin treatments similarly led to decreased functional responses (113). The physiological mechanisms of the reduced performances described in these results are not yet sufficiently clear. Nor is it clear that strategies to mitigate the influence of agricultural chemicals on functional responses can be developed. We suggest that this issue warrants valuable research in the future.

Some pesticides do not reduce natural enemy services. The herbicides cyclosulfamuron (JIN-QIU), bensulfuron-methyl, and acetochlor stimulated predation on the part of surviving spiders (62). Sublethal concentrations of triazophos, deltamethrin, and imidacloprid stimulated reproduction of the predator *C. lividipennis* (71). Long-term food and nutritional security depends on optimizing the use of agricultural chemicals in a way that leads to improved crop production and protection balanced by minimization of harmful and/or unexpected consequences. Such outcomes present substantial research opportunities and challenges.

2.1.3. Pesticides influence parasitoid behavior and fecundity. Parasitoid foraging capacity is influenced by sublethal doses of insecticides. In *A. nilaparvatae*, consuming an imidacloprid–honey mixture led to substantial parasitism reduction, which involves sensory responses (65). Sublethal concentrations of triazophos and deltamethrin similarly operate through sensory physiology (65). Surviving parasitoids were unable to distinguish *N. lugens*-infested from noninfested plants (65). The reduction of the capacity of *A. nilaparvatae* to find host eggs for parasitization reduces the wasp's impact on pests. Some other insecticides do not disrupt parasitoid foraging. For instance, chlorantraniliprole and pymetrozine had little impact on *A. nilaparvatae*.

2.1.4. New assessment tools. Mortality indices per se do not meaningfully represent the influence of insecticides on natural enemy services. A more meaningful approach is assessment of natural enemy functional decreases (FDs) (113, 123), modeled by the equation

$$FD(\%) = \sum_{t=1}^{TR} \frac{Dt + St \times FDt}{TR} \times 100.$$

Here,

$$FD_t (\%) = \frac{F_{ck} - F_R}{F_{ck}} \times 100,$$

where FD_t is the FD rate of surviving predator at time t ; F_{ck} is the predation function for untreated predator; F_R is the predation function for pesticide-treated predator; D_t is the mortality of predator at time t ; $FD_T = D_t + FD_t$ is the total function decrease rate of predator at time t ; TR is the time (day) needed for predation function restoration of pesticide-treated predator; and FD is the total function rate of predator after one pesticide treatment.

FD may exceed the influence of mortality on biocontrol services. For example, the mortality of *P. subpiraticus* at 7 days after 810 ppm bisultap treatments was 39%, while the reduction of FD was 72% (113). We infer from the model that bisultap caused relatively low mortality but led to substantial reduction of spider predation. Again, mortality alone is an inadequate index of insecticide impact actions on natural enemies.

At the agroecosystem level, insecticide-related FDs are complex because many species make up populations of natural enemies. Xu et al. (123) established another model of predatory functional reduction that considers the predation rate of individuals within the total natural enemy populations. Such models are useful, not strictly for their analytical capacity, but for a deeper appreciation of many biotic and abiotic factors operating in ecosystems.

2.2. The Influence of Pesticides on Physiology and Biochemistry of Rice Plants and Planthoppers

Pesticide applications kill and otherwise impact targeted pests. Pests not killed by pesticide applications may suffer paralysis, substantial behavioral changes, feeding and foraging disorders, and mating failures. Within the organisms, the applications lead to a range of changes at the physiological, biochemical, and molecular levels. In this section, we discuss the non-lethal impacts of pesticides on rice plants and on their planthopper pests.

2.2.1. Pesticides influence rice physiology and biochemistry. Oxalic acid (OA) is a dicarboxylic acid that acts in rice resistance to BPH (75). OA content is higher in planthopper-resistant rice varieties compared to susceptible ones. Some insecticides, such as triazophos and imidacloprid, lead to reduced OA content in rice (17, 111, 112). Buprofezin, imidacloprid, and decamethrin lead to higher reduction of sugars (112) and free amino nitrogen (6, 66), which benefits pests. Concentrations of the insect inhibitory neurotransmitter γ -aminobutyric acid in rice plants were reduced following treatments with the herbicides quinclorac and butachlorentazone, the antibiotic JGM, or bisultap (66). Buprofezin, imidacloprid, JGM, bisultap, and triazophos applications led to reduced chlorophyll and photosynthesis in rice leaves, possibly by inhibiting electron transport in photosystem II (73, 111, 112). Export of photosynthate was inhibited by JGM and triazophos treatments (73).

Some rice enzymes are influenced by pesticide applications. Overexpression of glutathione-S-transferase (GST) enhances plant resistance to stress (25, 80, 127). Imidacloprid led to enhanced GST activity in the BHP-resistant variety Zhendao 2 and to reduced GST activity in the susceptible variety Xiushui 63 (110). Sodium oxide dismutase (SOD) activity was reduced in rice for 10–15 days after separate applications of several herbicides (110).

2.2.2. Pesticides influence plant hormones. Pesticide-induced changes in plant hormones have the potential to drive changes at the whole-plant level (6). Cytokinins, including zeatin riboside (ZR), act in cell division and elongation and influence the intensity and direction of photosynthate flows (23). ZR content in rice leaves decreased significantly three days after separate foliar sprays with buprofezin, imidacloprid, JGM, or triazophos (83). Rice roots treated with JGM, buprofezin, or imidacloprid using hydroponic culture led to significant reductions in leaf ZR content. These reports indicate that pesticides may inhibit ZR production or its upward systemic transport from roots to shoots, although the inhibitory mechanism remains unclear.

2.2.3. Pesticides influence rice gene transcription profiles. Some pesticide-induced changes indirectly influence gene expression in rice. Cheng et al. (17) found 225 genes that were differentially expressed after an imidacloprid treatment; 117 were up-regulated, and 108 were down-regulated. Of these, specific expression of genes encoding plant lipid transfer protein, lignin peroxidase, and flavonol-3-o-methyltransferase was changed, and this type of change may be responsible for the imidacloprid-induced rice susceptibility to BPH, which inflicted more damage on treated than control rice plants. Work on the influence of agricultural chemicals on crop plants opens a new corridor into necessary research because increasing plant susceptibility to BPH may facilitate resurgence.

2.2.4. Pesticide-induced susceptibility to planthoppers. We define pesticide-induced susceptibility (PIS) as reduced rice resistance to planthoppers following pesticide application (115). PIS facilitates planthopper feeding, survival, and fecundity and may thereby promote resurgence. Separate applications of bisultap, imidacloprid, JGM, butachlor, bentazone, metolachlor, bensulfuron-methyl, cinmethylin, acetochlor, and quinclorac led to increased rice damage (17, 66, 115). Repeated pesticide applications extended the duration of PIS, which, again, may facilitate planthopper resurgence.

2.3. Population Characteristics of Planthopper Resurgence

After applications of resurgence-associated insecticides, planthopper populations were suppressed for approximately 3 days and then rapidly rebounded through increasing growth and development of survivors (69). The resurgent populations are influenced by interactions of insecticides with other factors, such as rice variety and timing and dosage of fertilization (139). Generally, the interactions between pesticide sprays and rice variety and between pesticide sprays and fertilization influenced planthopper development times from early nymph to late nymph and to adult in WBPH. Three patterns of WBPH population size changes follow triazophos (TZP) application: (a) a continuous population increase to a peak followed by a decline, (b) an immediate decline, and (c) a decline followed by a higher peak and then a decline. TZP sprays temporarily reduced the density of BPH populations in all test plots; this was followed by rapid recovery (139). Sublethal nitenpyram concentrations led to increased macropterous/brachypterous BPH ratios, although it did not directly stimulate reproduction (129). Our interpretation of this result is that larger numbers of flight-capable BPH may increase the risk of resurgence.

2.4. Community Characteristics of Planthopper Resurgence

The influence of insecticides extends beyond killing insects to the far broader impact of disturbing the organization of community food webs. Arthropod communities in rice agroecosystems form food webs the complexity and stability of which depend on species richness and evenness

(58). High arthropod diversity in these agroecosystems enhances their resilience and capacity to recover after challenges are removed (48–50). Nonetheless, rice ecosystem services are influenced by several perturbations, particularly pesticide application. The insecticide trimethacarb reduces species richness and evenness but leads to increases in herbivore abundance (67). Insecticide treatments led to irregular insect population dynamics (18).

3. MECHANISMS OF PLANTHOPPER RESURGENCE AT THE GUILD LEVEL

At its most basic level, enhanced planthopper reproduction seems to follow chemically induced changes in organismal energy flow. A large number of biochemical pathways are involved in energy processing, and expression of key genes within the few pathways that we investigated is influenced by agricultural chemicals. Among the three species within the guild, exposure to some agricultural chemicals leads to different reproductive outcomes.

3.1. Physiological and Biochemical Effects of Agricultural Chemicals on Planthopper Reproduction

Juvenile hormone (JH) is a pleiotropic hormone with many actions in juvenile (i.e., regulating developmental outcomes of molts) and adult (i.e., promoting ovarian development) insects. Circulating JH titers are regulated by factors that increase JH production in corpora allata and enzymes that catabolize JH, such as JH esterase. TZP and deltamethrin treatments led to increased circulating JH-III titers in BPH females over 1–3 days postemergence (PE). The increased hormone titers are due to reduced levels of active JH esterase during the first three days PE (35). JGM treatments led to increased JH titers (by approximately 45–50%) in BPH females over two days PE, and they decreased 20-hydroxyecdysone (20E) titers by 30–36% (121). Agricultural chemicals can increase BPH reproduction by influencing major hormone titers. Although JH influences reproductive output, the underlying mechanism is related to increased availability of energy resources to support energy-intensive reproduction.

Imidacloprid, TZP, and deltamethrin treatments led to increased protein contents, particularly vitellogenin, in BPH ovary and fat body (31, 53). The increases induced by two resurgence-causing insecticides, TZP and deltamethrin, were generally greater compared to imidacloprid. Insect vitellogenesis involves synthesis of yolk protein precursors in fat body, transport via hemolymph, and recognition and uptake by oocytes. Fat body protein content is related to RNA quantities, which also increased in females treated with the insecticides mentioned above (31). Protein contents in fat body and ovary varied with pesticide treatment methods. Foliar spray and topical application of TZP and JGM foliar spray (JGM-S) significantly increased fat body and ovarian protein levels, but JGM topical treatments (JGM-T) did not (137), suggesting that mode of entry (ingestion versus absorption) influences BPH resurgence. The practical point is that decisions to use foliar sprays should be based on timing the sprays to minimize their positive impact on BPH reproduction. We return to this point below.

Metabolism of lipids and carbohydrates supports oocyte development and flight. The amounts of unfractionated lipids were higher in adults that developed from nymphs treated with various concentrations of deltamethrin, TZP, and imidacloprid (124–126). Similarly, JGM treatments led to increased amounts of unfractionated lipids in BPH ovaries but not in fat bodies. Similarly, there were increased amounts of unfractionated lipids and fatty acids in TZP-treated female whole bodies (63). In biochemical terms, JGM also led to increases in saturated fatty acids in ovaries and fat bodies. Compared to unsaturated fatty acids (those with one or more double bonds in the

carbon chains), the saturated components are more readily catabolized in fatty acid β -oxidation pathways (63).

Unlike BPH reproduction, SBPH reproduction was suppressed by JGM. Fatty acid contents in JGM-treated female SBPH decreased by 11–82%, depending on the specific component (22), suggesting that fatty acids are positively related to pesticide-induced changes in planthopper reproduction. Transmission electron microscopy (TEM) images indicate that the sizes of lipid droplets in the oocytes of JGM-treated BPH females were reduced at one (by 32%) and two (by 30%) days PE, indicating that JGM promotes lipid metabolism in oocytes (121), leading to faster ovarian development in JGM-treated females relative to controls.

Similarly, treating third-instar BPH nymphs separately with deltamethrin, TZP, and imidacloprid led to increased soluble sugar contents in the corresponding adults (124, 125). Glucose content; soluble trehalase activity; and expression of the soluble, but not membrane-bound, trehalase gene (*NTT α -1*) in TZP-treated fifth-instar nymph BPH increased, while trehalose content decreased (35, 39). Soluble trehalase activity and *NTT α -1* mRNA accumulation in TZP-treated macropterous females were higher compared to brachypterous females (35). Again, these metabolites provide the energy that drives BPH reproduction and resurgence.

3.2. Flight Muscle and Oocyte Changes Associated with Pesticide-Induced Brown Planthopper Reproduction

Planthopper migratory capacity and distance are closely related to resurgence (86). TEM shows that the diameters of female muscle myofibrils are larger at days one (by 31%) and two (by 21%) PE following TZP treatment. Similarly, sarcomere lengths and mitochondrial volumes were larger (102). These TZP-induced changes are supported by increases in energy metabolites. TZP, imidacloprid, and deltamethrin treatments led to enhanced flight speed and distance (134). We infer that exposure to some insecticides can increase overall migratory potential, recognizing that flight distances are substantially influenced by wind and other weather conditions.

3.3. Proteomic Analysis of Pesticide Actions

Pesticide exposure leads to substantial changes in protein and gene expression in planthoppers (3) in a species- and pesticide type-related manner. Carbamate treatments led to elevated expression of nine proteins and reduced expression of four others (89). In BPH, JGM-S treatments led to 284 differentially expressed proteins (142 increases and 142 decreases). Pesticide treatment methods also influence protein expression. JGM-T led to expression changes in 267 proteins (130 increases and 137 decreases). In JGM-S, when compared to JGM-T, 114 proteins were differentially expressed (62 increases and 52 decreases) (63). JGM and CBM induced inverse effects on SBPH. JGM suppressed, and CBM increased, SBPH reproduction. JGM treatments led to differential expression of 95 proteins (62 increases and 33 decreases). CBM treatments led to changed expressions of 818 proteins (452 increases and 366 decreases). The results are more complicated for JGM versus CBM treatments. For a single example, CBM and JGM treatments led to opposite changes in vitellogenin expression (117).

At the gene level, 145 genes were differentially expressed (85 increases and 60 decreases) between JGM and untreated control BPH females (132). Transcriptomic analysis showed that 15,870 genes were differentially expressed (10,761 increases and 5,109 decreases) in WBPH between JGM and control groups, in agreement with the fact that JGM suppresses WBPH reproduction (132). The significant changes in expression of genes associated with reproduction and metabolism can be used as candidates for detailed research to investigate the molecular mechanisms of pesticide-induced changes in reproductive output (132).

3.4. Analysis of Gene Functions

Discovery of specific genes acting in pesticide-induced planthopper reproduction emerged from targeted knockdown of selected genes that reduced or eliminated the pesticide-induced influences on reproduction. Some specific genes have been identified. For example, hydroxysteroid dehydrogenase-like protein 2-like and long chain fatty acid coenzyme A ligase act in the CBM- and TZP-induced SBPH reproductive increases (117, 130). Other genes, such as L-3-hydroxyacyl coenzyme A dehydrogenase, glucose dehydrogenase, and carboxylesterase precursor (EST-1), act in the JGM-induced suppression of SBPH reproduction (22, 32, 117). Fatty acid synthase (FAS), adipose triglyceride lipase, acetyl-CoA carboxylase (ACC), and EST-1 participate in JGM-induced stimulation of BPH reproduction (32, 56, 57, 63, 126, 132). Acyl-coenzyme A oxidase mediates TZP-induced BPH reproductive stimulation (70). Silencing the pyruvate kinase gene led to reduced fecundity in BPH (33). All these genes act in energy metabolism, suggesting that the underlying genetic mechanism of enhanced reproduction is generation of energy that supports reproductive physiology.

3.5. Pesticides Lead to Increased Brown Planthopper Thermotolerance

One element in the syndrome of pesticide-driven BPH resurgence is their enhanced thermotolerance. This is an important insight into BPH resurgence because high temperatures ($>38^{\circ}\text{C}$) can limit population growth. The molecular basis of the temperature limitation lies in enzyme function because the environmental temperatures set the body temperatures of very small insects, such as planthoppers. High body temperatures destabilize enzymes and limit catalysis. This suppresses energy metabolism and attendant reproduction and survival (11, 21). The number of eggs laid by BPH females treated with 40 ppm TZP at high temperature (34°C) approximately doubled compared to untreated insects (12). JGM-treated and, separately, TZP-treated females experienced increased lethal mean times (LT_{50}) at 40°C (34, 126). Our interpretation of these results is that TZP and JGM treatments lead to increased stress responses, one of which is expression of heat-shock proteins (HSPs) that operate as molecular chaperones that stabilize enzymes. The thermotolerance of SBPH resistant to buprofezin increased with increasing buprofezin resistance; however, buprofezin resistance did not influence cold resistance (64). Cross-tolerance is a broadly applied concept in which increased tolerance to one stressor increases tolerance to others. Again, one molecular mechanism of increased BPH thermotolerance is increased expression of *Hsp70*. In general, there are many HSPs, which serve as molecular chaperones and help stabilize other proteins. Similarly, JGM treatments act through *ACC* and *Hsp70* expression (126). *Hsp70* influences BPH reproduction at high temperature (e.g., 34°C) but not at lower temperatures (e.g., 26°C) (126). HSPs may mediate thermotolerance via direct interactions with enzymes. The proteins encoded by *arginine kinase* and *ACC* act in energy sensing and metabolism, which provides the proximate energy metabolite, ATP, to support stress tolerance and reproduction.

4. PESTICIDES INFLUENCE MALE CONTRIBUTIONS TO BROWN PLANTHOPPER REPRODUCTION

Most inquiries into the physiological mechanisms of planthopper resurgence have focused on females. In this section, we discuss pesticide-induced increases in male contributions to reproduction, which act via sexual transfer of materials to females.

4.1. Pesticides Enhance Accessory Gland Proteins

Several studies have examined the influence of male mating factors [including sperm and accessory gland proteins (AGPs)] on female reproductive performance. Males transfer seminal fluids, which

include sperm and AGPs, to females via mating. AGPs influence several female behaviors, including oviposition (20, 40, 88, 95). TZP and deltamethrin treatments led to enhanced AGP contents in males prior to mating (1 and 2 days PE) (30, 36). Treating third-instar BPH nymphs with 25 and 50 ppm TZP led to roughly double the amounts of AGPs in the adult males prior to mating (105). Postmating AGP contents were substantially lower than controls, supporting the hypothesis that insecticide-treated males transferred more AGPs to females, where they contribute to enhanced egg production (35, 36, 105).

The increased egg production mediated by pesticide-induced AGPs is a new insight into resurgence mechanisms. Wang et al. (105) tested this with four mating treatments: Pair 1 consisted of untreated control parents ($\sigma_{ck} \times \varphi_{ck}$), Pair 2 consisted of an untreated male with a TZP-treated female ($\sigma_{ck} \times \varphi_t$), Pair 3 consisted of a TZP-treated male with an untreated female ($\sigma_t \times \varphi_{ck}$), and Pair 4 consisted of TZP-treated parents ($\sigma_t \times \varphi_t$). Female partners in Pair 3 laid 44% more eggs than their counterpart controls and 20% more eggs than Pair 2 females (105). We suggest that the insecticide-induced reproductive effects on the males are transferred to females via mating. Pesticide-driven reproduction occurs due to pesticide influences on both male and female planthoppers.

4.2. Proteomic Analysis

Proteomic analysis of TZP-treated unmated BPH males versus untreated unmated males and, in a separate case, TZP-treated unmated males versus treated mated males showed 16 differentially expressed proteins in the treated males compared to their untreated counterparts, 10 increases and 6 decreases (30). Expression of a few proteins was substantially increased. For example, Act-5C (P10987), which acts in flight muscle isoforms, sperm individualization, and mushroom body development, was upregulated approximately 19-fold. Similarly, spermatogenesis-associated protein 5 (Q8NB90) and testis development protein NYD-SP6 (Q9BWX1) were upregulated 3.1- and 5.5-fold, respectively. These, too, may act in enhancing male contributions to BPH reproduction.

These proteins are mainly involved in spermatogenesis, and they promote increased fecundity via mating. Silencing a gene encoding spermatogenesis-associated protein 5-like (*SPATAS*) and *PHF7* in BPH males led to decreased AGP contents and decreased fecundity of these males' female partners (37–39). Relative to females that mated with untreated control males, females that mated with *SPATAS*-silenced males also suffered decreased fat body and ovarian protein contents, reduced abundances of yeast-like symbionts, and reduced vitellogenin gene expression (38). The influence of agricultural chemicals on planthopper populations can be registered at virtually all levels of biological organization: molecular, protein, cellular, tissue, organismal, and population.

5. PROSPECTIVE RESEARCH DIRECTIONS

Despite the progress in developing target-focused insecticides, episodes of chronic resurgence continue to recur. The most urgent need is for further research on the physiological and molecular mechanisms discussed in this review. The results of such work needs to be incorporated into resurgence models that link molecular mechanisms to ecological effects. This research will be complex, and investigation of factors such as food quality, predator and parasite populations, and insect-linked plant microbes will yield valuable insights. Research into how these physiological changes, in conjunction with environmental conditions, may operate to expand planthopper biogeographical ranges is necessary.

Continued research into planthopper biology is urgently needed. Nonetheless, current insights can be applied in design of contemporary pest and disease control operations. The literature on planthoppers indicates that species within the guild have different responses to the same

agricultural chemicals. This is a valuable insight because it can be applied in designing combined disease and pest management programs without waiting for development of sophisticated predictive models. We mention above that JGM application to control rice disease should be avoided in the presence of BPH populations because JGM stimulates BPH reproduction. Alternatively, JGM can be used for rice disease control in the presence of WBPH because it suppresses both disease and WBPH reproduction. The current insights also point to urgently needed research. TZP application, for example, enhances reproduction in all three planthopper species. It also kills natural enemies or reduces their biological control efficacy. Based on the information on TZP actions that is currently available, we suggest that application of this pesticide be avoided.

Various pesticides are often mixed, including insecticides with fungicides. This common practice raises important questions, particularly, how the mixtures influence members of the planthopper guild. In this case, again, research is required at all levels of biological organization. The work reviewed above provides some, albeit limited, insights into how various agricultural chemicals influence some members of one guild. This is a small step toward long-term, sustainable food and nutrition security for billions of humans sharing a small, increasingly abused planet.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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