Rice Planthopper Project

Planthoppers: new threats to the sustainability of intensive rice production systems in Asia

Edited by K.L. Heong and B. Hardy

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Australian Government
Australian Centre for International Agricultural Research

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Foreword

Rice is the staple food for around half the world's people and about three-quarters of a billion of the world's poor depend on rice. Each year, an additional 50 million rice consumers are added to the world population, which means that rice production will need to increase markedly.

Lowland rice provides more than 75% of the world's annual supply. For the world rice supply, these areas are likely to intensify through new high-yielding varieties and improved cultivation practices. But they are also vulnerable to threats from pests.

With increases in agricultural labor and inputs, farmers face a dilemma as their income is squeezed. Adding more burden to their livelihoods are unstable yields caused by pest outbreaks. One of the most devastating pests that threatened the Green Revolution in the 1970s and '80s was the brown planthopper. In 1977, the International Rice Research Institute (IRRI) convened the first brown planthopper conference to outline management strategies that included rice varieties resistant to pests, cultural practices, and integrated pest management (IPM) measures. IRRI's research in the 1990s clearly demonstrated that brown planthoppers were secondary pests, brought about by insecticide misuse. IRRI therefore developed IPM and communication strategies using a heuristics approach to motivate farmers to reduce their early-season spraying. This campaign reduced farmers' insecticide use by 53% and lowered vulnerability to outbreaks on thousands of rice farms in Vietnam and Thailand. International agencies, such as FAO, the World Bank, and UNDP, provided IPM training that focused on conserving natural biological control and reducing pesticide use for thousands of farmers. These efforts seemed to keep planthopper pests below damaging levels in most countries. However, the past few years showed signs of a return of this potential threat to rice production. IRRI therefore convened a second conference on rice planthoppers in 2008 to explore new approaches to developing sustainable management strategies.

Today, three major species of rice planthoppers (brown planthopper, white-backed planthopper, and small brown planthopper) have been reported as a menace in Bangladesh, Cambodia, China, India, Indonesia, Japan, Korea, Laos, Malaysia, the Philippines, Thailand, and Vietnam. They transmit five virus diseases and can cause

massive damages. Researchers are working to determine why planthoppers are again threatening rice crops. Since the last planthopper conference at IRRI, many scientific articles and books on planthoppers and numerous developments in research on biology, ecology, and biotechnology have become available. This book provides summaries and analyses of the key works and issues and provides details on management approaches. Clearly, the world needs a "doubly green revolution" to ensure food security. I hope this book will help initiate research and development activities for achieving it.

IRRI is grateful to the Australian Centre for International Agricultural Research, which first answered our call by supporting a scoping study in Vietnam in 2007. This study paved the way for the development of a full proposal and we are grateful to the Asian Development Bank for supporting this work.

Robert S. Zeigler
Director General
International Rice Research Institute

Preface

The International Conference on *Planthoppers—new threats to the sustainability of intensive rice production systems in Asia* held at the International Rice Research Institute (IRRI), Los Baños, Philippines, in June 2008 came about as a result of numerous outbreaks of planthoppers occurring in China and Vietnam. Rice planthoppers, brown and whitebacked planthoppers (BPH and WBPH) and the small brown planthopper (SBPH), are pests that are normally kept in check by naturally occurring biological control services in the rice ecosystem. In large populations, planthoppers can completely destroy crops, an effect called "hopper burn." In addition, planthoppers are known vectors of virus diseases: grassy stunt, ragged stunt, rice dwarf, rice black streak dwarf, and, more recently, a new virus called southern rice black streak. Plants infected by these viruses become stunted and have zero yield.

In the 1970s, BPH became a threat to rice intensification programs in Indonesia, Thailand, India, the Solomon Islands, and the Philippines. IRRI organized the first international BPH conference in 1977, which brought together scientists from all rice-producing countries to tackle the problem. Activities triggered by this conference followed, including integrated pest management (IPM), reducing unnecessary insecticide use, and breeding resistant varieties. These contributed to improved management of the pest, which kept it under control for the next 20 years. However, in the past 5 years, problems from all three species of planthoppers have intensified in several countries, such as China, Thailand, Malaysia, and Vietnam. This might be due to factors such as increased fertilizer and pesticide misuse, climate, changes in rice varieties (hybrid rice), and cropping patterns. Growing insecticide resistance, especially to imidacloprid and fipronil, is also a concern.

The 2008 International Conference brought together 88 scientists, agricultural directors, and pesticide company representatives from Australia (1), Bangladesh (2), Cambodia (3), China (4), FAO (3), India (5), Indonesia (2), Japan (7), Korea (3), Laos (2), Malaysia (3), the Philippines (13), Singapore (1), Taiwan (1), Thailand (6), the United States (2), Vietnam (5), and IRRI (25). Two keynote addresses and 17 scientific papers were presented.

Dr. Peter Kenmore, chief of Plant Protection Services, FAO, Rome, in his keynote speech stressed that planthopper problems are induced by insecticides. Farmers

generally respond to cues from the public and private sector that instill fear of losing their production. In the 1970s and '80s, BPH was a huge problem in the rice intensification programs of the Philippines and Indonesia as a result of packaged seeds, fertilizers, and insecticides provided to farmers. The BPH problem in Indonesia had declined since 1986 and had remained low after significant policy interventions to remove insecticide subsidies and the implementation of IPM. Professor Geoff Gurr, professor of applied ecology at Charles Sturt Univeristy, Orange, Australia, introduced the principles of ecological engineering and discussed their potential applications in overcoming outbreak pests such as rice planthoppers. Dr. K. Kajisa, IRRI economist, provided the economic setting for the conference, discussing the current situation in the rice market and the lessons we can draw from the past. A similar rice price surge took place in the 1960s and it prompted the Green Revolution. At the same time, it also prompted heavy chemical usage and the first threat of the BPH occurred in several Asian countries.

The book has 19 chapters; of these, 17 are from papers presented at the conference. The first chapter is an invited contribution and it discusses the taxonomic and biological characteristics of planthoppers, with drawings of the important taxonomic parts, and it provides a key to species. Chapters 2, 3, and 4 report on the status of rice planthoppers in China, Japan, and some Asian countries. Chapter 5 introduces the ecosystem services concept and addresses the question whether planthopper outbreaks are in fact symptoms from ecological breakdowns. Chapter 6 reports on the alarming state of insecticide resistance development that has recently occurred in Asia.

Chapter 7 examines the responses of brown planthoppers to nitrogen-enriched situations and Chapter 8 addresses the responses of the whitebacked planthopper to Chinese hybrid rice varieties. The seed box test to screen for planthopper resistance has been adopted for more than 40 years and Chapter 9 discusses gaps in understanding of the mechanisms involved in insect-plant relationships in these tests. Chapter 10 describes the resistance-breaking abilities of Korean brown planthoppers and Chapter 11 discusses population variations among brown planthopper populations in Asia. Chapter 12 analyzes a unique insect-induced response in japonica rice varieties. Chapter 13 reports on the transoceanic migration of planthoppers from the Asian mainland to Japan and Korea and Chapter 14 describes the viruses that are carried by planthoppers. Chapter 15 studies a new approach called ecological engineering and its prospects for providing ecological management techniques for planthoppers. Chapter 16 describes the genetics of host-plant resistance to planthoppers and Chapter 17 discusses the breeding approaches to incorporate planthopper resistance into rice varieties. Chapter 18 analyzes the use of genomics as a tool to aid management and Chapter 19 introduces the concept of discontinuance of a learned behavior and how this can lead to pesticide abuse that induces planthopper outbreaks.

We hope that the information in this book will help in shifting paradigms in planthopper management and chart new sustainable approaches that will reduce the vulnerability of farmers' rice fields to hopper burn, virus infections, and economic losses. For more up-to-date information on rice planthoppers, visit http://ricehoppers.net/.

Acknowledgments

In preparing this book, many people made contributions. First of all, the editors would like to thank the authors and co-authors of the 19 chapters. Much of the work presented here came out of the International Conference on Rice Planthoppers held in Los Baños in June 2008 that many of the authors attended and we thank the sponsors of the presenters, in particular, the Japanese Government, the International Rice Research Institute (IRRI), the United Nations Food and Agriculture Organization (FAO), the Australian Centre for International Agricultural Research (ACIAR), and the private sector.

We thank our colleagues who helped at various stages of producing the book; special thanks go to Juan Lazaro III for the cover design, to Grace Cañas for assisting in editorial work, to S. Villareal and Jo Catindig for technical assistance, and to Nonnie Bunyi for secretarial assistance.

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Taxonomy, outbreaks, and current status

Taxonomy and general biology of delphacid planthoppers in rice agroecosytems

Aimee Lynn B. Dupo and Alberto T. Barrion

Sixty-five species of planthoppers representing three subfamilies—Asiracinae (4 species), Stenocracinae (4 species), and Delphacinae (57 species)—all associated with rice agroecosystems in tropical Asia are taxonomically treated. Of the total, three genera of Delphacinae—*Nilaparvata* Distant, 1906; *Laodelphax* Fennah, 1963; and *Sogatella* Fennah, 1964—are economically important. The reconstituted planthopper food web comprising 244 species—218 species of invertebrates (89.34%), 17 vertebrates (6.97%), 6 pathogens (2.46%), and 3 nematodes (1.23%)—and a key to the parasitic Hymenoptera attacking planthopper eggs, and a pictorial guide to 63 species of predators are presented.

The diverse species in nature perform specific nutritional functions as either autotrophs (= producers) or heterotrophs (= consumers). The latter group of life forms is exemplified by phytophagous insects such as the delphacid planthoppers. Most of these planthoppers are economically important pests that feed directly or serve as vectors of pathogenic microorganisms and viruses to host plants, resulting in significant damage and yield losses for farmers. On the other hand, in the economy of nature, these planthoppers serve as sources of food for other heterotrophic consumers such as parasites and predators. Thus, the optimum existence of planthoppers in nature and agroecosystems vitally requires regulated management. Such strategic management of planthopper populations needs base-line fundamental scientific knowledge, which is the focal practical implication of this chapter.

What is a planthopper?

The term "planthopper" is a collective terminology applied to all phloem-feeding invertebrates constituting 14 families in the Superfamily Fulgoroidea, Suborder Homoptera, and Order Hemiptera. Like all homopterans, a planthopper has elongate mouthparts for piercing and sucking plant fluids in the phloem and xylem vessel elements. These vessels may have poor nitrogen content (Schaefer and Panizzi 2000) and less nutri-

Table 1. Checklist of delphacid planthoppers and the virus diseases they transmit.

Virus disease	Delphacid planthopper vector	Distribution
Grassy stunt	*Nilaparvata lugens* (Stål)	Philippines and Sri Lanka
Stripe	*Laodelphax striatellus* (Fallen) *Unkanodes sapporonus* (Matsumura) *Terthron albifascia* (Matsumura)	Korea and Japan
Black streak dwarf	*Laodelphax striatellus* *Unkanodes sapporonus* *Terthron albifascia*	Japan

tion than pollen grains and other reproductive structures, yet today planthoppers as a group have been evolutionarily successful.

Family Delphacidae represents one member of the fulgoroid superfamily. Its members are appriopriately called "delphacid planthoppers" to technically distinguish them from the rest of the planthoppers. The primary distinguishing character of the delphacid family is the presence of a mobile spur at the tip of tibia III. It is the largest family in Fulgoroidea at the moment with approximately 2,000 nominal species described in 280 genera (Asche 1984, Yang 1989).

Economic importance

Osborn (1904) was first to presage the economic importance of planthoppers and even suggested that planthoppers would be more damaging to crops than previously forecast. The prediction was correct because planthoppers became the Green Revolution era's major insect pest to contend with. Planthoppers increasingly attracted attention from farmers, scientists, local government units, NGOs, and national institutes because the planthopper problem never dissipated but rather grew more threatening to crop production. Outbreaks of the brown planthopper became significant. Moreover, planthoppers vector a number of virus diseases that affect plant vigor and reduce yield. Table 1 shows the delphacid planthoppers and the virus diseases these insects transmit to the rice plant.

Morphology, classification, and key to genera/species

Figures 1 to 5 show the morphology of planthoppers.

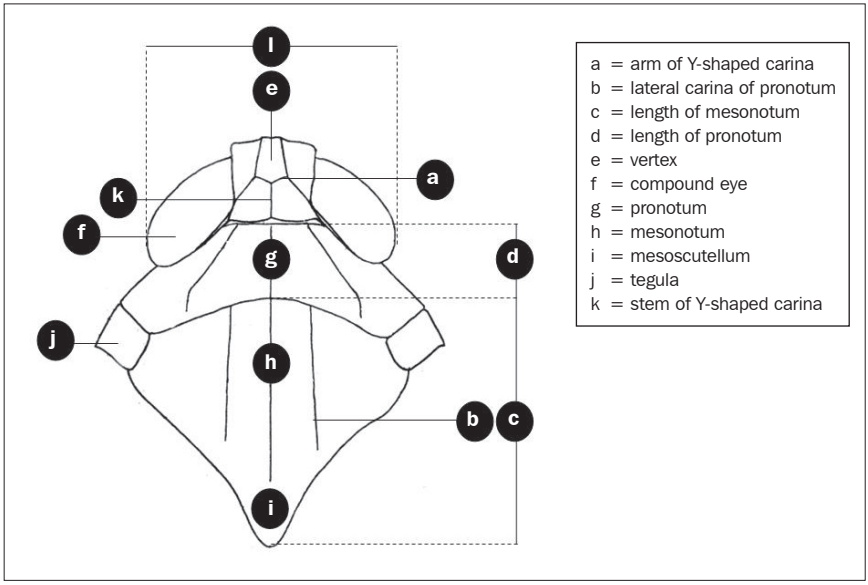

Fig. 1. Morphology of the head, pronotum, and mesonotum.

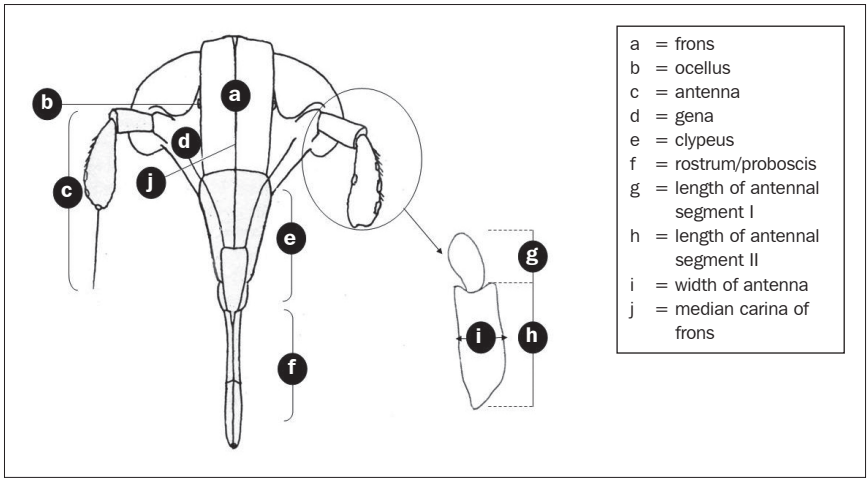

Fig. 2. Morphology of the frons, postclypeus (face), and antenna.

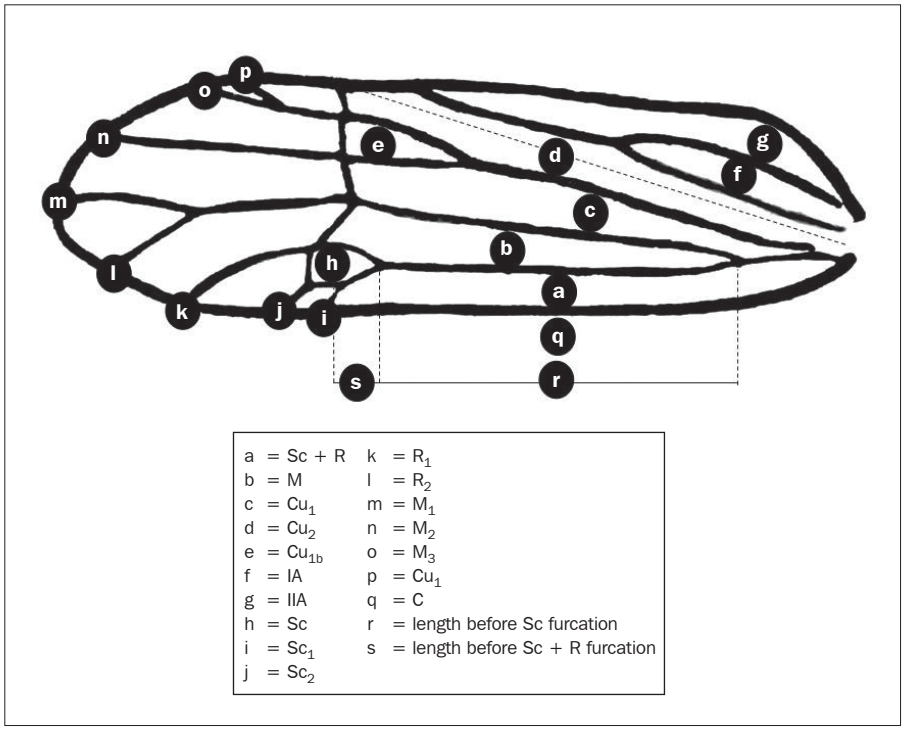

Fig. 3. Morphology of the forewing.

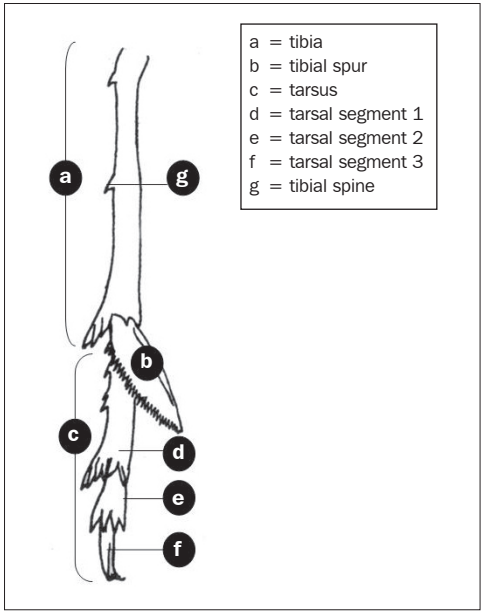

Fig. 4. Morphology of the tibia and tibial spine in leg 3.

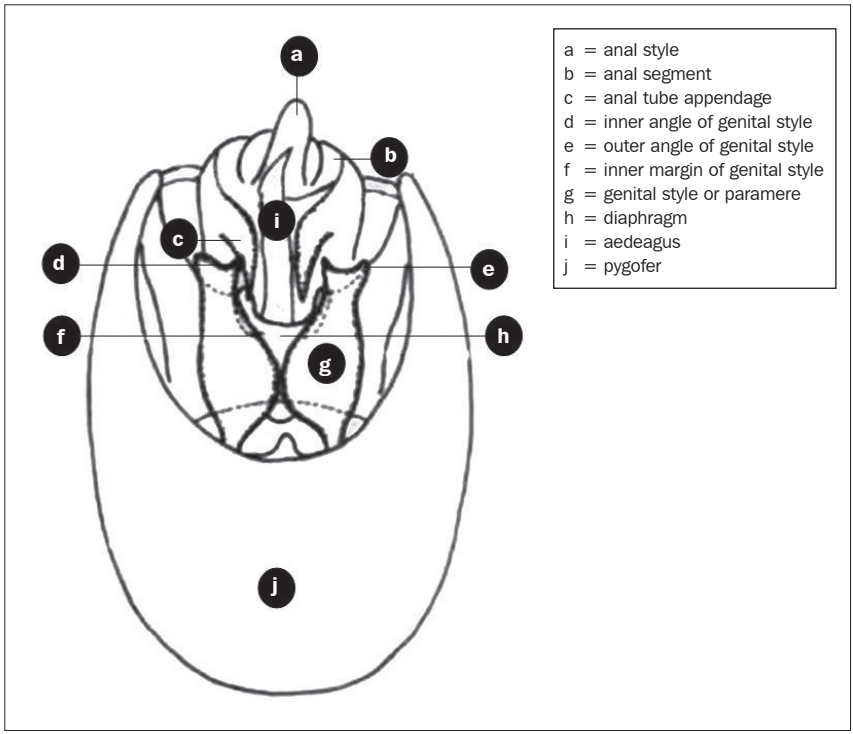

Fig. 5. Morphology of the male genital segment.

Checklist of delphacid planthoppers used in the key

1. *Melanesia pacifica* Kirkaldy
2. *Melanugyops* sp.
3. *Ugyops vittatus* (Matsumura)
4. *Ugyops tripunctatus* (Kato)
5. *Tropidocephala* sp.
6. *Tropidocephala flavovittata* Matsumura
7. *Tropidocephala nigra* (Matsumura)
8. *Tropidocephala dimidia* Yang & Yang
9. *Tropidocephala sinuosa* Yang & Yang
10. *Tropidocephala grata* Yang & Yang
11. *Tropidocephala formosa* Matsumura
12. *Tropidocephala brunnipennis* Signoret
13. *Tropidocephala saccharivoriella* Matsumura
14. *Tropidocephala festiva* (Distant)
15. *Arcofacies fullawayi* Muir
16. *Epeurysa abatana* Asche

17. *Epeurysa nawaii* Matsumura
18. *Tarophagus colocasiae* (Matsumura)
19. *Tarophagus persephone* (Kirkaldy)
20. *Sogatellana geranor* (Kirkaldy)
21. *Sogatellana quadrispinosa* (Muir)
22. *Sogatella furcifera* (Horvath)
23. *Sogatella vibix* (Haupt)
24. *Sogatella kolophon* (Kirkaldy)
25. *Latistria eupompe* (Kirkaldy)
26. *Tagosodes pusanus* (Distant)
27. *Terthron albovittatum* (Matsumura)
28. *Unkanodes albifascia* (Matsumura)
29. *Unkanodes sapporonus* Matsumura
30. *Stenocranu*s sp. A
31. *Stenocranus pacificus* Kirkaldy
32. *Stenocranus* nr. *pseudopacificus* Kirkaldy
33. *Stenocranus* sp. B
34. *Perkinsiella* sp. A
35. *Perkinsiella vastatrix* Muir
36. *Perkinsiella pseudomaidis* Muir
37. *Perkinsiella* nr. *bakeri* Muir
38. *Perkinsiella saccharicida* Muir
39. *Perkinsiella graminicida* Muir
40. *Peregrinus maidis* (Ashmead)
41. *Euidella* sp.
42. *Dicranotropis* sp.
43. *Numata muiri* (Kirkaldy)
44. *Nycheuma cognatum* (Muir)
45. *Metropis nigrifrons* Kusnezov
46. *Sardia rostrata* (Kirkaldy)
47. *Paradelphacodes paludosa* (Flor)
48. *Harmalia anacharsis* Fennah
49. *Harmalia heitensis* (Matsumura)
50. *Harmalia samesimae* (Matsumura & Ishihara)
51. *Toya propinqua* (Fieber)
52. *Euidellana celadon* Fennah
53. *Cemus sauteri* (Muir)
54. *Cemus nigromaculosus* (Muir)
55. *Cemus changchias* Kuoh
56. *Cemus* sp. A
57. *Cemus* sp. B
58. *Opiconsiva dodona* (Fennah)
59. *Laodelphax striatellus* (Fallen)
60. *Coronacella sinhalana* (Kirkaldy)

61. *Nilaparvata bakeri* (Muir)
62. *Nilaparvata muiri* China
63. *Nilaparvata albostriata* (Kirkaldy)
64. *Nilaparvata myersi* Muir
65. *Nilaparvata lugens* (Stål)

Key to the planthoppers of the rice agroecosystems in tropical Asia

1 Tibial spur of leg III subulate, circular, or angulate in cross section; antennae long 2
1' Tibial spur of leg III wedge-shaped with a single spine at apex or tectiform with teeth on hind margin; antennae relatively short 5

2 Antennae long and reaching midclypeus, second segment 3x longer than first; median carina of frons merged close to base; pygofer without midventral processes; parameres contiguous and swollen in basal one-third, curved outward forming a concavity at midlength, apices pointed almost touching one another ..... *Melanesia pacifica* Kirkaldy, 1907
2' Antennae very long, reaching beyond clypeus, second segment at least one-half longer than first; median carina of frons merged at about midlength; mid-ventral process of pygofer present; parameres not basally enlarged 3

3 Mesonotum with three carinae ..... *Melanugyops* sp.
3' Mesonotum with five carinae 4

4 Antennae as long as frons and clypeus combined; median carina of frons forked above midlength slightly in line to lower level of eyes; median ventral process of pygofer knob-like with rounded tip; parameres concave above mid-length with pointed apices subparallel to each other; body dirty light brown mottled with black spots on vertex and pronotum; body length 9–11 mm ..... *Ugyops vittatus* (Matsumura)
4' Antennae distinctly longer than combined length of frons and clypeus; median carina of frons bifurcates below midlength, way below lower level of eyes; median ventral process of pygofer apically broad and truncate; parameres slender and subparallel, tips meeting each other; body uniformly yellowish brown; pronotum lined with transverse row of three small and distinct reddish brown spots on each side; body length 8 mm ..... *Ugyops tripunctatus* (Kato)

5 Tibial spur of leg III solid, inner surface concave without teeth along posterior margin 6
5' Tibial spur of leg III tectiform with teeth on inner margin 18

6 Head noticeably extended in front of eyes, anterior end broadly rounded and snout-like; vertex without transverse to oblique connecting carina, subtriangular with lateral sides convex; frons long and reclined apically; clypeus as long as wide to longer than wide; pygofer with distinct medioventral process; parameres long, basal angles may bear long processes; forewings with small hair-bearing granules near veins; body length 3.1–4.25 mm 7

6' Head shortly developed in front of eyes, anterior end not snout-like; vertex with connecting carina; frons and clypeus different from above; pygofer without mediocaudal process; if present, anal segment with a pair of lateroapical processes; forewings without the hair-bearing granules 16

7 Head strongly projected forward far from eyes; face oblique almost at 45 degree angle viewed laterally 8

7' Head shortly porrect, close to the eyes; face in lateral view not at 45 degree angle 12

8 Vertex less than 2x longer than wide, 1.7–1.8x longer than the pronotum 9

8' Vertex 2-2.9x longer than wide, 2.5–3.3x longer than the pronotum 10

9 Vertex, frons except brown spot on frontoclypeal suture, upper gena, and pronotum green; vertex 1.7x longer than wide and 1.7x longer than the pronotum; postclypeus and base of gena dark brown; dorsal side of mesopleuron dark brown; forewing with knob-like protrusion on apical end of longitudinal vein M and subbasal area of longitudinal vein $R_2 + M_1$; body length 4 mm ..... *Tropidocephala* sp.

9' Vertex, frons, gena, and pronotum yellowish red; vertex 1.5x longer than wide and 1.8x longer than pronotum; postclypeus pale red; dorsal side of mesopleuron yellowish red; forewing without knob-like protrusions; parameres long, subparallel to each other except slightly enlarged base and diverging narrow apices; body length 3.6 mm ..... *Tropidocephala flavovittata* Matsumura

10 Vertex slightly 2x longer than wide, 2.5x longer than pronotum; pygofer with slender and pointed mediocaudal and laterocaudal processes; paramere with two concavities, subbasal inner cavity fused, apices rounded and slightly converging; body length 3.8 mm ..... *Tropidocephala nigra* (Matsumura)

10' Vertex 2.9x longer than wide, more than 3x longer than pronotum; pygofer and parameres differently shaped 11

11 Forewings with darker markings except hyaline vertical median band and black markings on apical ends of longitudinal veins Sc + R and $M + Cu_1$; knob-like protrusions more pronounced ..... *Tropidocephala dimidia* Yang and Yang

11' Forewings with light or pale markings, apical ends of Sc + R and $M + Cu_1$ without markings; knob-like protrusions indistinct ..... T*ropidocephala sinuosa* Yang and Yang

12 Vertex as long as to slightly longer than wide 13
12' Vertex distinctly longer than wide 15

13 Vertex as long as wide at midline, triangular in dorsal view; antennae not reaching the frontoclypeal suture; pygofer strongly concave viewed ventrally with a small medioventral process; parameres with an elongate basal process parallel to each other, more slender than the diverging outer processes with narrowed and outwardly curved apices; generally reddish brown except light brown face and gena; body length 3.2–3.4 mm ..... *Tropidocephala grata* Yang and Yang

13' Vertex slightly longer than wide; parameres diverging; body color not reddish brown; body length variable 14

14 Vertex greenish brown, as long as pronotum; pygofer with a short knob-like medioventral process, wing-like protrusions absent; parameres narrow and flattened basally with double concavities along the outer subbasolateral and subapicolateral areas, apices rounded; body length 3.7–3.9 mm ..... *Tropidocephala formosa* Matsumura

14' Vertex yellowish green, about 1.3x longer than pronotum; pygofer with a narrow and slender medioventral process and midlateral wing-like protrusions present; parameres flat, broad subapicolaterally forming a short, bluntly rounded tip, inner side with two short processes basally and basal one-third; body length 3.1–3.6 mm ..... *Tropidocephala brunnipennis* Signoret

15 Face with black markings only on apices of frons and base of clypeus; forewings more than 3x longer than wide, apical end narrow and acutely rounded; longitudinal veins M_2, M_3, and Cu_1 mat with brown bands; pygofer with a small, pointed, and granulate medioventral process; parameres subparallel to each other, inner bases each with a small spine, tip truncate laterocaudally; body length 3.5–3.7 mm ..... *Tropidocephala saccharivorella* Matsumura

15' Face black along apical and basal areas, clypeus, and gena; forewings barely 2.6x longer than wide, apical end broadly rounded, apices of longitudinal veins Sc + R and M with black markings; pygofer with strongly produced lateral margins, flattened medioventral processes with emarginated and granulate apices; parameres with a relatively long and slender subbasal process parallel to each other, main paramere body elongate and equally wide with apical one-sixth narrowed subapically and curved outward, tip oblique and sharply pointed at basal angle; body length 3.4–3.8 mm ..... *Tropidocephala festiva* (Distant)

16 Vertex distinctly quadrate, in profile at right angle to frons; lateral carina concave; submedian carina of vertex transverse; frons nearly twice as long as broad; apical half of first antennal segment and both ends of segment II dark brown; lateral carina of pronotum converging, posterior ends reach hind margin; forewings taper midapically, sinuate below apex; anal segment without paired processes; pygofer without mediocaudal process; parameres long and slender, inner basal one-third rounded but separated from each other, apical two-thirds slightly converging, apices twisted outward; general color green to yellowish green; body length 3.15–3.6 mm.....*Arcofacies fullawayi* Muir

16' Vertex obtusely rounded into frons forming rounded apical margins, lateral carina slightly convex; submedian carina of vertex converging toward frons; frons 1.4x longer than wide; antennal segments without bands; pronotal carina diverging, not reaching hind margins; mediocaudal process present; anal segment with a pair of short processes; parameres with inner process, diverging apically; body brown to pale yellow or reddish brown; body length 3–3.93 mm 17

17 Median medioventral processes as high as lateral ones; vertex 2.3x wider than long; forewing transparent or hyaline without bands; parameres moderately long with shorter mid-inner process wider at midlength, narrowing apically, outer process longer and broader with truncate to oblique apices projected outward; body length 3–3.13 mm; body color pale yellow to reddish brown .....*Epeurysa abatana* Asche

17' Median medioventral process higher than lateral ones; vertex 3x wider than long; forewings dark brown at apical half; parameres slender with basal inner processes uniform in diameter and distinctly lower than the outer process, with moderately rounded apices; body length 3.5–3.9 mm; body color brown .....*Epeurysa nawaii* Matsumura

18 Median carina of vertex, pronotum, and mesonotum with a broad to narrow white or yellowish white band.....19

18' Median carina of head, pronotum, and mesonotum without the above.....45

19 Frons with median carina simple or forked near the base 20

19' Frons with median carina forked near middle to basal one-third 25

20 Abdominal tergites VII-IX with a dorsomedian whitish yellow band; ventrocaudal margin of pygofer trilobate.....21

20' Abdominal tergites concolorous, without dorsomedian whitish yellow band; ventrocaudal margin of pygofer not trilobate 22

21 Lateral pair of ventrocaudal processes broadly rounded lateroventrally, distal margin projected medially forming a pointed inner edge; medioventral processes subtruncate, longer than the lateral ones; aedeagus with diverging reflected processes; female genitalia with a thumb-like basal process in valvifer VIII and strongly formed movable double-scale in abdominal sternite VI present..... *Tarophagus colocasiae* (Matsumura)

21' Lateral pair of ventrocaudal processes tapers apically as long as lateral ones; medioventral processes rounded apically; aedeagus with broadly fused reflected flag-like process at base, apically bifurcates into subequal spines; valvifer VIII of female genitalia with bases medially widely rounded; sternite VI with medially asymmetrical notch movable double-scale ..... *Tarophagus persephone* (Kirkaldy)

22 Median portion of head, pronotum, and mesonotum with a broad white longitudinal band..... 23

22' Head, pronotum, and mesonotum with a narrow, pale whitish yellow median stripe..... 29

23 Anal segment with two pairs of processes on the ventral side 24

23' Anal segment with one pair of processes on the ventral side 25

24 Forewings subhyaline with yellow tinge, subcosta and commissure yellowish white, membrane lightly developed; first antennal segment as long as second; anal segment with inner pair of processes slender and longer than the short and more robust outer pair, apices of outer pair converging and inner pair diverging; parameres cleft apically, mid-outer part wide, rounded to subtruncate; anal style distinctly long..... *Sogatellana geranor* (Kirkaldy)

24' Forewings hyaline with yellowish veins, small granulations sparse, apex of clavus with a light reddish brown tinge; first antennal segment distinctly shorter than second segment; anal segment with a distinctly long inner process, outer one small and short; parameres with an apico-inner tip strongly projected inward, outer tip tapers slightly and mid-outer trunk laterally truncate; anal style relatively short ..... *Sogatellana quadrispinosa* (Muir)

25 Pterostigma distinct; apicobasal half of forewing and apex of clavus with dark brown band; frons, gena, and clypeus black except whitish carina in frons and clypeus; parameres with a bulbous subbasal inner margin, unequally cleft apex with a small inner spine and more apically rounded outer part ..... *Sogatella furcifera* (Horvath)

25' Pterostigma indistinct; forewing with or without band; frons, gena and clypeus, and parameres different 26

26 Genital segment of male with a U-shaped mediodorsal margin of diaphragm; parameres usually broad at inner midlength, apex cleft; forewings usually banded along apicobasal half 27

26' Entirely not as above 28

27 Forewings transparent, unmarked; face whitish with dark brown genae; parameres with slim and petiolated base, apex strongly cleft with apico-outer side obliquely truncate, apico-inner sides acute and converging ..... *Sogatella vibix* (Haupt)

27' Forewings distinctly banded, dark brown along apicobasal half; face with yellow to dirty yellow frons and genae; parameres with relatively robust base, subbasal expansion, concave apex with a longer obliquely projected outer tooth and a much smaller, acute apico-inner tooth converging slightly ..... *Sogatella kolophon* (Kirkaldy)

28 Pterostigma indistinct; forewings hyaline without tinge; slender parameres strongly diverging, taper apically, almost reaching laterodorsal angle of genital segment, broad subbasally with a subtruncate inner part; diaphragm mediodorsally with broad W-shaped protrusion; clypeus yellow brown ..... *Latistria eupompe* (Kirkaldy)

28' Pterostigma distinct; forewings prominently banded along apicobasal half and claval suture extended to pterostigma, bands form four transparent spots between veins on the apical margins; basal compartment of vertex subrectangular; parameres almost uniformly broad, widely concave apex slightly narrower than subbase, outer tip higher than inner spine; diaphragm mediodorsally T-shaped; clypeus brown, lighter than dark brown base of frons ..... *Tagosodes pusanus* (Distant)

29 Head not narrowed in front of eyes; mediolateral carina of vertex meeting together on vertex forming one mediolongitudinal carina; forewing opaque to hyaline; parameres relatively broad, basally without outgrowth, apex subtruncate or with a short process and long processes 30

29' Head noticeably produced in front of eyes; median carina of vertex apically converged but not distinctly meeting on vertex, extended on to face except at extreme base; forewings mostly transparent; parameres slender, often with basal outgrowth, apices narrowed and acute 32

30 Vertex to scutellum with a moderately broad median longitudinal pale yellow-white band; antennae, face, and genae blackish brown; forewings subhyaline with a gray tinge, hind margin whitish and veins mostly light brown to dark brown; short and subglobose pygofer with a concave medioventral area; paramere subcontiguous basally, diverging apically with subtruncate tips viewed caudally, rounded viewed laterally; body dark brown; body length ..... 2.6–3.4 mm ..... *Terthron albovittatum* (Matsumura)

30’ Vertex to scutellum with a narrow median pale white stripe; antennae, face, and genae light brown; forewing opaque to hyaline; genitalia different 31

31 Forewings opaque, black except whitish apical and basal areas; vertex to scutellum with a fairly wide longitudinal band; face, clypeus, and genae deep black; base of parameres inwardly enlarged, rounded, directed to each other, narrow at midlength and apical one-third broad with a small outwardly projected inner end, a globose outer process viewed laterally; aedeagus sigmoid and hook-shaped with rounded tips; body length 1.8–2.5 mm ..... *Unkanodes albifascia* (Matsumura)

31’ Forewings hyaline with conspicuously white hind margin of clavus and broadly brownish hind margins, apical one-third of veins infuscated; vertex to scutellum with a narrow median longitudinal stripe; face, clypeus, and genae pale brown; base of parameres not enlarged, axe-like viewed laterally, inner margin uniformly concave and wide, forming a longer and rounded inner process directed upward, but one facing another in a subtruncate pattern, lower outer process subacute; aedeagus straight and arrow-like, barbed with subapical spines; body length 4.5–4.7 mm ..... *Unkanodes sapporonus* Matsumura

32 Forewings transparent except Cu_1 vein brownish below Cu_{1b} cell; frons, genae, and clypeus dark brown with white median and lateral carinae; frons 1.5x wider apically than base; parameres slender and curved outward anteriorly, narrowed inwardly at tip, then curved outwardly forming a hook; pygofer brown, midventrally V-shaped; tibial spur with 23 spines..... *Stenocranus* sp. A

32’ Forewings uniformly hyaline; frons, genae, and clypeus yellow-brown; frons 1.6–1.8x wider apically than base; parameres and pygofer different; tibial spur with about 21–30 spines..... 33

33 Frons with a broad white median longitudinal band and narrow brown lateral carina; clypeus white; genae yellowish brown; parameres slender, uniformly straight and diverging, contiguous basally, tips narrowed forming outwardly projected hooks; anal segment with two short processes; tibial spur with 24–25 spines; body length 6.8–7.8 mm .....*Stenocranus pacificus* Kirkaldy

33’ Without the combination of above characters..... 34

34 Face with two reddish brown longitudinal bands and three whitish yellow carinae, apex 1.6x wider than base; genae yellow-brown; clypeus swollen, yellow-orange; abdomen orange-yellow; tibial spur with 21 spines; base of parameres contiguous with a thin short spine, tips diverging, midpart long and slender outwardly hooked reaching beyond laterodorsal angle of pygofer; anal style relatively long; body length 6.12 mm .....*Stenocranus* nr. *pseudopacificus* Kirkaldy

34’ Face, clypeus, and genae uniformly yellowish brown; frons 1.8x wider than base; abdomen light to dark brown; tibial spur with 30 spines; base of parameres contiguous with a long, erect, sharply pointed spine at right angle, paramere body strongly concave along inner lateral margin, slightly converging apically forming a small hook at tip, projected laterally outward; anal style short; body length 5 mm ..... *Stenocranus* sp. B

35 Antennal segments somewhat flattened; forewings distinctly banded, and granulated; pygofer with two medioventral spines 36
35’ Antennal segments cylindrical; forewings usually without band, if banded, granulations very fine to indistinct; pygofer with none or three medioventral spines 41

36 Black species including legs and antennae; face black except light yellow-brown transverse band anterior of median Y-carina running to the genae, frons broadest at level of Y-median carina; pterostigma indistinct; forewings granulated, glossy light brownish yellow with two glassine spots on apical margins of cubital cell; medioventral part of black pygofer with two sharp processes curved caudally; bases of parameres robust and contiguous, inner margin concave forming 3–4 short spines at tip; anal segment with a pair of horn-like processes projected posteriorly; body length 7.7 mm ..... *Perkinsiella* sp. A
36’ Light brown species without the combination of above characters 37

37 Face with a single color pattern, mottled with pale yellow-brown spots, subapical part bears two pairs and four pairs toward base, and 2–3 spots on lateral carina; forewings weakly granulated tinged brown on veins along apical one-third; pterostigma prominent; tibial spur with 32 spines ..... *Perkinsiella vastatrix* Muir
37’ Face with two color patterns distinct 38

38 Small-bodied planthoppers, 5.4 mm long; frons with a transverse pair of interrupted white bands at level of simple eyes, four dots at subapex in line with two dots in each genae present, apex of frons white; median carina of clypeus white; antennae both blackish brown except yellow mediodorsal band on each segment; tibia I yellow with two brown bands subapically and subbasally; forewings strongly granulated, concave blackish brown band along median crossveins to vein M_1 present, apices of longitudinal veins also blackish brown; tibial spur with 27–28 spines…. *Perkinsiella pseudomaidis* Muir
38’ Large-bodied planthoppers, 7 mm or more long 39

39 Forewings with light or pale brown markings on M_1 to Cu_1 or opposite the cubital cell, 3–4 glassine spots present along apical margins 40

39’ Forewings with dark brown longitudinal band running along lower half of wings, darker along apical third opposite cubital cell; body length 7 mm ..... *Perkinsiella* nr. *bakeri* Muir

40 Apical half of frons whitish yellow extended to genae and sides of thorax, apex close to frontoclypeal suture with two triangular brown spots similar to genae; basal half of frons brown mottled with minute spots in four transverse rows; clypeus dark brown concolorous to base of coxa I and mesopleuron; forewings with alternating whitish yellow and brown dots, pale brown band opposite cubital cell forming four circular glassine spots along apical margins, granulations relatively sparse; body length 7.6 mm ..... *Perkinsiella saccharicida* Muir

40’ Apical half of frons brownish with white band below Y-median carina and along frontoclypeal margin; genae dull brown; clypeus brown; basal half of frons with indistinct white spots; forewings as above but granulations denser and closer to each other; body length 7 mm ..... *Perkinsiella graminicida* Muir

41 Forewings with distinct band and pterostigma 42

41’ Forewings with or without band, pterostigma indistinct 43

42 Forewings not granulated, banded opposite cubital cell marking the veins in apical half dark brown and with four oblong glassine spots; pygofer with distinctly concave medioventral margin without processes; parameres contiguous basally, basal two-thirds parallel to each other, apical one-third curved outward then inwardly converging, tips slightly cleft; head width narrower than pronotum; body length 6.5–7.6 mm ..... *Peregrinus maidis* (Ashmead)

42’ Forewings finely granulated, gray brown band covers Sc_1, R_1, M_1 to M_3, and Cu_1; medioventral margin rounded with three small teeth; parameres slender, broad basally projected caudally, diverging and twisted laterally, forming a narrow twisted apex directed laterally to the outside; head and pronotal width subequal; body length 5 mm ..... *Euidella* sp.

43 Lateral carina of pronotum visibly not reaching hind margin of pronotum; face broadest at apical one-third, lateral carina convex; clypeus and genae yellow-brown; second antennal segment less than twice as long as first; pygofer dark reddish brown with yellowish anal style; medioventral margin widely concave; parameres with a basal spur pointed posterad, midhalf rather flat and diverging, apical third thinly flat projected posteriorly; body length 4.2 mm ..... *Dicranotropis* sp.

43’ Entirely not as above 44

44 Forewings with a longitudinal pale brown band across wings, granulations distinct; scutellum brownish yellow; frons darker than clypeus, mottled and dark brown like the genae; medioventral processes absent; long and slender parameres basally wide protruding caudally, projected upward with sharply pointed tip gently diverging; anal segment with two processes and aedeagal spine very long extended outward from base of parameres; tibial spur with 29 teeth; body length 5.5 mm .....*Numata muiri* (Kirkaldy)

44' Forewings hyaline with dark brown vein in apical half, granulations feeble; scutellum whitish yellow; frons yellow-brown with mottles and more spots lining the lateral carinae; clypeus and genae uniformly yellow-brown; medioventral process with a long median and two short lateral spines; parameres strongly diverging with pointed base directed caudally, flat and wide medially and acute apically; anal segment with two brown processes and aedeagal spine curved downward from base of parameres, then curved upward at level to midlength of parameres, tip bifurcate; tibial spur with 36 teeth; body length 5 mm .....*Numata* sp.

45 Forewings mostly dark brown; vertex narrow and projected anteriorly or rounded in front of vertex; median carina of mesonotum present or obsolete 46

45' Forewings mostly hyaline; vertex not strongly projected in front of head, never rounded 47

46 Head in profile rounded; lateral carinae of pronotum diverging concavely away from hind margin; median carina of mesonotum absent, area distinctly grooved; body generally blackish except shiny brown forewings, blackish brown antenna, transparent small spots at apex of Cu_{1b} cell and a larger spot at Sc cell; broad transverse white band along posterior margins of pronotum; median carina of rectangulate frons obsolete on both ends; tibial spur with 27 spines or teeth .....*Metropis nigrifrons* Kusnezov

46' Head clearly narrowed in front, well protruded anterior of the eyes; forewings with a large transparent spot opposite subcostal cell and three round spots along apical margins; lateral carina of pronotum converging, not reaching hind margin of pronotum; body black to reddish brown with yellow antennae, thin yellow carina on vertex, anterior margin of pronotum, and tip of scutellum; median carina of frons entire and Y-shaped carina distinct; tibial spur with 17–19 spines.....*Sardia rostrata* (Kirkaldy)

47 Forewings without pterostigma.....48

47' Forewings with pterostigma.....53

48 Scutellum light brown lined with light net-shaped markings; lateral carinae of frons slightly convex; parameres narrow V-shaped, broad apically, bolo-shaped and parallel-sided with subtruncated tips diverging or outer lateral tips acute; pygofer rounded to slightly oblong, medioventral margin moderately concave; anal segment with a pair of short processes; body length 2.8–3 mm ..... *Paradelphacodes paludosa* (Flor)

48' Scutellum without net-shaped markings; lateral carina of frons usually subparallel sided; parameres, pygofer, and anal segment different 49

49 Pronotum pale whitish yellow, anterolateral margins near eyes dull brown concolorous to the vertex and mesonotum; tip of scutellum light to pale brown 50

49' Pronotum, vertex, and mesonotum with similar colorations 52

50 Parameres each with an inner basal node bearing a long process and erect processes, subparallel-bodied, anterior end bilobed, higher inner lobe converging apically, longer and rounded apically, outer lobe broadly rounded and diverging laterally ..... *Harmalia anacharsis* Fennah

50' Inner tips of parameres acute, lower than to subequal in height to outer tip ... 51

51 Body elongate brown including vertex, face, genae, and forewings; carinae and hind margins of pronotum and scutellum pale brown; pygofer narrowed midlaterally; anal style moderately long; parameres basally contiguous forming a V-shaped profile then slightly diverging, apex unevenly bifurcate with a small inner tip acute and outer tip shortly rounded and diverging; body length 3 mm ..... *Harmalia heitensis* (Matsumura et Ishihara)

51' Body light or pale brown including face, clypeus, and antennae; forewings subhyaline; margins of frontal carinae dark brown; pygofer broadest at mid-length, narrowed along basal one-third; anal style short; parameres U-shaped in profile with broad apex, inner tip relatively slender with blunt apex converging, outer tip rounded to subacute directed laterally; body length 1.7 mm ..... *Harmalia samesimae* (Matsumura et Ishihara)

52 Pale yellow to yellowish brown body including clypeus, antennae, and face except dark brown carina on frons; forewings visibly hyaline with feeble granulations; pronotum and mesonotum in fresh specimens may show yellowish orange light tinge at midscutellum between whitish lateral carinae; antennae barely reach frontoclypeal suture; pygofer reddish brown, slightly oblong without a median ventral process; parameres united and moderately broad basally, inner apical half concave, apices subtruncate forming converging inner and diverging outer tips; tibial spur with 19 spines..... *Toya propinqua* (Fieber)

52’ Brown, similar to *Nilaparvata lugens* (Stål); face, clypeus, and gena dirty brown; forewings granulated; pronotum without yellow-orange tinge extended to mesonotum; antennae with 2nd segment 1.6x times longer than blackish brown segment I, reach midclypeus; pygofer distinctly oblongate, median ventral area concave, extended outward, bears a small blunt process; parameres united at basal one-half, indented or concave, apically forming rounded apex with a small and pointed inner process converging; tibial spur with 27 spines..... *Euidellana celadon* Fennah

53 Forewings distinctly marked with bands, strongly granulated; head slightly narrower than pronotum; pronotal carinae yellow and midmesonotum with a longitudinal pale yellow band; pygofer with a thin but broad medioventral plate..... 54

53’ Forewings not marked as above; head visibly narrower than pronotum; pronotal carinae and mesonotum not yellowish; medioventral thin plate on pygofer absent 59

54 Males..... 55

54’ Females 58

55 Pygofer with thick yellowish white lateromedian area almost oblong..... 56

55’ Pygofer with thin yellow lateromedian area, subquadrate..... 57

56 Lateromedian area of pygofer yellow; parameres joined at base with a caudally projected small process, slender and tapers apically, narrow V-shaped in profile, outer lateral margin with a laterally projected blunt spine at midlength; propleuron white with five spots or dot marks; frons, clypeus, and genae blackish brown; frontoclypeal suture yellow; tibial spur with 36 spines..... *Cemus sauteri* (Muir)

56’ Lateromedian area of pygofer white to whitish yellow; parameres without laterally projected blunt spine along mid-outer lateral margin; anal segment with a pair of long and slender processes curved inside the segment; propleuron whitish yellow without spots; frons blackish brown; clypeus with yellow basal half and dark brown apical half; frontoclypeal suture white; tibial spur with 30–33 teeth..... *Cemus nigromaculosus* (Muir)

57 Forewings almost entirely dark brown except transparent areas between veins Sc and R_1 and veins M_1 and M_2; frons concolorous with genae and clypeus, all reddish brown; frons flat, 1.9x longer than wide; antennal segment II 1.4x longer than segment I; pygofer with straight midlateral areas; parameres merged basally and enlarged, midhalf constricted, apical one-half flat, diverging and tip rounded; aedeagus Y-shaped connective with long arms; body length 5.95 mm ..... *Cemus changchias* Kuoh

57’ Forewings with light brown and transparent areas, convex brown band runs from crossveins opposite Sc and Cu cells to apical margins, R_1 and R_2 veins brown; frons and clypeus paler than genae, frons with a shallow cavity subapically, nearly twice as long as wide; antennal length as above but segment 1 much darker than second; pygofer with concave midlaterals; parameres base moderately open, midhalf less constricted, apical half flat and blade-like, diverging with blunt tip; aedeagal Y-connective with short arm; body length 5.4 mm ..... *Cemus* sp. A

58 Vertex, pronotum, and mesonotum with a median longitudinal brown band, yellow brown in the scutellum; frons, clypeus, and genae reddish brown; frons with pale spots and genae none; antennal segment I black with yellow dorsal band..... *Cemus* sp. A

58’ Vertex, pronotum, and mesonotum with a median longitudinal yellow-brown band; scutellum tip brown; frons, clypeus, and genae brown with distinct yellow spots; genae each with two spots; antennal segment I dark brown.... *Cemus* sp. B

59 Basal segment of tarsi III spineless laterally; pronotum white to pale yellow; mesonotum black to blackish brown, tips never brown..... 60

59’ Basal segment of tarsi III with one or more spines laterally; pronotum, mesonotum, and tip of scutellum uniformly brown..... 62

60 Pronotum light to dark brown similar to vertex and mesonotum; vertex carina coarse with lateral margins straight; median carina of clypeus faded; forewings hyaline with fuscous tinge, veins fuscous and with a linear spot between claval vein and commissural margin dark reddish brown, lighter basad of the margins; antennal segment I yellow-brown; pygofer rounded with truncated mediocaudal area; parameres basally contiguous, inner lateral margins concave at most part, rather straight in outer part, apex emarginate with convergingly acute inner tooth, diverging subtriangular outer tooth; tibial spur with 19 teeth……..…..*Opiconsiva dodona* (Fennah)

60’ Without the combination of above characters..... 61

61 Central carina of frons pale colored; vertex brown with yellowish brown carinae but black between median and lateral carinae; antennal segment I pale yellow-brown; forewings subhyaline with light brown tinge on clavus; pterostigma dark brown; pygofer oblongate and seemingly bilobed; parameres widely diverging from base, outer lateral subapex indented forming bluntly rounded tips; short anal segment processes parallel to one another..... *Laodelphax striatellus* (Fallen)

61’ Central carina of frons deep black; vertex black; antennal segment I darkly pigmented; forewings hyaline; pterostigma indistinct to very light brown; pygofer subglobose without bilobed appearance; parameres swollen at base, almost touching each other, broad and uniform in width, concave inner margin with acute and converging inner lateral apices, oblique at tip; anal segment with diverging processes..... *Coronacella sinhalana* (Kirkaldy)

62 Submedian frons concave forming an incomplete median carina; forewings with dark brown tinge toward apical margins opposite cubital cell, and veins R_1 to M_1; pygofer with a distinctly pointed process and laterally barbed medioventral processes; parameres cleft apically, small inner lateroapical tooth converging, large outer lateroapical tooth acute and diverging; aedeagus bulbous apically with a small hook and spines close to the apex; tibial spur with 28–30 teeth.....*Nilaparvata bakeri* (Muir)

62’ Submedian of frons not excavated, median carina complete; pygofer with or without processes.....63

63 Medioventral margin of pygofer with three small processes; parameres cleft apically, apico-inner tip smaller than the apico-outer part with rounded tip; subapical part of parameres with a small spine projected caudally; aedeagus snoutlike at tip similar to a bird’s head; female genitalia with inner margin of first valvifer basally spatulate; tibial spur with 18–20 teeth ...*Nilaparvata muiri* China

63’ Pygofer without any processes on the medioventral margin 64

64 Pronotum opaque white; pygofer apically rotundate oval, thickened rim along anal third with a short spine; parameres broad, apically bifid with subapical inner lateral spine converging; tibial spur with 16 spines.....*Nilaparvata albostriata* (Kirkaldy)

64’ Pronotum brown to stramineous; pygofer and parameres different; tibial spur with 19–36 teeth.....65

65 Carina of vertex prominently developed; pygofer moderately long, dorsolateral angles not produced caudally, inflected mesad; parameres moderately long, broadly indented lateromedially along inner side, outer midlaterals produced laterad, nipple-like forming a concave cavity subapically, apex broad with a small upcurvedly projected outer process and a broadly tapered inner process; aedeagus moderately long, straight, lined with 7 teeth along dorsal margin, ventrally with a long narrow process at midlength; tibial spur with 19 teeth.....*Nilaparvata myersi* Muir

65’ Carina of vertex faintly developed; pygofer subovate, widest at about mid-length, dorsolateral angle slightly produced caudally; parameres relatively long, inner bases swollen almost touching each other, prominently concave at mid-inner area, slightly concave toward converging apices, outer apicolateral half moderately swollen; aedeagus long and slender, tapering apically, with teeth along caudal margins, broad medially, apex usually upturned left; tibial spur with 30–36 teeth. .. . . *Nilaparvata lugens* (Stål)

Systematic account of delphacid planthoppers

SUBFAMILY ASIRACINAE (Fieber 1872)

1. Genus *MELANESIA* Kirkaldy, 1907

Melanesia Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Exp. Stn. Entomol. Bull. 3:128
Haplotype: *Melanesia pacifica* Kirkaldy, 1907

Generic features: Head a little longer than wide viewed dorsally; vertex transverse, irregularly shaped, with two fairly deep but obscurely defined fovea; frons about two and a half times as long as wide apically and basally truncate, a single filiform carina forking close to the base, lateral margins widening a little toward the apex but narrowing slightly at the apical margin; genae not carinate, labium reaching beyond the coxae I; antennae long and reaching to about the middle of clypeus, somewhat flattened with a few circular sensory organs, but many short bristles; second segment 3x as long as the first, which is rather wider apically than basally; pronotum very transverse, lateral carina curving under the eyes; scutellum 4x as long as the pronotum with five carina; tegmina with forking radial vein much closer to base than the brachial, reforked basal of the subapical transverse line somewhat apical of the middle, the tegmina are bent in and there is a cross vein that cuts across the longitudinal ones, turning off obliquely toward the apex at the middle and turning off again, close to the apex of the clavus, into the commissure; tegmina closely and finely granulated both on and between the shortly piliferous veins; these are 1C apical veins, 4th and 5th reforking, 7, 8, and 9 having a common base; hind tibiae longer that the tarsi, with a basal spine and another basal of the middle; spur much as in genus *Ugyops*; basal segment of hind tarsi much longer than the other two together (reproduced from Kirkaldy 1907).

1.1 *Melanesia pacifica* Kirkaldy, 1907
Plates 1a, 5a, 10a, 18a, 24a, 32a, 35a-b

Melanesia pacifica Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Exp. Stn. Entomol. Bull. 3:129.

Features: Body length 6.25–7 mm. Vertex, pronotum, and scutellum yellowish fuscous, carina a little darker; frons yellowish, lateral carina very narrowly blackish brown; antennae, labium, legs, and sterna brownish yellow, tibia I and II obscurely

biannulate with fuscous; apices of first and second segments of hind tarsi more or less dark, tegmina brownish yellow except small dark spot about the middle of clavus, apical margin dark and often the subcosta; in male, sternites more or less ferruginous; last segment deeply rotundately emarginated; pygofer elongate, very sinuate in profile; anal tube elongately produced horizontally; parameres contiguous inwardly for a third of their length, then curving outward and recurving, apices acute and nearly contiguous; in female, sternites yellowish brown, sutured with black, few last segments deeply acute, angularly emarginated or ovipositor dark, much longer than pygofer (Kirkaldy 1907).

Host plants: Rice (Pawar 1972)
Economic importance: Not economically important (NEI)
Distribution: Fiji (Navua and Rewa) and the Philippines (new record)

2. Genus *MELANUGYOPS* Fennah, 1956

Melanugyops Fennah, 1956. Insects of Micronesia, Homoptera: Fulgoroidea 6:107-108.
Type: *Melanugyops erebea* Fennah, 1956

Generic features: Vertex quadrate, little longer than broad, slightly narrower at apex than base, a pair of oblique carinae arising at basal angles, and united medially distally, apical margin of vertex transverse, strongly interrupted by projecting median carina, basal margin transverse, near or before level of middle of eyes; frons longer than broad (about 2.5:1) with lateral margins shallowly convex, median carina and lateral margins subfoliate, the latter projecting laterad; frons and clypeus in profile forming a smooth shallow curve; eyes only slightly excavate below; ocelli absent; antennae cylindrical, not much shorter than frons and clypeus combined, second segment about 1.5x as long as first; rostrum with apex of subapical joint attaining post-trochanters; legs not at all foliate or compressed; post-tibiae laterally three-spined, apically four-spined, spur long, subulate, terminating in a spine; pronotum tricarinate, depressed between carinae, two-thirds as long as an eye behind eyes, lateral margins obsoletely bicarinate; mesonotum tricarinate; tegmina (brachypterous) scarcely reaching to apex of abdomen, Sc + R forked near node, M simple, Cu_1 forked near level of union of claval veins, no claval suture developed but vein Cu_2 distinct toward apex; claval area long, with claval veins united slightly basad of its middle; a few submarginal cross veins weakly present, but not forming a definite nodal line; veins not granulate or setose, but intervenal areas distinctly so in distal half; wings in brachypterous form, absent; male genitalia as in *Ugyops* (reproduced from Fennah 1956).

2.1 *Melanugyop*s sp.
Plates 1b, 10b, 18b, 24b, 40a

Features: Similar to *Ugyops* except for the tricarinate mesonotum; vertex in middle 1.65x wider than long, apex rounded, lateral margins straight with a small thickened spot before narrowing in front, carina yellow; frons, clypeus, and gena lined with two moderately broad longitudinal reddish brown bands running from vertex to clypeus and from vertex to pronotum and mesonotum; antennal segments subequal in length, first segment thinner than second with black and yellow alternating longitudinal stripes, second segment broader apically than yellow-brown base except for reddish brown band frontally; forewings subhyaline in most parts, light brown band on apical one-third, C-shaped from Sc_1 down to the cubital veins, subapex of M_3 to margins of M_2, R_2 with similar band.

Host: Rice
Economic importance: NEI
Distribution: Philippines (Luzon Island)

3. Genus *UGYOPS* Guerin-Meneville, 1834

Ugyops Guerin-Meneville, 1834. Voyage aux Indes Belanger 1:477
Type: *Ugyops percheronii* Guerin-Meneville, 1834

Ugyops Guerin-Meneville, 1834. Voyage aux Indes Belanger 1:477
_____. Burmeister, 1835. Handb. d. Entomol. 2:152
Hygyops. Amyot et Serville, 1843. Hist. Hem. 511
Ugyops. Matsumura, 1943. Cat. Araeopid. Imp. Jpn. 5
Ugyopus (!). Esaki et Ishihara, 1943. Ibid
Ugyops. Matsumura et Ishihara, 1945. Mushi 16
_____. Ishihara, 1945. Sci. Rep. Matsuyama Agric. Coll. 2:8
Bidis. Walker, 1857. J. Proc. Linn. Soc. 1:88
Jugodina. Schumacher, 1915. Suppl. Entomol. 4:141

Generic features: Head including eyes narrower than pronotum; vertex longer than wide, submedian carina arising nearly from base, uniting before apex; frons long, lateral carinae convex at apical three-fourths, median carina varies from simple to widely separated; postclypeus as wide as base as frons at apex; rostrum reaching to metatrochanters; ocelli obsolete; antennae long, cylindrical; pronotum with lateral carinae not reaching hind margin or laterals; mesonotum five-carinate; hind tibiae with 2–3 spines laterally, spinal formula of hindleg 4-5-4; anal segment large; pygofer with medioventral process; aedeagus with phyllobase indistinct, phyllus coil; supporting plate distinct, elongate; diaphragm very weakly sclerotized; opening of parameres incomplete; parameres simple.

3.1 *Ugyops vittatus* (Matsumura, 1905)
Plates 1c, 5b, 10c, 15a, 18c, 21a, 24c, 32b, 35c

Bidis vittatus Matsumura, 1905. Trans. Sapporo Nat. Hist. Soc. 1:31
Jugodina dictyophoroides Schumacher, 1915. Suppl. Entomol. 4:141
Bidis vittatus Matsumura, 1920. Illustr. Thous. Ins. Jpn. 1:54
B. vittatus Kato, 1933. Three col. Illustr. Ins. Jpn. Ser. 4, pl. 14. f. 1
Ugyopus (!) *vittatus* Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 5
Ugyopus (!) *vittatus* Matsumura et Ishihara, 1945. Mushi 16:59
Ugyops vittatus Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:9
U. v. Fennah, 1956. Proc. Calif. Acad. Sci. 4(28):463; Insects of Micronesia 6(3):95
U. v. Kuoh, 1983. Econ. Ins. Fauna China 27:29
U. v. Yang and Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:8-9

Features: Body length 9–11 mm. Body dirty light brown, scattered with black spots on vertex and on pronotum; a row of black spots in each side of pronotum indistinct; vertex along middle line 2.1x as long as broad as base just anterior to middle of eyes, base slightly narrower than apex; frons longer than broad (3–3.1:1); submedian carinae widest apart at base; second antennal segment 1.7x as long as basal, antennae as long as frons and clypeus; genae not tumid; ocelli obsolete; tegmina not long, but exceeding abdomen, Sc + R fork, Cu_1 fork, and union of claval veins at same level (reproduced from Matsumura and Ishihara 1945, Ishihara 1949, Fennah 1956).

Host plants: "Pteridophyta," rice
Economic importance: NEI
Distribution: Japan, Taiwan, and the Philippines (Luzon Island and Panay Island)

3.2 *Ugyops tripunctatus* (Kato, 1931)
Plates 15b, 21b, 28a, 35d

Bidis tripunctatus Kato, 1931. Bull. Biogr. Soc. Jpn. 2:165
Ugyops (!) *tripunctatus* Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 6
_____. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:10
Ugyops tripunctatus Yang and Yang, 1986. Taiwan Mus. Special Publ. Ser 6:9-15

Features: Body length 7.95–8.11 mm; yellowish brown with head marked on vertex and lateral areas before eyes; pronotum with median carina and along posterior margin red mottled with dark markings on each side; antennae yellowish brown, second segment subapically brown; genae reddish around base of antennae; frons dark brown basally; clypeus basally red; forewings hyaline, slightly mottled dark apically; vertex longer medially than wide basally (2.2:1), widely rounding subacutely into frons, distinctly wider at apex than at base, lateral margins concave at midhalf, apical margin truncate with merged submedian carinae distinct, submedian carinae united far before apex forming a common eminence, basal compartment of vertex shorter basally than median length (about 1:1.9), hind margin prominently angulate

medially; frons longer at midhalf than wide at broadest part by about 3:1, widest at basal three-fourths, lateral margins shallowly convex, median carina simple in apical fifth, forked in basal four-fifths with two arms widely diverging; rostrum reaching hind coxae, apical segment distinctly shorter than subapical about 1:1.8 and seemingly 4-segmented; antennae pass apex of clypeus, basal segment longer than wide by about 5:1, shorter than second by about 1:1.8; ocelli present as a scar; post-tibiae with three lateral spines; spinal formula in hind leg 4-5-4; forewings with 4-branched Sc anteriorly, Sc complete, M not fused with Cu_1 basally and apically, R-M basad M-Cu, Cu_1 forked before end of M-Cu, cu_{1a} forked apically; anal segment large, lateroapical angles rounded basally; pygofer in profile wider dorsally than ventrally; posterior margin longer below medioventral process than above, posteriorly with opening wider than long, lateral margin ill defined, medioventral process single and relatively wide; phallus circular with a long petiole viewed dorsally; supporting plate elongate, slightly widening along dorsal margins; diaphragm very lightly sclerotized; parameres simple, knife-like, and apically converging.

Host plants: Pteridophyta
Economic importance: NEI
Distribution: Taiwan

SUBFAMILY DELPHACINAE Jensen-Haarupt, 1915

4. Genus *TROPIDOCEPHALA* Stål, 1853

Tropidocephala Stål, 1853 Ofv. Ak. Forh. 10:266.
Type species: *Tropidocephala flaviceps* Stål, 1853.

Tropidocephala Stål, 1853. Ofv. Ak. Forh. 10:266
Nephropsia Costa, 1862. Ann. Mus. Zool. Napoli 1:76
Conicoda Matsumura, 1900. Entomol. Nachr. M. 26:258
Orchesma Melichar, 1903. Hom. Fauna Ceylon :94
Ectopiopterygodelphax Kirkaldy, 1906. Hawaii Sugar Plant. Assoc. Exp. Stn. Entomol. Bull. :412
Smara Distant, 1906. Fauna Brit. Ind. Rhynch. 3:478
Tropidocephala Matsumura, 1907. Ann. Mus. Hung. 5:57
_____. Kuoh, 1983. Econ. Insects Fauna China 27:31
_____. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser 6:15

Generic features: Head at eye level narrower than pronotum; vertex longer medially than wide at base, apex protruded in front of eyes distinctly, tricarinate, median carina simple, frons base to apex, lateral carinae converging apically, submedian carinae projected from apex of lateral carinae, uniting at apex developing the anterior margin of vertex; frons longer at middle line than wide at broadest part about 1.9–3:1; in profile more or less reclined apically, lateral carinae convex medially not connecting with lateral carinae of vertex, median carina forked at extreme base forming a small

cell; clypeus wider basally than frons at apex or subequal, prominently tricarinate but sometimes not; rostrum reaching to mesocoxae, apical segment slightly longer than wide; antennae short, cylindrical, second segment longer than first, often not reaching frontoclypeal suture; ocelli small but present; pronotum tricarinate, lateral carinae well developed, converging posteriorly and reaching hind margin; spinal formula of hind leg 5-6-4 or 5-7-4; forewings with small hair-bearing granules near veins; anal segment relatively large; pygofer in posterior view with opening longer than wide, lateral margin with or without protrusion, ventral margin with medioventral process; aedeagus with distinct phallobase, phallus slender, curved ventrad, phallobase wide basally, concave submedially to house phallus with very long process apically or basoventrally; aedeagus fastened to the anal segment, supporting plate indistinct; diaphragm membranous; parameres long, sometimes basal angles with long process; females without seventh abdominal sternite.

4.1 *Tropidocephala* sp.
Plates 1d, 10d, 18d, 24d, 40b

Features: Body length 5.4 mm; body greenish yellow, greenish tinge in the pronotum and midmesonotum; vertex, basal half of frons, and genae green; pale yellowish in apical half of frons, clypeus, and genae; blackish brown spot on midapex of frons, midbasal one-half of clypeus and genae, dorsal side of mesonotum; head in lateral view snout-like at 45-degree angle; antennae whitish yellow, apex of segment I with a brown ring, segment II longer than I with an oblique blackish brown stripe dorsolaterally; legs whitish; forewings subhyaline, granulated, claval base tinged pale yellow, vein M with a small, elevated, mound-like brown spot before and after cross veins, Sc + R with a pale white-yellow spine; anal style almost 2x longer than diameter of anal segment.

Host plant: Rice (Pawar, 1972)
Economic importance: NEI
Distribution: Philippines (Luzon Island)

4.2 *Tropidocephala flavovittata* Matsumura, 1907
Plates 15c, 21c, 28b, 35e

Tropidocephala flavovittata Matsumura, 1907. Ann. Hist. Nat. Mus. Hung. 5:63
_____. Schumacher, 1915. Mitt. Zool. Mus. Berlin 8:133
_____. Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 9; Syst. Stud. Jpn. Araeopid. 6
_____. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:14
_____. Kuoh, 1983. Econ. Insects Fauna China 27:37
_____. Yang & Yang, 1986. Taiwan Mus. Spec. Publ. Ser. 6:16-17

Features: Body length 3.6 mm; yellowish red in the vertex, pronotum, and mesonotum; median carina of vertex and carinae of pronotum and mesonotum dirty white; frons yellowish red with genae slightly darker and clypeus paler, median carina of frons dirty pale yellow; antennae white, apical margin of basal segment, subapical margin, and median of upper surface all dark brown; ventral surface of thorax and legs yellowish red, hind legs lighter in color; abdomen reddish yellow; vertex at midline longer than wide at about 1.5:1, longer than pronotum by about 1.8:1; frons longer than wide at broadest part about 3.3:1, broadest between eyes, median carina forked at basal one-third; clypeus slightly wider than frons at base; head set at about 45-degree angle viewed laterally; antennae short, not reaching frontoclypeal suture, segment I as wide as long, segment II longer than first by about 1.8:1; forewings with reddish brown to light brown tinge along the apical margins of M_3 and Cu_1 pygofer in posterior view with opening suboblongate, lateral margin not produced, medioventral process rather small, widening apically; parameres simple, long, narrowed, and diverged slightly apically; anal style relatively long.

Host plant: Unknown
Economic importance: NEI
Distribution: China and Taiwan

4.3 *Tropidocephala nigra* (Matsumura, 1900)
Plates 1e, 10e, 18e, 24e, 32c, 35f

Conicoda nigra Matsumura, 1900. Ent. Nachr. 26:251
_____. Oshanin, 1903. Verz. Palaark. Hemip. 2:300
Tropidocephala nigra Oshanin, 1910. Ibid. 451
_____. Esaki, 1932. Iconogr. Ins. Jpn. 1782. f. 3521
_____. Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jap. 8; Syst. Std. Jpn. Araeopid. 8
_____. Matsumura et Ishihara, 1945. Mushi 16:60

Features: Body length 4 mm; vertex more than 1.5x the length of pronotum vertex, pronotum, and scutellum brownish black to black except the whitish lateral carinae; median carina of vertex sometimes white too; female body light brown dorsally and ventrally, lateral carinae of pronotum bordered with black.

Host plant: Rice
Economic importance: NEI
Distribution: Japan and the Philippines (new record)

4.4 *Tropidocephala dimidia* Yang & Yang, 1986
Plates 15d, 21d, 28c

Tropidocephala dimidia Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:25-26.

Features: Body length 3.53–4.25 mm; general color pale yellow with base of antennal segment I and II ringed dark brown; vertex devoid of longitudinal markings between carinae; forewings dark apices on longitudinal veins with transparent vertical tinges before the cross veins and apical margins between veins from Sc_1 to M_1; cross vein Sc_2-R very feeble; vertex longer at midline than wide at base by about 2.9:1, longer than pronotum by about 3.3:1, strongly protruding in front of eyes, set at 45-degree angle viewed laterally; frons longer in midhalf than wide at broadest part by about 2.6:1, broadest at level of anterior margin of eyes; clypeus with lateral carinae distinct, median carina very light; antennae not reaching frontoclypeal suture; spinal formula of hind leg 5-6-4.

Host plant: *Imperata cylindrica* (L.) P. Beauv. var. *major* (Nees) Hubbard
Economic importance: NEI
Distribution: Taiwan

4.5 *Tropidocephala sinuosa* Yang & Yang, 1986
Plates 15e, 21e, 28d, 35g

Tropidocephala sinuosa Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:28-29

Features: Body length 3.89–4.59 mm; pale yellowish brown; forewings with pale markings, apical ends of longitudinal veins Sc + R, M, and Cu_1 unmarked; vertex very long, longer in midline than wide at base by 2.9:1, longer than pronotum by about 3.2:1, strongly protruding in front of eyes, rounded apically; frons elongated, longer at midlength than wide at broadest part by as much as 2.7:1, broadest above level of anterior eye margins; clypeus at base wider than frons at apex, carina very light; antennae not reaching the frontoclypeal suture; spinal formula of hind leg 5-6-4; pygofer in posterior view with opening wider than long, lateral margins acutely produced, ventrally the medioventral process small and acute apically, anterior margin strongly concave medially; aedeagus with slender phallus, phallobase with right side evenly formed viewed dorsally, in lateral (left) view right side produced into a lobe-like process apically, directed ventrally, another longer process emanates subbasally; anal style long, distinctly beyond anterior margin of the large anal segment; parameres slender, sinuate with small triangular process in the middle.

Host plant: *Imperata cylindrica* (L.) P. Beauv. var. *major* (Nees) Hubbard
Economic importance: NEI
Distribution: Taiwan

4.6 *Tropidocephala grata* Yang & Yang, 1986
Plates 15f, 21f, 28e, 35h

Tropidocephala grata Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:26-27

Features: Body length 3.21–3.40 mm; reddish brown planthopper; apex of frons, clypeus, genae, lateral parts of pronotum and legs, except coxa III, light brown; antennae yellowish to light brown, apex of segment I with dark brown ring and oblique ring at base of segment II; abdomen and pygofer reddish brown; forewings with dark brown longitudinal veins of Sc + R, M and Cu_1, and basal two-thirds, transparent spots distributed on the costal and apical areas, rest of apical third after the cross veins brown; vertex triangular, as long in middle line as wide basally, longer than pronotum by about 1.3:1, conical at apex, slightly protruded in front of eyes; head frontally oblong, longer in midline than wide at widest part about 1.9:1, broadest at level of simple eyes, in lateral view, very slightly oblique to subparallel to hind part of genae; antennae short, not surpassing the frontoclypeal suture; spinal formula of hind leg 5-6-4; pygofer with opening longer than wide, lateral margins obtusely produced into triangular plates viewed posteriorly, medioventral process small seen ventrally, ventral margin strongly concave; parameres parallel, basal part a little wider than apicals, curved outward medially, apically slender, narrowed, blunt, and diverging; aedeagus with slender phallus, phallobase with process arising from subbasal area ventrad.

Host plant: *Miscanthus* spp.; *Imperata cylindrica* (L.) P. Beauv. var. *major* (Nees) Hubbard
Economic importance: NEI
Distribution: Taiwan

4.7 *Tropidocephala formosana* Matsumura, 1910
Plates 15g, 21g, 28f, 35i

Tropidocephala formosana Matsumura, 1910. Schad. N. Nutz. Ins. Zucherrohr Formosas 16
T. f. Matsumura, 1911. Mem. Soc. Ent. Belg. 18:134
T. f. Schumacher, 1915. Mitt. Zool. Mus. Berlin 8:133
T. f. Kato, 1933. Three-col. Illustr. Ins. Jpn. 4. Pl. 15, f. 6
T. f. Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 10; Syst. Stud. Jpn. Araeopid. 69
T. f. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:13
T. f. Kuoh, 1983. Econ. Insects Fauna China 27:38
T. f. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:21-22

Features: Body length 3.67–3.98 mm; generally dark brown to reddish brown; vertex greenish brown but genae, clypeus, and lateral sides of anterior margin of pronotum black; frons reddish brown, median carina white with dark brown border from apex of vertex to end of mesonotum straight; apex of antennal segment I and middle of segment II ringed with brown; forewings brown with hyaline areas distributed; vertex slightly longer at midhalf than wide at base, as long as pronotum, conical at apex,

protruding in front of eyes; frons at midhalf longer than wide at broadest part by about 2.1:1 at level of ocelli; clypeus with indistinct carina; antennae short, not surpassing the frontoclypeal suture; spinal formula of hind leg 5-6-4; pygofer in posterior view with opening longer than wide, ventrally with medioventral process simple, ventral margin slightly incised near both sides of the process; aedeagus with slender phallus, phallobase with right side obtusely produced devoid of another process; parameres divergent, narrow, and flattened outside, reflected inside, reflection much wider and thicker basally, inner angle formed as a bent process, basal angle with large production digitate, directed inward; style cover granulate.

Host plant: *Miscanthus* spp. and *Saccharum officinarum* L.
Economic importance: NEI
Distribution: China and Taiwan

4.8 *Tropidocephala brunnipennis* Signoret, 1860
Plates 1f, 5c, 10f, 15h, 18f, 21h, 24f, 32d-e, 35j

Tropidocephala brunnipennis Signoret, 1860. Ann. Soc. Entomol. France 8:185
T. b. Stål, 1866. Hem. Afr. 4:178
Conicoda graminea Matsumura, 1900. Ent. Nachr. 26:259
Ectopiopterygodelphax eximius Kirkaldy, 1905. Hawaii Sugar Plant. Assoc. Exp. Stn. Entomol. Bull. 1:412
Tropidocephala eximius Kirkaldy, 1905. Ibid. 3:142
T. brunnipennis Matsumura, 1907. Ann. Hist. Nat. Mus. Hung. 5:59
Conicoda graminea Oshanin, 1908. Verz. Palaark. Hem. 2:300
Tropidocephala brunnipennis Oshanin, 1910. Ibid. 2:451
T. b. Muir, 1913. Proc. Hawaii Entomol. Soc. 2:245
T. b. Susuki, 1915. List Spec. Hanazono Entomol. Inst. 10
T. b. Matsumura, 1917. Appl. Entomol. For. Ser. 382
T. b (!) Kato, 1933. Three-col. Illustr. Ins. Jpn. 4
T. b (!) Wu, 1935. Cat. Ins. Sin. 2:119
T. b. Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 7; Syst. Stud. Jpn. Araeopid. 60
T. b. Matsumura et Ishihara, 1945. Mushi 16:60
T. b. Kuoh, 1983. Insects Fauna China 27:32
T. b. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:18-19

Features: Body length 3.11–3.61 mm; general body color greenish brown to dark brown, thorax greenish brown; vertex, pronotum, mesonotum, and deep base of forewings greenish yellow but blackish on the apical part, and both sides of median carina of frons, genae, coxae III, abdominal sternite, and pygofer; forewings with costal areas transparent, basal two-thirds dark brown; vertex longer at midline than wide at base by about 1.2:1, projected in front of eyes, conical at apex, longer than pronotum by 1.3:1; frons longer in middle line than wide at broadest part by about 1.6:1, widest at level above simple eyes; clypeus tricarinate; antennae not reaching frontoclypeal suture; spinal formula of hind leg 5-6-4; pygofer ovoid in posterior view with open-

ing longer than broad, lateral margins produced slenderly near base, in ventral view with medioventral process narrow and slender, ventral margin slightly concave at both sides with lateral extensions; anal style surpassing anterior margins of the long anal segment; aedeagus with slender phallus, phallobasal process arising from apical portion; diaphragm membranous; parameres flattened, apical third about twice as broad at base, inner margin almost straight, outer margin strongly produced laterad submedially, concave along basal third; each paramere with two short processes, one basal and another at basal third of inner margin directed mesodorsad.

Host plant: *Miscanthus* spp.; *Oryza sativa* L.; and *Saccharum officinarum* L.
Economic importance: NEI
Distribution: Australia, China, Japan, Malaysia, Philippines (new record), New Guinea, Madagascar, North Africa, S. Europe, and Taiwan

4.9 *Tropidocephala saccharivorella* Matsumura, 1907
Plates 15i, 21i, 28g, 35k

Tropidocephala saccharivorella Matsumura, 1907. Ann. Hist. Nat. Mus. Hung. 5:65
T. saccharivora (!) Matsumura, 1910. Schad. U. Nutz. Inst. Zuckerrohr. Formosas 28
T. saccharivorella Muir, 1913. Proc. Hawaii Entomol. Soc. 2:244
T. s. Schumacher, 1915. Mitt. Zool. Mus. Berlin 8:133
T. s. Dammerman, 1929. Agric. Zool. Malay. Archipelago 236
T. s. Wu, 1935. Cat. Ins. Sin. 2:120
T. s. Esaki et Ishihara, 1943. Syst. Stud. Jpn. Araeopid. 68
T. s. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:14
T. s. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:22-25

Features: Body length 3.52–3.73 mm; greenish yellow to reddish brown; apex of frons, around ocelli, base of clypeus and upper mesopleuron blackish; forewings hyaline, apical fourth excluding the costal area yellowish gray, apical part of longitudinal veins M_2, M_3, and Cu_1 covered with dark brown, apiculate brown in vein M indistinct, and small, round brown markings on middle of $Rs + M_1$; vertex long, longer in middle line than wide at base about 2:1, longer than pronotum by about 1.7:1, apically rounded and distinctly produced in front of eyes; frons longer in middle line than wide apart by about 2.4:1, widest at level of anterior eye margin; antennae short, reaching frontoclypeal suture; clypeus tricarinate; spinal formula of hind leg 5-6-4; forewings narrow, acutely rounded apically; pygofer opening wider than long viewed posteriorly, lateral margins without process, ventrally with medioventral process granulate and ventral margin straight, pointed at apex; aedeagus with slender phallus, phallobase with process arising at apex, in dorsal view forming a small digitate production at right side, in similar direction as phallus; parameres parallel, slightly wide at base, apical third narrowed and sinuate, basal angles each produced into a pointed process, in lateral view apex truncated, distinctly constricted subapically.

Host plant: *Miscanthus* spp. and *Saccharum officinarum* and *Saccharum* spp.
Economic importance: NEI
Distribution: China, Philippines, and Taiwan

4.10 *Tropidocephala festiva* (Distant, 1906)
Plates 1g, 5d, 10g, 18g, 24g, 35l

Smara festiva Distant, 1906. Fauna Brit. Ind. Rhynch. 3:478. f. 64
Tropidocephala festiva Matsumura, 1907. Ann. Hist. Nat. Mus. Hung. 5:62
T. f. Oshanin, 1912. Kat. Palaark. Hemip. 117
T. f. Muir, 1913. Proc. Hawaii Entomol. Soc. 2:224
T. f. Schumacher, 1915. Suppl. Entomol. 4:142
T. f. Wu, 1935. Cat. Ins. Sin. 2:119
T. f. Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 9; Syst. Stud. Jpn. Araeopid. 64
T. f. Matsumura, & Ishihara, 1945. Mushi 16:60
T. f. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:19-21

Features: Body length 3.44–3.82 mm; vertex and thorax yellowish green, median carinae of both bordered with brown and outside of lateral carinae similarly brown, a pair of short brown longitudinal markings inside the posterior part of lateral carinae of pronotum just in front of lateral carinae of mesonotum, and on lateral area; anterior part of pronotum marked with dark brown; apex of segment I and base segment II of rounded antennae brown; frons with black markings on basal part, apical part, and on genae below eyes; clypeus, sternum of metathorax, femora of legs, part of tibia III and abdomen, including pygofer, black and rest colored brown; forewings dark brown, nearest base yellowish green, hyaline areas distributed, three on costal area, five on apical part, and one next to end of claval line, three black and globular markings apiculate to longitudinal veins Sc + R, M, and Cu_1; vertex longer in midline than wide at base by about 1.9:1, longer than pronotum by about 1.8:1, acutely rounded at apex, produced in front of eyes; frons longer medially than wide between eyes by about 2.4:1, clypeus tricarinate; antennae short, reaching the frontoclypeal suture; rostrum surpassing procoxae; spinal formulae of hind leg 5-6-4; pygofer opening longer than wide viewed posteriorly, lateral margins strongly produced, most part of opening weakly sclerotized except above opening of parameres, in ventral view with medioventral process flattened, widened apically, slightly emarginated at apex and granulate; anal style moderately long, surpassing anterior margin of the relatively long anal segment; aedeagus with slender phallus, basal portion of phallobase in dorsal view bearing triangular process apically, process of phallobase arising apically; parameres in caudal view, slightly parallel, main body subequally wide, elongate, apical sixth narrowed and curved, basal angle forming a long process, in profile with subapical portion granulate, truncated apically and pointed at basal angle.

Host plant: *Imperata cylindrica* (L.) P. Beauv. var. *major* (Nees) C.E. Hubbard
Economic importance: NEI
Distribution: China, Indonesia, Japan, Malaysia, Philippines, Sri Lanka, Taiwan

5. Genus *ARCOFACIES* Muir, 1915

Arcofacies Muir, 1915. Can. Entomol. 47:319.
Type species: *Arcofacies fullawayi* Muir, 1915
Arcofacies Muir, 1915. Can. Entomol. 47:319
Arcofacies Kuoh, 1983. Econ. Insects Fauna China 27:45
Arcofacies Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:34

Generic features: Head including eyes narrower than pronotum; vertex with well-defined margins, wider basally than long submedially, apical margin distinctly emarginated at both sides of median point, lateral carinae concave, submedian carinae transverse; Y-shaped carina without stalk, arms very small, connecting submedian carinae formed a small cell, in profile vertex and frons at 90-degree angle; frons at midhalf longer than wide at broadest part more than 2:1, widest at level of simple eyes, lateral carinae convex basally, almost straight below level of ocelli, median carina poorly developed, forked at extreme base; clypeus slightly wider basally than frons at apex, at right angle to frons, tricarinate; rostrum not reaching over mesotrochanters; eyes in dorsal view with lateral margins emarginated medially; ocelli present; antennae cylindrical, basal segment distinctly longer than wide, shorter than segment II; pronotum with lateral carinae attaining hind margin, converging apically, median carina very fine; forewings at rest mode tectiform, M and Sc_1 with more than half-length common petiole, Cu_1 emanates from end of cross vein or basad; spinal formula of hind leg 5-6-4; pygofer viewed posteriorly with opening longer than wide, lateral margins strongly produced mediocaudally; medioventral process absent; aedeagus bears no phallobase, phallus tubular, simple and acute at apex; supporting plate sclerotized and pigmented, V-shaped; diaphragm wide and membranous; parameres long and simple, broad basally, slender and narrowed apically, subparallel and very slightly converging.

5.1 *Arcofacies fullawayi* Muir, 1915
Plates 1h, 5e, 10h, 24h

Arcofacies fullawayi Muir, 1915. Can. Entomol. 47:320
A. f. Muir, 1919. Philipp. J. Sci. 15:526
A. f. Fennah, 1956. Proc. Calif. Acad. Sci. 28(4):465
A. f. Kuoh, 1983. Econ. Insects Fauna China 27:45
A. f. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:34-37

Features: Body length 3.15–3.58 mm; green to yellowish green planthoppers; white median line runs from apex of frons to end of mesonotum, bordered with black; antennae with apical half of segment I and base and apex of segment II ringed dark brown; lateral parts of pronotum each with an oblique white band with brown borders; pygofer blackish brown; forewings hyaline with brown veins, light brown over basal third, rest hyaline, mottled with dark brown markings, in dark portions veins marked with white spots; vertex quadrate, wider basally than long submedially by about 1.4:1; submedian carinae present subapically; frons longer at midhalf than wide at broadest area about 1.9:1; antennae surpassing the frontoclypeal suture, basal segment longer than wide about 2:1, shorter than segment II by half; forewings sinuate below apex; pygofer strongly produced caudomedially; phallus simple, strongly concave on dorsal margin, acute at apex, directed ventrad; parameres long, slender, rounded at base, suddenly narrowing apically, slightly twisted subapically.

Host plant: *Bambusa multiplex* (Lour.) Raeuschel; *B. oldhamii* Munro; *B. multiplex* Raeuschel cv. "fernleaf" Young
Economic Importance: NEI
Distribution: China, Indonesia, Philippines, and Taiwan

6. Genus *EPEURYSA* Fieber, 1866

Eurysa Fieber, 1866. Verh. Zool. Bot. Ges. Wien. XVI:520.
Type species: *Eurysa lineata* (Signoret, 1857)

Eurysa Fieber, 1866. Verh. Zool. Bot. Ges. Wien. XVI:520
Eurysa Fieber, 1875. Rev. Mag. Zool. 3:374
Eurysa Ferrari, 1878. Ann. Mus. Stor. Nat. Genova 18:80
Eurysa Melichar, 1896. Cicad. V. Mit.-Eur. 67
Epeurysa Matsumura, 1900. Entomol. Nachr. 26:261 (type: *Epeurysa nawaii* Matsumura, 1900)
Eurysa Oshanin, 1908. Verz. Palaark. Hemip. 2:309
Epeurysa Oshanin, 1908. Ibid. 311; 1912. Kat. Palaark. Hem. 118
Eurysa Muir, 1915. Can. Entomol. 47:263, 298
Epeurysa Muir, 1915. Ibid. 263
Eurysa Matsumura, 1917. Appl. Entomol. Form. Ser. 379
Eurysa Muir & Giffard, 1924. Hawaii Sugar Plant. Assoc. Entomol. Bull. 15:5, 8

Eurysa Muir, 1926. Ann. Mag. Hist. Ser. 9(17):20
Eurysa Esaki & Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 41
Epeurysa Esaki et Ishihara, 1943. Ibid. 42
Eurysa Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:86
Epeurysa Asche, 1983. Marbuger. Entomol. Publ. 1(8):211-226
Epeurysa Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:44-45

Generic features: Body length 3–3.93 mm; generally brown, head across eye area as broad as pronotum; vertex distinctly short, and wider than long, rounded to obtuse toward frons, lateral margins concave, more or less diverging apically and basally, submedian carinae uniting at apex or not, Y-carina distinct; eyes fairly flat dorsally; frons longer medially than broadest part (1–1.4:1), broadest at level of simple eyes; lateral carinae convex medially, median carina simple to forked at extreme base; clypeus finely tricarinate; antennae simple, passing the frontoclypeal suture, second segment fairly swollen, about 2x as long as first; pronotum longer than vertex medially, wider than vertex including eyes; tricarinate, lateral carinae straight, posteriorly diverging and not reaching hind margin; pronotum and mesonotum moderately arched; scutellum large, longer than vertex and pronotum combined, apically triangular projected posterad; forewings ordinary, surpassing abdominal tip; legs simple, spurs thin, tectiform with minute teeth at apex; spinal formula of hind leg 5-6-4; anal segment ring-like, lateroapical angles moderately separated, each produced into a short and stout process; pygofer with three medioventral processes; aedeagus with phallobase, phallobasal process with subapical node, then forming a distal arm; phallus tubular, simple, apical part downwardly recurved; diaphragm membranous; parameres with strong process at basal angle.

6.1 *Epeurysa abatana* (Asche, 1983)
Plate 35m

Epeurysa abatana Asche, 1983. Marburger. Entomol. Publ. 1(8):211-226
E. a. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:49-50

Features: Body length 3.03–3.13 mm; pale yellow to reddish brown; forewings hyaline, devoid of any markings; vertex wider at base than long submedially about 2.3:1, obtusely rounding into frons, evenly convex along apical margins; frons at midline longer than wide at broadest part or subequal, base wider than apex, lateral margin slightly convex, median carina distinct; clypeus at base as wide as frons at apex, wider at base than long; rostrum reaching coxae II; antennae reaching level of basal third of clypeus, segment I cylindrical, slightly longer than wide, shorter than segment II by about 1:1.5; pygofer much longer ventrally than dorsally viewed ventrally, medioventral processes laterally triangular, median one lobe-like, apically rounded, widest of median process about one-fifth as wide as distance between highest points of lateral ones; anal segment relatively long, lateroapical angles each produced into convex lobe, line between them arched, in profile spinose-shaped and directed ventrad; aedeagus moderately long, phallus directed to left and curved ventrad in apical quarter, acute

apically, phallobasal process borne basally and protruding mediocaudad, forming a hemicircular apical node, after node, forming a long distal arm, in dorsal view turned right in 90-degree angle, 3x as long as wide of broadest part near node, very narrow, slightly dilated near apex and twisted, in posterior view, distal arm basally wide, gradually narrowing apically, dorsal margin evenly arched downward; parameres moderately long, bifurcated distinctly forming a short, blunt subparallel apico-inner arm and a large subtruncate apico-outer tip, diverging.

Host plant: *Bambusa dolichoclada* and *B. oldhamii*
Economic importance: NEI
Distribution: Philippines (Luzon Island) and Taiwan

6.2 *Epeurysa nawaii* (Matsumura, 1900)
Plates 15j, 22a, 35n

Epeurysa nawaii Matsumura, 1900. Entomol. Nachr. 26:261.
E. n. Oshanin, 1908. Verz. Palaark. Hem. 2:311
E. n. Oshanin, 1912. Cat. Palaark. Hemip. 113
Eurysa nawae (!) Susuki, 1915. List Spec. Hanazono Entomol. Inst. 10
E. n. (!) Matsumura, 1917. Appl. Entomol. Form. Ser. 381.
Eurysa (*Epeurysa*) *nawae* (!) Matsumura, 1920. Daippon Gaichu Zensho. Rev. & Addit. Ser. 260
Eurysa nawae(!) Matsumura,1931. Nippon Konchu Daizukan 1266
E. n. Cheo, 1935. Peking Nat. Hist. Bull. 10:106
E. n. Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 41
Epeurysa nawaii Esaki et Ishihara, 1943. Ibid. 42
Eurysa nawaii Matsumura et Ishihara, 1945. Mushi 16:72
Eurysa nawae Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:86
Epeurysa nawaii Fennah, 1975. Entomol. Scand. Suppl. 4:83
E. n. Asche, 1983. Marburger. Entomol. Publ. 1(8):211-226
E. n. Yang & Yang, 1986. Taiwan Mus. Special Publ. Ser. 6:45-47

Features: Body length 3.53–3.93 mm; general coloration brown, dark form with wings darker at apical half, pygofer and genitalia darker than other parts; female yellow toward the head and thorax; dark brown abdomen; vertex relatively short, wider at base than median length submedially about 3:1, obtusely roundish toward frons, apical margin evenly convex; greatest length of basal compartment longer than median length of basal compartment about 1.2:1; frons at midline longer than wide of widest part about 1.3:1, widest at level of eyes, median carina forked almost near basal margin; clypeus basally wider than midlength about 1.4:1; antennae with segment I longer than wide, shorter than segment II about 1:1.3; pygofer much longer ventrally than dorsally, laterodorsal angles not produced ventrally, medioventral process with median one longer than lateral ones about 3x, apically ovoid, widest part one-third the distance between the highest points of lateral ones; anal segment with spinal processes, each developed as a convex triangular lobe, ventrad; phallus directed caudad

and decurved to ventrad in apical quarter, apically blunt; phallobasal process rather more slender than phallus, passing mediocaudad to left caudad, forming a node at tip, extending a more slender distal arm, in caudal view directed ventrad then left, in dorsal aspect, the widest part of the phallobasal process near node narrower than length of distal arm about 1:1.4; parameres moderately long, with basal angles very strongly produced to mediocaudad, in caudal view about half as high as inner angle; in laterocaudal view, with a small production on inner margin at about halfway of parameres; entire paramere dark brown.

Host plant: *Phyllostachys makinoi* Hayata and *Chimonabambusa quadrangularis* (Fenzi) Makino
Economic Importance: NEI
Distribution: China, Japan, Sri Lanka, and Taiwan

7. *Genus TAROPHAGUS* Zimmerman, 1948

Tarophagus Zimmerman, 1948. Insects of Hawaii 4:245-247.
Type species: *Megamelus proserpina* Kirkaldy, 1907

Tarophagus Zimmerman, 1948. Insects of Hawaii 4:245-247
Tarophagus Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:45
Tarophagus Fennah, 1956. Insects of Micronesia 6(3):110
Tarophagus Fennah, 1965. Bull. Brit. Mus. (Nat. Hist.) 17(1):37
Tarophagus Asche & Wilson, 1989. Bull. Entomol. Res. 79:286-287

***Generic features*:** Body length around 4 mm; small to medium-sized blackish brown planthopper with a creamy white or pale yellowish longitudinal band running from vertex to the dorsal discs of pronotum, mesonotum to the tip of scutellum; distinctly broad whitish yellow dorso-median band present on abdominal tergites VII-IX, laterotergites yellow; vertex medially about as long as broad at base, lateral margins straight, anteriorly converge moderately; basal compartments about 0.6x the length of vertex, median carina weak to indistinct, area shallowly concave; apical cell distinct; frons about twice as high as broad, maximum width at frontoclypeal suture; carinae of frons prominent, median carina forked in upper quarter; frontal area shallowly concave, basally almost flat; clypeus slightly shorter than frons, surface convex; median carina of clypeus distinct; rostrum reaching anterior margin of postcoxae; antennal segments cylindrical, segment II slightly longer than segment I; number and arrangement of sensory fields of pedicel: 16 in 7 groups or rows; ocelli and blemmata present; pronotum wider than head, in midline about as long as vertex; carina distinct, lateral pair straight, diverging caudally, reaching posterior margin of pronotum; mesonotum medially longer than pronotum by about 1.6:1, lateral carinae straight, diverging caudad, median carina weak, not visible at tip of scutellum; post-tibial spur foliate with 28–36 teeth.

7.1. *Tarophagus colocasiae* (Matsumura, 1920)
Plates 16a, 22b, 28h, 36a

Liburnia (Delphax) *colocasiae* Matsumura, 1920, Dainippon Gaichi Zensho. 564; 1932
_____. Matsumura, 1932. Consp. Jpn. Injurious Ins. :225. (In Japanese.)
Delphalodex? *colocasiae* (Matsumura) Esaki et Ishihara, 1943. Dept. Agric. Kyushu Imp. Univ. Publ. 14:36
Megamelus proserpina Fullaway, 1937. Proc. Hawaii Entomol. Soc. 9:405
_____. Isaki, 1940. Botany Zool. Tokyo 3:278
_____. Esaki at Ishihara, 1943. Fukuoka Dept. Agric. Kyushu Imp. Univ. Publ. 14:19
_____. Matsumura & Ishihara, 1945. Mushi 16:71
_____. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:78-79
Tarophagus proserpina Zimmerman, 1948. Insects of Hawaii 4:247
_____. Fennah, 1956. Insects of Micronesia 6:110-111
_____. Fennah, 1970. Brit. Sol. Is. 6:60
_____. Fennah, 1971. Insects of Micronesia 6:571
_____. Fennah, 1978. Ann. Zool. (Wars.) 34:16
Tarophagus taiwanensis Wilson, Tsai, 1988. Pan-Pacif. Entomol. 64:54

Features: Body length of pygofer with medioventral processes longer than lateral ones; lateral ventrocaudal processes rounded laterodistally, distal margin slightly developed mediad forming an acute inner edge; reflected processes of aedeagus diverging with the longer right spine distally projected dorsocaudally; parameres short and small, basal two-thirds relative range apically narrowed, curved into thumb-like structure projected laterally; anal segment somewhat rounded and ring-like with w-shaped and short subparallel lateroapical angular (ventral side) processes; in females, the valvifer VIII has inner margins of bases developed into a long, finger-to-tongue-like process; sternite V bears a median membrane between the chitinized parts with two distinctly separated chitin-plates and the movable and double-scale of sternite VI bears a median straight incision.

Host plant: *Colocasia esculenta* L.
Economic importance: Relatively high
Distribution: Widespread in Southeast Asia: Indonesia, Myanmar, Philippines, Papua New Guinea, New Britain, Solomon Islands, Thailand, Guam, Micronesia, Marshal Islands, and Hawaii

7.2 *Tarophagus persephone* (Kirkaldy, 1907)
Plates 1i, 5f, 10i, 18i, 24i, 30a, 32f, 40c

Megamelus persephone Kirkaldy, 1907. Bull. Hawaii Sugar Plant. Assoc. Div. Entomol. 3:148
Megamelus proserpinoides Muir, 1917. Proc. Hawaii Entomol. Soc. 3:327
Tarophagus proserpina australis Fennah, 1965. Bull. Brit. Mus. Nat. Hist. Entomol. 17:37-39

***Features*:** Body length 2.8–3.2 mm; creamy white band runs from vertex to apex of scutellum; proboscis, margins of mesopleuron, coxae III, apex of tibiae, and second post-tarsal segment stramineous; forewings castaneous, with apical cells of R mostly transparent, margins of clavus white; rest of wings brownish gray including the veins; vertex at midlength as long as broad at base, subrectangular toward frons, distinctly narrower at apex than bases, lateral margins straight, apical margins shallowly convex with submedian carinae slightly prominent, Y-shape carina feeble, submedian carina not merging at apex of vertex, basal compartment of vertex wider posteriorly than broadest length 1.7:1 than median length 2:1; frons at midline longer than wide at broadest point 2.1:1, broadest apically, lateral margins shallowly sinuately diverging, median carina forked at basal fourth; clypeus basally narrower than frons at apex; clypeus as long as broad at base, very shallowly convex in profile, nearly straight, entire clypeus moderately convex; proboscis just reaches torchanter III; antennae reaching apical level of post-clypeus, basal segment longer than broad 2.1:1, segment II longer than segment I 1.4:1; ocelli small; pronotum shorter at midline than wide at anterior margin, lateral carinae straight, rarely reaching hind margin; mesonotum longer than scutellum by about 2.2:1; tibial spur with about 36 teeth; forewings much beyond abdomen, deeply rounded apically with Sc + R fork and Cu_1 fork at same level, slightly distad of middle, both much distad of fusion of claval veins; pygofer rather long, posterior opening about as long as broad, dorsolateral angles shortly produced, weakly inflected; diaphragm with dorsal margin excavate, lateral margins below midlength each produced strongly caudad in a stout process, tapering distad to an obliquely truncate apex; medioventral process knob-like on a stout stalk; aedeagus moderately long, compressed laterally, decurved in distal half, a short flagellum borne dorsoapically, reflected cephalad above aedeagus for about half its length, moderately expanding distad, bifurcate apically in two equal acuminate processes; parameres short, strongly divergent, basally wide, acute to narrow apically with outer angle more acutely produced laterally; anal segment short and collar-like, lateroapical angles contiguous, each projected ventrad into a stout pointed and spinose process.

Host plant: *Colocasiae esculenta*
Economic importance: Relatively low
Distribution: Widespread in Southeast Asia and Australia, Papua New Guinea, Borneo, Philippines, Solomon Islands, New Britain, Malaysia, and Indonesia

8. Genus *SOGATELLANA* Kuoh, 1980

Sogatellana Kuoh, 1980 in Huang et al 1930. Acta Zootaxonomica Sin. 5(2):169
Type species: *Sogatellana marginata* Kuoh

Sogatellana Kuoh, 1980 in Huang et al 1930. Acta Zootaxonomica Sin. 5(2):169
_____. Asche and Wilson, 1990. Systematic Entomol. 15:37

Generic features: Head including eyes distinctly narrower than pronotum; vertex longer submedially than wide at base about 1.3:1; submedian carinae merged at apex, basal compartment wider basally than greatest length 1.3:1; frons longer at midline than wide at widest portion about 2.1–2.4:1, widest at apical third; lateral carinae convex below ocelli, median carina may or may not be forked at base; clypeus as wide as or wider than frons apically; proboscis reaching trochanter II; ocelli present; antennae cylindrical, passing the frontoclypeal suture, basal segment longer than wide, shorter than segment II about 1:2.3; pronotum with lateral carinae not reaching hind margin; spinal formula of leg III 5-7-4; tibial spur with 16–23 teeth; short anal segment ring-like with lateroapical angles moderately separated producing two processes; phallus tubular, narrowed apically only slightly, armed with several teeth; suspensorium also ringlike without dorsal arms; diaphragm wide with dorsal margin produced medially, median area near dorsal margin convex, margin with distinct pigmented ring, along it armed with many small spines, rough on surface; parameres wide, relatively long, and slightly diverging, inner angle well developed.

8.1 *Sogatellana geranor* (Kirkaldy, 1907)
Plate 36b-c

Delphax geranor Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Div. Entomol. Bull. 3(1):158
Delphax sponsa Kirklady, 1907. Ibid. 148
Sogatella geranor Asche and Wilson, 1990. Syst. Entomol. 15:35 & 37

***Features*:** Similar to *Sogatella kolophon* (Kirkaldy) but median longitudinal stripes from head to scutellum whiter, body size narrower and longer; carinae more pronounced, frons intercarinally reddish brown, head slightly produced in front of eyes; antennae reaching well beyond clypeus, segments 1 and 2 nearly subequal in length; forewings subhyaline tinged with yellow, subcosta and commissure ivory white slightly beyond abdominal tip, membrane scarcely formed; pygoter elongate viewed posteriorly (end-on) and thickened inwardly at the sides; anal segments distinctly quadrispinose with a lateral spine on each side directed downward, and with converging tips, and two downwardly directed spines with diverging tips; aedeagus swollen basally, narrowed at midlength viewed laterally, tube-like viewed dorsally with 18–19 subapical spines; diaphragm knob-to-mound-like; parameres slightly narrowed subapically, cleft at tip forming acute apico-inner obliquely converging tips and rounded apico-outer diverging tips.

Host plant: Rice
Economic importance: Low
Distribution: Australia, Philippines, S. Mariana Islands (Saipan), Palau Islands (Koror), Yap Islands (Yap)

9.2 *Sogatella quadrispinosa* (Muir, 1919)
Plate 36d-e

Sogata 4-*spinosa* Muir, 1919. Can. Entmol. 51:526
Sogatellara quadrinspinosa Asche & Wilson, 1990. Syst. Entomol. 15:36-37

Features: Typically resembles *Sogatella* planthoppers in size and general appearance; forewings hyaline with yellowish veins, granulations small and sparse, apex of clavus with reddish brown markings; antennal segments I shorter than II, 2nd segment 1.7x longer than first; anal segment with a pair of short outer processes and a pair of long inner processes, outer pair not reaching lateral margins of pygofer and inner pair with indistinctly diverging apices; diaphragm elongate knob-like; parameres broad at mid-length, constricted thereafter subapically, apex with a strongly rounded apico-outer end and slightly blunt apico-inner tip; aedeagus short, spirally spinose toward apex.

Host plant: Unknown
Economic importance: Low
Distribution: Singapore

9. Genus *SOGATELLA* Fennah, 1956a

Chloriona (*Sogatella*) Fennah, 1956a. California Acad. Sci. Proc. IV 28(13):471
Type species: *Delphax furcifera* Horvath, 1899

Sogatella Fennah, 1964. Bull. Entomol. Res. 54:48
_____. Fennah, 1965. Bull. Brit. Mus. (Nat. Hist.) 17(1):47
_____. Fennah, 1978. Ann. Zool. (Wars.) 34(9):221
_____. Ascher & Wilson, 1990. Syst. Entomol. 15:5
_____. Wilson and Claridge, 1991. CAB Intern. and Nat. Resources Inst. :55
_____. Ding and Zhang, 1994. China Agric. Sci. Technol. 74

***Generic features*:** Body length 2.5–4.0 mm; small and slender planthoppers; vertex to mesonotum lined with a median longitudinal whitish band; lateral portions of pronotum and mesonotum brownish black; head slightly narrower than pronotum; vertex length and frons distinctly slender; frons longer than broad with median carina forked at about level of middle of eyes, lateral margins straight and subparallel; antennae cylindrical, moderately short, 1st segment distinctly longer than broad, 2nd segment longer than first; combined length of pronotum and carinae nearly straight, strongly diverging basally, not reaching hind margin; not parallel with mesonotal carinate; mesonotum

tricarinate, longer than vertex and pronotum together; legs terete and slender; post-tibial spur with about 20 small teeth, basal segment of post-tarsus linked by a dorsally slightly concave tuberosity forming a broad U-shaped structure; aedeagus moderately long, somewhat sinuate, bent dorsally at basal third, tips curved ventral, slightly compressed and twisted and pointed apically, two rows of teeth present ascending from the ventrodorsal third on both sides to the dorsal third; phallotreme located subapical on the left side; parameres diverging, apically tapering and bifurcated distally.

9.1 *Sogatella furcifera* (Horvath, 1899)
Plates 1j, 5g, 11a, 16b, 18j, 22c, 24j, 30b, 32g, 36f

Delphax furcifera Horvath, 1899. Terms Fuzetek 22:372
_____ Mastumura, 1899. Nippon-gaichuhen. 406. f. 206
Liburnia furcifera Matsumura, 1900. Entomol. Nachr. 26:262
Delphax furcifera Onuki, 1901. Spec. Rep. Jpn. Agric. Stn. 10:58
Liburnia furcifera Meliches, 1903. Hom. Faun. Ceylon 104
Liburnia albinosa Fowler, 1905. Biol. Cent. Am. Han. 1:135
Sogatella distincta Distant, 1912. Annu. Mag. Nat. Hist. 8th ser. 9:191
Sogatella pallescens Distant, 1912. Ibid. 9:192
Delphax furcifera Oshanin, 1912. Kat. Palaark. Hem. 9:192
_____. Schumacher, 1915. Mitt. Zool. Mus. Berlin 8:134
Megamelus ? *furcifera* Muir, 1917. Proc. Hawaii Entomol. Soc. 3:328
_____ Muir, 1921. Ibid. 4:486
Sogata furcifera Muir et Gifford, 1924. Hawaii Sugar Plant. Assoc. Exp. Stn. Bull. 5:13
Liburnia furcifera Muir, 1924. Kwngyo-mohanjo Kenyu-hokoku 12:23
Sogata furcifera Muir, 1926. Annu. Mag. Nat. Hist. Ser. 9, 17:34
Sogata pallescens Gater & Corbett, 1926. Feder. Malay State Str. Settlm. Bull. 33:5
_____ Dammerman, 1929. Agric. Zool. Malay Archipel. 235
S. furcifera Muir, 1930. Trebia 12:31
Delphacodes furcifera Esaki et Ishihara, 1931. Rep. Leafth. Injur. Ricepl. Nat. Enem. 2:5
Liburnia furcifera Wu, 1935. Cat. Ins. Sin. 2:119
_____ Metcalf. 1938. Bull. Mus. Comp. Zool. 82:300
Sogatella furcifera Matsumura et Ishihara, 1945. Mushi 16:64
Sogata tandojamensis Qadori & Misra, 1960. Proc. 4th Pan Ind. Ocean Sci. Cong. B. Biol. Sci. 1960:115
Chloriona (Sogatella) furcifera Fennah 1964. Bull. Entomol. Res. 54:48
_____. Fennah, 1978. Ann. Zool. (Wars.) 34(9):221
_____. Asche & Wilson, 1990. Syst. Entomol. 15:9-11
_____. Wilson & Claridge. 1991. CAB Intern. & Nat. Resources Inst. 56-58

Features: Yellow to yellowish brown; pronotum white with black areas behind eyes; frons, clypeus, genae, lateral areas of mesonotum, coxae I and II, and pleura all black; abdomen and pygofer dark brown; forewings hyaline with brown spot at end of clavus; vertex submedially almost as long as wide at base, obtusely rounded toward frons, lateral carinae straight, submedian carinae merged apically, basal compartment wider basally than greatest length 1.6:1; frons at midline longer than wide at broadest part

about 2.4:1, lateral carinae shallowly convex, median carina simple; clypeus basally wider than frons at apex; antennae surpassing frontoclypeal suture, segment I longer than wide at apex, shorter than segment II about 1:1.8; tibial spur with about 25 teeth; forewings longer than widest part about 3.3:1; pygofer slightly narrower dorsally than ventrally in profile, opening almost as long as wide viewed posteriorly, laterodorsal angle obtusely rounded, weakly produced; phallus laterally compressed, with around 18 teeth at left and 14 at right side, two rows separated basally; suspensorium elongate with hole at middle; diaphragm with dorsal margin evenly concave bearing a pair of peglike processes; anal segment short, lateroapical angles of pronotum distinctly separated, each produced ventrad in a moderately robust spinose process; opening of parameres with dorsal margin evenly curved upward, ventral margin with a broad lobe medially; parameres divergent, each with outer angle widely formed, obtuse apically, inner angle formed as long as outer one, apically acute.

Host plant: Rice, *Leersia hexandra, Echinochloa* spp., *Digitaria, Paspalum, Leptochloa chinensis*
Economic importance: High
Distribution: Bangladesh**,** Taiwan, China, Japan, Korea, Saudi Arabia, Siberia, Micronesia, Philippines, Laos, Cambodia, Myanmar, Nepal, Vietnam, Thailand, India, Indonesia, Pakistan, Fiji, Seychelles

9.2 *Sogatella vibix* (Haupt, 1927)
Plates 2a, 5h, 11b, 18k, 24k, 30c, 32h

Liburnia vibix Haupt, 1927. Homop. Palestine 1:13
L. matsumurana Metcalf, 1943. Gen. Cat. Hemiptera Facsim. IV(3):364
Delphacodes longifurcifera Esaki & Ishihara, 1947. Mushi :41
D. panicicola Ishihara, 1949. Sci. Rept. Matsuyama Agric. Coll. 2:51
D. dogensis Ishihara, 1952. Ibid. 8:47
Sogatella longifurcifera Fennah, 1969a. Bull. Entomol. Res. 54(1):53
S. vibix Fennah, 1963a. Ibid. 51
S. catoptron Fennah, 1963a. Ibid. 54-55
S. paniculata Fennah. 1963a. Ibid. 78
S. auzensis Linnavouri, 1964. Ann. Zool. Fennici 1:341
S. longifurcifera Fennah, 1965. Bull. Entomol. Res. 17(1):47
S. parakolophon Linnavouri, 1973. Notulae Entomol. Helsinki 53:108
S. matsumurana Nast, 1975. Ann. Zool. (Wars.) 33:2
S. longifurcifera Okada, 1977. Ibid. 11
S. diachenkea Kuo, 1977. Acta Zool. (Wars.) 34(9):222
S. vibix Asche & Wilson, 1990. Syst. Entomol. 15:22-24
S. v. Wilson & Claridge. 1991. CAB Intern. & Nat. Resources Inst. 62
S. v. Ding & Zhang, 1994. China Agric. Sci. Tech Press: 76-78

Features: Body length 3.33–4.16 mm; whitish yellow with black genae, large triangular area of mesopleura and round spot in metapleura, mesonotum with lateral fields pale brown to brown, apex of tarsi III black, abdomen and pygofer dark brown, forewings hyaline; vertex longer submedially than wide at base about 1.3:1, rounding into frons, wider at base than at apex, lateral carinae straight, arms of Y-shaped carinae distinct but the stem weak, submedian carinae not merged at apex, basal compartment of vertex wider at base than greatest length about 1.3:1; frons at midline longer than wide at broadest part about 2.4:1, median carina simple, forked at extreme base; clypeus basally wider than frons at apex, in middle line distinctly longer than wide at base; antennae passed frontoclypeal suture, segment I longer than wide at apex, shorter than segment II about 1:2.2; tibial spur with about 20 teeth; forewing longer than widest portion about 3.5:1; pygofer with dorsal margin almost as long as ventral in profile, laterodorsal angle rarely produced mesad, opening almost as wide as long viewed posteriorly; phallus similar in *S. furcifera* with around 18 teeth set in oblique pattern on left and 8 on right, two rows distinctly separated basally, not approximated; suspensorium with hole medially; diaphragm deeply concave along dorsal margin, median portion narrow, with a pair of peg-like processes, directed slightly caudad, apical portion strongly sclerotized; anal segment moderately short, lateroapical angles close but not contiguous, each produced ventrad in a moderately long spinose process; opening of parameres evenly concave ventrally with a small process medially; parameres with two apical processes, small inner one moderately converging, and large outer one strongly diverging.

Host plant: rice, maize, *Echinochloa crus-galli*, *Digitaria, Leersia*, *Phalacris,* and Setaria.
Economic importance: Low
Distribution: Oriental region: Bismark Islands, Cambodia, China, India, Indonesia, Laos, Pakistan, Philippines, Singapore, Thailand, Taiwan, Vietnam; Pacific region: Bonin Islands, Fiji Island, New Caledonia, Ryukyu Island, Solomon Islands, Tonga, Vanuatu: Australian region, Australia: Palaearctic region: Afghanistan, Cyprus, Egypt, Greece, Iran, Israel, Italy, Japan, Jordan, Korea, Lebanon, Mongolia, Morocco, Turkey, Saudi Arabia, former Soviet Union, Maritime Territory, and Yugoslavia; Ethiopian region: Kenya, Ethiopia, and Sudan

9.3 *Sogatella kolophon* (Kirkaldy, 1907)
Plates 2b, 6a, 11c, 18l, 24l, 30d, 32i, 36g-h

"Delphax" kolophon Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Entomol. Bull. 3(1):157
Opiconsiva insularis Distant, 1917. Trans. Linn. Soc. 2nd ser. Zool. 17:303
O. balteata Distant (in part), 1917. Ibid. 302
O. derelicta Distant, 1917. Ibid. 307
Delphacodes elegantissima Ishihara, 1952. Sci. Rep. Matsuyama Agric. Coll. 8:45
Sogata meridiana Beaver, 1952. J. Kansas Entomol. Soc. 25:111
Sogatella kolophon atlantica Fennah, 1963a. Bull. Entomol. Res. 54:58-59

S. k. insularis Fennah, 1963a. Ibid. 59
S. k. meridiana Fennah, 1963a. Ibid. 59
Sogatella balteata Fennah, 1963a. Ibid. 64
S. derelicta Fennah, 1963a. Ibid. 62
S. elegantissima Fennah, 1963a. Ibid. 76
S. nebris Fennah, 1963a. Ibid. 67
S. kolophon Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):47
S. k. Okada, 1977. Food & Fert. Tech. Centr. Asia Pac. Reg. 9
S. k. Fennah, 1978. Ann. Zool. (Wars.) 34(9):16
S.k. Asche & Wilson, 1990. Syst. Entomol. 15:16-20

Features: Body length 3.19–3.89 mm; yellowish brown with mesonotal lateral areas darker, coxae I and II, pleura and abdomen except laterally and pygofer brown to dark brown, forewings hyaline; vertex longer submedially than wide at base about 1.3:1, evenly rounded toward frons, slightly narrower apically than at base, basal compartment of vertex wider at base than greatest length about 1.4:1; frons in midline longer than widest part about 2.2:1, lateral carinae slightly concave, median carina forked at basal fifth; clypeus at base slightly wider than frons at apex; antennae extended to frontoclypeal, segment I longer than wide, shorter than segment II about 1:2; tibial spur with 15–22 teeth; pygofer wider dorsally than ventrally in profile, opening slightly longer than wide viewed posteriorly, laterodorsal angle typically inflected; phallus with 16 teeth arranged in oblique row on left, six on right margin, on caudal side left row obliquely reaching right side, two rows basally apart; suspensorium with a hole in the middle; diaphragm bears peglike process on each side, dorsal margin slightly arched, peglike processes and dorsal half of median part strongly sclerotized; anal segment short, lateroapical angles each produced ventrad into a short, stout spinose process; opening for parameres with dorsal margin arched upward, ventral margin with median projection obtuse; parameres with outer angle tapering to tip, basal angle forms distinct keel.

Host plant: Unknown
Economic importance: Low
Distribution: Oriental region: Cambodia, China, Hong Kong, India, Indonesia, Laos, Malaysia, Papua New Guinea, Philippines, Seychelles Islands, Sri Lanka, Thailand, Taiwan, and Vietnam; Pacific region: Belau Islands, Bonin Islands, Fiji Islands, Galapagos Islands, Guam, Hawaii Islands, Manganeva Islands, Marquesas Islands, Eniwetok Atoll, Micronesia, New Caledonia, Northern Marianas Islands, Pitcairn Islands, Solomon Islands, Tonga Island, Western Samoa; Australian Region: Australia; Nearctic region: Bermuda Islands; Neotropical region: Ecuador, Guyana, Jamaica, Mexico, Montserrat, Sta. Lucia, Venezuela; Atlantic Ocean: St. Helena Islands; Ethiopian region: Cape Verde Islands, Côte d'Ivoire, Nigeria, South Africa; Malagasian region: Mauritius, Rodrigues Islands; Palaearctic region: Azores Islands, Canary Islands, Japan, and Korea

10. Genus *LATISTRIA* Huang et al, 1980

Latistria Huang et al, 1980. Acta Zootaxon. Sin. 5(2):166
Type species: *Latistria testacea* Huang et al

Latistria Huang et al, 1980. Acta Zootaxon. Sin. 5(2):166
Latistria Asche & Wilson, 1990. Syst. Entomol. 15:37

Generic features: With strong resemblance to the small species of whitebacked planthoppers belonging to the *Sogatella albofimbriata* group characterized by having an acute anterior vertex; the main generic character of *Latistria* is the shape of the diaphragm forming mediodorsally a wide plate protrusion with rounded lobelike lateral edges or sinuate bilobed crossplate; parameres long, slender with tapering to truncate apices, in repose, parameres almost reach the laterodorsal margins of the anal segment, subbasally with latero-inner expansion projected laterally, apices strongly diverging; aedeagus in right lateral profile subbasal one-third curved, and aedeagal body bears two longitudinal rows of spines running from top to bottom, sometimes crossing each other at midlength, longer row with 16–25 teeth, and shorter row with 10–17 teeth.

10.1 *Latistria eupompe* (Kirkaldy, 1907)
Plates 16c, 22d, 36i-j

Delphax eupompe Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Div. Entomol. 3(1):162
D. ochrias Kirkaldy, 1907. Ibid. 157
Sogatodes infestus Yang, 1989. NSC Special Publ. 6:172
Latistria eupompe Asche & Wilson, 1990. Syst. Entomol. 15:37

Features: Body length 3–3.5 mm; general color pattern varies from dark reddish brown to blackish brown, sometimes yellowish white on antennae, pronotum, scutellum, between the lateral carinae, legs, and commissure; forewings dark reddish brown, a little paler in Sc + R, Sc_1 to Sc_2, R_1, and cubital area posterior of claval line; veins closely but flatly granulate; with nine apical cells, four and seven pedicellate; antennae short, segment I shorter than segment II, not reaching the apex of frons; tibial spur with 13 spines; pygofer opening longer than wide, thickened internally at the midlaterals, slightly diamond-shaped; anal segment with two medially strong straight spines between which arises the upward and outwardly directed aedeagus; parameres diverging, elongate, slender, and apically acute.

Host plant: Rice
Economic importance: Low
Distribution: Australia, China, Fiji, Indonesia, and the Philippines

11. Genus *TAGOSODES* Asche & Wilson, 1990

Tagosodes Asche & Wilson, 1990. Syst. Entomol. 15:32
Type species: *Dicranotropis cubanus* Crawford, 1914

Tagosodes Asche & Wilson, 1990. Syst. Entomol. 15:32
Tagosodes Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 62

Generic features: Body length 3–4 mm; external features basically similar to the members of the genus *Sogatella* Fennah, 1956 species complex; vertex, pronotum, and mesonotum lined medially by a longitudinal white band, laterals of pronotum and mesonotum blackish to brown; vertex slender, nearly parallel-sided, longer at midline than at base about 1.4–1.7 times, posterior compartment of vertex lightly concave with weak to indistinct median carina, anterior cell long and slender, anteriorly terminated at tip of vertex, sometimes extended to frons; vertex and frons form a moderate acute angle, transition toward frons mostly rounded; frons high and slender, about 2x to slightly more as high as maximum width, broadest at or toward frontoclypeal suture; median carina prominent along the transition point from vertex to frons; clypeus with distinct carina; proboscis reaching coxae III; segment II of antennae 1.8–2x longer than segment I, arrangement of sensory field 16 and 7; number of spines on tibial spur of leg III, proportions of hind tarsal segments and wings as in *Sogatella*; pygofer ringlike, subglobose to ovoid viewed caudally, laterodorsal angles moderately produced; mid-portion of diaphragm elevated, mediodorsal margin caudodorsally developed variably as T-shaped, triangular, rectangular, U- or W-shaped protrusion, central portion ovoidly bulbous, ridged and lined with many teeth; paramere opening broadly trapezoidal; anal segment with two spinous processes borne from the laterodorsal angles on the ventral side, processes toward each other medially, slightly curved ventrad viewed laterally; shape of parameres varies basally broad, middle part slender and dilated apically, often diverging from base then at least inner apical angle converging medially; aedeagus tubular, slightly flat, with spines irregularly forming rows.

11.1 *Tagosodes pusanus* (Distant, 1912)
Plates 2c, 6b, 11d, 18m, 25a, 30e, 32j, 36k, 40d

Sogata pusana Distant, 1912. Annu. Mag. Nat. Hist. 8(9):191
Kelisia fieberi Muir, 1917. Proc. Hawaii Entomol. Soc. 3(4): 331
Unkana formosella Matsumura, 1935. Insecta Matsumurana 9:72
Chloriona fieberi Fennah, 1956. Insects of Micronesia 6(3):120-121
Sogata striatus Qadri & Mizra, 1960. Proc. 4th Pan Indian Ocean Sci. Congr. B, Biol. Sci. 1960:117
Sogatella pusana Okada, 1977. Food & Fert. Tech. Centr. Asian Pac. Reg. 11
Himeunka chibana Tian & Kuoh, 1981. Acta Entomol. Sin. 24(2):193
Sogatodes assimilis Yang, 1989. NSC Special Publ. 6:178
Tagosodes pusanus Asche & Wilson, 1990. Syst. Entomol. 15:35
Tagosodes pusanus Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 63

Features: Body length 3.2–3.5 mm; pale yellow vertex about 1.7x as long as its basal width, lateral sides subparallel, carina yellow, outer areas from mediolateral carinae dark brown; frons dark brown with pale yellow carinae concolorous with genae, proboscis, and ocelli; clypeus dark brown with pale yellow carinae; pronotum with light yellow carinae, similarly pale yellow medially with a pair of dark impressions, laterally dark brown but paler along posterior margin; mesonotum as long as combined length of vertex and pronotum, pale yellow medially, dark brown laterally with blackish lateral carinae; forewings well developed, distinctly tinged at apex of clavus, apical cells crescently reddish brown or with finger-like markings toward apical margins near veins; apical veins dark brown; abdominal segments dark brown, pale yellow posteriorly; pygofer nearly rounded, medioventral area shallowly concave; parameres subbasally broad, constricted at midhalf along inner and outer sides, moderately concave at apex; diaphragm T-shaped; aedeagus basally wide and subglobose, slender and cylindrical at apical half, with four spines at midlength and 5–9 spines apically.

Host plant: Rice
Economic importance: Low
Distribution: Cambodia, China, India, Indonesia, Japan, Laos, Malaysia, Micronesia, Pakistan, Philippines, Sri Lanka, Taiwan, and Vietnam

12. Genus *TERTHRON* Fennah, 1965

Terthron Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):55-56
Type species: *Delphax anemonias* Kirkaldy, 1907

Terthron Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):55-56
Terthron Fennah, 1978. Ann. Zool. (Wars.) 34(9):222
Terthron Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 69
Terthron Ding & Zhang, 1994. China Agric. Sci. Tech. Press 96

Generic features: Body length 2.7–3.3 mm; general color blackish brown; broad ivory white median longitudinal band present dorsally on the head, pronotum, and mesonotum; segment I of antennae blackish brown, II dark reddish brown; forewings hyaline with pale reddish brown veins; vertex at midlength as long as broad at base, subacutely rounded toward frons, as wide at apex as at base, lateral margins straight to weakly concave, apical margin transverse with submedian carinae barely prominent; Y-carina present but feeble, submedian carinae merged at apex of vertex, basal compartment of vertex broader at hind margin than its greatest length about 2:1; at midline frons longer than wide at broadest part about 2:1, lateral margins shallowly convex, median carina simple; clypeus at base moderately wider than at apex of frons, clypeus as long as broad at base, in profile, shallowly convex, almost straight, entire clypeus in profile, moderately convex.

12.1 *Terthron albovittatum* (Matsumura, 1900)
Plates 2d, 16d, 22e, 37a-b

Dicranotropis albovittata Matsumura, 1900. Entomol. Nachr. 26:269
Delphax albovittata Susuki, 1915. List Spec. Hanazon. Entomol. Inst. 10
Liburnia albovittata Matsumura, 1917. Appl. Entomol. For. Ser. 379
Sogata albovittata Esaki, 1932. Iconogr. Ins. Jpn. 1734
Delphacodes albovittata Matsumura & Ishihara, 1945. Mushi 16:61
Terthron albovittatum Fennah, 1978. Ann. Zool. (Wars.) 34(9):222
T.a. Wilson & Claridge, 1991. CAB Inter. & Nat. Resources Inst. 69

Features: Body length 2.6–3.4 mm; dark to blackish brown planthoppers with a fairly broad pale yellow dorso-longitudinal median band running from vertex to apex of mesonotum; black face with white carina, genae, and clypeus; antennae mostly blackish brown, segment II slightly paler in color except base; vertex black between lateral and medio-lateral carinae; forewing subhyaline with a gray tinge, hind margin white, veins mostly light brown; vertex slightly longer than wide, forked toward frons; frons distinctly longer than wide, broadest at level of ocelli, slightly convex along lateral margins; median carinae forked nearly basad of frons; clypeus with distinct median carina; pronotum with distinct median and lateral carina, lateral carinae slightly concave, not reaching hind margin of pronotum, diverging; combined length of vertex and pronotum as long as to slightly shorter than length of mesonotum; pygofer oblongate, medioventral area concave housing base of basally merged parameres, the latter with subparallel sides, distinctly diverging, subtruncate at apex; aedeagus in lateral view, with a thumb-like apical process and a small acute one after concavity; anal segment with a pair of moderately long, acute, converging processes.

Host plant: Rice, *Panicum crus-galli* (barnyard millet)
Economic importance: High, vector of rice stripe virus and the black-streaked dwarf virus
Distribution: China, Japan, Korea, and Taiwan

13. Genus *UNKANODES* Fennah, 1956

Unkanodes Fennah, 1956. Proc. Calif. Sci. 28(13):474
Type species: *Unkana sapporona* Matsumura, 1935

Unkanodes Fennah, 1956. Proc. Calif. Sci. 28(13):474
Glymodelphax Wagner, 1963. Mitt. Hamburg. 2001. Mus. Inst. 60:167
Unkanodes Wilson and Claridge, 1991. CAB Intern. & Nat. Resources Inst. 69
Unkanodes Ding & Zhang, 1994. China Agric. Sci. & Tech. Press 109

Generic features: Body length 4.5–4.7 mm long, pale brown to blackish brown with a fairly wide white band or stripe running from vertex to scutellum; vertex slightly oblong, nearly 2x as long as wide, narrowed at about midlength, medio-lateral carinae arise from lateral carinae apically, united to each other on apex and extended to frons as single carina; face somewhat oblong, broadest under eyes about 2.5x as long as broadest width; antennae relatively long, reaching beyond fronto-clypeal suture, segment I distinctly shorter than segment II by less than half the length of the second; pronotum and vertex almost subequal in length, tricarinate lateral carinae diverging posteriorly but not reaching hind margin; mesonotum tricarinate; pygofer moderately oblongate, mediocaudal process absent; parameres with concave inner midlaterals concave, apically forming lobe-like process, inner one higher than the other; laterodorsal angle distinctly higher than the tip of paramere; ventrolaterals of pygofer sometimes well developed laterally; anal segment with a pair of downwardly processes, aedeagus arrow-like with subapical barb of spines directed downward or hook-like.

13.1 *Unkanodes albifascia* (Matsumura, 1900)
Plates 22f, 37c

Liburnia albifascia Matsumura, 1900. Entomol. Nachr. 26:268
Delphax a. Oshanin, 1908. Verz. Palaark. Hem. 2:330
D. a. Oshanin, 1912. Kat. Palaark. Hem. 120
Delphacodes albifascia Esaki et Ishihara, 1943, Cat. Araeopid. Imp. Jpn. 35
Chilodelphax albifascia Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 69
Ribautodelphax albifascia Ibid. 69

Features: Body length 1.8–2.4 mm; body dorsally with a distinctly conspicuous fairly broad white median longitudinal stripe running from vertex to scutellum; vertex light brown with black band each between lateral and medio-lateral carinae; pronotum and scutellum brown; frons and clypeus black with white longitudinal stripe along its median carinae; genae similar to frons in coloration except for the brown lateral carinae; antennae light brown, short, and not reaching the fronto-clypeal suture, segment I shorter than segment II; forewings opaque, blackish with basal portion whitish and apical margins bearing whitish tinge; pterostigma conspicuously black; pygofer subglobose with laterally expanded ventrolateral margins, latero-dorsal angle well developed; parameres visibly concave at about midlength of the inner lateral margins, apically forming an outwardly projected hook, apicolateral tip of the outer margin rounded; anal segment with a pair of short processes; aedeagus hook-like viewed ventrally, barbed with spines toward the apex.

Host plant: Rice and a wide range of Gramineae
Economic importance: Relatively high; vector of northern cereal mosaic virus, stripe disease, and black streaked dwarf virus
Distribution: Japan, Korea, maritime territory of former Soviet Union

13.2 *Unkanodes sapporonus* (Matsumura, 1935)
Plates 2e, 16e, 22g, 37d

Unkana sapporona Matsumura, 1935. Insecta Matsumurana 10:74
Unkanella sapporona Esaki et Ishihara, 1945. Cat. Araeopid. Imp. Jpn. 22
Unkanella sapporona Matsumura et Ishihara, 1945. Mushi 16:69
Delphacodes sapporona Ishihara, 1949. Cont. Sci. Rep. Matsuyama Agric. Coll. 2:57
Unkanodes sapporona Fennah, 1956. Proc. Calif. Acad. Sci. 28:4
Elymodelphax excise Anufriev, ? 1980. Zool. Zh. 59
Unkanodes sapporonus Wilson and Claridge, 1991. CAB Intern. & Nat. Resources Inst. 68
Unkanodes sapporona Ding & Zhang, 1994. China Agric. Sci. & Tech. Press 110-112.

Features: Body length 4.5–4.7 mm, generally pale yellow-brown-bodied planthopper; vertex longer than wide, narrow, visibly extending forward between eyes; white stripe lined the median longitudinal area of vertex running to pronotum and scutellum; frons and clypeus concolorous, more dark colored than pale brown genae, frons broadest subanteriorly, lateral margins slightly concave, median and lateral carinae distinct, median carina forked close to base of frons; antennae short pale brown, segment I narrower and shorter than segment II, not reaching frontoclypeal suture; clypeus longer than wide with median carina present; length of vertex and pronotum combined longer than mesonotum; pronotum tricarinate; forewings hyaline, hind margin broadly brownish, veins along apical one-third infuscated; pygofer with a short narrow basal lobe adjacent to base of parameres, widens as parameres diverge; parameres parallel-sided most of their length viewed caudally, axe-like seen laterally; apex constricted on both sides, laterally inner apical tip shortly bulbous at tip; aedeagus arrow-like with barbed spines subapically.

Host plant: Rice
Economic importance: Minor pest; vector of black streaked dwarf and stripe viruses
Distribution: China, Japan, Korea, maritime territory of former Soviet Union, Taiwan

14. Genus *STENOCRANUS* Fieber, 1866

Stenocranus Fieber, 1866. Zool.-Bot. Ges. Wien, Verh. 16:519
Type species: *Fulgora minutes* Fabricius, 1787

Stenocranus Fieber, 1866. Zool.-Bot. Ges. Wien, Verh. 16:519
Stenocranus Sahlberg, 1871. Not. Sallsk. Faun. Fenn. Forh. 12:413
Stenocranus Fieber, 1875. Rev. Mag. Zool. 370
Stenocranus Farrari, 1878. Ann. Mus. Stor. Nat. Genova 18:57
Stenocranus Ashmead, 1889. Entomol. Am. 5:27
Stenocranus Melicher, 1896. Cicad. v. Mit. Eur. 56

Stenocranus Van Duzee, 1897. Bull. Buffalo Soc. Nat. Sci. 5:230
Stenocranus Kirkaldy, 1907. Hawaii
Stenocranus Oshanin, 1912. Kat. Palaark. Hem. 118
Stenocranus Crawford, 1914. Proc. U.S. Mus. 46:587
Stenocranus Dozier, 1922. Ohio J. Sci. XXII (3):69
Stenocranus Muir et Griifard, 1924. Hawaii Sugar Plant. Assoc. Entomol. Bull. 15:11
Stenocranus Matsumura, 1935. Insecta Matsumurana 10:71
Stenocranus Esaki et Ishihara, 1943. Cat. Araeop. Imp. Jpn. 13
Stenocranus Matsumura & Ishihara, 1945. Mushi 16:68
Stenocranus Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:23-24
Stenocranus Fennah, 1956. Insects of Micronesia 6(3):113
Stenocranus Fennah, 1978. Ann. Zool. (Wars.) 34(9):219
Stenocranus Ding & Zhang, 1994. China Agric. Sci. Tech. Press 23

Generic features: Body length 2.6–7 mm; vertex projected in front of eyes, apex narrower than base, fairly oblong, usually 1.5–2x the width, with medio-lateral carina joining lateral carinae before reaching base and converging apically, but not meeting on vertex, continued on to frons, where they merge with each other inferiorly to base; head including eyes subequal to combined length of vertex and pronotum; eyes comparatively large; enlarged postero-laterally, Y-shaped median carina present; frons more than 2x as long as width at midlength, its widest point; eyes relatively large, swollen postero-laterally; clypeus wider basally than in frontal apex; antennae in most species short, not reaching fronto-clypeal suture, segment II longer than segment I by about 2:1; pronotum shorter than the length of vertex, wider than head, including eyes, lateral carinae convergingly curved posteriorly and distinctly reaching hind margin; mesonotum large, apex blunt to pointed, length about equal to combined length of vertex and pronotum; tricarinate but median carina indistinct toward apex; forewings well developed, distinctly protruded well beyond tip of abdomen; legs simple, basitarsus as long as or a little longer than the combined length of the other two tarsal segments; pygofer often oblongate with anal segment and long and large style projected outward, medioventral area deeply concave forming a distinctly sunken base of slender parameres; tips of parameres usually narrowed and pointed; aedeagus long, slender, and pointed apically.

14.1 *Stenocranus* sp. A
Plates 2f, 6c, 11e, 19a, 25b, 32k

Features: Body length 4.8 mm; body coloration pale yellow brown; head wider than long by about 1.34x at widest point; vertex, viewed dorsally, 1.8x longer than wide of broadest point along basad of vertex; submedian carina of vertex narrowed toward base of frons; basal compartment of vertex almost as wide as long, Y-carina faded to indistinct; eyes distinctly large; frons pale yellow brown except thin brown longitudinal stripe lining the side of lateral carina; 2.7x longer than wide at broadest subapical area, 4.5x at narrowed base of frons, anterior width 1.7x wider than base, median carina very thin yellow sigmoid-like toward fronto-clypeal suture, partly faded

before reaching the suture; lateral carinae of frons, clypeus, and genae thin black line; clypeus and genae pale yellow-brown; frontoclypeal suture sunken; clypeus strongly convex at middle, tricarinate; antenna yellowish, base of segment I narrower than its apex, segment II 2.3x longer than I, distinctly beyond frontoclypeal suture; length of vertex and pronotum together one-eighth shorter than mesonotum; pronotum tricarinate, lateral carinae straight and oblique, directed laterad, not reaching hind margin; mesonotum about 1.16x longer than vertex and pronotum, tricarinate, median carina fading toward scutellum, lateral sides light brown; forewings subhyaline with pale yellowish brown veins along apical margins, extended beyond tip of abdomen by about the length of abdomen; legs and abdomen yellowish; pygofer yellowish, darker in the anal segment; medioventral part widely and deeply concave, housing basally merged; apically diverging parameres; apical one-third of parameres moderately enlarged, tips pointed parallel to each other to slightly converging; laterodorsal angle of pygofer at level with the enlarging apical third of parameres; anal segment with a pair of short processes parallel to each other, tips hardly reaching laterodorsal angle; aedeagus brownish, thin, slender, and long; tibial spur with 23 spines.

Host plant: Rice
Economic importance: NEI
Distribution: Philippines (Luzon Island)

14. 2 *Stenocranus pacificus* Kirkaldy, 1907
Plates 2a, 6d, 11f, 19b, 25c, 32l-m, 37e-f

Stenocranus pacificus Kirkaldy, 1907. Hawaii Sugar Plant Assoc. Div. Entomol. 3(1):139
S. p. Fennah, 1956. Insects of Micronesia 6(3):114
Sogata hakonensis Pawar, 1972. Terminal Rep. Int. Rice Res. Inst.

Features: Body length 4–6.3 mm; light orange-yellow planthopper with a broad dorso-median longitudinal band running from head to scutellum; vertex frontally narrowed, produced in front of reddish eyes, 1.69x longer than wide at broadest basal area; basal compartment almost as wide as long basad; frons with a broad median white longitudinal band, including median carina, laterals, and lateral carina narrowly brown extended partly to vertex; widest subapically near the convex frontoclypeal suture, almost 3x longer than wide, anterior width 2x basal width; tricarinate; clypeus white medially as continued from frons, pale yellow-brown laterally; median carina present; genae brownish yellow; ocelli present, black; antennae yellow, segment II 1.75x longer than segment I, passing the frontoclypeal suture; forewing hyaline, tinged pale yellow, including veins, apical vein light reddish brown extended beyond abdominal tip by more than length of the dorsally orange abdomen; pygofer yellow, V-shaped toward medioventral margin, emarginate ventrally; anal segment prominent with a pair of processes subparallel to one another; parameres contiguous basally, diverging V-shaped toward apex, with a hooked tip directed lateroventrally; aedeagus elongate, subascending; legs yellow, tibial spur of leg III with 24–25 spines.

Host plant: Rice, *Saccharum officinarum*, and grass
Economic importance: Low
Distribution: Fiji Island, Western Caroline Island, Palau, and Philippines

14.3 *Stenocranus* near. *pseudopacificus* Kirkaldy
Plates 2h, 6e, 11g, 19c, 25d, 32n-o

Features: Body length 5.7–7.5 mm; pale yellow to light orange-yellow with a relatively narrow median longitudinal white band running from vertex to scutellum; eyes reddish brown to silvery brown with red tinge; mesonotum largely orange laterally; basal compartment pale yellow with margins brown; vertex whitish except for reddish brown band between median and lateral carinae running down to frons; frons reddish brown except for whitish median and yellow-brown carinae; clypeus orange; genae yellowish brown; antennae yellow; forewings hyaline, lightly granulated, veins pale brown toward apical margins; legs yellow; abdomen orange except for yellow pygofer; vertex slightly longer than wide, widest basad, frontally narrowed and projected in front of eyes; basal compartment at base 1.4x wider than long; median carina present forming bilobed area; combined length of vertex and pronotum about 0.6x length of mesonotum, the latter 1.65x longer than vertex and pronotum; lateral carina of pronotum very slightly concave to straight, not reaching hind margins; median carina of mesonotum faded before scutellum; frons at widest anterior, 2.66x longer than wide, almost parallel-sided except narrowed at base; ocelli black present; clypeus tricarinate, 1.44x longer than wide, apical half near the frontoclypeal suture bulbous, rounded, and swollen; antennae barely reached the frontoclypeal margin, segment II 2.1x longer than I; forewings extended beyond tip of abdomen by as much as 1.63x length of abdomen; pygofer subquadrate basally to moderately oblong, laterodorsal angle almost at midlength, U-shaped on apical end; parameres unique, large contiguous base forms thin spur with apically diverging tips, continued apically as slender process, curved outward laterally; anal segment with a pair of processes, horn-like curved toward the inside of pygofer; aedeagus long and slender, half-coiled subapically forming a transverse structure between horn-like process of anal segment; anal style relatively short. (Note: Quite similar to *S. pseudopacificum* Muir but genitalia pattern quite different.)

Host plant: Rice
Economic importance: Low
Distribution: Philippines (Luzon Island)

14.4 *Stenocranus* sp. B
Plates 2i, 6f, 11h, 19d, 25e, 33a-b

***Features*:** Body length 5.6 mm; pale yellow with light orange-red abdomen; pronotum whitish yellow; mesonotum with yellowish brown band along lateral carinae and sublaterals pale yellow-brown; a dorso-median longitudinal white band from vertex to scutellum distinct; frons, clypeus, and genae yellow-brown, including carinae; ocelli black; eyes silvery brown; antennae yellow; hyaline wings very finely granulate; vertex narrowly projected forward in front of eyes, 1.23x longer than wide taken across broadest basal area; basal compartment as a whole subquadrate, each cell almost 2x longer than wide; vertex and pronotum together shorter than mesonotum, the latter 1.33x longer than vertex and pronotum; pronotum and mesonotum tricarinate; lateral carinae of pronotum slightly convex, not reaching hind margin; median carina of mesonotum indistinct toward scutellum; frons at apical portion 2.58x longer than wide, lateral margins more widely separated apically, sinuate basally toward vertex; clypeus mildly swollen near frontoclypeal suture; antennae with base of segment I narrower than apex, segment II 2x longer than segment I; forewings extended beyond tip of abdomen by twice the length of abdomen; pygofer yellow except for brownish aedeagus and tips of parameres; obligate to basally subquadrate; parameres horn-like, basally contiguous, with emanating thin and slender, apically pointed spines; inner midlaterals deeply concave, curved inward and then slightly outward forming an oblique small hook-like diverging process; pair of anal segment processes apically thin and slender, projected downward to aedeagus and converging.

Host plant: Rice
Economic importance: Low
Distribution: Philippines (Luzon Island)

15. Genus *PERKINSIELLA* Kirkaldy, 1903

Perkinsiella Kirkaldy, 1903. Entomologist 36:179
Type species: *Perkinsiella sachariciда* Kirkaldy, 1903

Perkinsiella Kirkaldy, 1903. Entomologist. 36:179; 1906. Hawaii Sugar Plant. Assoc. Entomol. Bull. 1:404
Phalacastor Kirkaldy, 1906. Hawaii Sugar Plant. Assoc. Entomol. Bull. 1:408
Perkinsiella Kirkaldy, 1907. Ibid. 3:136
Perkinsiella Muir, 1910. Ibid. 9:4. 1913. Proc. Hawaii. Entomol. Soc. 2:240
Perkinsiella Matsumura, 1917. Appl. Entomol. Form. Ser. 378.
Perkinsiella Muir, 1927. Ins. Samoa 2:11
Perkinsiella Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 44
Perkinsiella Matsumura et Ishihara, 1945. Mushi 16:73
Perkinsiella Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:18

Perkinsiella Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:44
Perkinsiella, 1956. Insects of Micronesia 6(3):109
Perkinsiella Fennah, 1965. Bull. Brit. Mus. (Nat. Hist.) 17(1):16
Perkinsiella Fennah, 1978. Ann. Zool. (Wars.) 34(9):223
Perkinsiella Wilson and Claridge, 1991. CAB Intern. & Nat. Resources Inst. 70-72

Generic features: Moderately sized to large planthoppers, 5.0–7.7 mm long; easily recognized by head noticeably broad with a broad medio-longitudinal yellow to white band running from vertex to mesonotum; vertex slightly projected frontally in front of eyes, subparallel-sided, mediolateral carinae raised along lateral carinae, slightly posterior to middle, moderately converging anteriorly, continued to frons and branch near the lower margin of eyes; Y-shaped carina and usually faded to indistinct transverse carinae between mediolateral carina present; face about 2x as long as broad between eyes, the broadest area narrow and distinctly concave to excavated toward the apex; clypeus base about as wide as apex of frons; antennae large, nearly reaching apex of clypeus, sement I rather triangular (broader at apex than at base) and both segment I and II flattened, and segment II about 1.5x longer than first; pronotum slightly broader than vertex at eye region, a little shorter than vertex; lateral carinae diverging and curving posteriorly, fading before reaching lower margin; mesonotum relatively small obtusely projected posteriorly, length subequal to vertex and pronotum combined; legs simple, hind basitarsus more than 2x as long as the other two tarsal segments put together; spurs relatively small, thin, with many minute teeth along the hind margin; pygofer with two spines on vertical margin.

15.1 *Perkinsiella* sp. A
Plates 2j,11i,33c

Features: Body length 7.5 mm; black *Perkinsiella* form with brownish vertex, median plate of pronotum and scutellum, blackish brown legs, brownish median carina of mesonotum dorsum of femur I and wings particularly the veins and hyaline in the discal area and from Sc to M_{1+2}; vertex slightly produced in front of eyes, almost parallel sided, 1.23x wider than long at base, basal compartment wide, each slightly longer than wide to almost subequal median carina of compartment distinct; eyes large and distinct; frons black with very light yellow transverse band at level of simple eyes and a narrow line at frontoclypeal suture, 1.67x longer than wide, broadest at level of antennae, tricarinate, median carina forked at broadest point of frons, lateral carinae parallel-sided apically, widen medially and narrow basally; clypeus shiny black, median carina distinctly higher than lateral carinae; antennae typical of the genus except for color, segment I with yellowish brown longitudinal band laterally and ventrally, segment II yellow-brown along basal one-third; apex of segment I 1.8x wider than its base; segment II 1.5x longer than segment I; vertex and pronotum shorter than mesonotum, the latter 1.38x longer than combined length of pronotum and vertex; pronotum tricarinate, lateral carina sigmoid, posterior ends curve diverging, not reaching the hind margin; mesonotum tricarinate, median carina distinct up to scutellum, lateral carinae subparallel to one another, scutellum distinctly triangular, separated

by a transverse demarcation line from mesonotum; forewings 3.87x longer than broad, transparent in the discal area between veins R and M, subcostal cell, and Sc to M_{1+2} subcostal cell with two cells; pygofor black with yellow-brown style, subovate, narrowed in the medioventral margin with a pair of thin outerwardly curved spines; ventrolaterally strongly convex and rounded; parameres stout, contiguous basally, widen at midlength forming concave inner lateral margins, slightly converging to U-shaped apically, apex with small tooth-like protuberance projected upward; and segment with a pair of processes, slightly converging, then process projected caudad; and style leaf-like to pear-shaped, 2.5x longer than wide.

Host plant: Unknown
Economic importance: Low
Distribution: Philippines (Luzon Island)

15.2 *Perkinsiella vastatrix* (Breddin, 1896)
Plates 2k, 6g, 11j, 19e, 25f, 37g-h

Dicranotropis vastatrix Breddin, 1896. Deutsch. Entomol. Zeitschr 1896:109
D.v. Krueger, 1899. Zuckerrohr. U.S. Kultune 312
D.v. Brusse, 1904. Arb. Boil. About Land. Kais. Ges. Amt. 4:319
Perkinsiella vastatrix Kirkaldy, 1906. Hawaii Sugar Plant. Assoc. Exp. Stn. Entomol. Bull. 1:407; 1907. Ibid. 3:135,137
P. (*Dicranotropis*) v. Matsumura, 1910. chad. U. Nutz. Ins. Zuckerrohr. Formosa 15
P. v. Muir, 1910. Hawaii Sugar Plant. Assoc. Exp. Sta. Entomol. Bull. 9:5,9
P. v. Gater et Corbett, 1926. Fed. Malay. State Straits Settlm. Bull. 38:5
P. (*Dicranotropis*) v. Dammerman, 1929. Agric. Zool. Malay. Archipel. 235
P. v. Takano et Yanagihara, 1938. Spec. Rep. Tokyo Exp. Stn. 2:122
P. v. Esaki & Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 45
P. v. Ishihara, 1945. Sci. Rep. Matsuyama Agric. Coll. 2:21

Features: Body length 8 mm; brownish yellow with dark brown pterostigma, hyaline wings, brown markings on the apical one-third of forewings; dark brown antennal segment I except for yellow basolaterals; I and II legs yellow except tibia with subapical and subbasal blackish brown bands and tarsi I and II completely blackish brown; femur III with brown longitudinal lateral stripe vertex very slightly projected in front of eyes, 1.4x wider than long, 1.32x broader posteriorly than anteriorly; basal compartment visibly deep and concave, as wide as long, median carina present; frons, clypeus, and genae brownish, sometimes basal one-half of clypeus yellow; frons mottled with yellowish spots, 4–5 pairs at base, to level of Y-carina, 2–3 pairs at midlateral carina and 1–2 pairs subapically, 2.13x longer than wide at broadest point, just above level of distinctly black ocelli, tricarinate similar to clypeus, genae with a yellow spot subapically; antenna with apex of segment I almost 2x wider than its base, segment II 1.9x longer than I lightly passing the frontoclypeus suture; vertex and pronotum together about 0.7 length of mesonotum, the latter being 1.48x longer than vertex to pronotum; pronotum tricarinate, lateral margins sinuate, curved outward laterally, not

reaching hind margin, propleuron with four yellowish white spots just behind eyes; mesonotum tricarinate with whitish yellow tip of scutellum, without demarcation line between mesonotum and scutellum, median carina reaches scutellum; forewings beyond abdominal tip by about 0.8 length of abdomen; pygofer subovate, wider ventrally and somewhat elongate apically; medioventral process with a pair of thin and slenderly long bifurcating processes; parameres basally large and bearing two diverging processes; anal tube with a bifurcate spin; anal style short; venter of anal segment brown medially; tibial spur with about 30 teeth.

Host plant: *Andropogon sorghum*, rice, *Saccharum officinarum*, *Zea mays*
Economic importance: Relatively low
Distribution: Indonesia, Japan, Malaysia, New Guinea, Philippines, Taiwan, East Africa

15.3 *Perkinsiella pseudomaidis* (Kirkaldy, 1906)
Plates 2l, 6h, 12a, 19f, 25g, 40e

Phacalastor pseudomaidis Kirkaldy, 1906. Hawaii Sugar Plant. Assoc. Entomol. Bull. 1:408
Perkinsiella pseudomaidis Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Entomol. Bull. 3:136

Features: Body length 4 mm; typical pattern of *Perkinsiella*, broad whitish yellow dorsomedian band runs from vertex to pronotum and narrows to the mesonotum; lateral side of pronotum and mesonotum brownish; propleuron with three short white bands and a white spot; scutellum whitish yellow; eyes brownish silvery; antennae brown-yellow except for dark brown to black apex of segment I and base of II; frons blackish brown with two yellow transverse bands at eye level, genae blackish brown with two yellow spots; clypeus brown with yellow carinae; legs blackish brown with yellow apical median and basal bands in tibia I and II, sides of thorax and abdomen pale dark brown with whitish yellow patches; forewing transparent with distinct dark brown granulations; brown band anterior of cubital cell and just after cross veins present extending concavely but lightly to Cu_1 up to M_3; vertex slightly wider than long; frons 2.28x longer than broad, widest at level of simple eyes; vertex and pronotum together shorter than mesonotum, the latter 1.6x longer than vertex and pronotum; pronotum tricarinate, lateral carina posteriorly curved laterally, not reaching margins; mesonotum tricarinate but very low; pygofer with two relatively short ventral spines, in profile, ventral margin acutely developed; parameres twisted; ventral wall of anal tube bears four spines, dorsal ones longer than ventrals; valvifer VIII of female with inner margin of the base produced upright and vertical forming lobe-like tube extension.

Host plant: *Saccharum officinarum* L. and rice
Economic importance: Low
Distribution: Fiji and Philippines (Luzon Island)

15.4 *Perkinsiella* near *bakeri* Muir, 1916
Plates 3a, 7a, 12b, 19g, 25h, 33d, 40f

Features: Body length 4.5–5.2 mm; generally blackish brown with a broad whitish yellow median longitudinal band running from basal compartment of vertex, pronotum, and tip of scutellum; pronotal band wider than in mesonotum; lateral margins of pronotum and mesonotum dark brown, propleuron with three transverse white bands and a spot; meso- and metapleuron with more whitish areas than other species; eyes blackish red to dark brown; frons with a broad tranverse yellowish white band on apical half extended laterally to genae, edge of pronotum, and pleuron; subapex of frons with transverse brown line extended to genae, dark brown in basal half; clypeus brownish yellow aligned to the blackish brown band on midcoxa I; antennae brownish black with yellow ventral line and black apex of segment I, segment II with a yellow spot subbasofrontally; femora I and II with alternating whitish yellow and dark brown longitudinal bands; tibia I and II with a basal and subapical blackish brown band; all tarsi black; leg III with brown markings on laterals and apex of femur, base, and apex of tibia near the spines; spur brown but whitish yellow before the spines; forewings granulated, transparent except for brown marking on apical one-third after the cross veins, apices of cells between Sc to half of $R_2 + M_{1+2}$ transparent; vertex shortly protruded in front of large eyes, 1.26x wider than long at widest point, submedian carina fused down to frons, each cell of basal compartment slightly wider than long; vertex and pronotum together shorter than mesonotum, the latter 1.36x longer than combined length of vertex and pronotum; lateral carina of pronotum sinuate, curved laterally not reaching hind margins; mesonotum tricarinate as in pronotum, median carina forked toward scutellum; frons at widest point 1.85x longer than wide across level of ocelli; lateral carina parallel-sided anteriorly, convex medially, and narrowed apically; median carina forked almost at level of ocelli; pygofer obovate, medioventral area V-shaped with a pair of outwardly projected processes, ventrolateral margins strongly concave laterally; parameres relatively short and broad, apex with three small processes, inner one projected inward laterally, apical one slightly diverging, longest outer one curved caudad; anal segment with a pair of ventrally located processes, parallel to one another, projected caudally.

Host plant: Rice
Economic importance: Low
Distibution: Philippines (Luzon Island and Panay Island)

15.5 *Perkinsiella saccharicida* Kirkaldy, 1903
Plates 3b, 7b, 12c, 16f, 19h, 23g, 25i, 28i, 33e, 37i-j, 40g

Perkinsiella saccharicida Kirkaldy, 1903. Entomologist 36:179
Perkinsiella saccharicida Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Entomol. Bull. :137
Perkinsiella saccharicida Muir, 1910. Hawaii Sugar Plant. Assoc. Entomol. Bull. 9:5
Perkinsiella saccharicida Kirkaldy, 1910. Faun. Hawaii 2:578
Perkinsiella saccharicida Melichar, 1913. Notes Leyd. Mus. 36:111
Perkinsiella saccharicida Matsumura, 1917. Appl. Ent. Form. Ser. 378
Perkinsiella saccharicida Singh-Pruthi. 1925. Trans. Entomol. Soc. London (1925):228
Perkinsiella saccharicida Gater et Corbett, 1926. Fed. Malay. State Straits Settlm. Bull. 8:5
Perkinsiella saccharicida Matsumura, 1932. Dainippon Gaichu Zusetsu 228
Perkinsiella saccharicida Esaki & Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 45
Perkinsiella saccharicida Matsumura et Ishi, 1945. Mushi 16:73
Perkinsiella saccharicida Fennah, 1965. Bull. Brit. Mus. (Nat. Hist.) 17(1):17

***Features*:** Body length 4.8–5.2 mm; dull yellowish brown except for blackish red eyes, transparent wings with brown granulation, basal margins of forewings, and pterostigma marked brown in midapical area of forewings in males; frons brown in basal half, whitish yellow in apical half with brown diamond-like spots close to the fronto-clypeal suture and genae; basal half of frons lined with three pairs of yellow spots arranged longitudinally to vertex and four transversely above ocelli level; clypeus chocolate brown parallel to the band on midcoxa I; antennae yellow except for brown ring on apex and ventral band of segment I; femora I-III with alternating yellow and brown longitudinal stripes; side of thorax with round brown spot in metapleuron; vertex only slightly protruded in front of eyes, 1.14x wider than long, basal compartment as long as broad; vertex and pronotum combined shorter than mesonotum, the latter 1.62x longer than two taken together; pronotum and mesonotum tricarinate; lateral carinae of pronotum curved laterad posteriorly, not reaching hind margin; forewings extended beyond abdominal tip by 1.27x length of abdomen; venter of abdomen of female white except for brown ovipositor sheath and lateral margins of sternites; pygofer ovate, medioventral area without a concavity, base of parameres with a pair of widely separated spines; parameres short and subtruncate apically; anal segment has a pair of upwardly projecting spines.

Host plant: Rice, *Saccharum officinarum* (L.), *Zea mays* (L.)
Economic importance: Low
Distribution: Australia, Fiji, Hawaii, Indonesia, Malaysia, New Guinea, Philippines, and South Africa

15.6 *Perkinsiella graminicida* Kirkaldy, 1906
Plates 3c, 7c, 12d, 19i, 25l, 33f, 37k-l

Perkinsiella graminicida Kirkaldy, 1906. Hawaii Sugar Plant. Assoc. Entomol. Bull. 1:406
Perkinsiella graminicida Kirkaldy, 1907. Ibid. 3(1):137
Perkinsiella graminicida Muir, 1910. Ibid. 9:5

Features: Similar to *P. saccharicida* except for brownish apical one-half of frons below the Y-median band and along the frontoclypeal margin; basal half of frons with indistinct white spots; genae dull brown; clypeus and antennae brown to yellowish brown, apex of antennal segment II with black ring; vertex at its greatest width 1.35x wider than long; vertex and pronotum combined shorter than mesonotum, the latter 1.4x longer than vertex and pronotum; pronotum and mesonotum tricarinate; lateral carinae of pronotum curved laterad posteriorly, not reaching hind margin; forewings extended beyond tip of abdomen by 1.35x length of abdomen; forewings with thicker granulations, apical third with a convex brown band from crossveins Cu_1 to M_3; pygofer brownish red, medioventral area with a pair of short subparallel spines; parameres with large contiguous black and rough base, U-shape in profile, with brown apical half forming two spines at right angles, outer one subapical and projected laterally, other one directed upward; anal segment with two long curved spines from the ventral side of the tube; aedeagus quite small.

Host plant: Rice
Economic importance: Low
Distribution: Fiji and Philippines (Luzon Island)

16. Genus *PEREGRINUS* Kirkaldy, 1904

Peregrinus Kirkaldy, 1904. Entomologist 37:175
Type species: *Delphax maidis* Ashmead, 1890

Dicranotropis Van Duzee, 1897. Bull. Buffalo Soc. Nat. Sci. 5:228
Peregrinus Kirkaldy, 1904. Entomologist 37:175
Peregrinus Crawford, 1914. Proc. U.S. Mus. 46:593
Peregrinus Muir, 1915. Canad. Entomol. 47:299
Peregrinus Muir & Giffard, 1924. Hawaii Sugar Plant. Assoc. Entomol. Bull. 15:11
Peregrinus Osborn, 1935. New York Acad. Sci. 14:234, 240.
Peregrinus Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 39
Peregrinus Matsumura et Ishihara, 1945. Mushi 16:71
Peregrinus Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:79
Peregrinus Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:44
Peregrinus Fennah, 1956. Insects of Micronesia 6(3):109
Peregrinus Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):18
Peregrinus Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 70

Generic features: Body length 3.7–5 mm; light brown to yellow-brown; frons, genae, clypeus, antennal segment I, and laterals of pronotum and mesonotum darker in shape; forewings subhyaline, tinged brown; vertex almost as long as wide, slightly converging toward truncate apex, mediolateral carina convergent apically but distinctly not uniting on vertex, continued on to frons where carinae unite slightly at midlength, U-shaped median carina visible; frons relatively wide, its length 2x the width at midlength, its broadest point; clypeus base clearly wider than apex of frons; antennae comparatively long, protruding from base of face, segment I much longer than half of the second; pronotum almost as long as vertex, much broader than vertex, including eyes, tricarinate, lateral ones converging curved posteriorly and entirely reaching the hind margin; scutellum large, much longer than vertex and pronotum combined; legs simple, hind basitarsus longer than the other two margins; pygofer ovoid with truncate anterior end, small anal segment, parameres converging apically.

16.1 *Peregrinus maidis* (Ashmead, 1890)
Plates 3d, 7d, 12e, 16g, 19j, 23b, 25k, 28j, 33g-h, 38a-b, 40h

Delphax maidis Ashmead, 1890. Psyche 5:323
D. psylloides Lethierry, 1896. Ind. Mus. Notes 3:106
Dicranotropis maidis Van Duzee, 1897. Bull. Buffalo Soc. Nat. Sci. 5:240
Liburnia psylloides Melichar, 1903. Hom. Faun. V. Ceylon 104
Peregrinus maidis Kirkaldy, 1904. Entomologist 37:176
Pundaluoya simplicia Distant, 1906. Faun. Brit. Ind. Rhynch. 3:468
Liburnia psylloides Distant, 1906. Ibid. 484
Peregrinus maidis Distant, 1907. Ann. Soc. Entomol. Belg. 51:221
P. m. Van Duzee, 1909. Bull. Buffalo Soc. Nat. Sci. 9:197
P. m. Kirkaldy, 1910. Faun. Hawaii 2:577
Pandaluoya simplicia Melichar, 1913. Notes Leyd. Mus. 36:109
Liburnia psylloides Melichar, 1913. Ibid. 111
Peregrinus maidis Melichar, 1913. Ibid. 111
Dicranotropis maidis Crawford, 1914. Proc. U.S. Mus. 46:595
Peregrinus maidis Metcalf, 1915. J. Elisha Mitsch. Soc. 31:12
P. m. Van Duzee, 1917. Cat. Hem. Am. 769
P. m. Giffard, 1922. Proc. Hawaii Entomol. Soc. 5:109, 110, 116, 118
P. m. Muir, 1926. Ann. Mag. Nat. Hist. Ser. 9 :17, 80
P. m. Dammerman, 1929. Agric. Zool. Malay Archipel. 235
P. m. Esaki, 1940. Bot. Zool. 8:276
P. m. Swezey, 1940. Hawaii Plant. Rec. 44:158
P. m. Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 39
P. m. Matsumura et Ishihara, 1945. Mushi 16:71
P. m. Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:44.
P. m. Fennah, 1956. Insects of Micronesia 6(3):109
P. m. Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):18
P. m. Fennah, 1978. Ann. Zool. (Wars.) 34(9):223
P. m. Wilson & Claridge. 1991. CAB Intern. & Nat. Resources Inst. 70

Features: Body length 3.7–5 mm; light yellow-brown to yellow-orange in some specimens, mesonotum with a pair of orange longitudinal bands between the white median and yellow-brown lateral carina, with transparent ungranulated wings banded brown on apical one-third radiating from apex of cubital cell to longitudinal vein Cu, M_3, M_2, M_1, and R_2 and Sc_1 but shaded areas form four white spots, one each between Cu_1 and M_3 and M_1 and M_2 and two between M_2 and M_3; pterostigma present; abdomen including pygofer dark brown to dark reddish brown; femora yellow-brown, tibiae yellowish; vertex truncate anteriorly, 1.25x wider than long basally, the broadest part; basal compartment with each cell as long as wide, both cells deeply concave; frons, clypeus, and genae yellow-brown with lateral carinae thinly black; ocelli black; frons at widest point at level of Y-median carina, 1.8x longer than wide; median carina forked nearly at midlength, boldly higher than lateral carinae, carinae with sharp edges; clypeus tricarinate similar to frons; vertex and pronotum combined length shorter than mesonotum, the latter 1.47x longer than the two together; lateral carinae of pronotum slightly convex posteriorly, not reaching hind margin; mesonotum's median carina fades in the base of scutellum; lateral carinae widen posteriorly and narrow anteriorly; segment I of antennae shorter than II, apex with black ring band; II about 1.85x longer than I, base black, narrower than apex, with apical one-third black; overall antennae reach a little beyond the frontoclypeal suture; forewings beyond abdominal tip by as long as total length of mesonotum to tip of abdomen; pygofer slightly oblong to rounded; parameres small, bases sunken into deeply concave medioventral area, parallel basally, the apical one-third curved out and bent inward, truncated to slightly cleft apices face each other; anal style short and relatively small.

Host plant: Maize, sorghum, sugar cane, *Bronus unicoides, Cynodon dactylon, Rottboellia cochinchinensis,* and occasionally on upland rice
Economic importance: High
Distribution: Cosmotropical species found in Africa, Bangladesh, Cambodia, India, Indonesia, Caroline Island, Hawaii, Laos, Malaysia, Micronesia, North and South America, Palau Island, Philippines, Sri Lanka, Taiwan, and Tahiti

17. Genus *EUIDELLA* Puton, 1886

Euidella Puton, 1886. Cat. Hem. Pal. 72
Type species: *Euidella basilinea* (Germar, 1819)

Euides Fieber, 1866. Verh. Zool-Bot. Ges. Wien. 16: 519 (nom. preocc.)
Euides Sahlberg, 1871. Not. Sallsk. Faun. Fenn. Forh. 12:402
Euides Fieber 1875-76. Rev. Mar. Zool. (1875):373
Euidella Puton, 1886. Cat. Hem. Pal. 72
Euides Melichar, 1896. Cicad. V. Mit.-Gur. 66
Euidella Oshanin, 1908. Verz. Palaark. Hem. 2:308
Euidella Muir, 1915. Can. Entomol. 47:263, 300
Euidella Muir et Giffard, 1924. Hawaii Sugar Plant. Assoc. Entomol. Bull. 25:6, 10

Epunka Matsumura, 1935. Insecta Matsumurana 10:77
Toyoides Matsumura, 1935. Ibid. 78
Epunka Matsumura et Ishihara, 1945. Mushi 16:70
Eudes Ding & Zhang, 1994. China Agric. Sci. Tech. Ser. 50

***Generic features*:** Body length 6–7 mm; head relatively wide, about as wide as pronotum; vertex almost subquadrate or slightly longer than width; carinae fairly distinct except for the fading median carina; mediolateral carina merged with lateral carina before base; eyes moderate in size; face oblong, broadest almost medially, of length 2.5x the largest width, apex slightly narrower than base, mediolongitudinal carina furcate a little strongly to the midline; clypeus oblongate, base slightly wider than apex of frons; antennae very long, protruding apex of frons and almost reaching apex of clypeus, first segment distinctly longer than half of the length of segment II; pronotum shorter than vertex, with lateral carinae fading slightly posterior to the middle, before reaching hind margins; mesonotum relatively large, longer than combined length of vertex and pronotum, tricarinate, with apex moderately acute projecting posteriorly; forewings large, protruding well beyond abdominal tip; legs slender, simple spur thin, tectiform, hind margin with about 30 teeth; hind basitarsus much longer than combined length of second and third segment.

17.1 *Euidella* sp.
Plates 3e, 7e, 12f, 19k, 26a, 33i, 40i

Features: Body length 5 mm; eyes reddish brown similar to abdomen and pygofer; vertex, pronotum, and mesonotum tinged with orange to yellowish markings; frons, genae, clypeus, antennae, and legs yellowish brown; forewings hyaline with light brown band or apical half opposite cubital cell and vein R_1; segment and style yellow; vertex as long as wide, basal compartment deeply concave, 1.33x longer than pronotum; frons with median carina forked above midlength of frons, closer to base, mottled with yellowish white spots, four subapically in between the median carina, two each on the lateral carinae at level of Y-shaped carina and ocelli, a few fading ones at base of frons; genae each with two similar spots; antenna distinctly beyond frontoclypeal suture, almost up to midclypeus; pronotum tricarinate, one-third length of mesonotum, lateral carina curved posteriorlaterally but not reaching hind margin; mesonotum tricarinate, 1.29x longer than combined length of vertex and pronotum; pygofer ovoid, medioventral margin with three equally sized and long thin spines; base of paramere with a flattened part extended caudally, midhalf concave latero-caudally, twisted apically and diverging, forming tip with series of minute spike-like processes; anal segment with a pair of thin and long spines curved inward to the concave area of paramere; aedeagus long and slender with an apically long process curved inward parallel to the aedeagal body.

Host plant: Rice
Economic importance: low
Distribution: Philippines (Luzon Island)

18. Genus *DICRANOTROPIS* Fieber, 1866

Dicranotropis Fieber, 1866. Verh. Zool. Bot. Ges. Wien. 16:521
Type species: *Delphax hamata* Boheman (subsequent designation by Distant, 1906)

Dicranotropis Fieber, 1866. Verh. Zool. Bot. Ges. Wien. 16:521
Dicranotropis Sahlberg, 1871. Not. Sallsk. Faun. Fenn. Forh. 12:469
Dicranotropis Ferrari, 1878. Ann. Mus. Stor. Mat. Genova 18:88
Dicranotropis Edward, 1886. Trans. Entomol. Soc. London 1:92
Dicranotropis Ashmead, 1886. Entomol. Am. 5:27
Dicranotropis Melichar, 1896. Cicad. V. Mit.-Eur. 96
Dicranotropis Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Entomol. Bull. 3:132
Dicranotropis Matsumura, 1917. Appl. Entomol. Form. Ser. 379
Dicranotropis Muir & Giffard, 1924. Hawaii Sugar Plant. Assoc. Entomol. Bull. 15:6, 7.
Dicranotropis Muir, 1927. Insects of Samoa 2:13
Dicranotropis Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 48
Dicranotropis Matsumura et Ishihara, 1945. Mushi 16:67
Dicranotropis Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:70
Dicranotropis Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:43
Dicranotropis Ossiannilsson, 1978. Fauna Entomol. Scand. 7(1):152
Dicranotropis Kuoh, 1983. Econ. Insects Fauna China 27:83
Dicranotropis Yang, 1989. NSC Special Publ. 6:315

Generic features: Body length 2.5–5.3 mm; body mostly light brown, pale dirty brown to gray; vertex as long as wide to longer than wide; frons with or without scattered mottles of light-colored spots; mediolongitudinal carina of frons forked close to the midlength or near to the level of ocelli, but never forked at base of frons; forewing hyaline with or without markings toward the apex; parameres with apices mutant or conspicuously forked; ventral margin of pygofer usually without hooks, some may have hooks on ventral margin of anal tube.

18.1 *Dicranotropis* sp.
Plates 3f, 7f, 12g, 19l, 30f, 33j

Features: Body length 4.2 mm; pale yellowish brown with transparent wings without markings, pale yellow legs with antennae, brown eyes, reddish ocelli, reddish brown pygofer, and yellow anal segment and style; vertex moderately projected in front of the eyes, rounded in front viewed dorsally, 1.2x longer than wide basally, basal compartment concave, each cell about 1.57x longer than broad; vertex longer than pronotum by 1.2x, together with pronotum combined length slightly shorter than or as long as mesonotum; lateral carinae of pronotum curved posteriorlaterally not reaching hind margins; mesonotum tricarinate like pronotum; frons broadest along apical one-fourth; 1.95x longer than wide; pygofer with a widely concave medioventral area; paramere with a basal spur directed latero-outward, flat and slightly convex at midlength, apical one-third thin and projected caudally, in profile, parameres apically

diverging moderately; anal segment with a pair of long and slender ventral processes converging toward tip of aedeagus, then joining parallel to one another reaching base of parameres.

Host plant: Rice
Economic importance: Low
Distribution: Philippines (Luzon Island)

19. Genus *NUMATA* Matsumura, 1935

Numata Matsumura, 1935. Insecta Matsumurana 9:139
Type species: *Stenocranus sacchari* (Matsumura)

*Numat*a Matsumura, 1935. Insecta Matsumurana 9:139
Unkana Matsumura, 1935. Ibid. 10:73
Numata Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 18
Numata Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:35
Numata Fennah, 1978. Ann. Zool. (Wars.) 34(9):222
Numata Kuoh, 1983. Econ. Insects Fauna China 27:77

Generic features: Body length 3.5–5.17 mm, grayish to light reddish brown planthoppers; head across eyes slightly narrower than pronotum; vertex about as long submedially as wide at base, anterior margins transverse, submedian carinae not merging apically; basal compartment wider at base than maximum length about 1.7:1; frons longer than broad at widest midline point about 2.3:1, median carina forked above level of ocelli; postclypeus wider basally than frons apically; rostrum reaching mesotrochanter; ocelli present; antennae cylindrical, bypassing the frontoclypeus suture, basal segment longer than wide, shorter than second about 1:2; pronotum with lateral carinae not reaching hind margin; spinal formula of leg III 5-7-4; tibial spur with 17–35 teeth; anal segment ring-like, lateroapical angle each forming a stout process; pygofer longer ventrally than dorsally, ventrally deeper concave, without medioventral process; phallus large, flat laterally, acute apically, incised subapically in ventral margin; diaphragm short; parameres long and diverging, basally projected caudad then abruptly dorsad.

19.1 *Numata muiri* (Kirkaldy, 1907)
Plates 3g, 7g, 12h, 19m, 26b, 30g, 33k-l, 38c-d

Dicranotropis muiri Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Entomol. Bull. 3:134
Stenocranus sacchari Matsumura, 1910. Schad. U. Nutz. Ins. Zuckerrohr Formosas 16
Dicranotropis muiri Muir, 1916. Hawaii Sugar Plant. Assoc. Div. Entomol. Bull. 13:153
D. m. Muir, 1917. Proc. Hawaii Entomol. Soc. 3:317
Numata sacchari Matsumura, 1935. Insecta Matsumurana 9:139
Unkana sacchari Matsumura, 1935. Ibid. 10:73

Numata sacchari Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 18
N. s. Matsumura et Ishihara, 1945. Mushi 16:70
N. s. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:36
Numata muiri Fennah, 1978. Ann. Zool. (Wars.) 34(9):222
N. m. Yang, 1989. NSC Special Publ. 6:59-61

Features: Body length 4.10–5.17 mm; light yellowish brown with a spherical black spot on each metapleuron; forewing subhyaline with basal end of claval suture, apices of apical veins dark brown and pale to light brown membrane between M_{3+4} and Cu_{1a}; abdomen dark brown; vertex as long submedially as wide as base, narrowed apically than base, submedian carina not merging at apex; Y-shaped carina with weak stem, basal compartment of vertex broader basally than greatest length about 2:1; frons at midline longer than wide by about 2.3:1, subparallel-sided except for narrow base, median carina forked at basal third; clypeus very long, longer than wide at base; antennae extended beyond frontoclypeal suture, basal segment longer than wide, segment II about 2x as long as first; tibial spur with about 30 teeth; forewings longer than widest part about 4:1; pygofer prominently longer ventrally than dorsally, opening wider than long; viewed posteriorly, lateral margins not clearly defined; phallus very large, strongly compressed laterally, reflected cephalad distally bearing two processes, upper one surpassing base and lower one not reaching it; diaphragm very narrow, angulated along dorsal margin, forming a V-shaped area weakly sclerotized; parameres long and narrow, dorsally directed, basally contiguous and apically diverging; anal segment short, ring-like, lateroapical angles separated, each produced ventrad forming a stout spinose process.

Host plant: *Saccharum officinarum* L. and rice
Economic importance: Low
Distribution: China, Japan, Philippines, Taiwan, and Vietnam

20. Genus *NYCHEUMA* Fennah, 1964

Nycheuma Fennah, 1964. Trans. R. Entomol. Soc. Lond. 116(7):145
Type species: *Dicranotropis capensis* Muir

Nycheuma Fennah, 1964. Trans. R. Entomol. Soc. Lond. 116(7):145
Nycheuma Kouh, 1983. Econ. Insects Fauna China 27:31
Nycheuma Yang, 1989. NSC Special Publ. 6:95

Generic features: Body length 2.56–3.40 mm; head slightly wider than or as wide as pronotum; vertex shorter submedially than wide at base about 1:1.2, moderately rounded toward frons, about as broad apically as at base, apical margin transverse with submedian carinae distinct, Y-shaped carina weak, submedian carina not merging apically; frons at midline longer than wide at broadest portion about 2:1, widest at level of simple eyes; lateral margins straight and converging distad beyond this point, median carina forked at base; antennae cylindrical, passing shortly beyond fronto-

clypeal suture, segment I longer than wide, about 2:1, shorter than segment II about 1:2; pronotum tricarinate, lateral margin not reaching hind margin; spinal formula of hindleg 5-7-4; tibial spur with about 20 teeth; anal segment short, lateroapical angles widely separated, each produced ventrad in a spinose process; pygofer dorsally short, long and strongly convex ventrally, posterior opening as long as wide, laterodorsal angle not produced, lateral margins weak, medioventral process present, small to long, sometimes complex; long phallus compressed laterally, reflected cephalad at apex in a flagellum; diaphragm deeply impressed with membranous dorsal margin; parameres simple, narrow, distally tapering, rectangulately or subacutely bent dorsad.

20.1 *Nycheuma cognatum* (Muir, 1917)
Plates 3h, 7h, 12i, 20a, 26c, 33m

Dicranotropis cognata Muir, 1917. Proc. Hawaii Entomol. Soc. 3:317
D. c. Muir, 1921. Ibid. 4:575
D. c. Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:43
D. c. Fennah, 1956. Insects of Micronesia. 6(3):111
Nycheuma cognatum Fennah, 1964. Trans. R. Entomol. Soc. Lond. 117(4):145
N. c. Fennah, 1969. Pacif. Ins. Mongr. 21:37
N. c. Fennah, 1971. Insects of Micronesia 6(9):571
N. c. Fennah, 1973-1975. Entomol. Scand. Suppl. 4:89
N. c. Kuoh, 1993. Econ. Insects Fauna China 27:81
N. c. Yang, 1989. NSC Special Publ. 6:96

Features: Body length 2.56–3.26 mm; uniformly brown with subhyaline forewings; vertex slightly shorter submedially than wide at base about 1:1.1, Y-shaped carina relatively distinct, basal compartment of vertex wider basally than widest length about 1.8:1; frons at midline longer than wide at widest point about 1.7:1, widest at level of ocelli; postclypeus wider at base than frons at apex, slightly wider than base, than length in midline; rostrum reaching trochanter III, apical segment shorter than subapical segment; antennae extend beyond midpostclypeus, basal segment longer than wide about 1.7:1, segment II shorter about 1.8:1; tibial spur with about 27 teeth; pygofer with posterior margin strongly produced caudad medially, opening small viewed posteriorly, distinctly wider than long; lateral margin weakly defined, ventral margin shallowly concave, with three distinct medioventral processes, middle the longest; phallus tubular and long, arched slightly upward medially, reflected cephalad at apex in a flagellum on right side, top of flagellum slightly turned mesad then laterad, apically pointed, with a large stout process at middle left, smaller one near apex right; opening of parameres oblongate; parameres slender, blade-like, widely divergent, pointed apically, inner margin straight, outer margin moderately produced lateromedially; anal segment long, collar-like, lateroapical angles very widely apart, each projected caudad and partly mesad in stout spinose processes.

Host plant: Rice
Economic importance: Low
Distribution: Australia, Bonin Island, China, Fiji, New Caledonia, Philippines, Sri Lanka, Taiwan, West Caroline Island

21. Genus *Metropis* Fieber, 1866

Metropis Fieber, 1866, Oshanin. Kat. Palaark. Hemip. 120
Type species: *Metropis mayri* Fieber, 1866

Generic features: Body length 3.3–5 mm; blackish brown to dark reddish brown planthopper with eyes, frons, and genae reddish brown, yellow clypeus and legs; forewings almost uniformly yellowish brown except for transparent subcostal cell and small cubital cell; head visibly rounded in front of eyes, moderately produced in front; vertex distinctly rounded in front viewed dorsally, wider than long by about 1.45 times, anterior and posterior width subequal, basal compartment with each cell as long as wide; submedian carina visible; frons almost subquadrangle, longer than wide at midlength by about 1.12x, Y-median carina not visible toward base and median carina partly erased anteriorly, absent in some species; clypeus lower than frons, median carina absent; ocelli absent; antennae cylindrical, segment 1<11, slightly exceeded the frontoclypeal suture; vertex almost as long as to slightly shorter than pronotum; combined length of vertex and pronotum shorter than mesonotum, the latter only 1.06x longer than vertex and pronotum; forewings beyond abdominal tip by about one-third its length, long, about 4x longer than wide; pygofer ovoid, medioventral margin V-shaped, laterodorsal angle weak; paramere relatively slender, distinctly diverging apex slightly narrowed forming a small outwardly directed hook; aedeagus slender, almost parallel-sided with apical subtriangular spine.

21.1 *Metropis nigrifrons* Kusneaov, 1929
Plates 3i, 8a, 13a, 16h, 20b, 23c, 26d, 38e, 40j

Metropis nigrifrons Kusneaov, 1929. Vien. Entomol. Zeitg. 46(3):167
Stiroma nigrifrons Dlabola, 1966. Acta Entomol. Bohemoslov 63:443
M. nigrifrons Ding & Zang, 1994. China Agric. Sci. Ser. 36

Features: As described above in the generic features, however, the specimens examined have frons rough with transverse striae and median carina distinct, Y-shaped median carina absent; posterior margin of pronotum with a narrow yellow transverse band.

Host plant: Rice
Economic importance: Low
Distribution: China and the Philippines (new record)

22. Genus *SARDIA* Melichar, 1903

Sardia Melichar, 1903. Hom. Fauna v. Ceylon 96
Type species: *Sardia rostrata* Melichar, 1903

Sardia Melichar, 1903. Hom. Fauna v. Ceylon 96
Sardia Distant, 1906. Faun. Brit. Ind. Rhynch. 3:475
Hadeodelphax Kirkaldy, 1906. Hawaii Sugar Plant. Assoc. Entomol. Bull. 1:410
Hadeodelphax Kirkaldy, 1907. Ibid. 3:140
Sardia Muir, 1913. Proc. Hawaii Entomol. Soc. 2:246
Sardia Muir, 1915. Can. Entomol. 47:267, 301
Sardia Distant, 1916. Faun. Brit. Ind. Rhynch. 6:141
Sardia Muir, 1927. Insects of Samoa 2:11
Sardia Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 38
Sardia Matsumura & Ishihara, 1945. Mushi. 16:75
Sardia Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:82
Sardia Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:41
Sardia Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):44
Sardia Yang, 1989. NSC Special Publ. 6:280
Sardia Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 72

Generic features: Body length 3.8–4.5 mm; head prominently narrower than pronotum, strongly produced in front of eyes; vertex medially longer than wide at narrowest point between eyes by as much as 2:1, lateral sides subparallel, apical margin acutely developed medially, submedian carinae uniting on vertex; Y-shaped carina weak; basal compartment narrower basally than greatest length; frons at midline longer than widest part about 3:1; rostrum reaching trochanter III; short antennae cylindrical; ocelli distinct; pronotum with lateral carinae reaching hind margin; spinal formula of leg III 5-7-4; tibial spur with around 20 teeth; pygofer in profile ventrally wider than dorsal, ovoid; parameres simple, inner sides concave to straight; anal segment ring-like, borne medially; aedeagus short and robust.

22.1 *Sardia rostrata* Melichar, 1903
Plates 3j, 8b, 13b, 20c, 23d, 26e, 29a

Sardia rostrata Melichar, 1903. Hom. Fauna v. Ceylon 96
S. r. Schumacher, 1915. Suppl. Entomol. 4:142
S. r. Esaki & Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 38
S. r. Matsumura et Ishihara, 1945. Mushi 16:75
S. r. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:83
S. r. Kuoh, 1983. Econ. Insects Fauna China 27:123
S. r. Yang, 1989. NSC Special Publ. 6:282
S. r. Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 72

Features: Body length 4.3–4.5 mm; black planthopper except for yellowish white antennae, rostrum, femora I and II, tibiae, and tarsi; whitish along leg III, apex of scutellum, and basal two-thirds of hind claval margins; forewings opaque, pale black, whitish to transparent between Sc and another three areas along anterior margins between Sc_2 and R_1, R_1 and Rs, and Rs and M_1, and darker toward tip of clavus; head distinctly narrowed frontally forming a subacute and ridge-like tip; vertex at base and anterior of eyes 2.35x longer than wide; basal compartment with indistinct arm of Y-carina but stem visible; pronotum a little shorter than half length of vertex; combined length of vertex and pronotum longer than mesonotum by about 1.33x; lateral carina of pronotum concave to slightly converging before reaching the hind margin; basal segment of antennae distinctly shorter than segment II; pygofer visibly wider ventrally than dorsally, laterodorsal angle not produced, lateral margins weakly defined; aedeagus short but robust with few subapical teeth; anal segment with lateroapical angles each developed medially into long spinose processes, wide apart, directed ventrad; parameres subparallel, rounded upper area, inner margin slightly concave, basal angle obtuse laterocaudally.

Host plant: Rice
Economic importance: Low
Distribution: China, India, Indonesia, Iran, Philippines, Taiwan, Sri Lanka

23. Genus *PARADELPHACODES* Wagner, 1963

Paradelphacodes Wagner, 1963. Mitt. Hamburg Zool. Mus. 60:169
Type species: *Delphax paludosa* Flor, 1861

Generic features: Body length 2.8–3 mm; pale brown planthopper as reflected in the frons, clypeus, genae, and antennae; forewings hyaline; head moderately projected in front of eyes; vertex as long as wide to slightly longer than wide; basal compartment with each cell a little longer than wide, median carina present; submedian carina united in the frons; frons distinctly longer than wide; widest at midlength, median carina forked closer to base than midlength, lateral carina slightly convex; antennae cylindrical, base of segment I slightly narrower than apex; segment II about 2x longer than segment I and exceeded the frontoclypeal suture; vertex longer than pronotum; combined length of vertex and pronotum shorter than mesonotum, the latter about 1.2x longer than vertex and pronotum; lateral carina of pronotum curved posteriorlaterally, not reaching hind margins; mesonotum tricarinate with subparallel lateral carinae; pygofer ovoid, laterodorsal angle distinct to weakly produced; medioventral margin moderately concave; paramere diverging, with apicolateral tip pointed blunt, inner margins curved; anal segment with a pair of ventral processes, short and acute at tips; aedeagus simple with a ring-like suspensorium.

23.1 *Paradelphacodes paludosa* (Flor, 1861)
Plates 23e, 38f

Delphax paludosa Flor, 1861. Rhynch. Livlands. 2:82
Liburnia paludosa Scott, 1870. Ent. Monthly Mag. 7:75
*Delphacodes kuwahara*i Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:58
Paradelphacodes paludosa Wagner, 1963. Mitt. Hamburg Zool. Mus. 60:169
P. p. Okada, 1977. Food & Fert. Tech. Cen. Asia & Pac. Reg. 15
Kakuna kuwaharai Kuoh & Ding, 1980. Acta Entomol. Sin. 23(4):301
P. paludosa Ding & Zhang, 1994. China Agric. Sci. Tech. Press 59

Features: Body length 2.8–3 mm; body light brown with subhyaline wings, slightly darkened along apical half, veins with coarse granulated areas; vertex longer than wide with fairly wide apex, carinae indistinct except for mediolateral ones relatively visible; frons subparallel-sided, slightly narrowed above eyes, of length about 2.5x the width; antennae relatively long, almost reaching apex of clypeus, segment II slightly less than twice the length of segment I; pronotum slightly shorter than vertex; mesonotum smaller, the length less than vertex and pronotum combined; forewings short, slightly protruding abdominal apex; tibia III with a small spine near base and the other about the middle; basitarsus clearly longer than the other two tarsal segments combined; tibial spur rather thin with only 17 teeth along hind margin; pygofer ovoid except for subtruncate ventral end, widest at midlength; paramere bolo-like, subbasally concave in the inner side, broadens with straight sides apically almost parallel with other lateral sides, apico-inner tip concave to flat and apico-outer one forming a blunt spine; aedeagus bent at midlength with spines lining at apical half in sigmoid pattern; suspensorium ring-like; anal segment with a pair of short acute ventral processes.

Host plant: Unknown
Economic importance: Low
Distribution: China and Japan

24. Genus *HARMALIA* Fennah, 1969

Harmalia Fennah, 1969. Pacif. Ins. Monogr. 21:37
Type species: *Sogata thoracica* Distant, 1916

Harmalia Fennah, 1969. Pacif. Ins. Monogr. 21:37
Harmalia Fennah, 1978. Ann. Zool. (Wars.) 34(9):221
Paracorbulo Tian & Ding, 1980. Entomotaxonomia 2(4):315
Harmalia Kuoh, 1983. Econ. Ins. Fauna China 27:113
Harmalia Yang, 1989. NSC Special Publ. 6:198
Harmalia Wilson and Claridge, 1991. CAB Intern. & Nat. Resources Inst. 66
Harmalia Ding & Zhang, 1994. China Agric. Sci. Tech. Press 80

24.1 *Harmalia anacharsis* Fennah, 1969
Plate 17a, 38g-h

Harmalia anacharsis Fennah, 1964. Pac. Ins. Monogr. 21:38
Harmalia anacharsis Fennah, 1978. Ann. Zool. (Wars.) 34(9):221
Harmalia anacharsis Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 66

Features: Body length 3–3.6 mm; dark to light brown planthopper; pronotum pale dirty white, mesonotum dark reddish brown with white scutellum; forewing uniformly pale brown; head including eyes narrower than pronotum, moderately projected in front of eyes; vertex at widest point longer than wide; slightly longer than pronotum; combined length of vertex and pronotum slightly less than length of mesonotum; pronotum and mesonotum tricarinate; lateral carina of pronotum projected posteriorlaterally but not reaching the hind margins; pygofer longer than wide, oblongate with a long ventral portion, medioventral area somewhat truncate, lateral margins not expanded, somewhat parallel-sided; laterodorsal angle developed; paramere with latero-inner base expandedly truncate in posterior view, apices each bear a setaceous process, extended upward subparallel to one another, apical end forming a long thumb-like inner process and the lower outer one broadly rounded; oval segment rather tube-like with a pair of ventral spines that converge basally and diverge apically; aedeagus in lateral view, long and cylindrical.

Host plant: Rice
Economic importance: Low
Distibution: New Caledonia, Indonesia, Philippines, Sri Lanka, and Vietnam

24.2 Harmalia heitensis (Matsumura & Ishihara, 1945)
Plates 3k, 8c, 13c, 17b, 20d, 23f, 26f, 30h, 38i, 40k

Sogata heitensis Matsumura & Ishihara, 1945. Mushi 16:66
S. h. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:66
Harmalia h. Fennah, 1973-75. Entomol. Scand. Suppl. 4:105
H. h. Fennah, 1978. Ann. Zool. (Wars.) 34(9):15
H. h. Yang, 1989. NSC Special Publ. 6:200-201

Features: Body length 2.13–3.33 mm; body blackish brown; pronotum with posterior half white, carinae of frons and clypeus, proboscis, antennae, and legs brown except for dark brown and light tibiae; forewings brown, granulose, concolorous with veins; vertex as long submedially as wide at base, lateral carinae straight, submedian carina merged on vertex far before apical margin, basal compartment wider at base than greatest length about 1.7:1; frons longer at midline than wide at widest part about 2.5:1, broadest at apical third, lateral carinae distinctly convex below simple eyes; antennae overpass frontoclypeal suture, basal segment longer than wide about 1.6:1, shorter than segment II by about 1:1.9, tibial spur with about 19–21 teeth; forewings about

2.9x longer than wide; pygofer in profile wider dorsally than ventrally, laterodorsal angle strongly produced and reflected, opening wider than viewed posteriorly, lateral margins convex; aedeagus long, tubular without tooth; diaphragm narrow, dorsal margin rounded and small; parameres wide, slightly divergent, outer margin developed medially, inner margin convex, outer angle forms a broad triangulate lobe, inner angle short and acute; anal segment collar-like, lateroapical angles approximate, each produced into a strong spinose process, ventrally directed.

Host rice: Rice
Economic importance: Low
Distribution: Philippiines, Taiwan, and Vietnam

24.3 *Harmalia samesimae* (Matsumura & Ishihara, 1945)
Plate 38j

Unkuna sameshimai Matsumura et Ishihara, 1945. Mushi 16(10):68
Kakuna sameshimai Matsumura et Ishihara, 1945. Mushi 16(10):69
Delphacodes sameshimai Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:54
Harmalia sameshimae (sic) Fennah, 1971. Insects of Micronesia 6(8):582
Harmalia samesimae Okada, 1977. Food & Fert. Tech. Cen. Asia & Pac. Reg. 15
Harmalia sameshimai Yang, 1989. NSC Special Publ. 6:202-203

Features: Body length 3.33 mm; pale brown planthopper with yellowish white pronotum between lateral carinae and posterior margin; dark brown to black frons except carinae, coxae, and abdomen; forewings semihyaline and light brown; vertex at submedian as long as wide at base, at apex slightly narrower than at base, apical margin acutely formed medially, submedian carinae merged apically, basal compartment wider at base than greatest length about 1.5:1, widest apical third; proboscis passed trochanter II; antennae bypassed the frontoclypeal suture, basal segment longer than wide, shorter than second about 1:2; tibial spur with about 19 teeth, very wide, half as wide as long; forewings longer than broadest part about 2.8:1; pygofer in profile rather broad, laterodorsal angle widely formed, opening wider than long viewed posteriorly, lateral margins ill-defined; aedeagus without tooth, tubular; suspensorium acutely rounded dorsally, ring-like in ventral two-thirds; parameres relatively long, slightly sinuate, outer angle with lobe-like process, inner angle with rod-like process and basal angle forms a distinct small process; anal segment collar-shaped, lateroapical angles each forming into a strong spinose process with right corner angulated at base.

Host plant: Unknown
Economic importance: Low
Distribution: Japan, Taiwan, and South Mariana Island

25. Genus *TOYA Distant, 1906*

Toya Distant, 1906. Fauna of India 3:472
Type species: *Toya attenuata* Distant, 1906

Toya Distant, 1906. Fauna of India 3:472
Toya Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):56
Toya Fennah, 1978. Ann. Zool. (Wars.) 34(9):221
Toya Kuoh, 1983. Econ. Insects Fauna China 27:153
Toya Yang, 1989. NSC Special Publ. 6:219
Toya Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 73
Toya Ding & Zhang, 1994. China Agric. Sci. Tech. Press 121

Generic features: Body length 1.13–3.50 mm; pale yellow-brown with dark brown area between carina; forewings hyaline; head narrower than pronotum; vertex as wide as to slightly broad at base than long submedially, apical margin transverse, submedian carinae merge at apex, Y-shaped carina distinct to weak; frons longer at midline than broad, widest part about 2:1; lateral carinae slightly convex; clypeus at base wider than frons at apex; rostrum reaching coxae III; antennae cylindrical, basal segment longer than wide, and shorter than segment II; ocelli distinct; pronotum with lateral carinae not reaching hind margin; tibial spur with around 20 teeth; pygofer with strongly developed laterodorsal angle, directed mesad, lateral margins concave and ventral margin shallowly concave; medioventral process absent; aedeagus short and stout, with or without teeth; parameres moderately long, flattened, and diverging; anal segment deeply sunken in dorsal cavity of pygofer.

25.1 *Toya propinqua* (Fieber, 1866)
Plates 3l, 8d, 13d, 20e, 26g, 30i, 33n-o

Delphax (*Delphacodes*) *propinqua* Fieber, 1866. Verh. Zool. Bot. Ges. Wien. 16:525
Delphax hamulata Kirschbaum, 1868. Cicad. Wiesbadem 38
Liburnia propinqua Fieber, 1875. Rev. Mag. Zool. 79:135
Liburnia propinqua Melichar, 1896. Cicad. V. Mit.-Eur. 79
L. terminalis Van Duzee, 1907. Bull. Buff. Soc. Nat. Sci. 8:49
Delphax propinqua Oshamin, 1908. Verz. Pallark. Hem. 2:317
D. p. Matsumura, 1910. Schad. U. Nutz. Ins. Zuckerrohr Formosas 29
Liburnia tuckeri Van Duzee, 1912. Bull. Buff. Soc. Nat. Sci. 10:506
L. propinqua Matsumura, 1917. Appl. Entomol. Form. Ser. 38
Delphacodes neopropinqua Muir, 1917. Proc. Hawaii Entomol. Soc. 7:335
D. subfusca Muir, 1919. Can. Entomol. 51:38
Liburnia (*Delphax*) *propinqua* Matsumura, 1920. Dainippon Gaichu Zencho 263
Delphacodes propinqua Wolcott, 1923. J. Dept. Agric. Puerto Rico 8:111
Liburnia p. Matsumura, 1932. Dainippon Gaichu Zusetsu 224
Liburnia albicallis Haupt, 1935, nec Motschulsky, 1863. Tiewelt Mittoleuropas 4(3):44
Delphacodes propinqua Esaki et Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 33

D. p. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:52
Delphacodes shirozui Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:53
Calligypona propinqua Wagner, 1954. Bull. Soc. Faud ler Entomol. Kairo 38:217
D. propinqua Fennah, 1956. Insects of Micronesia 6(3):122
Metadelphax propinqua Wagner, 1963. Mitt. Hamburg Zool. Mus. Inst. 60:70
Toya propinqua Fennah, 1964. Trans. R. Entomol. Soc. Lond. II6(7):142
Toya propinqua Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):56
T. p. Fennah, 1971. Insects of Micronesia 6(8):581
T. p. Fennah, 1973-75. Entomol. Scand. Suppl. 4:115
T. p. Yang, 1989. NSC Special Publ. 6:219-223
T. p. Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 73
T. p. Ding & Zhang, 1994. China Agric. Sci. Tech. Press 122-123

Features: Body length 1.13–1.34 mm (brachypterous form); 2.87–3.40 mm (macropterous form); pale yellowish brown with brownish frons and darker stripes along both sides of carinae; forewings hyaline; abdomen dark brown, including pygofer with whitish laterodorsal projection; vertex almost as long submedially as with whitish laterodorsal projection; vertex almost as long submedially as wide at base, obtusely rounded toward frons at apex as wide as at base, basal compartment wider basally than greatest length about 2:1; frons longer at midhalf than wide at widest part by about 2:1, broadest at midlength, apically wider than at base, lateral carinae convex; clypeus slightly wider at base than frons at apex, shorter than wide at base; antennae reaching midclypeus, segment I longer than wide about 1.6:1, shorter than segment II about 1:1.8; tibial spur with 14–18 short and weak teeth; pygofer with laterodorsal angle strongly developed, as long dorsally as ventrally, opening wider than long in posterior view; aedeagus relatively short, armed with six distinct teeth dorsally, sometimes 2–6 dorsally and 0–5 ventrally; parameres moderately long and wide, strongly divergent, inner margin shallowly concave, inner angle slightly formed mesad, outer angle slightly produced obtusely lateral, apex truncate, in lateroventral view basal production apically rounded; anal segment with lateroapical angles narrowly apart, each projected ventrally into a long spinose process, directed ventrocaudal and slightly laterad.

Host plant: rice, *Saccharum officinarum*, *Setaria* sp., and *Echinochloa crus-galli*
Economic importance: Low
Distribution: Widespread and had been reported in Africa, Americas, Australia, Cambodia, China, Japan, India, Laos, Philippines, Taiwan, Vietnam, Western Micronesia, Malaysia, Sri Lanka, Pakistan, and Europe

26. Genus *EUIDELLANA* Metcalf

Euidellana Metcalf, 1950. B. P. Bishop Mus. Occ. Pap. 20(5):61
Type species: *Euidellana carolinensis* Metcalf, 1950

Euidellana Metcalf, 1950. B. P. Bishop Mus. Occ. Pap. 20(5):61
Euidellana Fennah, 1978. Ann. Zool. (Wars.) 34(9):220
Euidellana Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 72

Generic features: Body length 3.4–4.3 mm; brown-bodied planthopper with hyaline wings; head including eyes wider than pronotum about 1.09x; vertex slightly projected in front of eyes; wider at base than long about 1.3:1, apical margin truncate, submedian carina slightly prominent uniting at base of frons; Y-shaped carina distinct, stem feeble; frons broader apically than base about 1.33:1, longer than wide by 2.75x at widest subapical point, lateral carinae subparallel apically, narrowed basally, fork of median carinae almost at level of ocelli; vertex longer than pronotum by 1.19x; mesonotum 1.14x longer than combined length of vertex and pronotum; clypeus wider at base than apex of frons, median carina very prominent, somewhat sharp; rostrum reaching trochanter III; antennae both cylindrical, segment I shorter than II, the latter about 2.2x longer than the first; pronotum with lateral carinae not reaching hind margin; tibial spur with 26–29 teeth; pygofer oblongately narrow, viewed caudally, opening longer than wide, venter strongly rounded; anal segment distinctly sunken in apex of pygofer; parameres simple, subparallel to slightly converging apically, apices blunt.

26.1 *Euidellana celadon* Fennah, 1975
Plates 4a, 8e, 13e, 20f, 26h, 30j, 34a, 40l

Euidellana celadon Fennah, 1975. Entomol. Scand. Suppl. 4:89
E. c. Fennah, 1978. Ann. Zool. (Wars.) 34(9):220
E. c. Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 72

Features: Body length 3.4–4.3 mm; pale brown-bodied planthopper with uniformly transparent wings except for light brownish veins and granulations, head including eyes wider than pronotum about 1.09x; vertex slightly projected in front of eyes; wider at base than long about 1.3:1, apical margin truncate, submedian carina slightly prominent uniting at base of frons; Y-shaped carina distinct, stem feeble; frons broader apically than base about 1.3:1, longer than wide by 2.75x at widest subapical point, lateral carinae subparallel apically, narrowed basally, fork of median carinae almost at level of ocelli; vertex longer than pronotum by 1.19x; mesonotum 1.14x longer than combined length of vertex and pronotum; clypeus wider at base than apex of frons, median carina very prominent, somewhat sharp; rostrum reaching trochanter III; antennae both cylindrical, segment I shorter than II, the latter about 2.2x longer than the first; pronotum with lateral carinae not reaching hind margin; tibial spur with 26–29 teeth; pygofer oblongately narrow, viewed caudally opening longer than wide, venter strongly rounded; anal segment distinctly sunken in apex of pygofer;

parameres simple, subparallel to slightly converging apically, apices blunt; aedeagus with a short spinose process ventrally on left subapically, directed lateroventrally; tip forming two spines viewed laterally.

Host plant: rice
Economic importance: low
Distribution: Bangladesh, India, Philippines, Sri Lanka, and Vietnam

27. Genus *CEMUS* Fennah, 1964

Cemus Fennah, 1964. Trans. R. Entomol. Soc. Lond. 116(7):147
Type species: *Cemus leviculus* Fennah, 1964

Cemus Fennah, 1964. Trans. R. Entomol. Soc. Lond. 116(7):147
Cemus Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):19
Cemus Fennah, 1978. Ann. Zool. (Wars.) 34(9): 227
Cemus Kuoh, 1983. Econ. Insects Fauna China 27:63
Cemus Yang, 1989. NSC Special Publ. 6:123
Cemus Wilson & Claridge, 1991. CAB Intern. and Nat. Resources Inst. 70
Cemus Ding & Zhang, 1994. China Agric. Sci. Tech. Press 42

Generic features: Body length 1.60–4.03 mm; pale brown to dark brown, wings subhyaline with C-shaped brown band on apical areas; head including eyes narrower than pronotum; vertex submedially shorter than wide at base, widely and obtusely rounding into frons, submedian carinae not merged apically; Y-shaped carina visible, basal compartment wider basally than greatest length about 2.5:1; frons at midline longer than broad at widest part about 1.8:1, broadest at level of simple eyes; median carina bifurcate at level of ocelli; clypeus at base slightly wider than frons at apex, about as long at middle as wide at base; rostrum extended to trochanter III, apical segment as long as subapical; antennae almost reaching apex of postclypeus, segment I longer than wide more than 2:1, segment III longer than I, ocelli distinct, very close to anterior margin of genae; pronotum with lateral carinae not reaching hind margin; fore and middle femora and tibiae somewhat compressed; spinal formula of leg III 5-7-4; tibial spur with about 30 teeth; pygofer distinctly long and strongly convex ventrally, rather short dorsally, posterior opening relatively small, prominently longer than wide, weakly developed laterodorsal angle, strongly inflected, medioventral process short, quadrate, and wider than long; anal segment distinctly ring-like, lateroapical angles each projected ventrally forming a slender spinose process; parameres simple, short to narrow, often tapering distally to acute apex, dorsally projected, slightly diverging viewed posteriorly; aedeagus long, somewhat distally decurved, bearing a long flagellum borne at apex, directed cephalad.

27.1 *Cemus sauteri* (Muir, 1917)
Plates 4b, 8f, 13f, 20g, 26i, 29b, 31a, 34b

Phyllodinus sauteri Muir, 1917. Proc. Hawaii Entomol. Soc. 3:319
P. s. Esaki & Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 44
P. s. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:76
P. s. Fennah, 1950. Bernice P. Bishop Mus. Bull. 202:44
Cemus sauteri Fennah, 1964. Trans. R. Entomol. Soc. Lond. 116(7):147
C. s. Fennah, 1973-1975. Entomol. Scand. Suppl. 4:87
C. s. Fennah, 1978. Ann. Zool. (Wars.) 34(9):21
C. s. Yang, 1989. NSC Special Publ. 6:127

Features: Body length 1.66–2.50 mm (brachypterous), 3.16–3.86 mm (macropterous); black planthopper with yellowish brown head, thorax; spots on frons, base, and apex of tibiae, tibial spur, and second segment of metatarsi; antennae with black segment I, dorsally with elongate oval yellowish band, segment II dark brown, lateral lobes of pronotum and tegulae creamy white; forewings hyaline, black tinge from node to anal angle then submarginally to apex of tegmen, end of Sc, along both sides of R_1, Rs, and end of clavus, granulose black; pygofer black with cresentric whitish yellow band on each lateral side of genital opening; vertex shorter than broad at base, broadly and obtusely rounded toward frons; basal compartment wider, greatest length about 3:1; submedian carinae meeting on frons; at middle frons longer than wide at broadest point about 1.8:1, widest just above ocelli level, straight lateral margins below level of simple eyes; segment I of antennae longer than wide, shorter than II about 1:1.7; tibial spur with 21–24 teeth; forewings longer than broadest part about 3:1; pygofer distinctly longer ventrally than dorsally in profile, laterodorsal angle narrowly developed caudally, opening quite small, longer than wide; aedeagus long, dorsally curved with broad flagellum borne subapically, directed dorsad and cephalad, at midlength with a hooked process emanating at left side, projected mesad, a long process formed at right side, parallel with aedeagus; parameres slender, slightly diverging, apical third of outer margin with a large obtuse process, strongly sinuate viewed laterally; anal segment with lateroapical angles each formed into a strong short spinose process, projected ventrally.

Host plant: Rice
Economic importance: Low
Distribution: Philippines (new record), Fiji, Sri Lanka, Taiwan, and Vietnam

27.2 *Cemus nigromaculosus* (Muir, 1917)
Plates 4c, 8g, 13g, 20h, 26j, 31b, 34c, 40m

Phyllodinus nigromaculosus Muir, 1917. Proc. Hawaii Entomol. Soc. 3:319
P. n. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:76
P. n. Fennah, 1956. Insects of Micronesia 6(3):111
Cemus nigromaculosus Fennah 1964. Trans. R. Entomol. Soc. Lond. 116(7):148
C. m. Fennah, 1971. Insects of Micronesia 6(8):572
C. m. Yang, 1989. NSC Special Publ. 6:135-136

Features: Body length 2–2.7 mm; dark brown planthopper except for light brown to yellowish lateral areas of pronotum, carinae of head and thorax, segment II of antenna, spots on frons, anterior and posterior ends of femora and tibiae, hind tarsi and along hind tibiae, base of abdomen and anal tube; forewings hyaline, light yellowish brown, fuscous toward apical area, veins white with distinct black granules, each bearing a whitish yellow hair; head as wide as long close to midlength; antennae surpass middle of clypeus to slightly beyond, segment I shorter than II, the latter slightly clavate; femora and tibiae of legs I and II clearly compressed moderately, forewings not much protruded beyond abdominal tip, just reach pygofer; pygofer short viewed dorsally, ventrally long, opening longer than broad; medioventral margin with a small quadrate thin lip; anal segment large with a pair of long curved spines; parameres with slightly wide base, slender and thin becoming acute toward apex, knife-like in lateral view, slightly sinuate; aedeagus complex, basally thin, apex forming a large barb with corners directed basad, left side with a curved spine, right side with a longer and slender spine and a shorter one near base.

Host plant: Rice
Economic importance: Low
Distribution: Fiji, Japan, Philippines, New Guinea, New Caledonia, Taiwan, Tonga, and West Micronesia

27.3 *Cemus changchias* Kuoh, 1981
Plates 4d, 8h, 13h, 20i ,26k, 34d

Cemus changchias Kuoh, 1981. Acta Entomol. Sin. 24(4):422
C.c. Kuoh, 1983. Econ. Insects Fauna China 27:66
C.c. Yang, 1989. NSC Special Publ. 6:133-134

Features: Body length 4–4.4 mm; uniformly pale brown, darker on genae; intercarinal areas of frons mottled with yellowish spots; forewings hyaline, marked black from anterior margin along nodal line to posterior apical half margin, along R_1 and Rs, below Cu_1 and a short diagonal stripe at base; vertex wider at base than long submedially about 1.4:1; apical margin transverse, lateral carinae concave, submedian carinae not merging apically; basal compartment wider at base than longer part about 2.5:1; frons

at midlength longer than wide at broadest part about 1.8:1 at ocelli level; median carina bifurcate at level of simple eyes; basally clypeus as wide as apex of frons; basal segment of antenna longer than broad by about 2:1; shorter than segment II about 1:1.7; tibial spur with 27–32 teeth; forewings 3x longer than greatest width; pygofer roundish to slightly ovoid, in profile about as wide ventrally as dorsally, opening as long as wide viewed posteriorly, medioventral process broad and slightly cleft medially; aedeagus tubular, reflected cephalad in two processes apically, left side lobe-like, apex curved left, right one directed right then cephalad, outer margin medially with a small blunt structure; suspensorium Y-shaped with short arms; parameres rather short, gradually diverging at apex, outer margins strongly concave at midlength; anal segment deeply embedded in pygofer, lateroapical angles each form a long spinose process extended to base of parameres.

Host plant: Rice
Economic importance: Low
Distribution: China, Philippines (new record), and Taiwan

27.4 *Cemus* sp. A
Plates 4e, 9a, 13i, 20j, 26l, 31c, 34e, 40n

Features: Body length 3.8–4.0 mm; generally brown but darker in the lateral sides of pronotum and mesonotum; light brown wings with transparent areas toward apical margins; granulations brown with white hairs; head including eye slightly wider than the pronotum; vertex at base 1.35x wider than long, submedian carina not united in front of vertex; basal compartment visibly deep and each lobe-like, wider basally than long; pronotum at median point shorter than vertex; mesonotum at median line 1.33x longer than combined length of vertex and pronotum; frons 2.05x longer than wide at broadest part at level of ocelli and junction of median Y-carina; frons with two pairs of yellowish spots at apical one-half; similar to *C. changchias* Kuoh except for differently structured pygofer, parameres, and process on anal segment; in particular the lateroapical angle not produced; lateral margins of pygofer constricted at midlength, thin and whitish yellow, brown medioventral process thin, broad, and evenly emarginated; parameres moderately constricted in outer midlength; anal segment with thick and brown margins and short, brown style, the pair of processes long and thin curved outward after tip of parameres, then curved downward subcoiling bases of parameres toward the inside.

Host plant: Rice
Economic importance: Low
Distribution: Philippines (Luzon Island and Leyte Island)

27.5 *Cemus* sp. B
Plates 4f, 9b, 14a, 20k, 27a, 31d, 40o

Features: Body length 3.8 mm; similar to *Cemus* sp. A but basal compartment of vertex and midanterior one-third of pronotum and midposterior mesonotum with yellow-orange tinge; pronotum with hind inner margins of lateral carinae with whitish spots; posterior submedian part of mesonotum with a black spot and entire lateral part pale brown; head narrower than pronotum taken across eyes; vertex 1.76x wider than long at base, slightly longer than pronotum; mesonotum twice as long as combined length of vertex and pronotum; frons mottled with 16 whitish yellow spots, 8 spots on each side, 2x longer than wide, widest across level of antennal bases, slightly above ocelli level and bifurcation of median carina; antenna with basal segment shorter than segment II, its base distinctly narrower than apex; spinal formula of hind leg 5-7-4.

Host plant: Rice
Economic importance: Low
Distribution: Philippines (Luzon Island)

28. Genus *OPICONSIVA* Distant, 1917

Opiconsiva Distant, 1917. Trans. Linn. Soc. Lond. Zool. 17:301
Type species: *Opiconsiva fuscovaria* Distant

Opiconsiva Distant, 1917. Trans. Linn. Soc. Lond. Zool. 17:301
Opiconsiva Fennah, 1964. Ibid. 116(7):143
Corbulo Fennah, 1965. Bull. Brit. Mus. Nat. Hist. (Entomol.) 17:48
Opiconsiva Fennah, 1978. Ann. Zool. (Wars.) 34(9):20
Opiconsiva Ding, 1980. Econ. Insects Fauna China 27:130
Opiconsiva Yang, 1989. NSC Special Publ. 6:214
Opiconsiva Wilson and Claridge, 1991. CAB Intern. & Nat. Resources Inst. 73
Opiconsiva Ding & Zhang, 1994. China Agric. Sci. Tech. Press 78

Generic features: Head including eyes wider than pronotum; vertex slightly longer submedially than wide at base, about as wide at apex as at base, apical margin truncate, Y-shaped carina distinct or with its stem feeble, submedian carinae merged at apex or extreme base of frons; frons longer at midline than wide at broadest part about 2:1, widest near middle; proboscis passed the trochanter II; ocelli present; antennae cylindrical with segment I slightly longer than wide; pronotum with lateral carinae not reaching the hind margin; spinal fomula of leg III 5-7-4; tibial spur with about 20 teeth; pygofer in profile moderately short, opening longer than wide viewed posteriorly; phallus tubular, dorsobasal half thickened; suspensorium ringlike; diaphragm with dorsal margin produced dorsad medially; anal segment small but ringlike as well, sometimes collarlike, lateroapical angles each produced into a spinose process; parameres short.

28.1 *Opiconsiva dodona* (Fennah, 1965)
Plates 17c, 23g, 39a

Corbulo dodona Fennah, 1965. Bull. Brit. Mus. Nat. Hist. Entomol. 17:48
Opiconsiva dodona Fennah, 1978. Ann. Zool. (Wars.) 34 (9):220

Features: Body length 2.85–3.6 mm; pale brown to grayish brown planthopper except for pallid yellow to dirty white vertex, disc and hind margin of pronotum, carinae of frons and clypeus, basal segment of rostrum, ventrites at posterolateral angles and dorsal angles of pygofer; apical segment of proboscis, legs, and antennae reddish brown; forewings hyaline with very dilate fuscous tinge, veins reddish brown, a linear spot between common claval vein and commissural margin dark gray-brown; vertex as long medially as broad at base or slightly longer than wide; subrectangularly obtuse rounding into frons, somewhat narrower at apex than at base, lateral margins straight, apical margin truncate with moderately distinct submedian carinae similar to Y-shaped carinae; submedian carina merged at apex of vertex; basal compartment of vertex wider at hind margin than greatest length; frons at midline longer than wide at widest part 2.2:1, broadest at two-thirds from base, lateral margins shallowly convex, median carina simple; clypeus slightly wider than frons at apex; clypeus moderately convex; proboscis passed trochanter II only; antennae slightly pass the frontoclypeal suture, segment II longer than I; ocelli distinct; pronotum slightly longer at midline than broad at anterior margin; lateral carinae weakly concave, not reaching hind margin; mesonotum distinctly longer than scutellum by about 2.4:1; tibial spur with around 19 teeth; pygofer ovoid, wider laterally and strongly convex with medioventral area rather truncate, without any process; parameres basally contiguous, medially concave in inner side, emarginate at apex, inner part smaller than outer part; anal segment with a pair of diverging processes; laterodorsal angle distinct.

Host plant: Rice
Economic importance: Low
Distribution: Australia and the Philippines, may be widespread in the Oriental region

29. Genus *LAODELPHAX* Fennah, 1963

Laodelphax Fennah, 1963. Proc. R. Entomol. Soc. Lond. (B) 32:15
Type species: *Delphax striatella* Fallen

Laodelphax Fennah, 1963. Proc. R. Entomol. Soc. Lond. (B) 32:15
Callidelphax Wagner, 1963. Mitt. Hamburg Zool. Inst. 60:167
Laodelphax Kuoh, 1983. Econ. Insects Fauna China 27:147
Laodelphax Yang, 1989. NSC Special Publ. 6:216
Laodelphax Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 66
Laodelphax Ding & Zhang, 1994. China Agric. Sci. Tech. Press 112

Generic features: Head including eyes narrower than pronotum; vertex quadrate, as long as wide submedially at base, apical margin transverse, lateral carinae straight to parallel to each other, submedian carinae not merged at apex, Y-shaped carina distinct; basal compartment longer at base than widest length about 1.4:1; frons at middle line longer than wide at widest point about 2:1, widest below level of ocelli; clypeus as wide at base as frons at apex; proboscis just passes trochanter II; ocelli present; antennae cylindrical, segment I longer than wide, shorter than segment II about 1:1.9; pronotum with lateral carinae not reaching hind margin; spinal formula of leg III 5-7-4; tibial spur with about 17 teeth; pygofer very short dorsally, longer and convex ventrally in profile, in posterior view, lateral margins strongly produced caudad basally, without medioventral process; phallus tubular, compressed laterally, broad along basal half, pointed apically; suspensorium ringlike with two long arms along dorsal margins, directed dorsocephalad; diaphragm very wide; anal segment ringlike, lateroapical angles each produced into a spinose process; parameres short and simple.

29.1 *Laodelphax striatellus* (Fallen, 1826)
Plates 4g, 14b, 27b, 34f, 40p

Delphax striatellus Fallen, 1826. Hem. Suec. Cicad. 75
Liburnia s. Sahlberg, 1842. Acta Soc. Sci. Fenn. 1:435
Achortile striatella Oshanin, 1870. Mem. Soc. Amis. Sci. Nat. Moscow 6:48
Liburnia striatella lateralis Fieber, 1878. Cicad. d'Europe 4:72
Delphax striatella fimbriata Rey, 1894. Echarge 10:14
Liburnia devastans Matsumura, 1900. Entomol. Nachr. 26:262
L. nipponica Matsumura, 1900. Ibid
L. minomensis Matsumura, 1900. Ibid. 26:263
L. marginata Haupt, 1935. Tier. Mitteleuropas 4(3):142
L. haupti Lindberg, 1936. Comm. Boil. 4(9):17
Delphacodes striatella reyana Metcalf, 1943. Gen. Cat. Hemip. Fasc. IV (3):518
Delphacodes striatella Esaki & Ishihara, 1943. Cat. Araeopid. Imp. Jpn. 31
D. s. Matsumura & Ishihara, 1945. Mushi 16:60
D. s. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:49
Laodelphax striatella Fennah, 1963. Proc. R. Entomol. Soc. Lond. (B)32:15
Callidelphax s. Wagner, 1963. Mitt. Hamburg Zool. Mus. Inst. 60:175

Laodelphax striatellus Nasu, 1967. Major Insect Pests of Rice 493
L. s. Okada, 1977. Food Fert. Tech. Cen. Asia Pac. Reg. 12
L. s Yang, 1989. NSC Special Publ. 6:217
L. s. Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 66
L. s. Ding & Zhang, 1994. China Agric. Sci. Tech. Press 112

Features: Body length 3.33–4 mm; general color black; vertex, carinae of frons, antennae, tip of mesoscutellum, and legs yellowish white; pronotum white with areas behind eyes black; forewings hyaline, yellowish brown, near end of clavus with black markings; vertex as long submedially as wide at base, obtusely rounded toward frons, as wide at apex as at base, lateral carinae straight, submedian carinae not merging at apex of vertex, basal compartment wider at base than greatest length about 1.4:1; frons in middle line longer than wide at widest point about 2.1:1, broadest just below ocelli; lateral carina very slightly convex; clypeus as wide at base as apex of frons, little longer than wide basally; antennae passed the frontoclypeal suture, segment I longer than wide about 1.6:1, shorter than segment II about 1:1.9; tibial spur with 17–20 teeth; forewings longer than widest part about 3.3:1; pygofer in profile distinctly longer ventrally than dorsally, in posterior view with opening wider than long, laterodorsal angle slightly formed mesad; phallus very wide at basal two-fifths, abruptly attenuate apically, apical fifth slender, pointed apically; suspensorium elongate oval, narrowed ventrally, with long arms at dorsal side; diaphragm very broad, median area strongly produced caudad, each midlateral area strongly sclerotized and produced caudad, dorsal margin produced dorsad and apically truncated; anal segment short, lateroapical angles each produced ventrad in a stout process; parameres very short, transverse, outer angles each widely produced laterally.

Host plant: Rice and *Saccharum officinarum* L.
Economic importance: High
Distribution: Taiwan, China, Mongolia, Ryukyu Island, Japan, Micronesia, Philippines, Korea, Siberia, Europe, and former Soviet Union

30. Genus *CORONACELLA* Metcalf, 1950

Coronacella Metcalf, 1950. B. P. Bishop Mus. Occ. Pap. 20(5):59
Type species: *Coronacella bella* Metcalf, 1950

Coronacella Metcalf, 1950. B. P. Bishop Mus. Occ. Pap. 20(5):59
Coronacella Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):47
Coronacella Yang, 1989. NSC Special Publ. 6:313
Coronacella Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 73

30.1 *Coronacella sinhalana* (Kirkaldy, 1906)
Plates 17d, 39b-c

Liburnia frontalis Melichar, 1903. Homop. Faun. v. Ceylon 100
Delphacodes sinhalanus Kirkaldy, 1906. Can. Entomol. 38:156
Delphax puella Kirkaldy, 1907 [nec van Duzee]. Hawaii Sugar Plant Assoc. Div. Entomol. Bull. 3:1
Kelisia kirkaldyi Muir, 1917. Proc. Hawaii Entomol. Soc. 3:329
Coronacella bella Metcalf, 1950. B. P. Bishop Mus. Occ. Pap. 20(5):59
Coronacella sinhalana Fennah, 1973-75. Entomol. Scand. Suppl. 4:108

Features: Body length 2.86–3.26 mm; pitchy black; lateral carina of vertex and frons, median line of pronotum and mesonotum white, segment II of antenna and legs yellowish brown except femora III slightly brownish to dark brown; forewings subhyaline, yellowish brown, near end of clavus with distinct black markings; vertex submedially longer than wide at base about 1.3:1, at apex narrower than at base, lateral carinae slightly convex, Y-shaped carina moderately distinct, submedian carinae merged at apex, basal compartment wider posteriorly than greatest length about 1.2:1; frons at middle line longer than wide at widest point about 2.4:1, widest just below level of ocelli, lateral carina slightly convex, median carina simple; clypeus basally wider than apex of frons, about as wide as long; antennae surpassing frontoclypeal suture, basal segment longer than wide about 1.5:1, shorter than segment II about 1:2; tibial spur with about 18 teeth; pygofer with posterior margin slightly incised near base, laterodorsal angle obtusely rounded, not reflected mesad, opening wider than long in posterior view, lateral margins not very distinct; phallus short, tubular with several teeth dorsally near apex; orifice on lower side near apex; diaphragm broad, dorsal margin evenly convex medially; anal segment long, lateroapical angles closely approximated, each process ventrad in a slender spinose process, slightly projected laterally; parameres short, inner angle strongly projected mesad, inner margin strongly concave at apical half, outer margin almost straight.

Host plant: Rice
Economic importance: low
Distribution: Australia, Fiji, Gilbert Island, Micronesia, Philippines, Taiwan, Sri Lanka, Samoa, Tahiti, New Caledonia, and New Hebrides

31. Genus *NILAPARVATA* Distant, 1906

Nilaparvata Distant, 1906. Fauna Brit. Ind. 3:473
Type species: *Nilaparvata greeni* Distant, 1906

Nilaparvata Distant, 1906. Fauna Brit. Ind. Rhynch. 3:473
Kalpa Distant, 1906. Ibid. 474
Hikona Matsumura, 1935. Insecta Matsumurana 9:139
Nilaparvata Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:67
Nilaparvata Nasu, 1967. Major Insect Pests of Rice Plant 500
Nilaparvata Okada, 1977. Food Fert. Tech. Cen. Asia & Pac. Reg. 2
Nilaparvata Fennah, 1978. Ann. Zool. (Wars.) 34(9):219
Nilaparvata Mochida & Okada, 1979. Int. Rice Res. Newsl. 22
Nilaparvata Yang, 1989. NSC Special Publ. 6:275
Nilaparvata Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 49
Nilaparvata Ding & Zhang, 1994. China Agric. Sci. Tech. Press 82

Generic features: Body length 3.5–4.8 mm; generally brown planthopper; head including eyes narrower than pronotum; vertex slightly longer submedially than wide at base, sometimes subequal, submedian carinae not merged apically, Y-shaped carina distinct; frons longer at midline than wide at widest point about 2.4:1, widest at middle, median carina forked at base, sometimes not; clypeus at base slightly wider than frons at apex; proboscis reaching trochanter II; ocelli present; antennae cylindrical, only a little beyond frontoclypeal suture, with basal segment longer than wide, shorter than segment II about 1:2; pronotum with lateral carinae not reaching hind margin; spinal formula of leg III 5-7-4; first tarsal segment with 1–5 teeth; tibial spur with 15–33 teeth; pygofer longer ventrally than dorsally in profile, laterodorsal angle slightly projected, opening wider than long viewed posteriorly, medioventral process present or absent; phallus shape variable; suspensorium with broad stem, ventral half ring-like; parameres long and complex.

31.1 *Nilaparvata bakeri* (Muir, 1922)
Plates 29c, 39d

Delphacodes bakeri Muir, 1917. Proc. Hawaii Entomol. Soc. 3:336
Nilaparvata bakeri Muir, 1922. Rec. Indian Mus. 24:351
N. b. Muir, 1923. Philipp. J. Sci. 22:158
N. b. Ishihara, 1949. Sci. Rep. Matsuyama Agric. Coll. 2:69
N. b. Okada 1977. Major Insect Pests of Rice 4
N. b. Mochida & Okada, 1979. Intern. Rice Res. Newsl. 24
N. b. Yang, 1989. NSC Special Publ. 6:278
N. b. Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 52
N. b. Ding & Zhang, 1994. China Agric. Sci. Tech. Press 88

Features: Body length 4.26 mm; dark brown to blackish brown; vertex, frons, antennae, and legs paler in color; forewings hyaline, with apex of claval area black; vertex slightly wider at base than long submedially, apical margin transverse, submedian carina not merging apically, basal compartment wider at base than greatest length about 2:1; frons longer than wide at broadest point about 2.4:1, widest at level of ocelli, lateral carinae slightly convex, median carina forked along basal one-fourth; antennae surpassing frontoclypeal suture, with segment I longer than wide about 1.7:1, shorter than segment II about 1:2; tibial spur with about 33 teeth; forewings longer than widest portion about 3.2:1; pygofer with laterodorsal angle strongly projected, hind margin above medioventral process roundish caudally, medioventral process large, broad basally, narrowed at apical one-half in profile; opening wider than long, lateral margins ill-defined, medioventral process with both sides toothed, attenuating apically, viewed posteriorly; phallus tubular, apical third curved downward, apical half with 5 dorsal teeth, 6 ventrally; orifice terminal, right; suspensorium with broad stem, ventral ring normal; diaphragm broad, dorsal margin evenly incised medially; anal segment small, lateroapical angles separated, each forming into strong but short spinose process; parameres large, inner margin with process medially, pointing ventrally, apical fourth attenuating to apex.

Host plant: *Leersia japonica* Makino and *Leersia hexandra* Swartz.
Economic importance: Low
Distribution: China, Taiwan, Japan, Indonesia, India, Korea, Malaysia, Philippines, Thailand, Sri Lanka

31.2 *Nilaparvata muiri* China, 1925
Plates 29d, 39e

Nilaparvata muiri China, 1925. Ann. Mag. Nat. Hist. 9(16):480
N. m. Okada, 1977. Food Fert. Tech. Cen. Asia Pac. Reg. 4
N. m. Fennah, 1978. Ann. Zool. (Wars.) 34(9):219
N. m. Mochida & Okada, 1979. Int. Rice Res. Newsl. 28
N. m. Ding, 1983. Econ. Insects Fauna China 27:139
N. m. Yang, 1989. NSC Special Publ. 6:280
N. m. Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 52
N. m. Ding & Zhang, 1994. China Agric. Sci. Tech. Press 86

Features: Body length 3.5–3.83 mm; pale yellowish brown with brown abdomen, hyaline wings except black end of clavus; vertex almost as long submedially as wide at base, at apex slightly narrower than at base, submedian carinae not merged at apex, basal compartment wider at base than greatest length 2:1; frons longer in midline than wide at widest portion about 2.2:1; widest at level of ocelli, median carina forked basally; clypeus wider at base than frons at apex; antennae reaching over frontoclypeal suture, segment I longer than wide about 2:1, shorter than segment II about 1:1.5; tibial spur with about 26–30 teeth; forewings longer than widest portion about 3.15:1;

in profile pygofer slightly wider ventrally than dorsally, laterodorsal angle concave, medioventral process simple, distinct with the distinct process at level of base of parameres, in posterior view, opening wider than long; phallus slightly sinuate in dorsal view, dilate at apical half with right side armed with 11 teeth, left with 6, basal left membranous, right side at apex with beak-like process; suspensorium asymmetrical, inverse Y-shaped, left arm directed left, membranous apically; diaphragm somewhat broad, dorsal margin sharply incised medially; anal segment quite small, collar shaped; parameres stout, bifurcate apically, above middle with a short process.

Host plant: Rice and other Graminae such as *Digitaria, Echinochloa, Isachne,* and *Phalaris*
Economic importance: Low
Distribution: China, Japan, Korea, Taiwan, and Vietnam

31. 3 *Nilaparvata albostriata* (Kirkaldy, 1907)
Plates 17e, 39f-g

"*Delphax*" *albostriata* Kirkaldy, 1907. Hawaii Sugar Plant Assoc. Entomol. Bull. 3:154
Nilaparvata albostriata Okada, 1977. Food Fert. Tech. Cen. Asia & Pac. Reg. 3
Nilaparvata albostriata Mochida & Okada, 1979. Int. Rice Res. Newsl. 27

Features: Body length 2.25–2.75 mm; dark grayish brown to blackish, slightly paler on the vertex; eyes castaneous or gray brownish castaneous; antennae, carinae on frons, clypeus, legs all fuscotestaceous; pronotum, posterolateral margins of scutellum, subcostal vein, apical margin of forewings and last two to three abdominal tergites opaque white; carinae all very prominent including those in clypeus; head dorsally longer than wide, produced a little in front; frons broadening curvedly toward the apex but narrowing very slightly at the apical margin; pronotal carinae divergent, not curving under the eyes and not reaching the hind margin; scutellum shorter than pronotum; forewings nearly squarish, extending to about half the length of the abdomen, subtruncate apically and contiguous along the commissure; tibial spur with about 16 well-developed spines; pygofer apically roundish to ovate, the rim thickened about the anal third and forming a short spine; parameres broad, bifid at apex.

Host plant: Unknown
Economic importance: Low
Distribution: Australia, Guam, and New Caledonia

31.4 *Nilaparvata myersi* Muir, 1923
Plate 39h

Nilaparvata myersi Muir, 1923. Trans. New Zealand Inst. 54:258
N. m. Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1): 25
N. m. Okada, 1977. Food Fert. Tech. Cen. Asia & Pac. Reg. 3
N. m. Mochida & Okada, 1979. Int. Rice Res. Newsl. 28

Features: Body length 3.5 mm; generally stramineous but paler along vertex, pronotal disc and mesonotum, abdominal terga V-VII glossy brownish black except in middle line and tergum VIII shiny brownish black only along margins, pygofer castaneous-glossy brownish black except at dorsolateral angles, parameres and diaphragm piceous; vertex longer submedially than broad at base about 1.2:1, subacutely rounded toward frons, distinctly narrower apex of vertex, basal compartment of vertex wider at hind margin than greatest length about 1.5:1, and than median length about 1.7:1; frons in midline longer than wide at widest part about 2:1, broadest at middle, lateral margins shallowly convex, median carina simple or at most forked only at extreme base; clypeus wider at base than frons at apex, disc as broad at base as long; moderately convex in profile; anteclypeus rather strongly convex with entire clypeus in profile strongly interrupted convex or biconvex; antennae moderately surpassing frontoclypeal suture, basal segment longer than broad about 1.7:1, segment II longer than segment I about 1.5:1; ocelli small; pronotum with disc longer in midline than broad at anterior margin almost 1.3:1, lateral carinae concave, diverging laterally but not reaching hind margin; tibial spur with 19 teeth; pygofer moderately long, posterior opening about as broad as long, dorsolateral angles not produced caudad, inflected mesad; diaphragm with dorsal margin feebly convex; medioventral process absent; aedeagus relatively long, straight with about seven teeth along dorsal margin; a long narrow process arising ventrally near middle and extending caudad below main axis of aedeagus and parallel with it; anal segment relatively long, distinctly broad, lateroapical angles wide apart, each forming ventrad in a curved spinose process; parameres moderately long, stout, in posterior view each asymmetrically Y-shaped, strongly formed caudad subbasally; process of inner apical angle strongly curved cephalad.

Host plant: Unknown
Economic importance: Low
Distribution: New Zealand

31.5 *Nilaparvata lugens* (Stål, 1854)
Plates 4h, 9c, 14c, 17f, 23h, 29e, 34g, 39i

Delphax lugens Stål, 1854. Ofv. Svenska Vet. Ak. Forh. 11:246
D. sordescens Motschulsky, 1863. Bull. Soc. Nat. Moscow 36:109
D. oryzae Matsumura, 1906. List Injur. Insects Jpn. 13
Nilaparvata greeni Distant, 1906. Fauna Brit. Ind. 3:486
Kalpa aculeata Distant, 1906. Ibid. 474
Dicranotropis anderida Kirkaldy, 1907. Hawaii Sugar Plant. Assoc. Entomol. Bull. 3:133
Delphax ordovix Kirkaldy, 1907. Ibid. 3:152
D. parysatis Kirkaldy, 1907. Ibid. 153
Nilaparvata lugens Muir & Giffard, 1924. Ibid. 15:16
Hikona formosana Matsumura, 1935. Insecta Matsumurana 9:139
Nilaparvata lugens Fennah, 1956. Insects of Micronesia 6(3):121
N. l. Fennah, 1965. Bull. Brit. Mus. Nat. Hist. 17(1):24
N. l. Okada, 1977. Food & Fert. Tech. Cen. Asia & Pac. Reg. 3
N. l. Mochida & Okada, 1979. Int. Rice Res. Newsl. 25
N. l. Fennah, 1978. Ann. Zool. (Wars.) 34(9):219
N. l. Yang, 1989. NSC Special Publ. 6:276
N. l. Wilson & Claridge, 1991. CAB Intern. & Nat. Resources Inst. 50
N. l. Ding & Zhang, 1994. China Agric. Sci. Tech. Press 83

Features: Body length 3.7–5 mm (macropterous), 2.4–3.3 mm (brachypterous); brown to dark brown; forewings hyaline, with apex of claval area black; vertex quadrate, nearly as long as wide, apical margin transverse, submedian carinae not merged apically, basal compartment wider than base and than its greatest length about 1.7:1; frons longer in middle line than wide at widest point about 2.2:1, widest at level of ocelli, lateral carinae almost straight, median carina forked at basal fourth; antennae passed frontoclypeal suture, with basal segment longer than wide about 2:1, shorter than segment II about 1:2; tibial spur with 24–29 teeth; forewing longer than widest point about 3.3:1; pygofer with opening wider than long in posterior view, lateral margins not well defined, medioventral process absent; phallus tubular, slender, narrowed, and upturned at apical third; orifice at apical third, right, below orifice with five small teeth; suspensorium with slender stem, ventral ring turned right angle to stem, left side sclerotized, remainder membranous; diaphragm very broad, dorsal margin evenly incised medially; anal segment in deep emargination of pygofer, lateroapical angles separated, each produced into a long, spinose process; parameres large, inner margin roundly emarginate at middle, inner angle strongly projected, apex pointed, viewed caudolaterally.

Host plant: Rice
Economic importance: High
Distribution: Australia, Bangladesh, Cambodia, China, East Timor, Fiji, India, Indonesia, Japan, Korea, Laos, Malaysia, Myanmar, New Guinea, Pakistan, Palau, Philippines, Taiwan, Thailand, Vietnam, and Yap Island

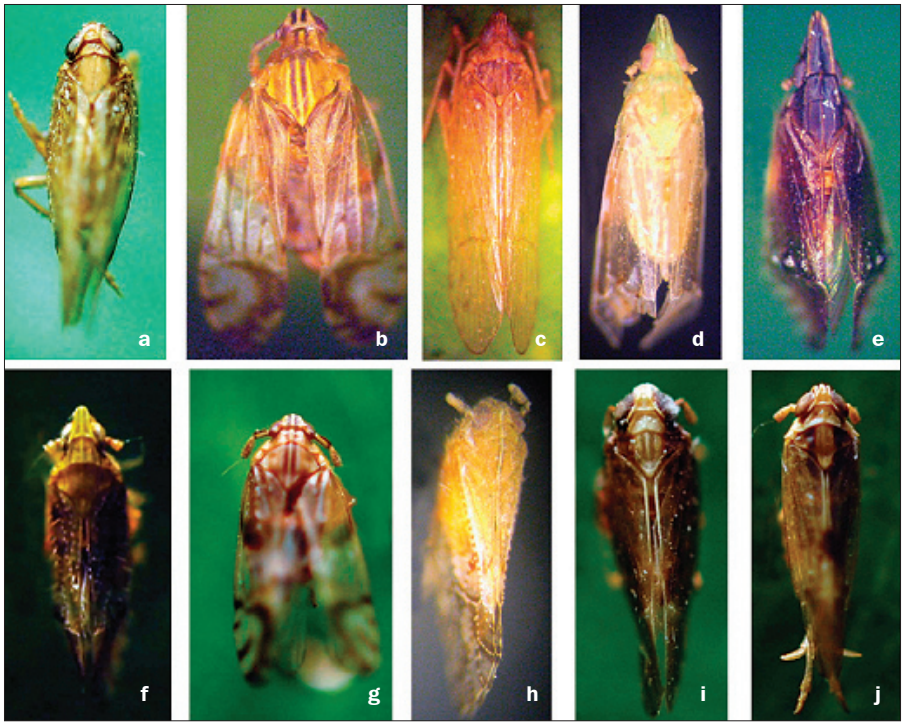

Plate 1. General habitus: (a) *Melanesia pacifica* Kirkaldy; (b) *Melanugyops* sp.; (c) *Ugyops vittatus* (Matsumura); (d) *Tropidocephala* sp.; (e) *Tropidocephala nigra* (Matsumura); (f) *Tropidocephala brunnipennis* Signoret; (g) *Tropidocephala festiva* (Distant); (h) *Arcofacies fullawayi* Muir; (i) *Tarophagus persephone* (Kirkaldy); (j) *Sogatella furcifera* (Horvath).

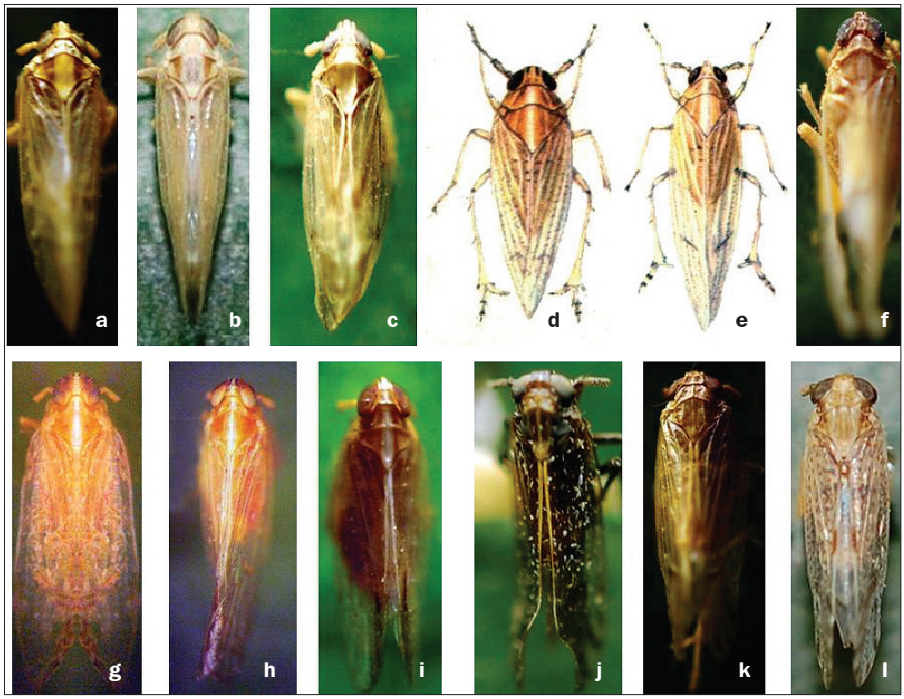

Plate 2. General habitus: (a) *Sogatella vibix* (Haupt); (b) *Sogatella kolophon* (Kirkaldy); (c) *Tagosodes pusanus* (Distant); (d) *Terthron albovittatum* (Matsumura); (e) *Unkanodes sapporonus* Matsumura; (f) *Stenocranus* sp. A; (g) *Stenocranus pacificus* Kirkaldy; (h) *Stenocranus* nr. *pseudopacificus* Kirkaldy; (i) *Stenocranus* sp. B; (j) *Perkinsiella* sp. A; (k) *Perkinsiella vastatrix* Muir; (l) *Perkinsiella pseudomaidis* Muir.

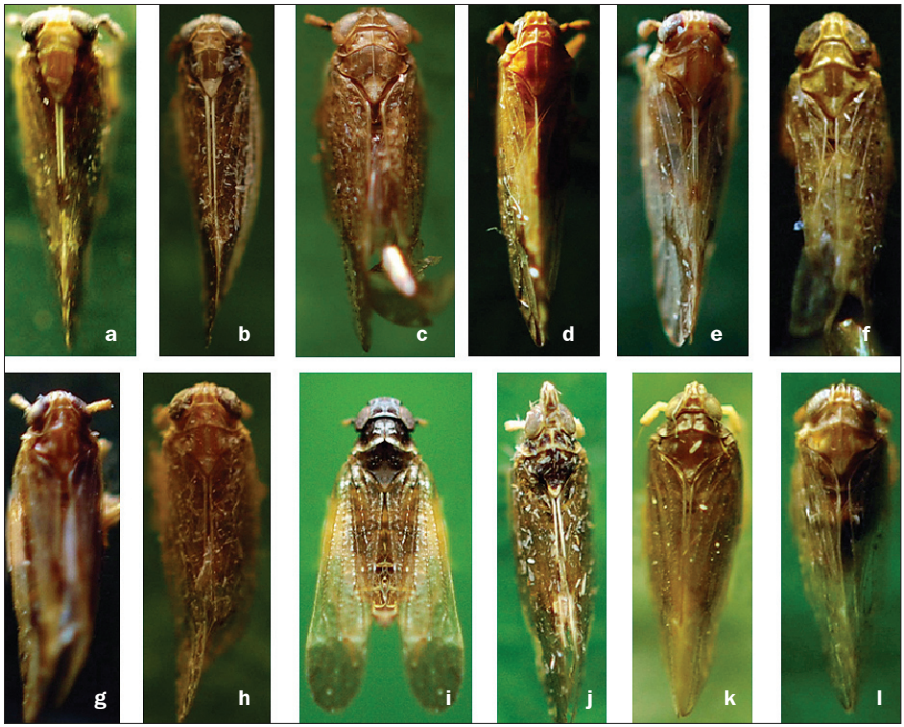

Plate 3. General habitus: (a) *Perkinsiella* nr. *bakeri* Muir; (b) *Perkinsiella saccharicida* Muir; (c) *Perkinsiella graminicida* Muir; (d) *Peregrinus maidis* (Ashmead); (e) *Euidella* sp.; (f) *Dicranotropis* sp.; (g) *Numata muiri* (Kirkaldy); (h) *Nycheuma cognatum* (Muir, 1917); (i) *Metropis nigrifrons* Kusnezov; (j) *Sardia rostrata* (Kirkaldy); (k) *Harmalia heitensis* (Matsumura); (l) *Toya propinqua* (Fieber).

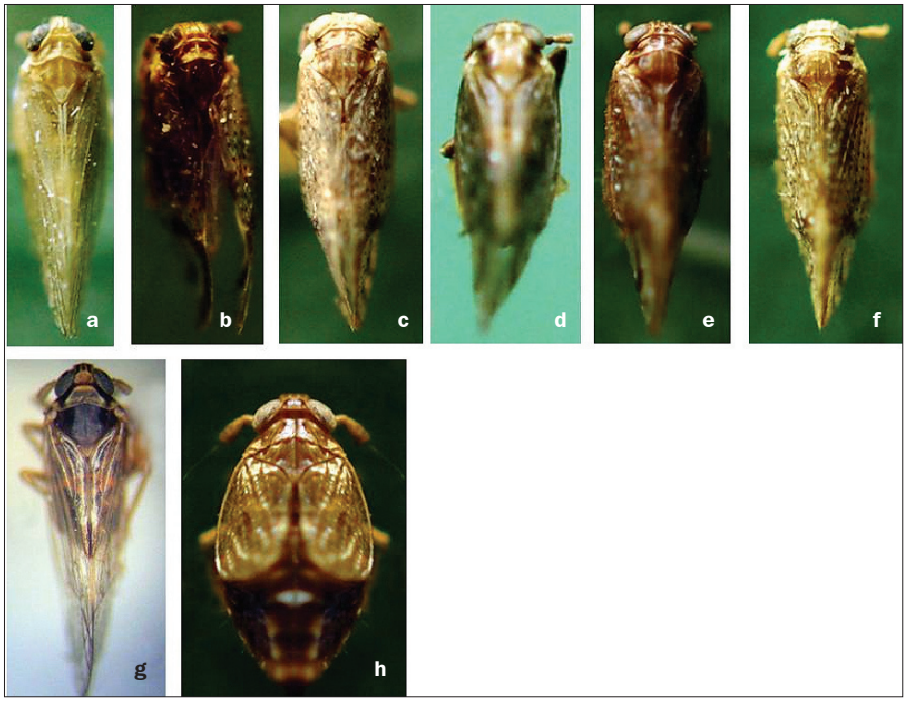

Plate 4. General habitus: (a) *Euidellana celadon* Fennah; (b) *Cemus sauteri* (Muir); (c) *Cemus nigromaculosus* (Muir); (d) *Cemus changchias* Kuoh; (e) *Cemus* sp. A; (f) *Cemus* sp. B; (g) *Laodelphax striatellus* (Fallen); (h) *Nilaparvata lugens* (Stål).

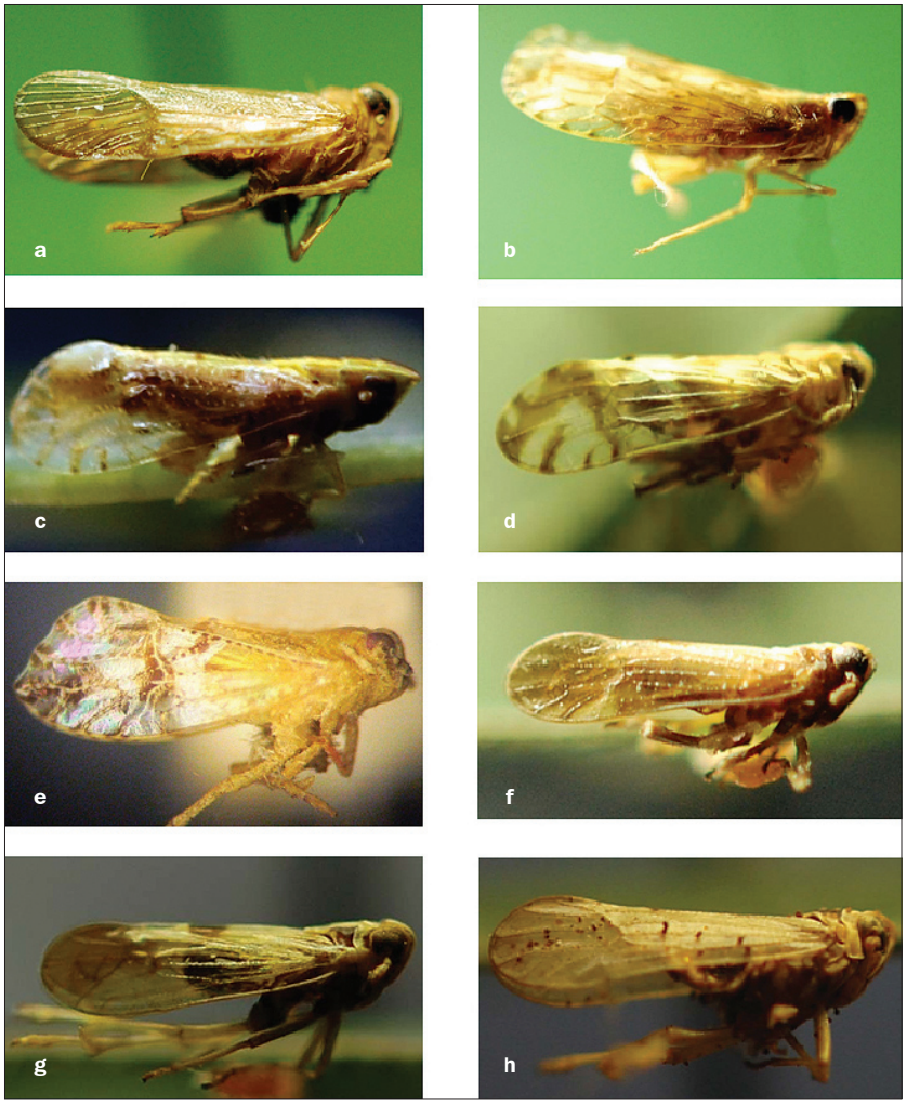

Plate 5. Lateral view of body: (a) *Melanesia pacifica* Kirkaldy; (b) *Ugyops vittatus* (Matsumura); (c) *Tropidocephala brunnipennis* Signoret; (d) *Tropidocephala festiva* (Distant); (e) *Arcofacies fullawayi* Muir; (f) *Tarophagus persephone* (Kirkaldy); (g) *Sogatella furcifera* (Horvath); (h) *Sogatella vibix* (Haupt).

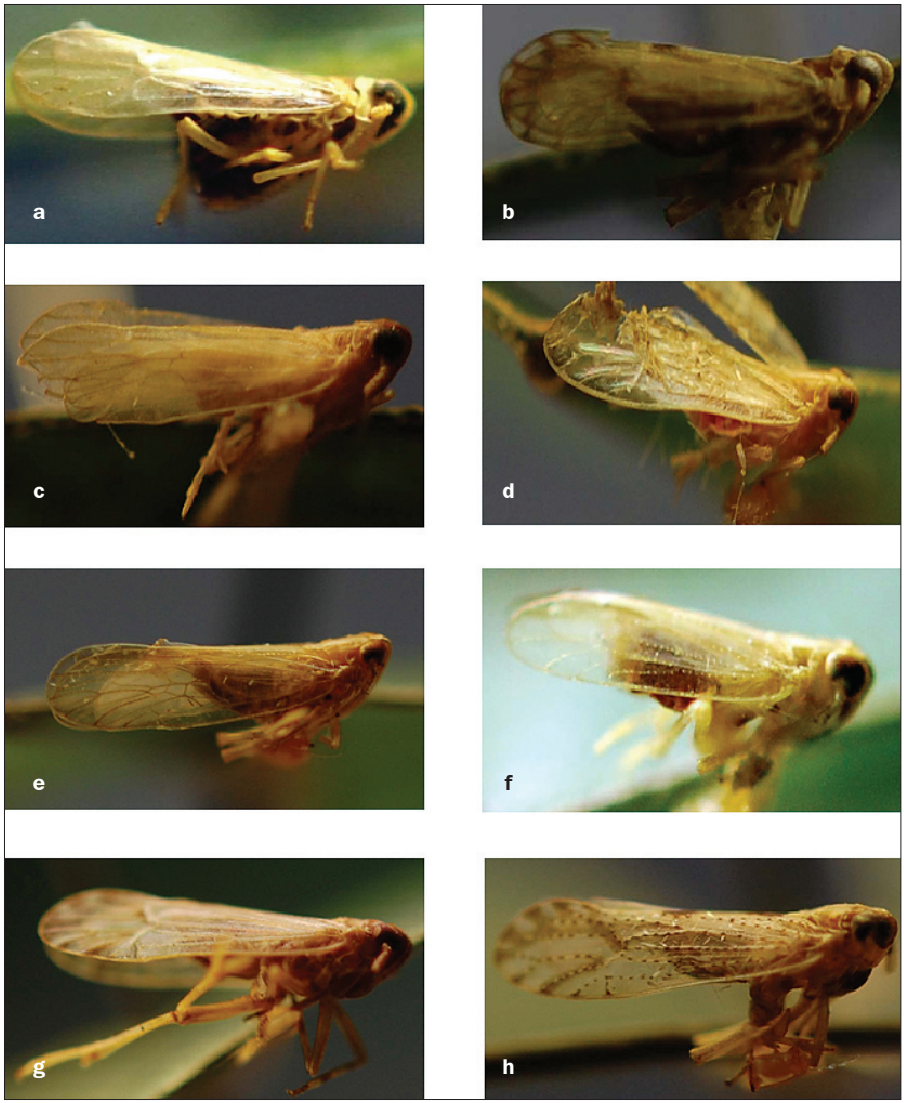

Plate 6. Lateral view of body: (a) *Sogatella kolophon* (Kirkaldy); (b) *Tagosodes pusanus* (Distant); (c) *Stenocranus* sp. A ; (d) *Stenocranus pacificus* Kirkaldy; (e) *Stenocranus* nr. *pseudopacificus* Kirkaldy; (f) *Stenocranus* sp. B; (g) *Perkinsiella vastatrix* Muir; (h) *Perkinsiella pseudomaidis* Muir.

Plate 7. Lateral view of body: (a) *Perkinsiella* nr. *bakeri* Muir; (b) *Perkinsiella saccharicida* Muir; (c) *Perkinsiella graminicida* Muir; (d) *Peregrinus maidis* (Ashmead); (e) *Euidella* sp.; (f) *Dicranotropis* sp.; (g) *Numata muiri* (Kirkaldy); (h) *Nycheuma cognatum* (Muir).

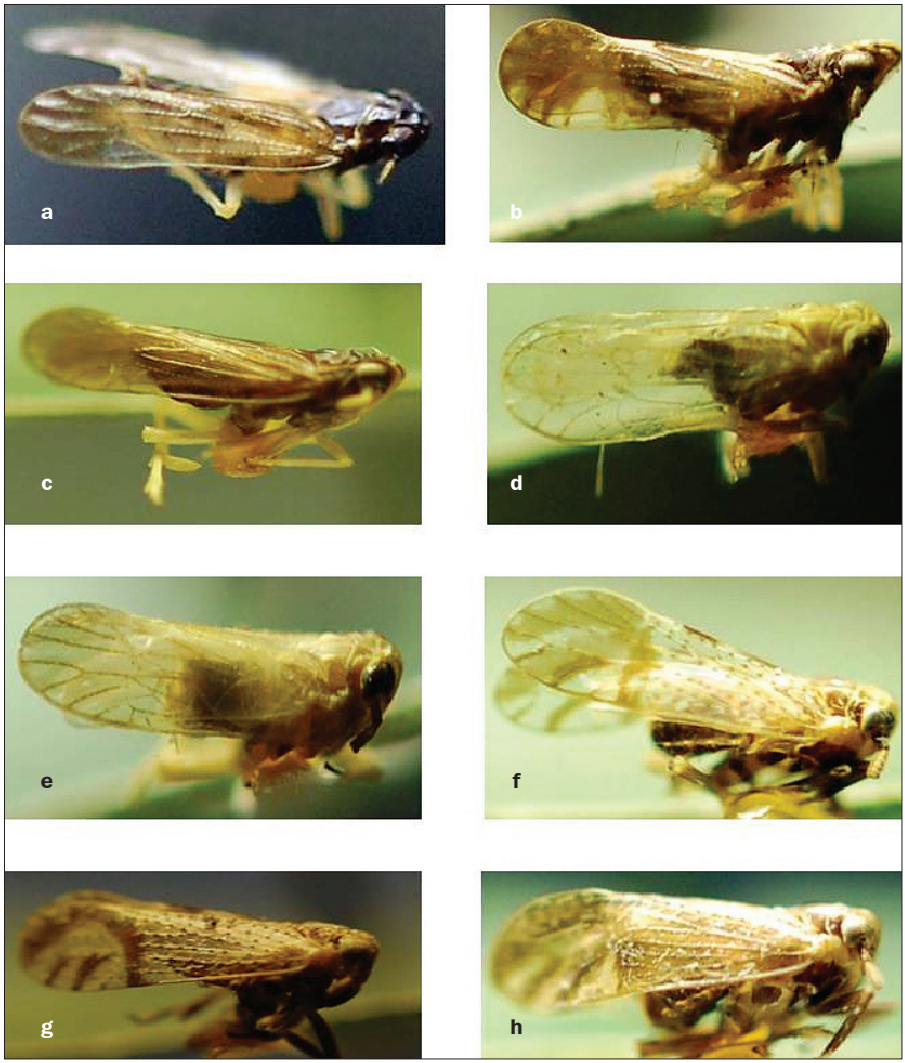

Plate 8. Lateral view of body: (a) *Metropis nigrifrons* Kusnezov; (b) *Sardia rostrata* (Kirkaldy); (c) *Harmalia anacharsis* Fennah ; (d) *Toya propinqua* (Fieber); (e) *Euidellana celadon* Fennah; (f) *Cemus sauteri* (Muir); (g) *Cemus nigromaculosus* (Muir); (h) *Cemus changchias* Kuoh.

Plate 9. Lateral view of body: (a) *Cemus* sp. A; (b) *Cemus* sp. B; (c) *Nilaparvata lugens* (Stål).

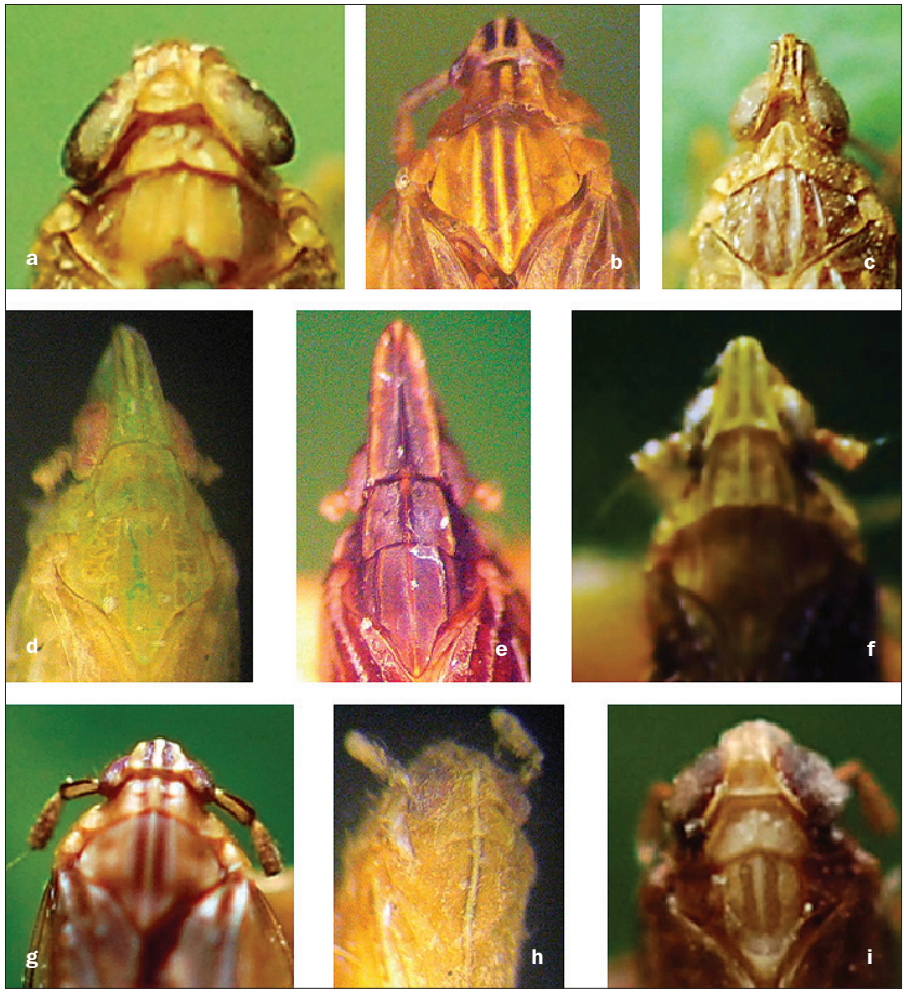

Plate 10. Dorsal view of head and thorax: (a) *Melanesia pacifica* Kirkaldy; (b) *Melanugyops* sp.; (c) *Ugyops vittatus* (Matsumura); (d) *Tropidocephala* sp.; (e) *Tropidocephala nigra* (Matsumura); (f) *Tropidocephala brunnipennis* Signoret; (g) *Tropidocephala festiva* (Distant); (h) *Arcofacies fullawayi* Muir; (i) *Tarophagus persephone* (Kirkaldy).

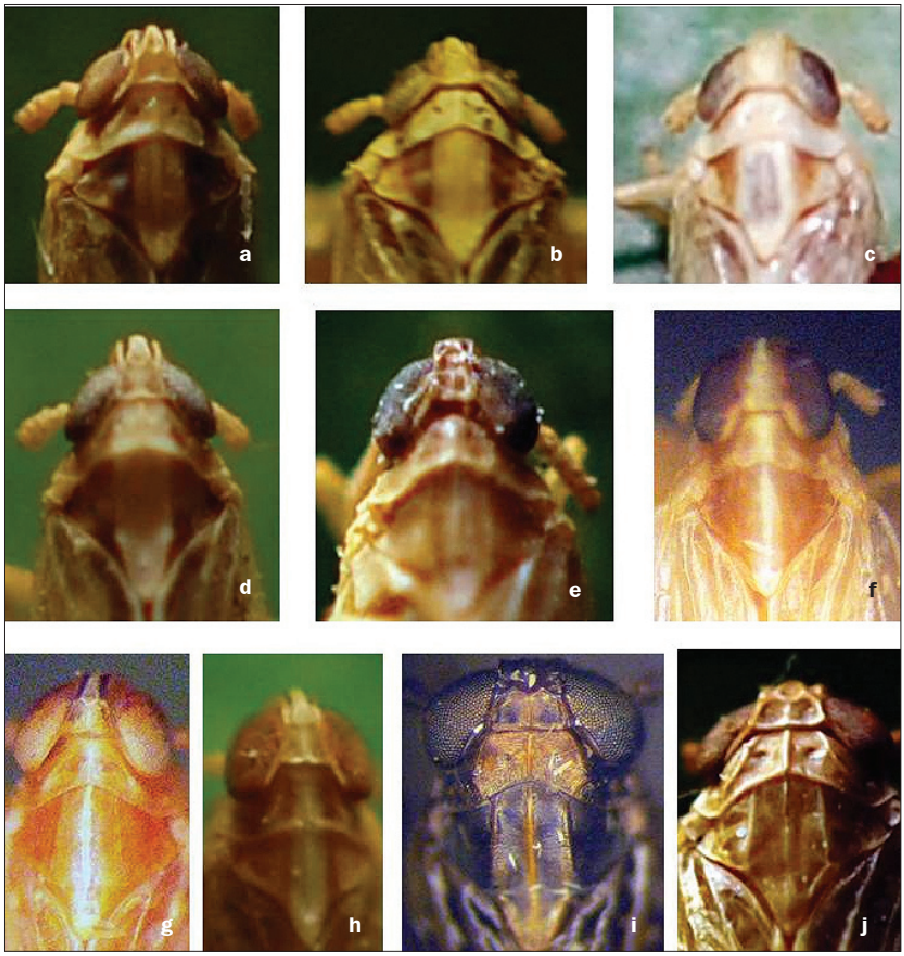

Plate 11. Dorsal view of head and thorax: (a) *Sogatella furcifera* (Horvath); (b) *Sogatella vibix* (Haupt); (c) *Sogatella kolophon* (Kirkaldy); (d) *Tagosodes pusanus* (Distant); (e) *Stenocranus* sp. A; (f) *Stenocranus pacificus* Kirkaldy; (g) *Stenocranus* nr. *pseudopacificus* Kirkaldy; (h) *Stenocranus* sp. B; (i) *Perkinsiella* sp. A; (j) *Perkinsiella vastatrix* Muir.

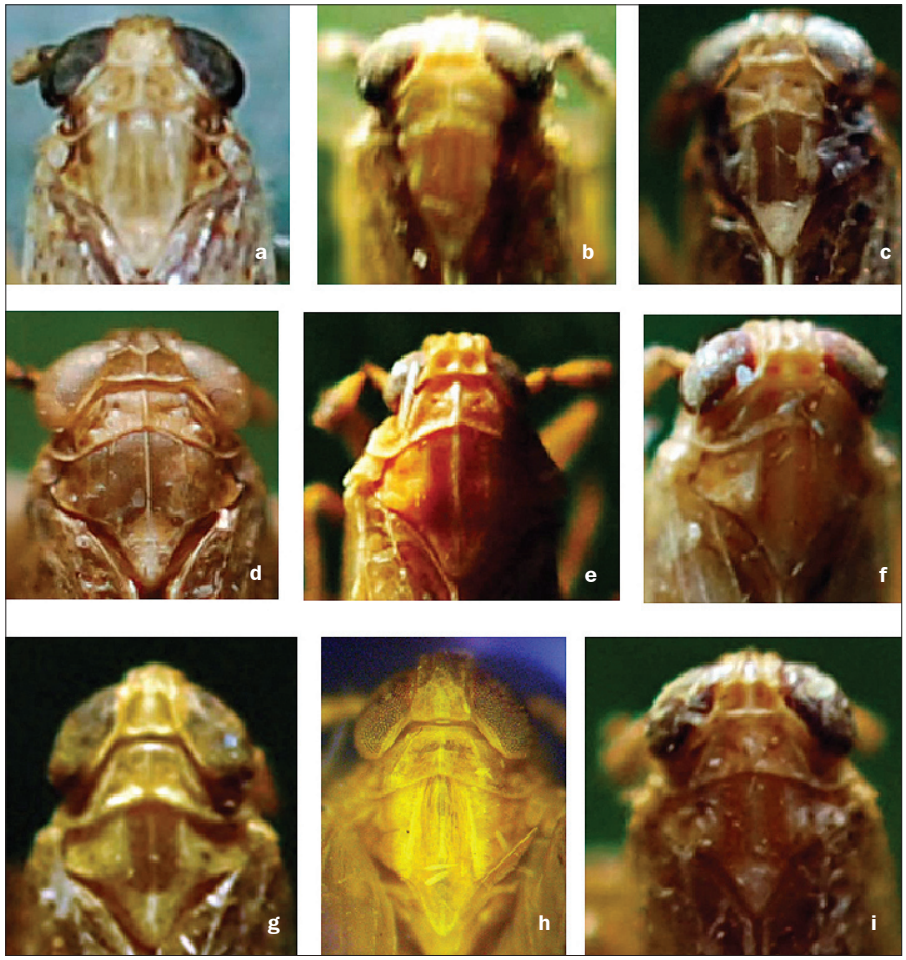

Plate 12. Dorsal view of head and thorax: (a) *Perkinsiella pseudomaidis* Muir; (b) *Perkinsiella* nr. *bakeri* Muir; (c) *Perkinsiella saccharicida* Muir; (d) *Perkinsiella graminicida* Muir; (e) *Peregrinus maidis* (Ashmead); (f) *Euidella* sp.; (g) *Dicranotropis* sp.; (h) *Numata muiri* (Kirkaldy); (i) *Nycheuma cognatum* (Muir).

Plate 13. Dorsal view of head and thorax: (a) *Metropis nigrifrons* Kusnezov; (b) *Sardia rostrata* (Kirkaldy); (c) *Harmalia heitensis* (Matsumura); (d) *Toya propinqua* (Fieber); (e) *Euidellana celadon* Fennah; (f) *Cemus sauteri* (Muir); (g) *Cemus nigromaculosus* (Muir); (h) *Cemus changchias* Kuoh; (i) *Cemus* sp. A.

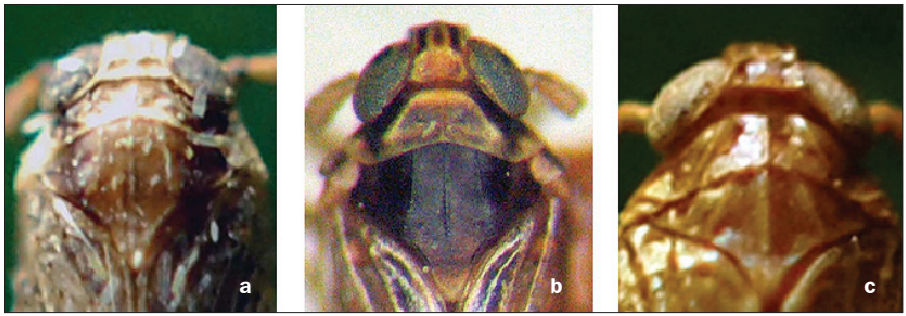

Plate 14. Dorsal view of head and thorax: (a) *Cemus* sp. B; (b) *Laodelphax striatellus* (Fallen); (c) *Nilaparvata lugens* (Stål).

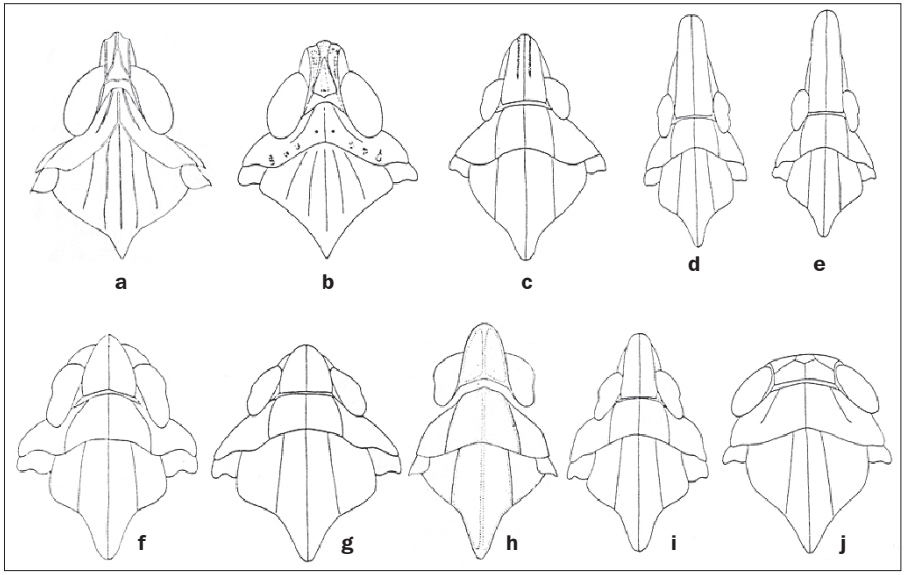

Plate 15. Dorsal view of head and thorax (line drawing): (a) *Ugyops vittatus* (Matsumura); (b) *Ugyops tripunctatus* (Kato); (c) *Tropidocephala flavovittata* Matsumura; (d) *Tropidocephala dimidia* Yang & Yang; (e) *Tropidocephala sinuosa* Yang & Yang; (f) *Tropidocephala grata* Yang & Yang; (g) *Tropidocephala formosa* Matsumura; (h) *Tropidocephala brunnipennis* Signoret; (i) *Tropidocephala saccharivoriella* Matsumura; (j) *Epeurysa nawaii* Matsumura.

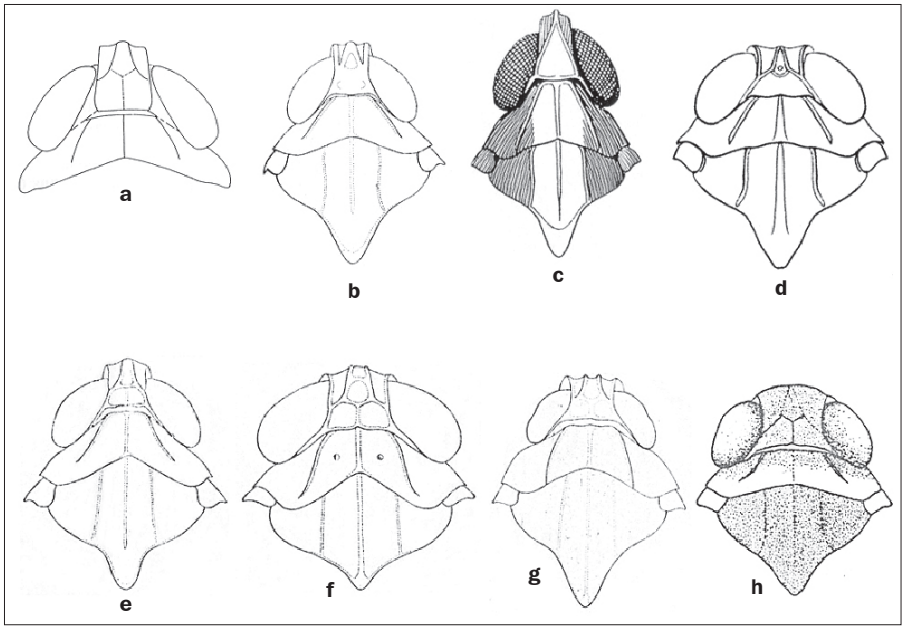

Plate 16. Dorsal view of head and thorax (line drawing): (a) *Tarophagus colocasiae* (Matsumura); (b) *Sogatella furcifera* (Horvath); (c) *Latistria eupompe* (Kirkaldy); (d) *Terthron albovittatum* (Matsumura); (e) *Unkanodes sapporonus* Matsumura; (f) *Perkinsiella saccharicida* Muir; (g) *Peregrinus maidis* (Ashmead); (h) *Metropis nigrifrons* Kusnezov.

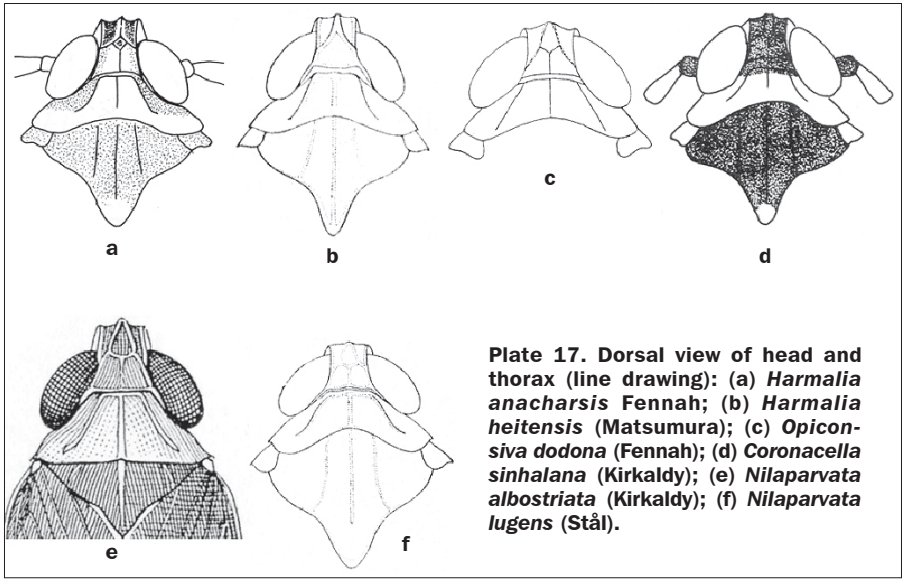

Plate 17. Dorsal view of head and thorax (line drawing): (a) *Harmalia anacharsis* Fennah; (b) *Harmalia heitensis* (Matsumura); (c) *Opiconsiva dodona* (Fennah); (d) *Coronacella sinhalana* (Kirkaldy); (e) *Nilaparvata albostriata* (Kirkaldy); (f) *Nilaparvata lugens* (Stål).

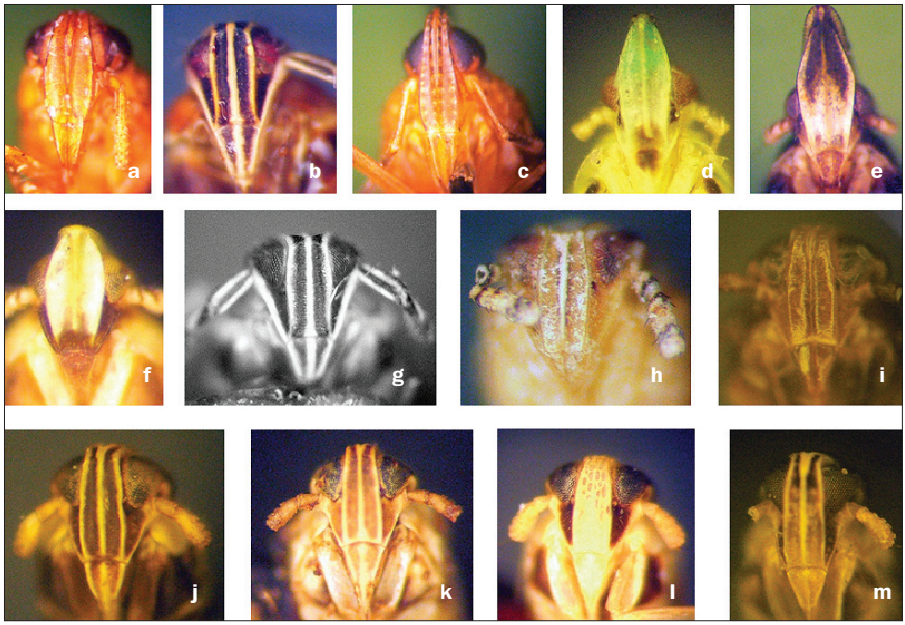

Plate 18. Frontal view of head: (a) *Melanesia pacifica* Kirkaldy; (b) *Melanugyops* sp.; (c) *Ugyops vittatus* (Matsumura); (d) *Tropidocephala* sp.; (e) *Tropidocephala nigra* (Matsumura); (f) *Tropidocephala brunnipennis* Signoret; (g) *Tropidocephala festiva* (Distant); (h) *Arcofacies fullawayi* Muir; (i) *Tarophagus persephone* (Kirkaldy); (j) *Sogatella furcifera* (Horvath); (k) *Sogatella vibix* (Haupt); (l) *Sogatella kolophon* (Kirkaldy); (m) *Tagosodes pusanus* (Distant).

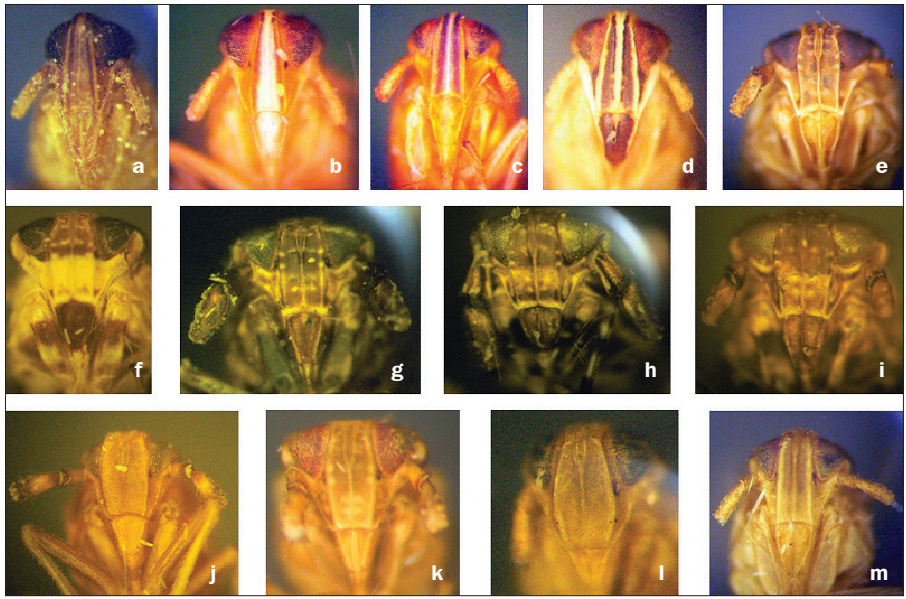

Plate 19. Frontal view of head: (a) *Stenocranus* sp. A; (b) *Stenocranus pacificus* Kirkaldy; (c) *Stenocranus* nr. *pseudopacificus* Kirkaldy); (d) *Stenocranus* sp. B; (e) *Perkinsiella vastatrix* Muir; (f) *Perkinsiella pseudomaidis* Muir; (g) *Perkinsiella* nr. *bakeri* Muir; (h) *Perkinsiella saccharicida* Muir; (i) *Perkinsiella graminicida* Muir; (j) *Peregrinus maidis* (Ashmead); (k) *Euidella* sp.; (l) *Dicranotropis* sp.; (m) *Numata muiri* (Kirkaldy).

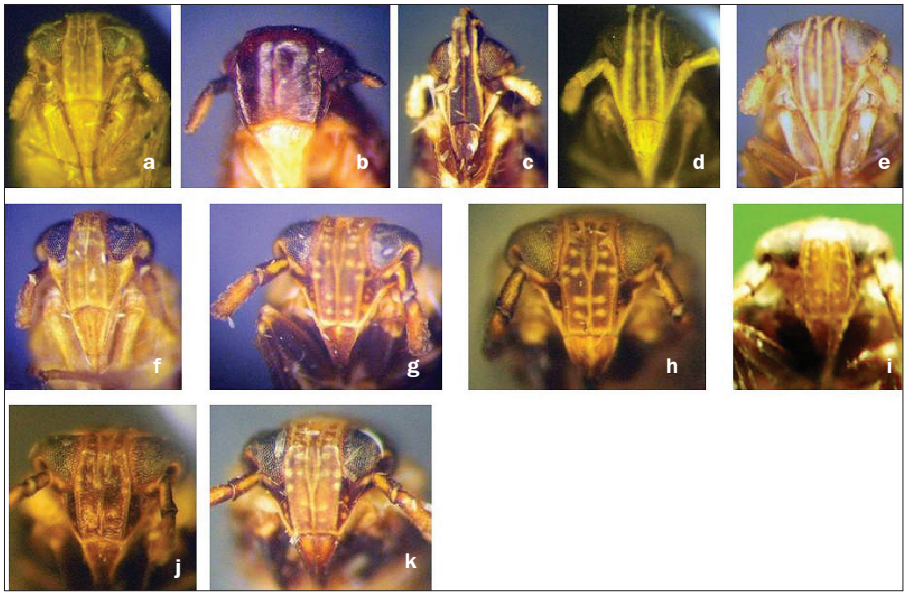

Plate 20. Frontal view of head: (a) *Nycheuma cognatum* (Muir); (b) *Metropis nigrifrons* Kusnezov; (c) *Sardia rostrata* (Kirkaldy); (d) *Harmalia heitensis* (Matsumura); (e) *Toya propinqua* (Fieber); (f) *Euidellana celadon* Fennah; (g) *Cemus sauteri* (Muir); (h) *Cemus nigromaculosus* (Muir); (i) *Cemus changchias* Kuoh; (j) *Cemus* sp. A; (k) *Cemus* sp. B.

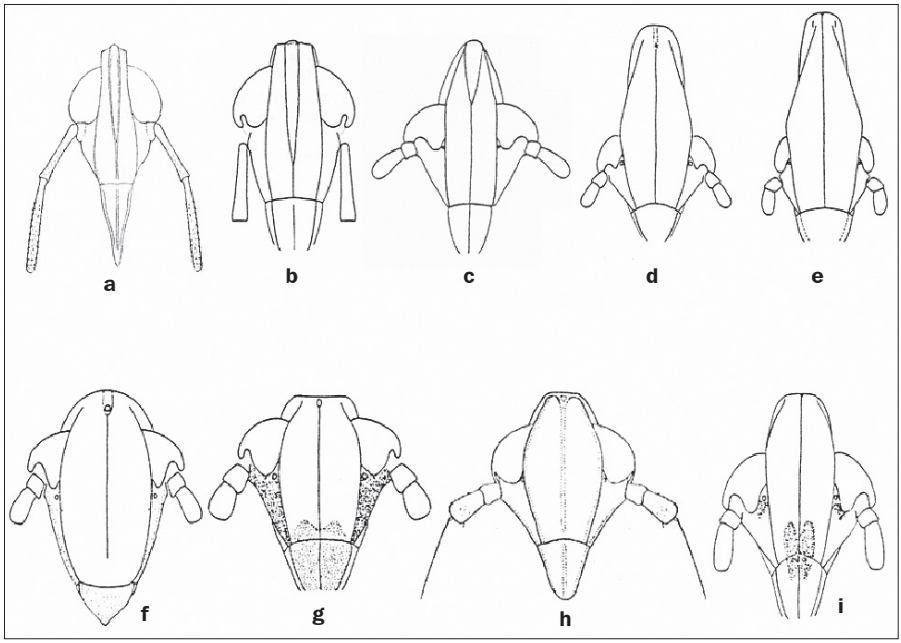

Plate 21. Frontal view of head (line drawing): (a) *Ugyops vittatus* (Matsumura); (b) *Ugyops tripunctatus* (Kato); (c) *Tropidocephala flavovittata* Matsumura; (d) *Tropidocephala dimidia* Yang & Yang; (e) *Tropidocephala sinuosa* Yang & Yang; (f) *Tropidocephala grata* Yang & Yang; (g) *Tropidocephala formosa* Matsumura; (h) *Tropidocephala brunnipennis* Signoret; (i) *Tropidocephala saccharivoriella* Matsumura.

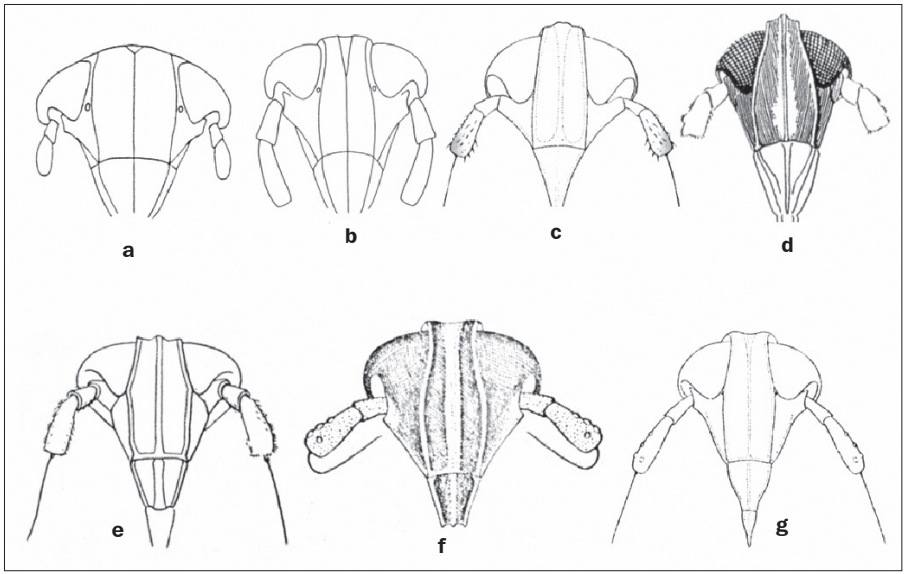

Plate 22. Frontal view of head (line drawing): (a) *Epeurysa nawaii Matsumura*; (b) *Tarophagus colocasiae* (Matsumura); (c) *Sogatella furcifera* (Horvath); (d) *Latistria eupompe* (Kirkaldy); (e) *Terthron albovittatum* (Matsumura); (f) *Unkanodes albifascia* (Matsumura); (g) *Unkanodes sapporonus* Matsumura.

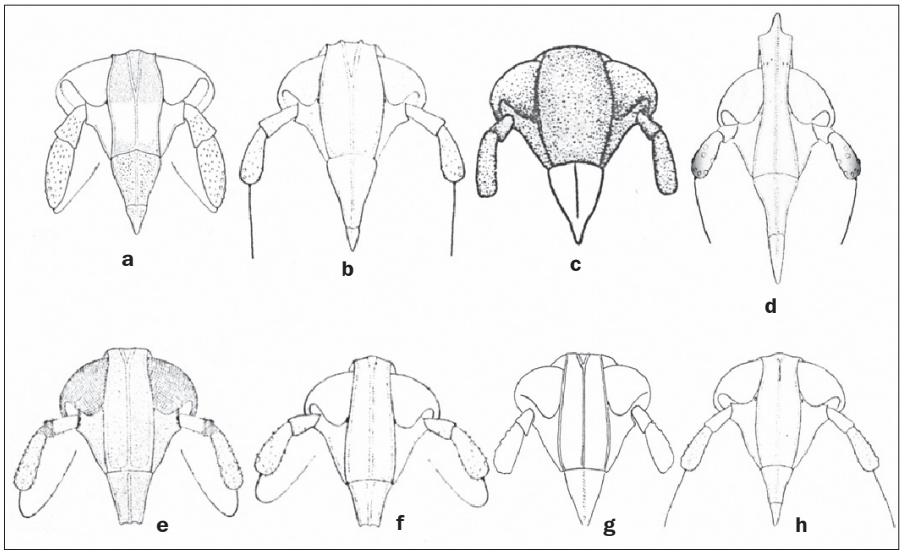

Plate 23. Frontal view of head (line drawing): (a) *Perkinsiella saccharicida* Muir; (b) *Peregrinus maidis* (Ashmead); (c) *Metropis nigrifrons* Kusnezov; (d) *Sardia rostrata* (Kirkaldy); (e) *Paradelphacodes paludosa* (Flor); (f) *Harmalia heitensis* (Matsumura); (g) *Opiconsiva dodona* (Fennah); (h) *Nilaparvata lugens* (Stål).

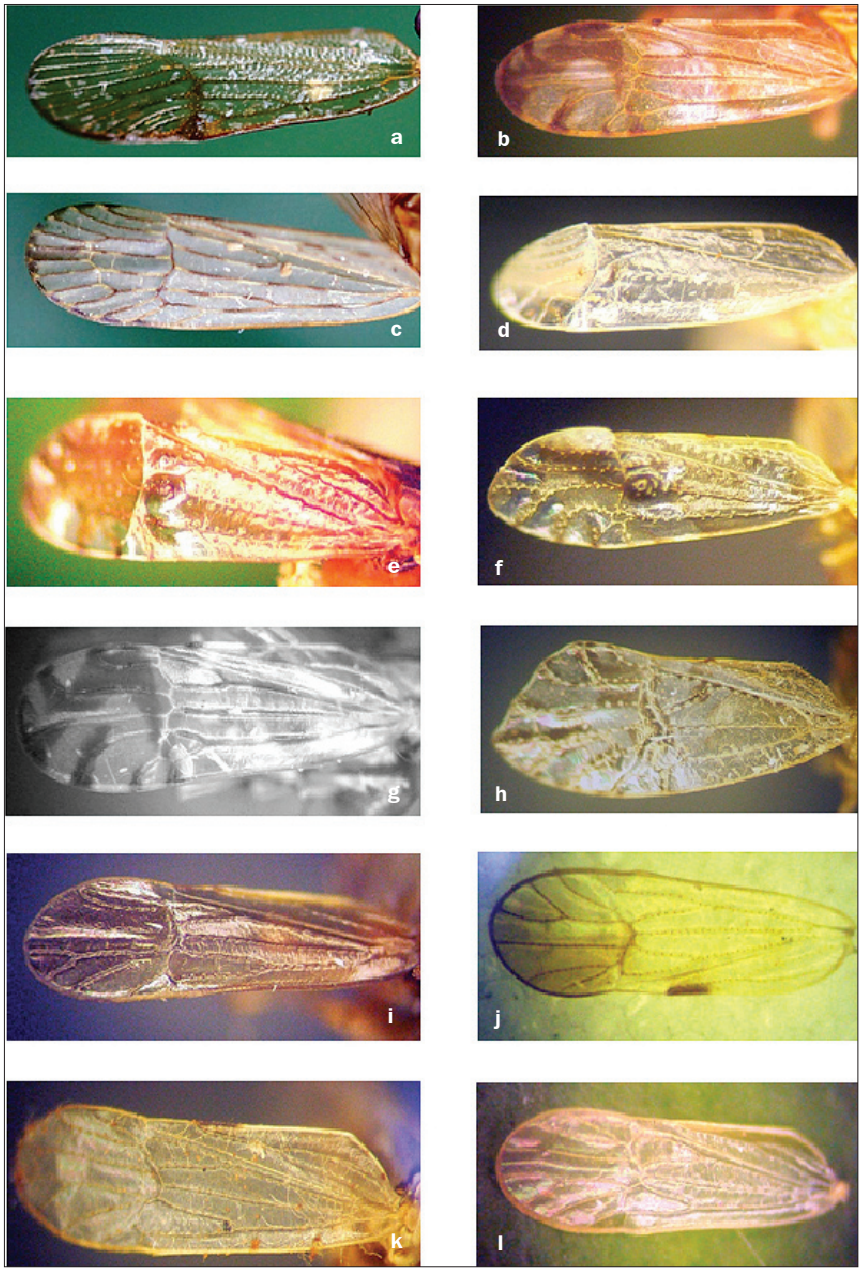

Plate 24. Wing venation: (a) *Melanesia pacifica* Kirkaldy; (b) *Melanugyops* sp.; (c) *Ugyops vittatus* (Matsumura); (d) *Tropidocephala* sp.; (e) *Tropidocephala nigra* (Matsumura); (f) *Tropidocephala brunnipennis* Signoret; (g) *Tropidocephala festiva* (Distant); (h) *Arcofacies fullawayi* Muir; (i) *Tarophagus persephone* (Kirkaldy); (j) *Sogatella furcifera* (Horvath); (k) *Sogatella vibix* (Haupt); (l) *Sogatella kolophon* (Kirkaldy).

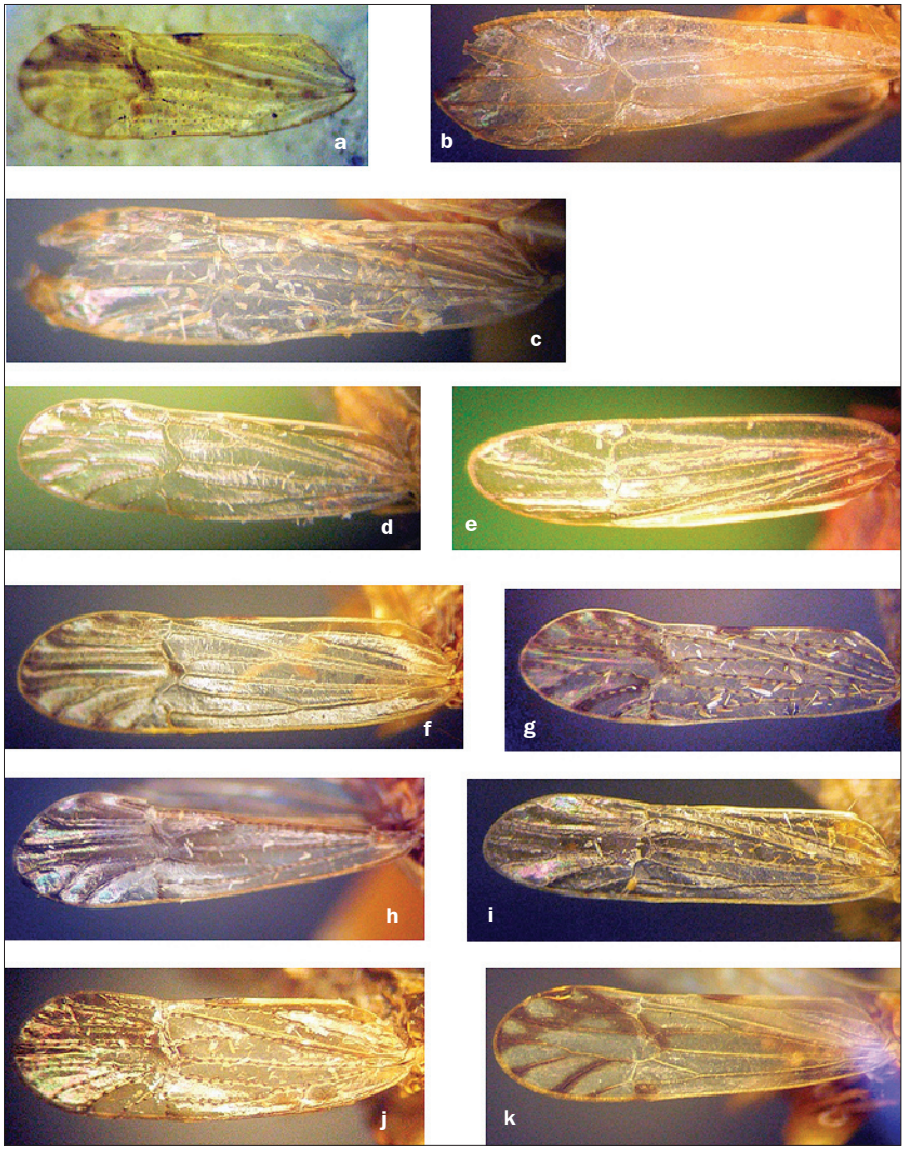

Plate 25. Wing venation: (a) *Tagosodes pusanus* (Distant); (b) *Stenocranus* sp. A; (c) *Stenocranus pacificus* Kirkaldy; (d) *Stenocranus* nr. *pseudopacificus* Kirkaldy; (e) *Stenocranus* sp. B; (f) *Perkinsiella vastatrix* Muir; (g) *Perkinsiella pseudomaidis* Muir; (h) *Perkinsiella* nr. *bakeri* Muir; (i) *Perkinsiella saccharicida* Muir; (j) *Perkinsiella graminicida* Muir; (k) *Peregrinus maidis* (Ashmead).

Plate 26. Wing venation: (a) *Euidella* sp.; (b) *Numata muiri* (Kirkaldy); (c) *Nycheuma cognatum* (Muir); (d) *Metropis nigrifrons* Kusnezov; (e) *Sardia rostrata* (Kirkaldy); (f) *Harmalia heitensis* (Matsumura); (g) *Toya propinqua* (Fieber); (h) *Euidellana celadon* Fennah; (i) *Cemus sauteri* (Muir); (j) *Cemus nigromaculosus* (Muir); (k) *Cemus changchias* Kuoh; (l) *Cemus* sp. A.

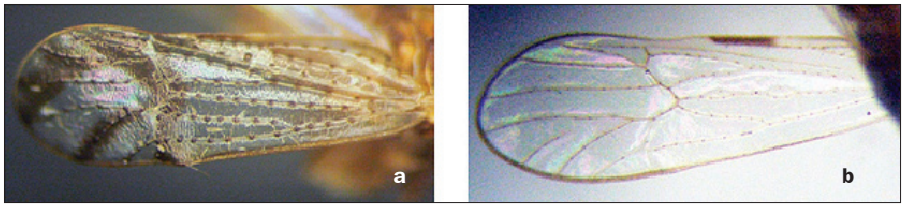

Plate 27. Wing venation: (a) *Cemus* sp. B; (b) *Laodelphax striatellus* (Fallen).

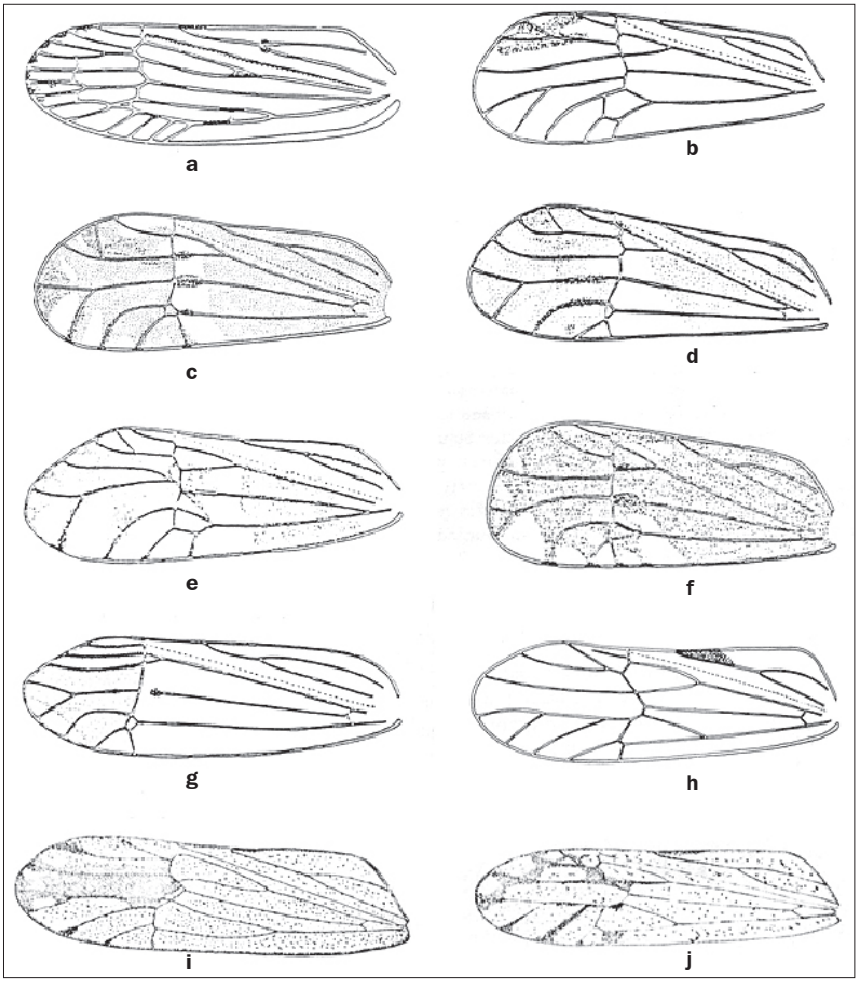

Plate 28. Wing venation (line drawing): (a) *Ugyops tripunctatus* (Kato); (b) *Tropidocephala flavovittata* Matsumura; (c) *Tropidocephala dimidia* Yang & Yang; (d) *Tropidocephala sinuosa* Yang & Yang; (e) *Tropidocephala grata* Yang & Yang; (f) *Tropidocephala formosa* Matsumura; (g) *Tropidocephala saccharivoriella* Matsumura; (h) *Tarophagus colocasiae* (Matsumura); (i) *Perkinsiella saccharicida* Muir; (i) *Peregrinus maidis* (Ashmead).

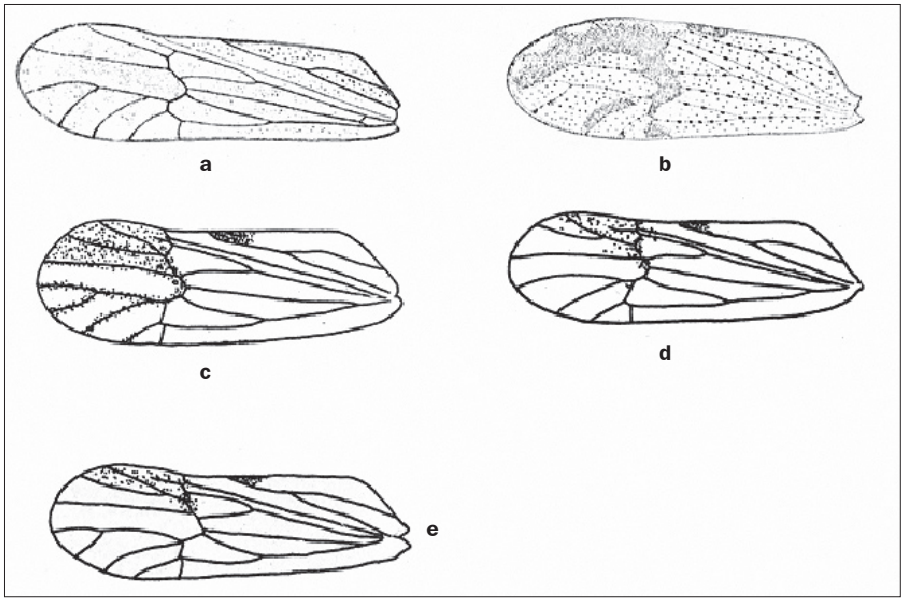

Plate 29. Wing venation (line drawing): (a) *Sardia rostrata* (Kirkaldy); (b) *Cemus sauteri* (Muir); (c) *Nilaparvata bakeri* (Muir); (d) *Nilaparvata muiri* China; (e) *Nilaparvata lugens* (Stål).

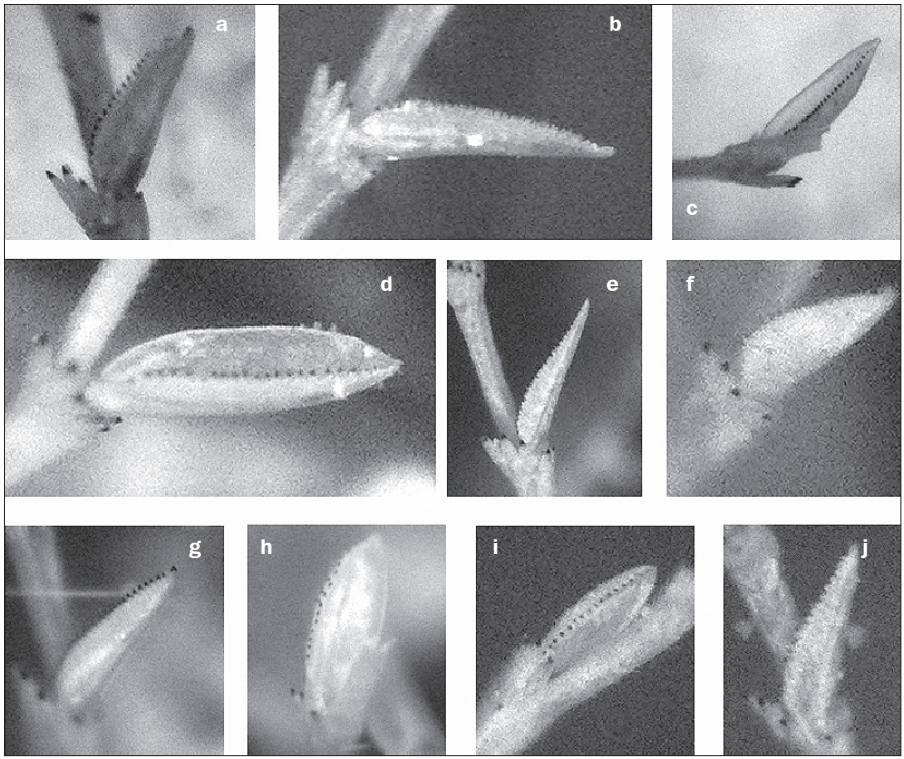

Plate 30. Tibial spur: (a) *Tarophagus persephone* (Kirkaldy); (b) *Sogatella furcifera* (Horvath); (c) *Sogatella vibix* (Haupt); (d) *Sogatella kolophon* (Kirkaldy); (e) *Tagosodes pusanus* (Distant); (f) *Dicranotropis* sp.; (g) *Numata muiri* (Kirkaldy); (h) *Harmalia heitensis* (Matsumura); (i) *Toya propinqua* (Fieber); (j) *Euidellana celadon* Fennah.

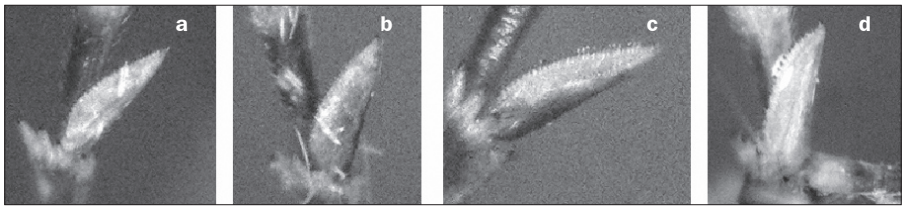

Plate 31. Tibial spur: (a) *Cemus sauteri* (Muir); (b) *Cemus nigromaculosus* (Muir); (c) *Cemus* sp. A; (d) *Cemus* sp. B.

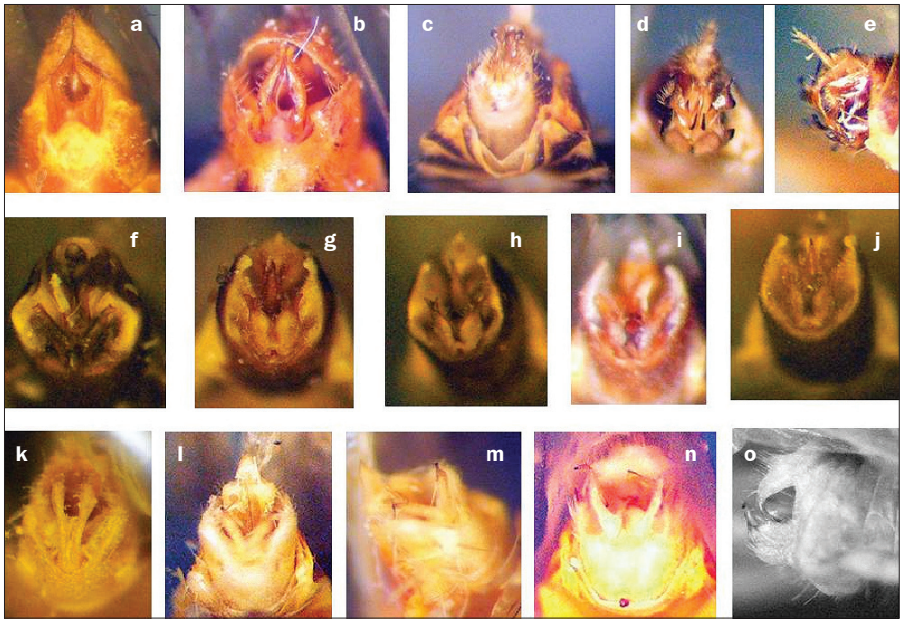

Plate 32. Male genitalia: (a) ***Melanesia pacifica*** **Kirkaldy;** (b) ***Ugyops vittatus*** **(Matsumura);** (c) ***Tropidocephala nigra*** **(Matsumura);** (d,e) ***Tropidocephala brunnipennis*** **Signoret;** (f) ***Tarophagus persephone*** **(Kirkaldy);** (g) ***Sogatella furcifera*** **(Horvath);** (h) ***Sogatella vibix*** **(Haupt);** (i) ***Sogatella kolophon*** **(Kirkaldy);** (j) ***Tagosodes pusanus*** **(Distant);** (k) ***Stenocranus*** **sp. A;** (l,m) ***Stenocranus pacificus*** **Kirkaldy;** (n,o) ***Stenocranus*** **nr.** ***pseudopacificus*** **Kirkaldy.**

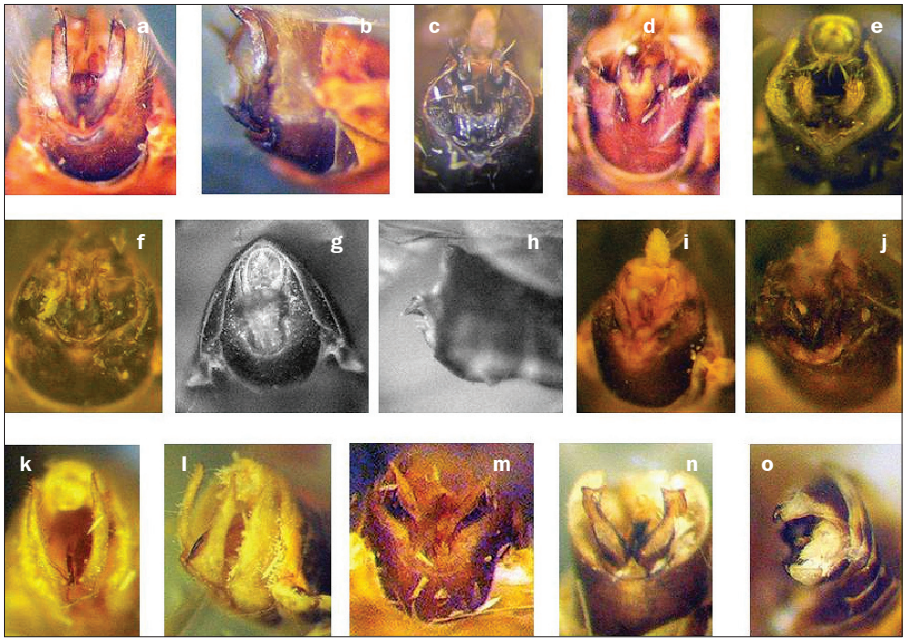

Plate 33. Male genitalia: (a,b) *Stenocranus* sp. B; (c) *Perkinsiella* sp. A; (d) *Perkinsiella* nr. *bakeri* Muir; (e) *Perkinsiella saccharicida* Muir; (f) *Perkinsiella graminicida* Muir; (g,h) *Peregrinus maidis* (Ashmead); (i) Euidella sp.; (j) *Dicranotropis* sp.; (k,l) *Numata muiri* (Kirkaldy); (m) *Nycheuma cognatum* (Muir); (n,o) *Toya propinqua* (Fieber).

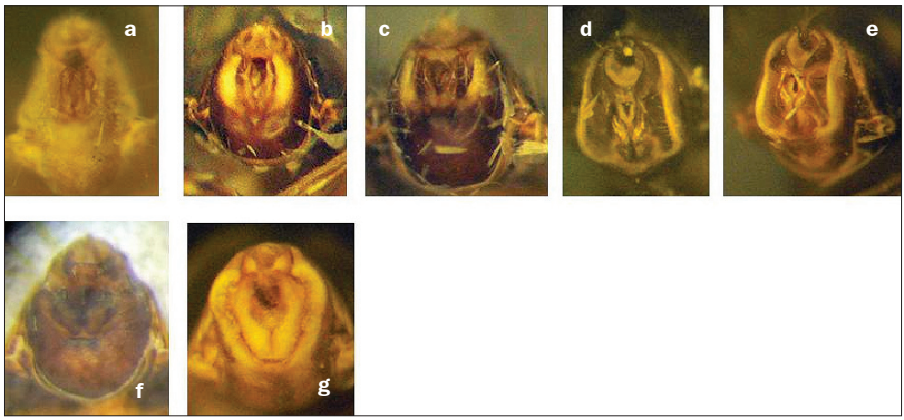

Plate 34. Male genitalia: (a) *Euidellana celadon* Fennah; (b) *Cemus sauteri* (Muir); (c) *Cemus nigromaculosus* (Muir); (d) *Cemus changchias* Kuoh; (e) *Cemus* sp. A; (f) *Laodelphax striatellus* (Fallen); (g) *Nilaparvata lugens* (Stål).

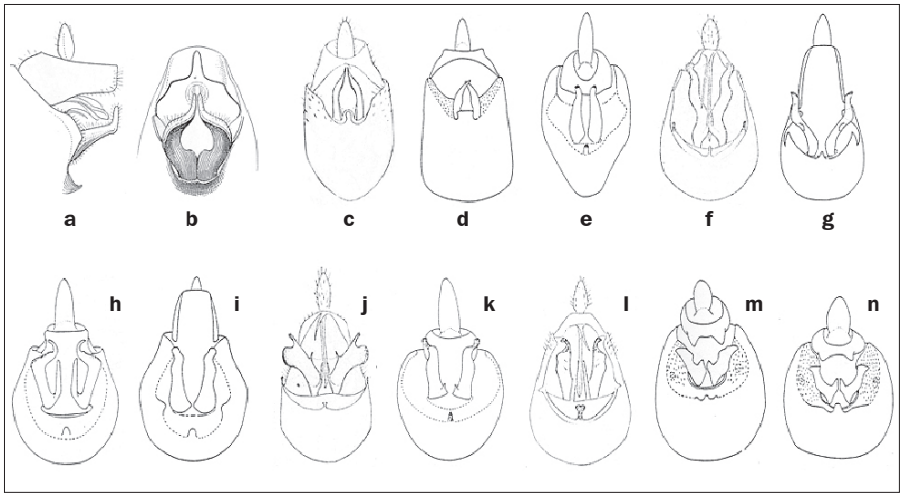

Plate 35. Male genitalia (line drawing): (a,b) *Melanesia pacifica* Kirkaldy; (c) *Ugyops vittatus* (Matsumura); (d) *Ugyops tripunctatus* (Kato); (e) *Tropidocephala flavovittata* Matsumura; (f) *Tropidocephala nigra* (Matsumura); (g) *Tropidocephala sinuosa* Yang & Yang; (h) *Tropidocephala grata* Yang & Yang; (i) *Tropidocephala formosa* Matsumura; (j) *Tropidocephala brunnipennis* Signoret; (k) *Tropidocephala saccharivoriella* Matsumura; (l) *Tropidocephala festiva* (Distant); (m) *Epeurysa abatana;* (n) *Epeurysa nawaii* Matsumura. Sources: Kirkaldy (1907), Ishikara (1949), Yang and Yang (1986), Yang (1989).

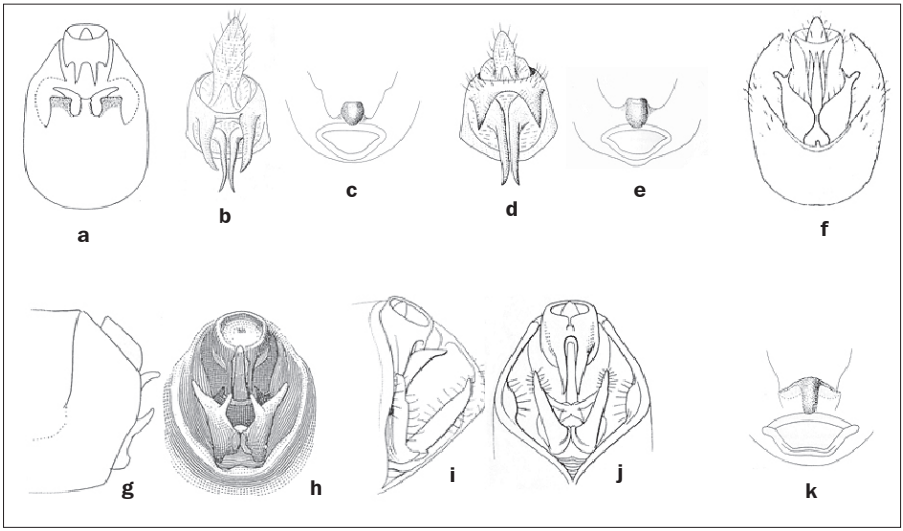

Plate 36. Male genitalia (line drawing): (a) *Tarophagus colocasiae* (Matsumura); (b,c) *Sogatellana geranor* (Kirkaldy); (d,e) *Sogatellana quadrispinosa* (Muir); (f) *Sogatella furcifera* (Horvath); (g,h) *Sogatella kolophon* (Kirkaldy); (i,j) *Latistria eupompe* (Kirkaldy); (k) *Tagosodes pusanus* (Distant) [c, e, and k = diaphragms of pygofer]. Sources: Kirkaldy (1907), Asche and Wilson (1990), Wilson and Claridge (1991).

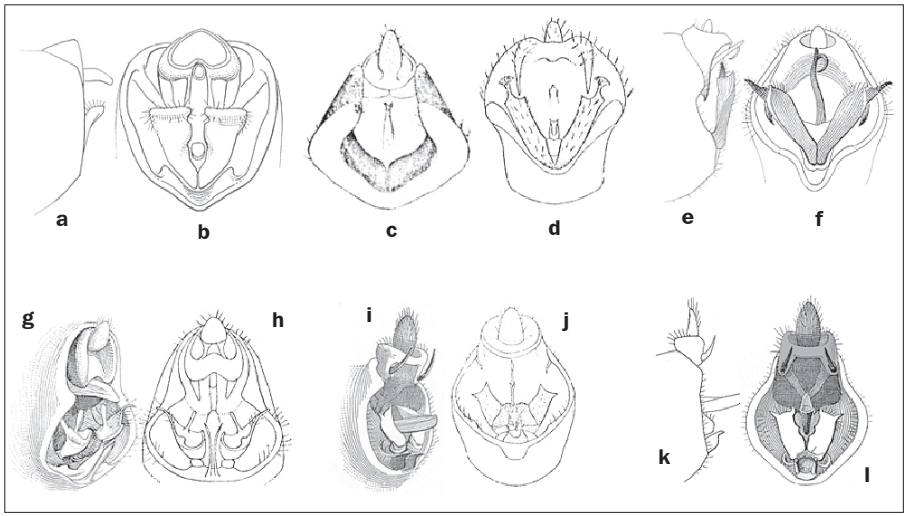

Plate 37. Male genitalia (line drawing): (a,b) *Terthron albovittatum* (Matsumura); (c) *Unkanodes albifascia* (Matsumura); (d) *Unkanodes sapporonus* Matsumura; (e,f) *Stenocranus pacificus* Kirkaldy; (g,h) *Perkinsiella vastatrix* Muir; (i,j) *Perkinsiella saccharicida* Muir; (k,l) *Perkinsiella graminicida* Muir (a, e, g, i, and k in lateral view). Sources: Kirkaldy (1907), Ishikara (1949), Fennah (1978), Yang (1989).

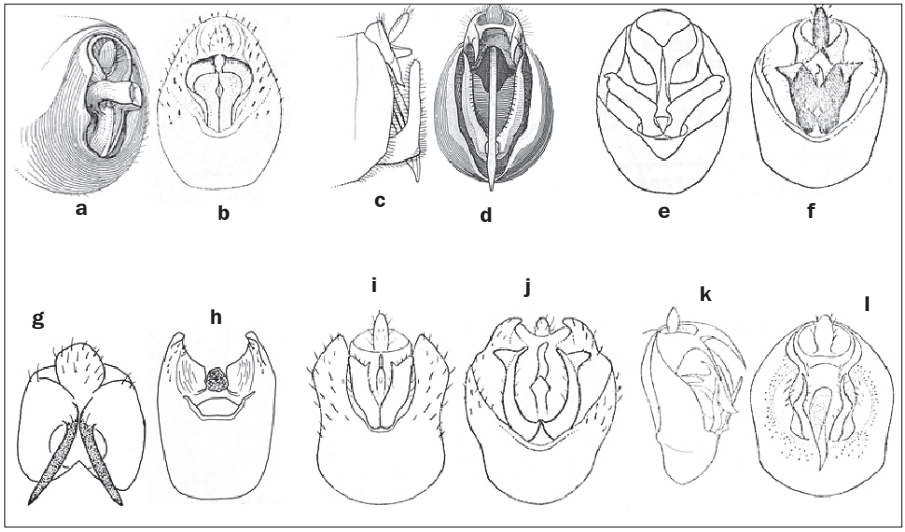

Plate 38. Male genitalia (line drawing): (a,b) *Peregrinus maidis* (Ashmead); (c,d) *Numata muiri* (Kirkaldy); (e) *Metropis nigrifrons* Kusnezov; (f) *Paradelphacodes paludosa* (Flor); (g,h) *Harmalia anacharsis* Fennah; (i) *Harmalia heitensis* (Matsumura); (j) *Harmalia samesimae* (Matsumura & ishihara); (k,l) *Cemus sauteri* (Muir). Sources: Kirkaldy (1907), Ishikara (1949).

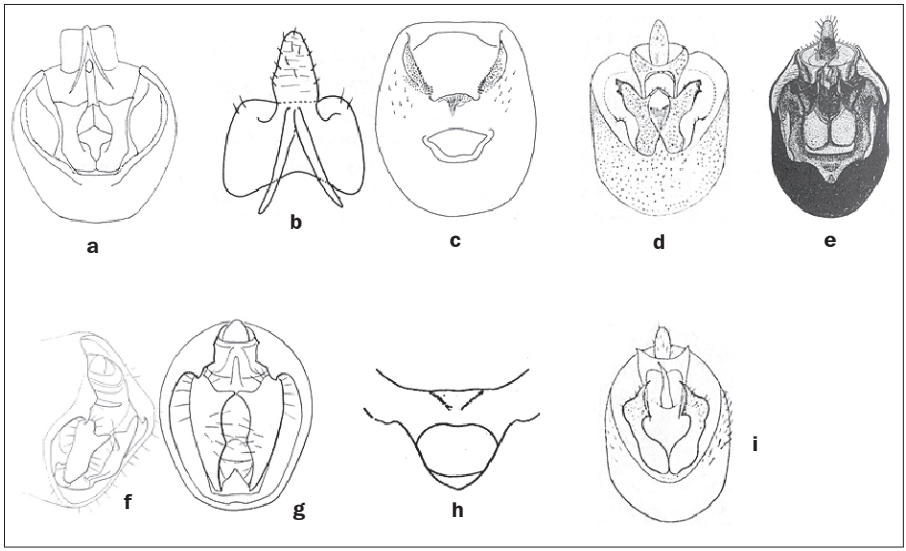

Plate 39. Male genitalia (line drawing): (a) *Opiconsiva dodona* (Fennah); (b,c) *Coronacella sinhalana* (Kirkaldy); (d) *Nilaparvata bakeri* (Muir); (e) *Nilaparvata muiri* China; (f,g) N*ilaparvata albostriata* (Kirkaldy); (h) *Nilaparvata myersi* Muir; (i) *Nilaparvata lugens* (Stål). Sources: Kirkaldy (1907), Mochida and Okada (1979), Wilson and Claridge (1991).

Plate 40. Female genitalia: (a) *Melanugyops* sp.; (b) *Tropidocephala* sp.; (c) *Tarophagus persephone* (Kirkaldy); (d) *Tagosodes pusanus* (Distant); (e) *Perkinsiella pseudomaidis* Muir; (f) *Perkinsiella* nr. *bakeri* Muir; (g) *Perkinsiella saccharicida* Muir; (h) *Peregrinus maidis* (Ashmead); (i) *Euidella* sp.; (j) *Metropis nigrifrons* Kusnezov; (k) *Harmalia heitensis* (Matsumura); (l) *Euidellana celadon* Fennah; (m) *Cemus nigromaculosus* (Muir); (n) *Cemus* sp. A; (o) *Cemus* sp. B; (p) *Laodelphax striatellus* (Fallen).

Biology of planthoppers

A major salient feature in the biology of planthopper species is their ontogenetic development. This is the universal process in planthoppers occurring immediately after bisexual reproduction. It consists of sequential stages—from the immediate product of reproduction (= fertilized egg or zygote), instar nymphs, till the formation of mature dimorphic adults (= fully-winged macropterous and truncate-winged brachypterous forms) of both sexes. Planthoppers exhibit incomplete or hemimetabolous development. The duration of each stage depends on temperature and host cultivars. In the case of *Nilaparvata lugens* (Stål), Nasu and Suenaga (1956) and Mochida (1970) described its embryonic development.

Egg stage

Upon emergence of adult planthoppers, for instance, for the brown planthopper, *N. lugens*, bisexual mating occurs and their oviparous female starts laying eggs from the day following mating. The pre-oviposition period of planthoppers ranges from 3 to 8 days. Brachypterous females have a shorter pre-oviposition period (3 to 4 days) than macropterous females (3 to 10 days) under cool conditions. Brachypters begin to oviposit earlier than macropters. More eggs (60 to 500) are laid as egg-groups by brachypterous females than the macropters. In most cases, the eggs are thrust in a straight line, generally on the lower part of the host plant along the mid-region of the leaf sheath, though sometimes eggs are laid in clusters of 4–10 in longitudinal rows within the leaf midribs. For instance, the female rice delphacid, *Tagasodes orizicolous* (Muir), lays 300 to 500 eggs in batches of 7 in the midribs of rice leaves (Dale 1994). *N. lugens* females lay 100 to 500 eggs depending on the stage of growth of the rice plant (Van Der Laan 1981). In the greenhouse, each female lays about 100 to 200 eggs. The number of eggs laid by female delphacids during their life span ranges between 0 and 1,474. The number of eggs laid is correlated to life span and ovipositional period.

Eggs are covered with a dome-shaped egg plug secreted by the accessory glands of the female. The white eggs of planthoppers are similar in shape (oblong or longitudinally ovate and slightly curved) and size (0.1 mm) but may vary in egg plug, wherein the whitebacked planthopper, *Sogatella furcifera* Horvath, has a longer and more pointed egg plug than *N. lugens*. Only the tips or minute operculum of eggs protrude from the plant surface. The number of eggs laid at a site varies in different countries. For instance, *S. furcifera* laid 164 eggs in India (Vaidya and Kalode 1981) and 300 to 350 in Japan (Suenaga 1963). The egg of *N. lugens* consists of the chorion, vittelline membrane, protoplasm, nucleus, yolk, and mycetocyte. Because of its shape, the mycetocyte is set apart from the other egg contents. Meanwhile, steps involved in embryo formation start to proceed after maturation, fertilization, and cleavage. This happens at the posterior pole of the egg on the first and second day after oviposition. A pit or depression appears on the posterior pole at 28 to 32 hours after oviposition and then develops into a deep slender tube. The mycetocyte remains situated on top of the vagination as invagination progresses. The process continues in such a way that the ventral surface of invagination faces the egg's dorsal side. On the other hand, the

posterior portion is in the direction of the egg's anterior pole. By the second day, the invagination develops; the movement of the mycetocyte is toward the anterior pole. The third day allows observers to distinguish the head, thoracic, and abdominal parts, and, by the fourth and early fifth day, the invagination's top and tail are bent. At the same time, the mycetocyte movement is along the egg's ventral side—specifically the posterior pole. With the original position of the embryo reversed, the mycetocyte goes back to its original position. At this point, blastokinesis is said to be complete (Mochida and Okada 1979). Prior to hatching, red eye spots appear at the end of the eggs. In about 4 to 15 days, the eggs of planthoppers hatch. The egg stage of *N. lugens* is about 7 to 11 days in the tropics.

The hatchability and survival of planthopper eggs occur at around 25 °C. Eggs are very sensitive to dessication and soon shrivel when the host plant starts wilting (Kisimoto 1977). The embryonic and postembryonic developments of planthoppers occur at 10.8 and 9.0 °C, respectively.

The eggs in diapause were defined as those still alive after 24 hours at −4 °C. Diapause in the egg stage was reported to occur in planthoppers. Female planthoppers were induced to deposit diapausing eggs under low temperature coupled with short photoperiod in rice plants at the ripening stage (Miyake and Fujiwara 1962, Okamura 1963, Sugimoto 1967). Nasu (1967) studied the eggs in diapause in seven delphacids. In diapause eggs, embryonic development stopped just before the blastokinesis stage. Embryonic development ensued when eggs were kept at 25 °C within several days and the eggs hatched. These phenomena were not observed in the eggs of *N. lugens*.

Nymphal stage

After embryonic development, the eggs of planthoppers hatch into first-instar nymphs after being laid. The shell is normally burst open by the muscular activity of the nymph, which may swallow air or amniotic fluid, and thus increase its volume as the pressure exerts. Planthoppers have five-instar nymphs that actively feed on the host plant's phloem sap to become adults. In the case of *S. furcifera*, the nymphs prefer weeds for feeding. Usually, the newly-hatched first-instar nymph is cottony white and turns purple-brown within an hour in *N. lugens*, whereas, in *S. furcifera*, from white, it is transformed into strongly mottled dark gray or black and white in color.

In the case of *N. lugens*, the five nymphal stadia are distinguished by shapes of the mesonotum, and body size. Both embryonic and postembryonic development are influenced considerably by temperature. The nymphal period of planthoppers varies widely depending on food conditions, density during development, and other environmental factors. For example, *N. lugens* in the tropics takes about 10 to 18 days from the hatching of the first-instar nymph till adult stage, while *S. furcifera* takes 12 to 17 days. On seedlings of susceptible high-yielding cultivar Pelita 1-1, the periods of planthopper development are as follows: egg (8–9 days), nymphs (13–15 days), macropterous males (8–9 days), and macropterous females (11–12 days). In *N. lugens*, the nymphal period is shorter for the brachypterous form than for the macropterous form in both sexes and, even at high densities, the nymphal period of the brachypter-

ous insect is fairly constant, whereas that of the macropterous insect is lengthened by greater density (Kisimoto 1957).

The temperature conditions in the nymphal stage affect the longevity and oviposition of adult hoppers (Mochida 1964). At a temperature of 25 °C, the nymphal period of *L. striatellus* is about 2 weeks. In the case of *N. lugens,* the minimum growth of nymphs is at a temperature range of 28 to 30 °C in the daytime and at a slightly lower temperature at night. In warm humid climates, planthoppers remain active throughout the year and their population fluctuates according to the availability of host plants, activity of natural enemies, and other prevailing environmental factors. When fifth-instar female nymphs are irradiated at 15 to 20 Krad Cobalt 60, egg formation is interrupted (Mochida 1973).

Adult stage

The nymphs stay on the lower parts of host plants and the emergence of adults takes place at the basal part of the host plant. However, when the population is very high, for instance in Java with 500 hoppers per hill, adults were observed to swarm even on flag leaves, the uppermost internodes of panicles, and panicle axes. The dimorphic adults with two wing forms may have either the male longer (3.5 mm) than the female (2.0 mm) as in *L. striatellus* or vice versa as in *N. lugens*, wherein the male is shorter (4.5 mm) than the female (5.0 mm).

Female planthoppers initiate copulation by producing abdominal vibrations from a distance of 80 cm. Male *N. lugens* can mate with a maximum of nine females for 24 hours and an individual female can copulate more then twice during its lifetime (Mochida and Okada 1979).

The total life cycle of planthoppers is about 9 to 26 days or 3 to 4 weeks and a new generation may appear monthly. In Java, four to five generations of hoppers may develop in one rice crop. Mochida et al (1977) reported that *N. lugens* may have two to eight generations during one rice cropping season in tropical lowlands. In fact, *N. lugens* has five generations on a single rice crop in southern Japan (Mochida 1964), five or six generations in the central part of China (Lei and Wang 1958), and four or five generations in Java (Mochida et al 1977). *L. striatellus* has six to seven generations in a year and, in Japan, it hibernates as last-instar nymphs in winter wheat. The emerging adults then move into transplanted rice in late May and early June (Dale 1994).

Adult planthoppers live for 18 to 20 days, while a generation takes 3 to 4 weeks. The adult longevity of *N. lugens* differs considerably between laboratory and field conditions, the maximum values being 36.6 and 9.0 days, respectively. (For a more detailed discussion on the biology and ecology of planthoppers, please refer to Denno and Perfect [1994].)

The delphacid planthopper food web

Of the delphacid planthoppers dwelling in rice agroecosystems, the brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae), is the first to have its food web

constructed (IRRI 1980, Barrion et al 1981). The BPH food web is simple and has only 76 taxa represented by 11 parasitoids, 11 secondary natural enemies, and the rest are predators dominated by 50 species of spiders (65.8% of total taxa in the web). In 1981, Yasumatsu et al (1981) reported the food chain relationship between planthoppers and leafhoppers of rice and their natural enemies in Thailand. The web reported 12 species of parasitic Hymenoptera attacking the egg stage, namely, *Paracentrobia* (two species) and *Oligosita* (three species) in the family Trichogrammatidae; *Anagrus* (three species), *Gonatocerus, Mymar, Gonatocerus,* and *Polynema* in family Mymaridae; and *Tetrastichus formosanus* Timberlake in family Eulophidae. At the nymphal stage, the dryinids (*Haplogonatopus orientalis, Pseudogonatopus hospes,* and *Echthrodelphax fairchildii*), a strepsipteran (*Elenchus yasumatsui*), and an unidentified nematode are listed. Although three big-headed flies—*Tomosvaryella oryzaetora*, *T. subvirescens,* and *Pipunculus mutillatus*—are included in the food chain, these flies are specific to green leafhoppers, *Nephotettix* and *Balclutha*. Within the same web are the predators represented by more than 20 species of insects and series of unidentified taxa of invertebrates (ants, damselflies, and spiders) and vertebrates (fishes, birds, and bats). It is surprising that toads and frogs are excluded in the planthopper and leafhopper food chain in Thailand.

In 1988, the International Rice Research Institute (IRRI) reported the second planthopper food web representing *Sogatella* spp. (*S. furcifera, S. vibix*, and *Tagosodes pusanus*). The whitebacked planthopper (WBPH) food web has 199 species consisting of 139 predators and 33 parasitoids. Of total predators, spiders once again are the major players and most abundant, accounting for as much as 70% (63 species) of total taxa. We presume that spiders must have played a major regulatory function against planthoppers. Overall, the key predators in the WBPH food web are similar to those of the brown planthopper.

The present version of the delphacid planthopper food web (Fig. 6) is an expanded model of the intricate relationships of the invertebrates (insects, mites, and spiders), vertebrates, nematodes, and pathogens in the rice agroecosystems in tropical Asia. It consists of 244 species, with 89.34% (218 species) invertebrates, 6.97% (17 species) vertebrates, 2.46% (6 species) pathogens, and 1.23% (3 species) nematodes (Table 2). This excludes the 48 taxa of hyperparasites/hyperpredators and the spiders that may behave as hyperpredators as well.

Egg parasitoids of delphacid planthoppers

Members of the superfamily Chalcidoidea are among the parasitic Hymenoptera that play an important role in regulating planthopper populations in the agricultural landscape of rice agroecosystems. These are often called "little murderers" as their parasitic action disables planthopper eggs from developing ahead and becoming adults. Members of the group are basically parasitoids and parasitic in their pre-imaginal stages and free-living as adults. Similar to leafhoppers (Freytag 1983), planthoppers are heavily regulated by egg parasitoids.

About 56 species of parasitic Hymenoptera use the eggs of some 23 species of planthoppers in tropical Asia (Table 3). The egg parasitoids belong to four chalcidoid

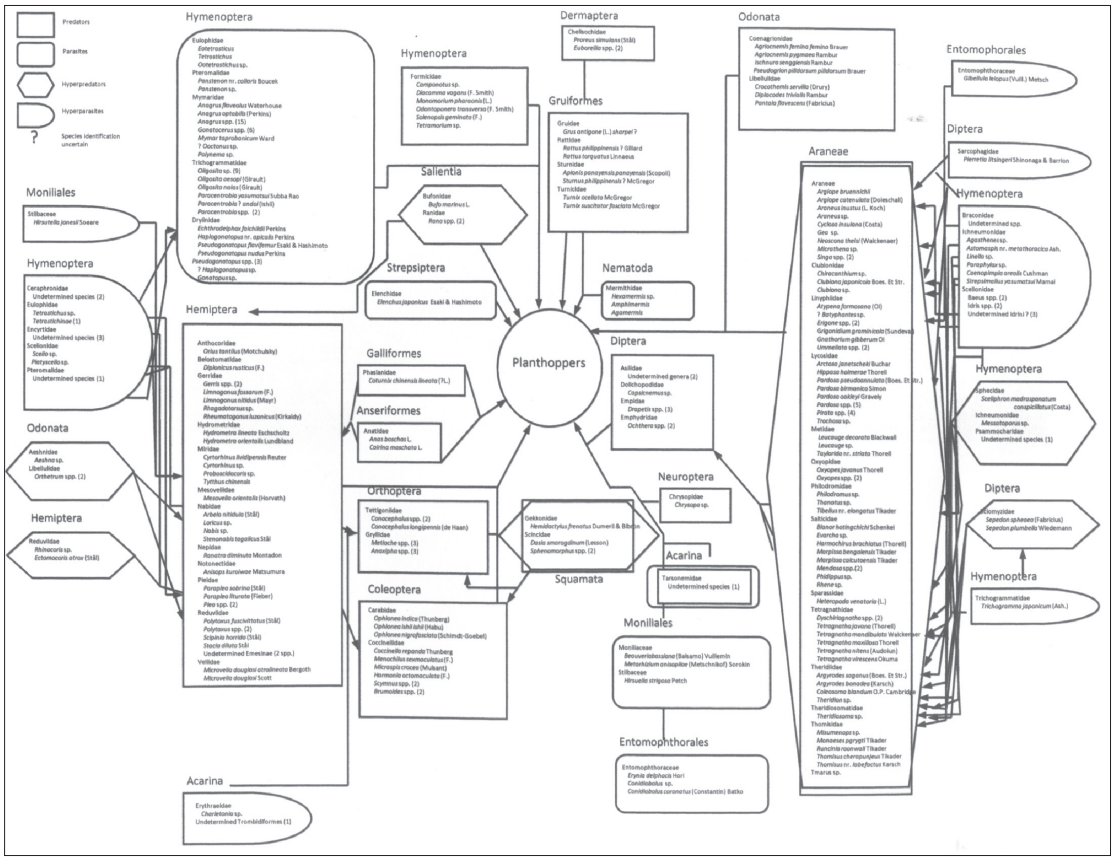

Fig. 6. Food web of planthoppers in the rice agroecosystems of tropical Asia.

Table 2. Summary of natural enemies of delphacid planthoppers in tropical Asia.

Group	No. of species	Composition (%)
Invertebrates	(218)	(89.34)
Parasitic Hymenoptera	66	27.04
Strepsiptera	1	0.41
Acarina	1	0.41
Predators	150	61.48
Araneae	72	29.51
Hemiptera	34	13.93
Coleoptera	11	4.51
Orthoptera	9	3.69
Odonata	7	2.87
Diptera	7	2.87
Hymenoptera	6	2.46
Dermaptera	3	1.23
Neuroptera	1	0.41
Vertebrates	17	(6.97)
Gruiformes	7	2.87
Salientia	3	1.23
Squamata	3	1.23
Anseriformes	2	0.82
Galliformes	2	0.82
Nematodes	3	(1.23)
Nematoda	3	1.23
Pathogens	6	(2.46)
Entomophthorales	3	1.23
Moniliales	2	0.82
Stilbaceae	1	0.41
Total	244	100

Table 3. Summary of the parasitic Hymenoptera egg parasitoids of delphacid planthoppers and their host range.

Parasitoids	Species (no.)	Composition (%)	Delphacid hosts
Family Mymaridae			
Anagrus	17	30.4	*L. striatellus, Toya* sp., *Delphacodes* sp., *U. sapporonus, Dicranotropis nagaragawana, Stenocranus* sp., *N. lugens, N. bakeri, Stenocranus minutus, Delphacidae, Sogatella vibix, P. maidis, Hirozunka japonica, Tagosodes pusanus, Perkinsiella saccharicida* *Tarophagus proserpina, Sogatella furcifera, T. propinqua* *Pundaluoya simplicia, Harmalia sameshimai*
Gonatocerus	6	10.7	*N. lugens, U. sapporonus, T. pusanus, N. bakeri* *Sogatella vibix, ?Perkinsiella/?Peregrinus, Toya* sp., *Sogatella furcifera*
Mymar	3	5.4	*N. lugens, T. pusanus, Sogatella furcifera*
Acmopolynema	2	3.6	*T. pusanus, Toya propinqua*
Anaphes	1	1.79	*N. lugens*
Camptoptera	1	1.79	*Tarophagus colocasiae*
Eomymar	1	1.79	Undet. Delphacidae
?Ooctonus	1	1.79	*N. lugens, Sogatella furcifera*
Polynema	1	1.79	*N. lugens,* Undet. Delphacidae
Family Trichogrammatidae			
Oligosita	11	19.6	*N. lugens, T. pusanus,* planthopper, *N. bakeri* *S. furcifera, Toya* spp. *(2), U. sapporonus, S. vibix, Tarophagus colocasiae*
Paracentrobia	4	7.14	*N. lugens, N. bakeri, Toya* spp. (2), planthopper *H. sameshimai, S. furcifera, S. vibix, T. pusanus*
Aphelinoidea	1	1.79	*N. lugens*
Trichogramma	1	1.79	*N. lugens*
Family Eulophidae			
Ootetrastichus	2	3.6	*N. lugens*
Eotetrastichus	1	1.79	*N. lugens, S. furcifera, T. pusanus*
Tetrastichus	1	1.79	Undet. Delphacidae
Family Pteromalidae			
Panstenon	2	3.6	*N. lugens, N. bakeri, Toya* spp. (2), *S. vibix, U. sapporonus*

families—Mymaridae (33 species and 9 genera), Trichogrammatidae (17 species and 4 genera), Eulophidae (4 species and 3 genera) and Pteromalidae (2 species and 1 genus). Among the mymarids, the most dominant egg parasitoids are in two genera—Anagrus (17 species) and Gonatocerus (6 species). Other members of the family Mymaridae reported on eggs—*Acmopolynema, Anaphes, Camptoptera, Eomymar, Mymar, Ooctonus,* and *Polynema* played a small role in natural control of planthoppers based on their records of occurrence on reared egg masses. Equally important are the tiny wasps in the family Trichogrammatidae best represented by two genera—Oligosita (11 species) and Paracentrobia (four species). Occasionally reared from the eggs are the eulophids and pteromalids with four and two species, respectively. However, the latter group is considered an egg predator rather than egg parasitoid. An example is *Panstenon* sp. (Hymenoptera: Pteromalidae), reported by Claridge (1987) as an egg predator.

We conclude that the four genera of chalcidoids—*Anagrus* and *Gonatocerus* (family Mymaridae) and *Oligosita* and *Paracentrobi*a (family Trichogrammatidae)—are the key egg parasitoids that inflict heavy pressure on planthoppers. Egg parasitization, however, may vary from 12% to 100% depending on the environmental quality and perturbations (Otake 1977, Chandra 1978, Miura et al 1979, Vungsilabutr 1981, Kim et al 1982, Claridge 1987).

Nymphal-adult parasitoids/parasites of delphacid planthoppers

Table 4 documents the parasitoids and parasites attacking the nymphs and adults of planthoppers in rice agroecosystems. There are 21 species of natural enemies at the nymphal-adult stage of planthoppers. In terms of species richness, the order of preponderance of these natural enemies is as follows—Drynidae (10 species) > pathogens (6 species) > nematodes (3 species) > mite and strepsiptera (2 species). The dryinids are perhaps the most interesting among the parasitoids of nymphs and adults because of their dual type of behavior, namely, as a parasitoid and as a predator. In both cases, the dryinids incapacitate or kill the host. Planthoppers parasitized by dryinids show an enlarged encapsulation called "thylacium" attached to the body of the host. This structure contains the larva of the dryinid. The color (varying from black to reddish brown or brown) and skin design (smooth and shiny or netted) of the thylacium can be used to identify the species at the generic level. It (thylacium) bursts and opens when the larva is ready to pupate. Pupae wrapped by light brown or whitish silken threads are commonly seen attached on or glued to the rice or grass foliage. Dryinids have two forms—wingless with chelate leg I and winged. The winged form (except for *Echthrodelphax*) is often identified as a braconid wasp belonging to the genus *Cotesia*. But the number of antennal segments (only about 10) and the distinctly long segments are unique among winged dryinids, and these features isolate them from braconids.

In rice agroecosystems, the most common species of dryinids belong to the four genera, namely, *Pseudogonatopus* (five species), *Haplogonatopus* (three species), and one each for *Echthrodelphax* and *Gonatopus*. Olmi (1984) provided a solid understanding of the taxonomy of family Dryinidae at the world level.

Table 4. Checklist of parasitoids and parasites attacking the nymphal-adult stages of planthoppers.

Parasitoid/parasite	Delphacidae hosts
Hymenoptera: Dryinidae	
Echthrodelphax fairchildii Perkins	*N. lugens, S. furcifera, L. striatellus, P. saccharicida*
Haplogonatopus apicalis Perkins	*N. lugens, L. striatellus, S. furcifera, T. pusanus*
Gonatopus yasumatsui Olmi	*N. lugens*
Haplogonatopus oratorius (Westwood)	*L. striatellus*
Haplogonatopus atratus Esaki & Hashimoto	*L. striatellus*
Pseudogonatopus sarawaki Moczar	*N. lugens, Sogatella* sp.
Pseudogonatopus nudus Perkins	*N. lugens, S. furcifera*
Pseudogonatopus fulgori (Nakagawa)	*S. furcifera, L. striatellus*
Pseudogonatopus flavifemur Esaki & Hashimoto	*N. lugens, S. furcifera, S. vibix, T. pusanus*
Pseudogonatopus hospes Perkins	*N. lugens, S. furcifera*
Strepsiptera: Elenchidae	
Elenchus japonicus Esaki & Hashimoto	*Harmalia* sp., *N. lugens, S. furcifera, S. vibix, L. striatellus*
Acarina: Erythraeidae	
Charletonia sp.	*N. lugens, S. furcifera, L. striatellus*
Nematoda: Mermithidae	
Agamermis sp.	*N. lugens*
Amphimermis sp.	*N. lugens*
Hexamermis sp.	*N. lugens*
Moniliales: Moniliaceae	
Beauveria bassiana (Balsamo) Vuillemin	*N. lugens*
Metarhizium anisopliae (Metchnikoff) Sorokin	*N. lugens, S. furcifera, T. pusanus*
Moniliales: Stilbaceae	
Hirsutella strigosa Petch	*N. lugens, S. vibix, S. furcifera, T. pusanus*
Entomophthorales: Entomophthoraceae	
Erynia delphacis Hori	*L. striatellus, N. lugens*
Conidiobolus sp.	*N. lugens*
Conidiobolus coronatus (Constantin) Batko	*N. lugens*

The biological control potential of the four genera *Echthrodelphax, Gonatopus*, *Haplogonatopus,* and *Pseudogonatopus* has been well recognized in China (HAAI 1978), Taiwan (Chiu 1979), Japan (Esaki 1932, Une et al 1989), Thailand (Yasumatsu et al 1981), Malaysia (Pagden 1934, Van Vreden and Ahmadzabidi 1986), and the Philippines (Chandra 1980, Chua and Dyck 1982). The potential for biocontrol of *Pseudogonatopus flavifemur* Esaki & Hashimoto against the brown planthopper was assessed only at the International Rice Research Institute in 1982. It was reported that *P. flavifemur* is a strong biocontrol agent because of the following attributes: (1) voracious feeder that can kill 38.8 brown planthoppers in a day, (2) strong preference for *N. lugens* compared with *Sogatella furcifera* (Horvath) and *Nephotettix* spp., (3) demonstrated a sigmoid functional response curve and positive aggregative behavior, (4) reduced *N. lugens* populations in the field and damage of planthopper to plants, and (5) short handling time and ease for mass rearing.

Pathogens and nematodes represent the other mortality factor for planthoppers. Their occurrence on planthoppers is relatively uncommon but they may at times impact the population of planthoppers if environmental conditions are conducive to their growth. Occasionally, *Metarhizium, Hirsutella,* and *Beauveria* are observed on the brown, whitebacked, and maize planthoppers while *Entomophthora* is on the taro planthopper. Overall in the tropics, the contribution of pathogens and nematodes to the control of planthoppers remains low, similar to the strepsipterans. Enhancing the effectiveness of these nymphal-adult parasitoids/parasites in mitigating planthopper populations in the agricultural landscape is a gray area for research.

Predators of planthoppers

Planthoppers in rice agroecosystems have an estimated total of 167 species of predators distributed into nine orders of invertebrates and five orders of vertebrates (Table 2). In terms of species richness, the top two invertebrate predators of planthoppers are in order Araneae (spiders) and order Hemiptera (true bugs), represented by 72 and 34 species, respectively. The rest belong to the third group with about 1–11 species. These are Coleoptera (11 species), Orthoptera (9), Odonata (7), Diptera (7), Hymenoptera (6), Dermaptera (3), and Neuroptera (1).

Among the predatory spiders, the family Lycosidae is the most known, being commonly abundant in rice agroecosystems and unique not only because it is species rich in having 15 species represented by at least five genera—*Arctosa, Hippasa, Pardosa, Pirata,* and *Trochosa*—but also because of its strong predatory attributes. These attributes are (1) excellent hunting behavior brought about by the 3-row eye arrangement with powerful vision exerted by the large posterior eyes—the posterior median (PME) and posterior lateral (PLE) eyes; (2) voracious and gregarious predator; (3) at home in both dryland and wetland environments; and (4) highly competitive. In tropical Asia, the most widespread species of wolf spiders (family Lycosidae) are *Pardosa pseudoannulata* (Boesenberg and Strand) and several species of *Pirata*. Both the biology and ecology of these taxa are well studied. Irregardless of crop age, lycosids are present in rice ecosystems where planthoppers may be present. However,

these spiders are highly visible during the vegetative to maximum tillering stages of the rice plant. Being semiaquatic, these lycosids can live under water submerged for quite some time if endangered. For the young nymphs of planthoppers, the predatory specialists belong to four families: Linyphiidae (*Atypena, Erigone, Gnathonarium, Ummeliata, Erigonidium*), Theridiidae (*Enoplognatha*, *Theridion,* and *Coleosoma*), Theridiosomatidae (*Theridiosoma* and *Wendilgardia*), and Tetragnathidae (*Tetragnatha* and *Dyschiriognatha*). Migrating populations of planthoppers do not escape predatory spiders. To a certain extent, a number of migrant populations get entangled in the network of spider webs nicely laid on the plant canopy in the early morning or late in the day when the weather is good. Those caught by these specialists belonging to the family Araneidae (*Araneus, Neoscona,* and *Argiope*) and Tetragnathidae (*Tetragnatha, Leucauge,* and *Taylorida*) succumb to death in the web, others are wrapped, while others are devoured by the spiders.

In the vertebrates, the order of preponderance is Gruiformes (seven species) > Salientia and Squamata (three each) > Anseriformes and Galliformes (two each).

In the true bugs, the spiders are perhaps best equaled in their capacity to control planthopper populations by the aquatic and semiaquatic bugs belonging to the families Gerridae, Veliidae, Mesoveliidae, Pleidae, Hydrometridae, and Miridae. However, except for the mirid bug, *Cyrtorhinus lividipennis* Reuter, and the veliid bug, *Microvelia douglasi atrolineata* Bergroth, and the spiders, *Pardosa pseudoannulata* (Boesenberg and Strand) and *Pirata* spp., little is known about their biology, their interactions with other players in the agroecosystems, the role of competition within and among predators, and the impact of the wide taxonomic array of predators on planthopper control.

Among the invertebrate predatory groups, the other notable species that prey on planthoppers are the larvae and adults of coccinellid beetles—*Micraspis, Harmonia,* and *Coccinella* (Coccinellidae), *Ophionea* (Carabidae), and *Paederus* (Staphylinidae) in order Coleoptera; *Conocephalus* (Tettigoniidae), *Metioche,* and *Anaxipha* (Gryllidae) in Orthoptera; *Agriocnemis, Ischnura,* and *Pseudagrion* (Coenagrionidae), and *Diplacodes*, *Crocothemis,* and *Pantala* (Libellulidae) in Odonata; *Ochthera* (Ephydridae) and *Drapetis/Elaphropeza* (Empididae) in Diptera; *Solenopsis* and *Monomorium* (Formicidae) in Hymenoptera; *Proreus* and *Euborellia* (Chelisochidae) in Dermaptera; and *Chrysopa* (Chrysopidae) in Neuroptera. Their collective effort in predation on planthoppers in the natural environment may have been undocumented but long hours of field observation on the natural history of these predators provided the proof of their important role in agroecosystems. Hence, we conclude that the combined network of predation by this broad array of predators thriving sympatrically in rice agroecosystems provides heavy pressure on the nymph and adult populations of planthoppers. These invertebrates are like well-oiled machines in terms of predation and they use the agroecosystem as a niche to effectively hunt their prey.

In general, delphacid planthoppers at various growth stages—instar I to adult—are good food supplements that comprise the nutritional diet requirements of predators. However, in terms of host (delphacid planthoppers)-natural enemy associations, most

records (>93%) are biased to a few taxa of delphacids, namely, *Nilaparvata lugens, Laodelphax striatellus,* and *Sogatella furcifera*.

Key to the parasitic Hymenoptera egg parasitoids (only for Trichogrammatidae and Mymaridae)

Plate 41a-e

1 Tarsi 3-segmented (Family Trichogrammatidae).....2
1' Tarsi 4-5 segmented (Family Mymaridae).....11

2 Antennal funicle with 2 ring-like segments and 2 longer segments; discal ciliation on forewings varies from sparse but arranged rows of cilia to a dense mat with short and randomly distributed cilia; marginal fringe of forewings short, distinctly less than half wing width 3
2' Antennal funicle of female with 2-segmented funicle (ring + funicle only); discal ciliation sparse but usually in rows; marginal fringe of forewings at least one-half width of the wings at its broadest point.....4

3 Forewing with a narrow smoky or brownish tinge across wing beneath stigma vein; scape as long as combined length of pedicel and funicle; gaster pale yellow with tergites laterodorsally dark brown ..... *Paracentrobia yasumatsui* Subba Rao
3' Forewing with a rounded brown mark beneath stigma vein; scape a little longer than combined length of pedicel and funicle; abdominal tergites I-IV uniformly brown .....*Paracentrobia andoi* Ishii

4 Marginal fringe of forewings one-third to one-half the maximum width of wings.....5
4' Marginal fringe of forewings slightly shorter or longer than maximum width of wings.....6

5 Discal cilia long and coarse; marginal fringe of forewing about half maximum width of wings and always greater than one-third; pedicel 3x as long as funicle segment, the latter prominently wider than long; scape broadened basally, funicle and basal two clubs bisected medially by a transverse row of long setae; light yellowish brown .....*Oligosita brevicilia* Girault
5' Discal cilia short, fine, and very sparse, at least 10 rows visible; marginal fringe barely one-third maximum width; pedicel about half of scape; stigma vein knoblike with subtruncate apex; orange-bodied species with light yellow-brown legs.....*Oligosita consanguinea* Girault

6 Pedicel as long as the short and clavate scape; funicular segment longer than broad; forewings with distinct and large substigmal cloud; yellow except for fuscous tips of coxae and midfemora, and dark brown basal half of abdomen ..... *Oligosita manii* Viggiani

6' Pedicel usually much shorter than scape 7

7 Pedicel almost as long as the narrow funicle; club as long as the combined length of pedicel, ring, and funicle segments; cilia on discal area very few and scarce, a single complete row lining the apical end of wing and 10 more cilia irregularly scattered at the distal end ..... *Oligosita shibuyae* Ishii

7' Pedicel at least twice as long as funicle 8

8 Marginal fringe of forewing as long as or longer than maximum width of wings; discal cilia moderately sparse 9

8' Marginal fringe of forewing more than 0.7 maximum width of wing 10

9 Marginal fringe of forewing distinctly longer than maximum wing width; pedicel more than twice the length of funicle, the latter slightly wider than pedicel; sheath of ovipositor not exserted ..... *Oligosita naias* Girault

9' Marginal fringe and maximum width of forewing equally long; funicle half the length of pedicel; sheath of ovipositor distinctly exserted ..... *Oligosita yasumatsui* Viggiani & Subba Rao

10 Marginal fringe of forewing only slightly shorter than maximum wing width; discal ciliation rather thick opposite subtriangular stigma vein, moderately scattered toward distal end; pedicel more than 2x longer than funicle ..... *Oligosita aesopi* Girault

10' Marginal fringe almost as in *O. aesopi*; funicle subglobular and less than half of pedicel; discal ciliation more evenly scattered toward distal end, without dense ciliation opposite the knoblike stigmal vein. *Oligosita nephotettica* Mani

11 Gaster with more or less distinct petiole, convexly rounded or subglobular basally; mesopostphragma not projecting into the gaster; tarsi 4-5 segmented 12

11' Gaster broadly connected to propodeum; mesopostphragma plainly projecting into gaster; a pair of distinctly separated plates behind scutellum; antennae 9-segmented in females, 13-segmented in males; tarsi 4-segmented (*Anagrus*) 22

12 Tarsi 5-segmented 13

12' Tarsi 4-segmented 20

13 Petiole long and slender; propodeum prominently carinated; antenna 11-segmented with 8 funicular segments and undivided club ..... *Ooctonus* sp.

13’ Petiole short, wider than long; antennae of male 13-segmented and female 11-segmented, with 8 funicular segments; marginal vein not elongated, venation not reaching basal one-third of wing; gaster subsessile (*Gonatocerus* spp.) ... 14

14 Anal plate with 4 long hairs ... 15
14’ Anal plate with more than 4 long hairs ... 17

15 Apical 4 funicular segments as long as or slightly shorter than the basal 4, 4th to 6th segment equally long and cylindrical, without sensory ridge; segments VII and VIII with a pair of sensory ridges each; median mesoscutum with a subglobular brown band in apical half; forewing 4.5x as long as wide; anal plate large, tapers apically and pygostyle indented sub-basally inside ... *Gonatocerus uttardecanus* Mani & Saraswat
15’ Apical 4 funicular segments distinctly longer than basal 4 ... 16

16 Funicular segments V-VIII cylindrical to subcylindrical and longer than 4 basal segments, equally long with a pair each of sensory ridges; entire median area of mesoscutum occupied by a brown band except lateral margin near parapsidal furrow; forewing 3x longer than wide; anal plate short hairs in 2 rows, apex of plate pointed; pygostyle without indention; postphragma very flat ... *Gonatocerus narayani* (Subba Rao & Kaur)
16’ Funicular segments V-VIII globular, each with sensory ridges except segment VI, and segment VIII with a cavity; mesoscutum moderately produced and rounded apicomedially with a brown band above tip of parapsidal furrow; forewing rather concave along anterior margin, about 4x as long as wide; marginal vein 7.4x as long as wide; proximal sensillium midway of distal sensilla and distal macrochaeta; 4 anal plate hairs in a transverse row in apical one-third and with cleft apex ... *Gonatocerus devitatacus* Mani & Saraswat

17 Anal plate triangular with 7 long hairs, mostly along margins; apicomedian band of mesoscutum reaching only the anterior pair of setae; forewing slightly constricted near stigma vein, nearly 4x as long as wide; marginal vein 14x as long as wide; stigma vein bears 3 distal sensilla; pedicel as long as funicular segment III, F6 = F7; club nearly as long as radicula and scape; abdomen light yellow except blackish brown tergites V and VI ... *Gonatocerus munarus* Mani & Saraswat
17’ Anal plate subovoid to ovoid; funicular segments of various lengths ... 18

18 Anal plate ovoid with 5 hairs in 3 transverse rows; basal funicular segment of antennae shortest in both sexes, 0.7 as long as 2nd, 2nd and 3rd subequal, 4th to 8th equally long, a pair of sensory ridges only in segments V to VIII in female, all segments in male except scape and pedicel; lateral side of mesoscutum behind parapsidal furrow entirely yellowish brown to brown; forewing 4x as long as wide; proximal sensillium just below distal macrosetae; ovipositor highly exserted ..... *Gonatocerus cicadellae* Nikolskaya

18' Anal plate subovoid; basal 3 funicular segments equally long 19

19 Anal plate bluntly conical with 5 long hairs in 2 transverse rows medially; female antennae with 4th and 6th funicular segments globular and equal in length, 6th the shortest, paired sensory ridges in segments V, VII, and VIII; shortest funicular segment 1 (F1) as long as scape, club = F3 = F4 = F8 = F10 in male; discal hairs a little beyond base of marginal vein in origin; abdomen with alternating yellow and brown transverse bands ..... *Gonatocerus cincticipitis* Sahad

19' Anal plate narrowly conical with a subacute apex; female funicular segments IV, V, and VI globular and equally long, paired sensory ridges only in VII and VIII segments; funicular segment X (F10) as long as club, and longer than F6 to F8 in male; discal hairs emanate from base of marginal vein and form a prominent oblique line to posterior margin; abdomen with 4 brown interrupted transverse bands ..... *Gonatocerus miurai* Sahad

20 Hindwings abbreviated, filiform, and highly reduced, poorly developed into a whiplike process without the wing blade; forewing oarshaped, distal half of broad part dark brown with 1 clear row of setae traversing middle from shaded to light area and 2–3 short rows of setae dorsad shaded portion; marginal fringe 4x maximum wing width; scape medially thin, enlarged on both ends, funicle II longest and segment III to VI short and together with undivided club longer than F2 ..... *Mymar taprobanicum* Ward

20' Without the combination of above characters 21

21 Scape without scalelike structures; marginal vein thickened; prothoracic spiracle in normal position ..... *Polynena* sp.

21' Scape with scalelike markings, pedicel broad, funicles I-III long and in decreasing length, and in increasing diameter toward club; marginal vein thin; prothoracic spiracles positioned toward midbody, on the line between pronotum and mesoscutum ..... *Stephanodes imbricatus* (Narayanan & Subba Rao)

22 Funicular segment I long, usually 2x as long as wide; scape smooth without transverse ridges 23

22' Funicular segment I very short, subglobular; scape transversely carinated 24

23 Funicular segment I slender and longer than pedicel; antennae long and narrow; ovipositor hardly exserted, ratio of ovipositor and exserted part 20:1; disc of forewing narrow, nearly parallel-sided, with 1 row in basal two-thirds and 2 rows in apical one-third ..... *Anagrus optabilis* (Perkins)

23' Funicular segment I shorter or as long as pedicel 24

24 First funicular segment as long as pedicel; ovipositor highly exserted; apical 2 segments of tarsi III as long as the exserted part of ovipositor; disc of forewing with slightly dilated apical third, ciliation in an irregular row toward basal half and in 2–3 irregular rows in apical third ..... *Anagrus perforator* Perkins

24' First funicular segment distinctly shorter than pedicel; ovipositor just moderately exserted, length of exserted part as long as apical segment of tarsus III; ratio of ovipositor and exserted part 5.4:1; proximal two-thirds of forewing parallel after marginal vein, distal one-third gradually expanded and curved with long marginal cilia, a long midlongitudinal line of discal hairs from discal end of marginal vein to wing apex present, accompanied by another irregular short line of 6–8 hairs dorsad of long line ..... *Anagrus panicicolae* Sahad

25 Distal end of forewing disc dilated 26

25' Distal end of forewing disc not dilated; second funicular (F2) segment longest 28

26 Marginal vein with 2 long setae; forewing with 3–4 rows of discal hairs with distinct small bare space at widest part; F1 very small and subglobular, F2 longer than F3 and the longest; gaster conical; ovipositor moderately exserted ..... *Anagrus flaveolus* Waterhouse

26' Marginal vein with only 1 long seta 27

27 Forewing with 8–9 irregular rows of discal hairs and without bare or hyaline space at its widest part; 3rd funicle segment with only 1 sensory ridge; ovipositor moderately exserted, ratio of ovipositor and its exserted part 9.2:1 ..... *Anagrus incarnatus* Haliday

27' Forewing with 2 regular rows (rarely 3) of discal hairs and with hyaline space in its widest part; ciliation moderately more toward proximal end; ovipositor clearly exserted beyond tip of abdomen; club with a single sensorium ..... *Anagrus* sp. A

28 Funicular segment II longest; segment IV to VI subequal in length and diameter; discal ciliation 2 lines, forms a long clear hyaline area distally; marginal fringe almost 3x the maximum width of wing; ovipositor short to slightly exserted ..... *Anagrus frequens* Perkins

28' Funicular segment II as long as segment IV; may or may not be as long as segment VI; ovipositor short to long 29

29 Ovipositor long, prominently exserted beyond tip of abdomen; ovipositor length a little over twice the length of apical segment of ovipositor sheath; 2nd funicular segment as long as 4th but shorter and much more slender than the broad 6th segment; 1 row of discal ciliation visible along the clear area ..... *Anagrus* sp. B

29' Ovipositor short, slightly exserted beyond abdomen; funicular segment II, IV, and VI subequal in length; distal end of forewing with a hyaline area; marginal fringe a little longer than the maximum wing width ..... *Anagrus armatus* (Ashmead)

Key to the Dryinids in rice agroecosystems

Plate 42a-f

1 Both sexes fully winged; notaulices completely distinct and jointed posteriorly in male; female with testaceous head, antennae, and pronotum; abdomen similarly testaceous except tergites 1, 2, and 4 partly brown; propodeum and petiole black; forewing transparent without dark transverse bands; maxillary palpi 3–4-segmented and labial palpi 2-segmented; segment I and 4 foretarsus equal in length; enlarged claw with subapical tooth and 4–5 lamellae; segment V of foretarsus with a single row of 9–12 lamellae, apex with a group of 6–11 lamellae; aedeagus with a deeply cleft apicomedian process..... *Echthrodelphax fairchildii* Perkins

1' Female apterous; male winged; other characters not as above 2

2 Enlarged claw without subapical tooth, with or without small tooth at the end of the longitudinal furrow 3

2' Enlarged claw with subapical tooth 6

3 Pronotum not crossed by a transverse depression, if so, impression feeble; labial palp 2-segmented 4

3' Pronotum with a prominent transverse depression 5

4 Maxillary palpi 2-segmented; enlarged claw with 3 bristles at end of longitudinal furrow; segment V with a row of 6 minute lamellae on distal half, apex with 6 lamellae; segment I of foretarsi longer than segment IV (11:9); black except for testaceous antennae and yellow legs ..... *Tetrodontochelys sakaii* (Esaki and Hashimoto)

4' Maxillary palpi 3-segmented; enlarged claw as above but with 5 peglike hairs; segment V with a row of 16–20 lamellae and a group of 8–10 lamellae at apex, proximal region with an inner serrate margin; segment I of foretarsi as long as segment IV; reddish testaceous antennae with black petiole; brown vertex and abdomen ..... *Tetrodontochelys lucens* Olmi

5 Maxillary palpi 3-segmented; labial palpi 2-segmented; enlarged claw with a bristle and 3 peglike hairs at end of longitudinal furrow; segment V of foretarsi with innerside proximally not serrate, with 2 rows of 12 lamellae and a group of 6 lamellae at apex; 1st segment of tarsi I longest, 2x longer than 4th and slightly longer than 5th; black species except for yellow malar area, clypeus, mandibles, and front of vertex and brownish antennae and legs ..... *Gonatopus yasumatsui* Olmi

5' Maxillary palpi 6-segmented; labial palpi 3-segmented; enlarged claw with 6 peglike hairs, innerside with 18–19 lamellae in 2 rows, apex with 14 lamellae in a group; 1st segment of tarsi I two-thirds of 4th, 5th segment 4x longer than 1st; head brownish red with yellow mandibles, clypeus, and front vertex; antennae brown with segments 1 and 2 yellow; thorax and abdomen blackish brown ..... *Gonatopus lucidus* (Rohwer)

6 Pronotum without or with very weak transverse depression; labial palpi 1-segmented; maxillary palpi 2-segmented 7

6' Pronotum clearly with a prominent depression; labial palpi 2-segmented; maxillary palpi 2- to 4-segmented 9

7 Female abdomen entirely testaceous to occasionally brown; propodeum yellow testaceous; enlarged claw with 3–6 lamellae, segment V with 2 rows of 7–10 lamellae and a group of 2–7 lamellae at apex; male with dorsal process of gonoforceps distally broadened and serrated ..... *Haplogonatopus apicalis* R.C.L. Perkins

7' Female abdomen uniformly black; male dorsal process of gonoforceps distally serrated or not serrated 8

8 Dorsal process of gonoforceps distally serrated but not broadened; segment V with 12 lamellae ..... *Haplogonatopus atratus* Esaki & Hashimoto

8' Dorsal process of gonoforceps long and slender, apex without a serrated margin; segment V with 11 lamellae, enlarged claw with 4 lamellae ..... *Haplogonatopus oratorius* (Westwood)

9 Legs testaceous; thorax and pronotum red testaceous with yellow scutum; maxillary palpi 2- to 4-segmented; sides of metanotum rounded; metathorax + propodeum with a feeble tract of median furrow; enlarged claw with subapical tooth and 6–7 lamellae, segment V of foretarsi with 2 rows of 19–20 lamellae and a group of 5–8 lamellae at apex; basal segment of foretarsi as long as 4th; dorsal process of gonoforceps slender, pointed at apex and with a subapical point ..... *Pseudogonatopus sarawaki* Moczar

9' Legs mostly yellow; thorax, propodeum, and abdominal coloration more or less different; metapleuron rounded or protruding; dorsal process of gonoforceps different from above 10

10 Metapleuron protruding, metathorax + propodeum without median furrow; maxillary palpi 4-segmented; enlarged claw with a subapical tooth and 6 lamellae; segment V of foretarsus with 2 rows of 14 lamellae and a group of 6 lamellae apically; basal segment of foretarsi as long as 4th segment; generally reddish testaceous except for black petiole and brown-red abdomen ..... *Pseudogonatopus nudus* R.C.L. Perkins

10' Metapleuron rounded; body black to brownish black 11

11 Head, thorax, and propodeum brownish black; abdomen black; maxillary palpi 2-segmented; mandible tetradentate; metathorax and propodeum weakly granulated; enlarged claw with subapical tooth and 4–5 lamellae, segment V of foretarsi with 2 rows of 10–12 lamellae and a group of 5 or more at apex; basal segment of foretarsi one-fifth longer than 4th; dorsal process of gonoforceps broad and long, rounded at apex and with a lateral point ..... *Pseudogonatopus fulgori* (Nakagawa)

11' Without the combination of above characters 12

12 Body uniformly black except for brown head; propodeum without yellow area at apex; metathorax and propodeum dull and granulated; maxillary palpi 4-segmented; enlarged claw with a subapical tooth and 5 lamellae; segment V of foretarsi with 2 rows of 13 lamellae, apex with a group of 7 lamellae; segment I of foretarsi 1.24x longer than 4th; dorsal process of gonoforceps very short and pointed ..... *Pseudogonatopus flavifemur* Esaki & Hashimoto

12' Thorax and propodeum black; propodeum with a yellow patch apically; abdomen brownish black and head brown; metanotum and propodeum with a tract of median furrow and indistinctly sculptured; maxillary palpi 2- to 4-segmented; enlarged claw with 4–9 lamellae; segment V of foretarsi with 2 rows of 20–25 lamellae, apex with a group of 7–10 lamellae; dorsal process of gonoforceps broadly long, pointed, and blade-like ..... *Pseudogonatopus hospes* R.C.L. Perkins

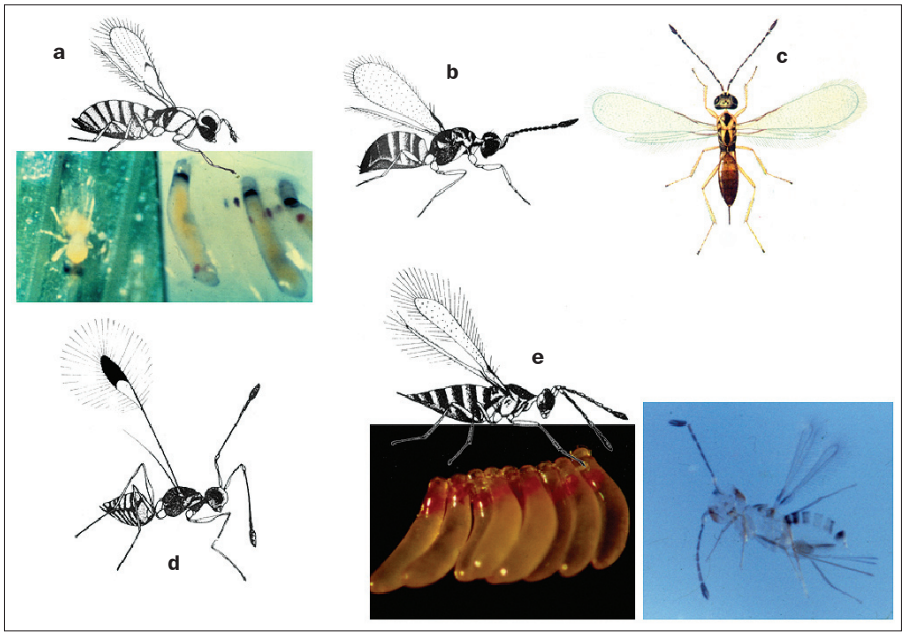

Plate 41. Representative examples of egg parasitoids: (a) *Oligosita naias* Girault (plus parasitized BPH eggs); (b) *Gonatocerus* sp.; (c) *Gonatocerus munna*rus Mani & Saraswat; (d) *Mymar taprobanicum* Ward.; (e) *Anagrus* spp. (plus parasitized BPH eggs).

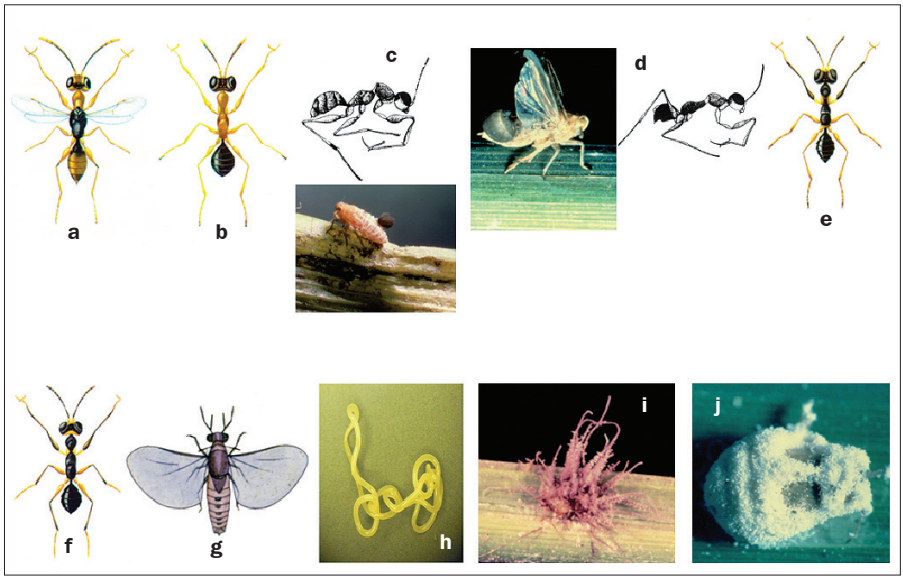

Plate 42. Representative examples of nymphal and adult parasitoids/parasites: (a) *Echthrodelphax fairchildii* R.C.L. Perkins; (b) *Haplogonatopus atratus* Esaki & Hashimoto; (c) *Haplogonatopus* sp. (plus parasitized BPH nymph); (d) *Pseudogonatopus nudus* R.C.L. Perkins (plus parasitized BPH nymph); (e) *Pseudogonatopus fulgori* (Nakagawa); (f) *Pseudogonatopus flavifemur* Esaki & Hashimoto; plus (g) *Elenchus japonicus* Esaki & Hashimoto; (h) *Hexamermis* sp.; (i) *Hirsutella citriformis* Speare, (j) *Beauveria bassiana* (Balsamo) Vuillemin.

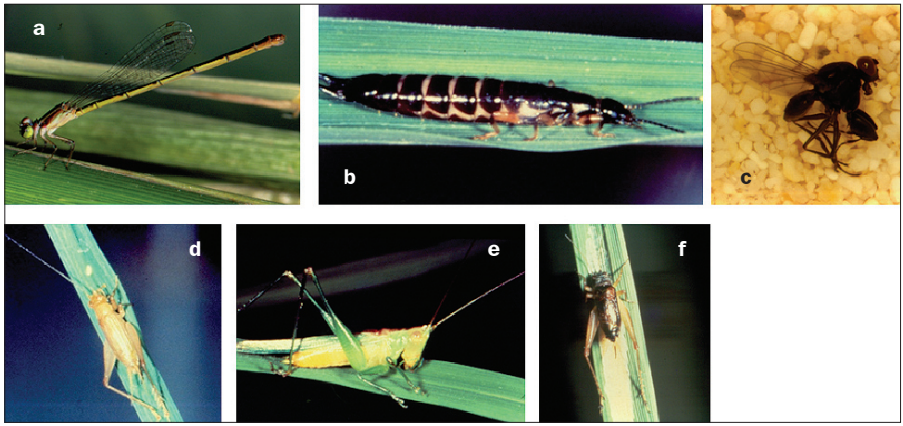

Plate 43. Insect predators: Odonata: (a) *Agriocnemis* sp.; Dermaptera: (b) *Euborellia stali* (Dohrn); Diptera: (c) *Ochthera sauteri* Cresson; Orthoptera: (d) *Anaxipha longipennis* (Serville); (e) *Conocephalus longipennis* (de Haan); (f) *Metioche vittaticollis* (Stål).

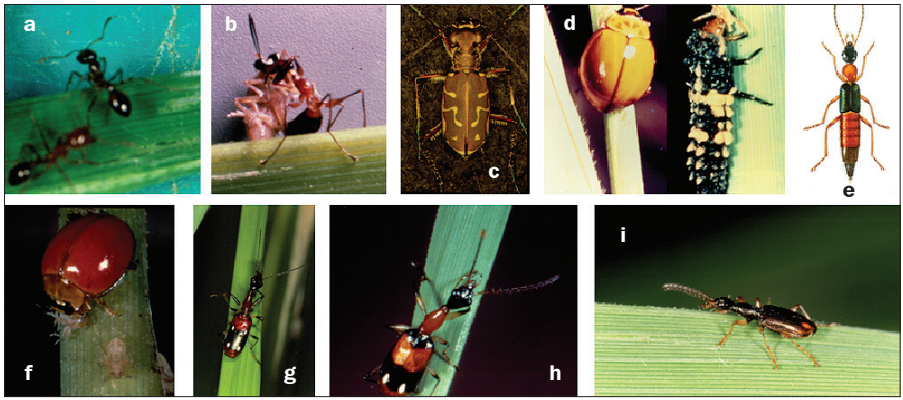

Plate 44. Insect predators: Hymenoptera: (a) *Solenopsis geminata* Fabricius; (b) *Pseudogonatopus* sp.; Coleoptera: (c) *Cicindela sumatrensis* Herbst; (d) *Harmonia octomaculata* (Fabricius) (adult and nymph); (e) *Paederus fuscipes* Curtis; (f) *Micraspis crocea* (Mulsant); (g) *Ophionea interstitialis* Schmidt-Goebel; (h) *Ophionea indica* (Thunberg); (i) *Anoplogenius* sp.

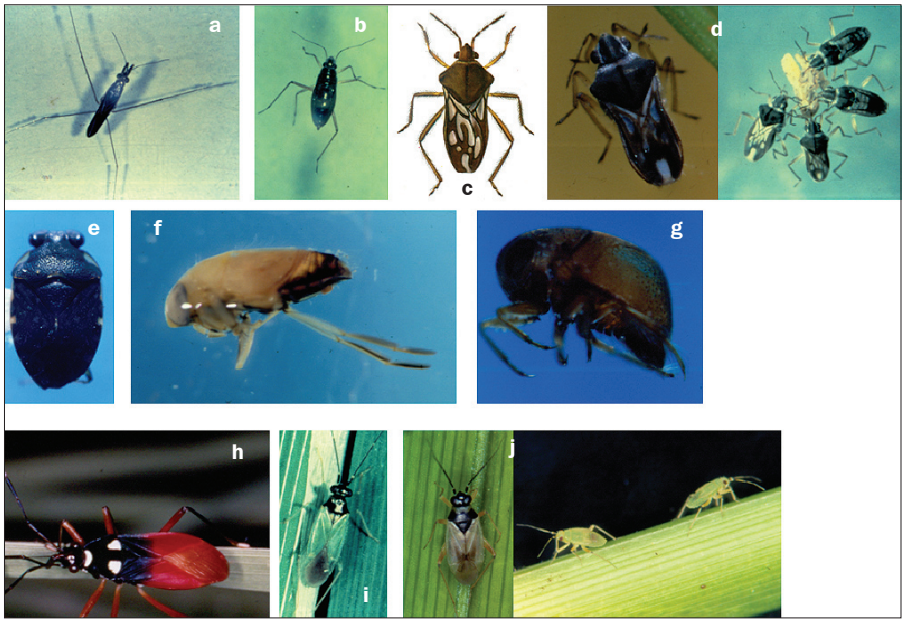

Plate 45. Insect predators: Hermiptera: (a) *Limnogonus fossarum* (Fabricius); (b) *Mesovelia vittigera* (Horvath); (c) *Microvelia douglasi* Scott; (d) *Microvelia douglasi atrolineata* Bergroth; (e) *Ochterus marginatus* (Latreille); (f) *Anisops kurowae* Matsumura; (g) *Paraplea sobrina* Stål; (h) *Dindymus pulcher* Stål; (i) *Cyrtorhinus lividipennis* Reuter; (j) *Tytthus chinensis* Stål (adult and nymphs).

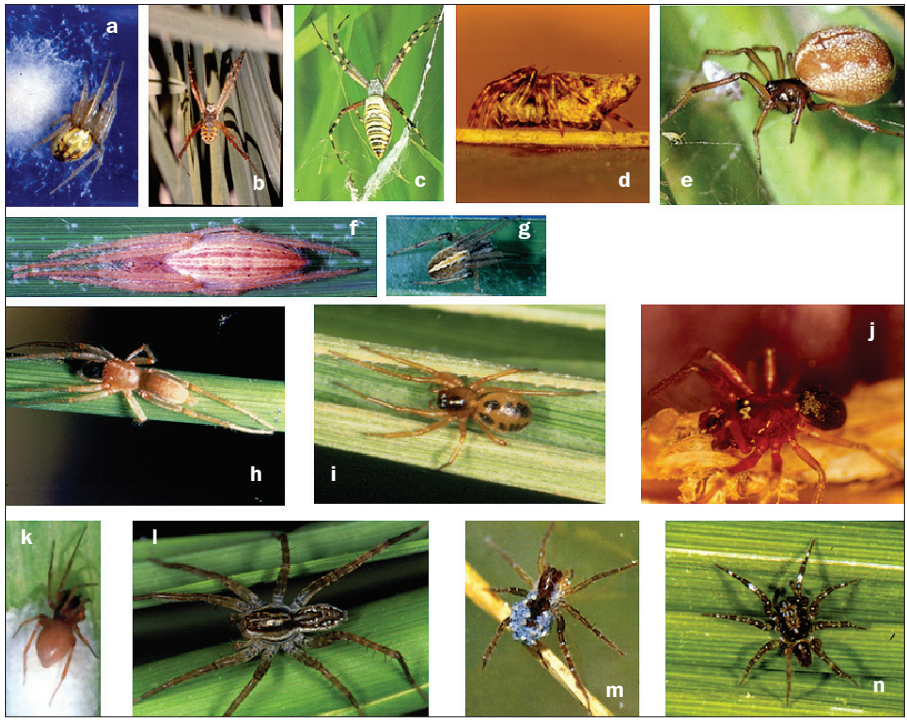

Plate 46. Family Araneidae: (a) *Araneus inustus* (C.L. Koch); (b) *Argiope catenulata* (Doleschall); (c) *Argiope bruennichii*(Scopoli); (d) *Cyclosa* sp.; (e) *Singa* sp.; (f) *Larinia phithiscica*; (g) *Neoscona theisi* (Walckenaer); Family Clubionidae: (h) *Clubiona japonicola* (Boesenberg & Strand); Family Linyphiidae : (i) *Atypena formosana* (Oi); (j) *Erigone prominens* (Boesenberg & Strand); (k) *Erigonidium graminicola* (Sundevall); Family Lycosidae: (l) *Pardosa pseudoannulata* (Boesenberg & Strand); (m) *Pirata subpiraticus* (Boesenberg & Strand); (n) *Arctosa tanakai* Barrion & Litsinger.

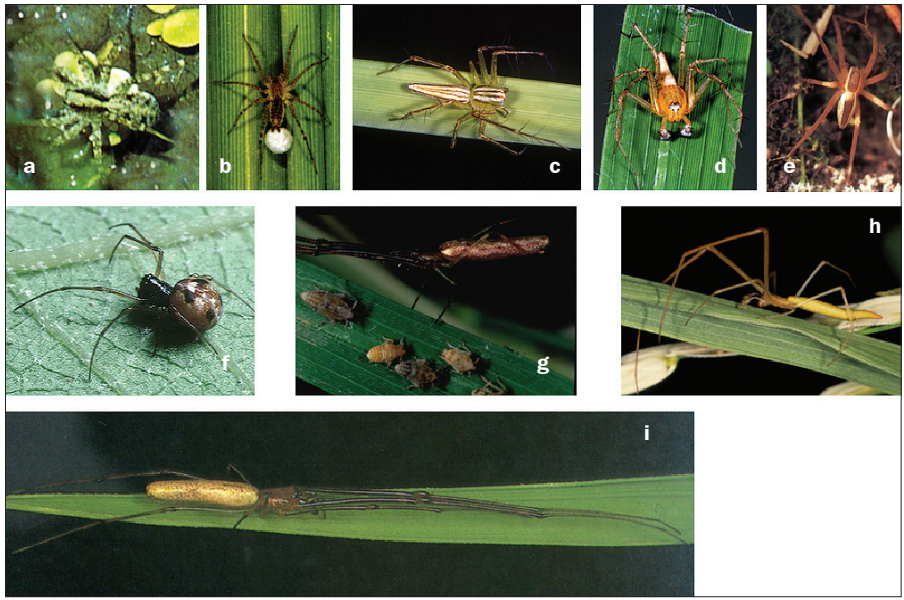

Plate 47. Family Lycosidae: (a) *Pardosa* sp.; (b) *Hippasa holmerae* Thorell; Family Oxyopidae: (c) *Oxyopes lineatipes* (C.L. Koch); (d) *Oxyopes javanus* Thorell; Family Pisauridae: (e) *Dolomedes* sp.; Family Tetragnathidae: (f) *Dyschirionatha dentata* Zhu & Wen (source: Akio Tanikawa); (g) *Tetragnatha maxillosa* Thorell; (h) *Tetragnatha javana* (Thorell); (i) *Tetragnatha nitens* Auduoin.

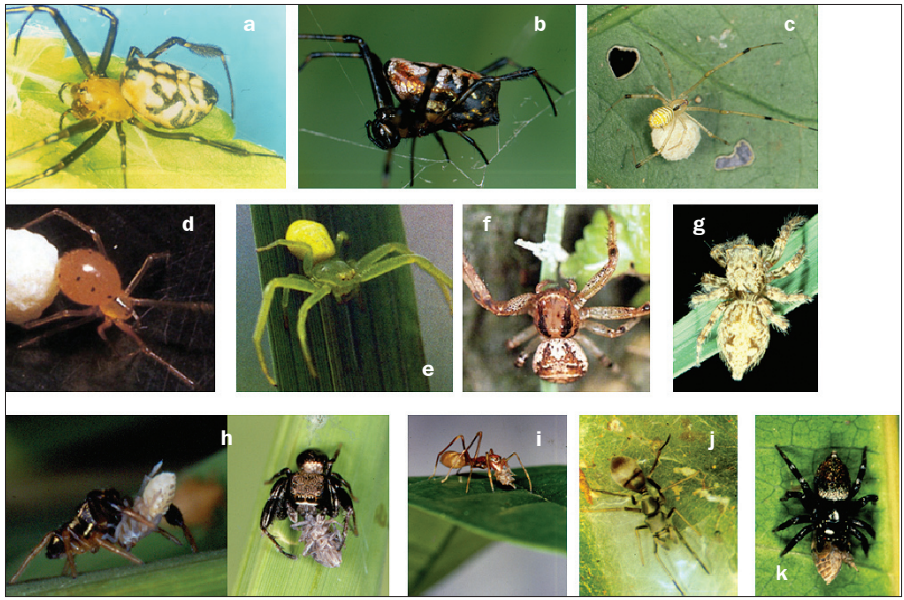

Plate 48. Family Tetragnathidae: (a) *Leucauge* sp.; (b) *Leucauge fastigata* (Simon); Family Theridiidae: (c) *Chrysso* sp.; (d) *Coleosom octomaculatum* (Boesenberg & Strand); Family Thomisidae: (e) *Misumena* sp.; (f) *Xysticus* sp.; Family Salticidae: (g) *Plexippus paykulli* (Audouin); (h) *Harmochirus brachiatus* (Thorell); (i) *Myrmarachne assimilis* Banks; (j) *Myrmarachne bidentata* Banks; (k) *Thiania* sp.

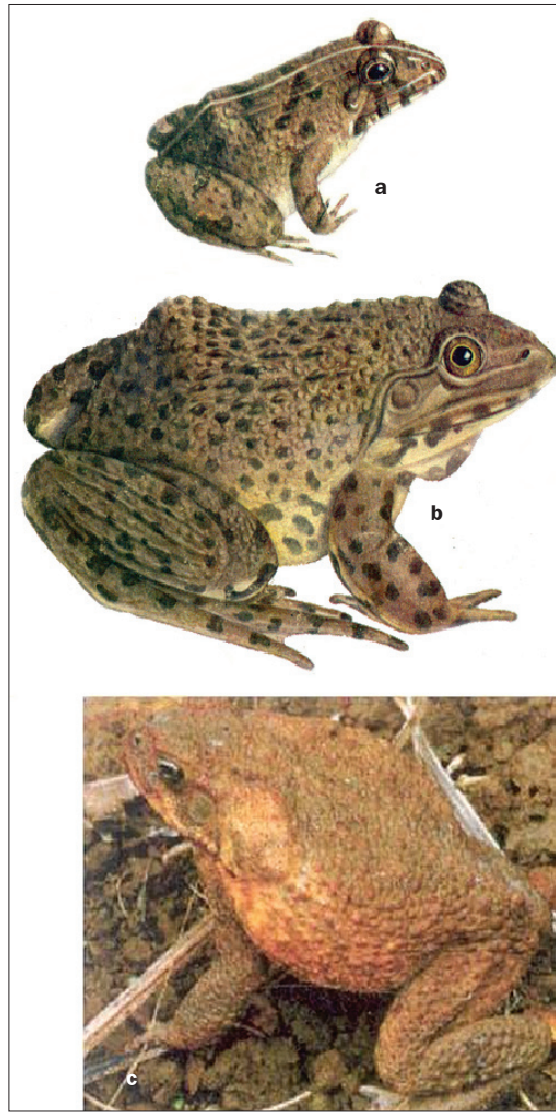

Plate 49. Family Ranidae: (a) *Rana limnocharis* Boie; (b) *Rana tigrina rugulosa* (Wiegmann); Family Bufonidae: (c) *Bufo marinus* Linnaeus.

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Notes

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Rice planthopper problems and relevant causes in China

Jiaan Cheng

The new development of three rice planthopper species, including small rice planthopper, brown planthopper, and whitebacked planthopper, and historical profiles of relevant environmental factors in rice ecosystems in China were analyzed. The results indicated that the changes in cropping system and increase in susceptible hybrid varieties, fertilizers, pesticides, and temperature created vulnerable rice ecosystems, which increased initial populations and growth rates and resulted in high population sizes and frequency of outbreaks. The main parameters for higher initial population are earlier starting time, longer immigration period, and higher immigration size; those for higher growth rate are higher fecundity, more generations, and lower mortality; and those for lower control efficiency are changes in species structure, genetic structure, and temporal structure. The approaches for improving planthopper management by modifying cropping systems, building up system resistance, developing new control strategies, and strengthening international collaboration were discussed.

Keywords: small brown planthopper, brown planthopper, whitebacked planthopper, environmental factors, management

Laodelphax striatellus Fallen (small brown planthopper, SBPH), *Nilaparvata lugens* Stål (brown planthopper, BPH), and *Sogatella furcifera* Horvath (whitebacked planthopper, WBPH) have become major pests successively in the rice-growing areas of Asia and extensive studies have been carried out to develop control programs since the 1960s. Much money has been invested to prevent yield losses caused by rice planthoppers, for example, a national program for BPH control using resistant varieties and pesticides in Indonesia invested more than US$100 million per year between 1980 and 1987, but did not prevent planthopper outbreak and exacerbated problems of varietal breakdown, insecticide resistance, and resurgence in BPH (Kenmore 1991). It further demonstrated that rice planthoppers were typical artificial pests. The implementation of the Intercountry Rice IPM program sponsored by FAO in the late 1980s as well as the Farmer Participatory Research Program sponsored by IRRI in the 1990s changed farmers' perceptions in tropical countries on rice planthoppers,

promoted natural biological control in rice ecosystems, and reduced risks of planthopper outbreak (Kenmore 1991, Escalada and Heong 2004). However, chemical control is still the main tactic for planthopper control in subtropical and temperate regions, such as China, Japan, and South Korea. Although field experiments showed that unreasonable use of insecticides could also cause BPH resurgence in subtropical and temperate areas, insecticides have still been extensively used in these countries (Wang et al 1994, Cheng 1995). Development of imidacloprid, a new insecticide with higher efficiency and a longer residual period, even stimulates negligence in applying insecticides and imidacloprid has been widely used in all the rice-growing areas of Vietnam, China, South Korea, and Japan since the early 1990s (Liang et al 2007). The frequency of BPH outbreak declined after the outbreak in the early 1990s and it seems that the BPH problem was solved by the new insecticide. However, the dream of solving the BPH problem by applying the new insecticide was shattered by the serious outbreak of BPH that resulted from high resistance to imidacloprid and other reasons in 2005 (Cheng and Zhu 2006). The continued outbreaks of rice planthoppers in 2006 and 2007 indicated the importance of redesigning a planthopper management program. This paper covers new developments in rice planthoppers in recent years and interactions between planthopper problems and ecological factors in rice ecosystems in China, as well as management strategies.

New planthopper problems in rice ecosystems in China

It has been more than 40 years since SBPH caused serious yield losses by transmitting virus diseases, such as rice stripe virus disease (RSV) and rice black streaked dwarf virus disease (RBSDV), in the mid-1960s in the Yangtze Delta area of China. BPH and WBPH became major pests in the late 1960s and late 1970s, respectively, and all three planthoppers have had frequent outbreaks since then. Figure 1 shows a historical profile of rice planthoppers based on data collected in 10 fields without using any insecticide applications every year in Jiaxing, Zhejiang Province, China (Cheng et al 2008). The value of the ordinate is the average peak density of total planthoppers per 100 hills. BPH or WBPH is ranked for 5 grades and grade 5 (more than 3,000 per 100 hills) is considered as an outbreak (Zhang 1995).

According to the data in Figure 1, the developmental history of rice planthoppers in the Yangtze Delta of China could be separated into three stages: exposure (from 1964 to 1978), development (from the late 1970s to early 2000s), and exacerbation (after the early 2000s). In the first stage (exposure), SBPH, BPH, and WBPH became major pests from potential pests successively, but only one species caused yield losses in some areas in the same year and BPH was considered as the number-one pest in the rice ecosystem (Cheng 1995). In the second stage (development), both BPH and WBPH caused yield losses in the same year and the occurring area of WBPH was continually expanding. WBPH became the number-one pest, especially in South China (Tang et al 1995), but SBPH occurred only occasionally in small areas. However, all three species were causing serious yield losses every year in the third stage (exacerbation). In the Yangtze Delta area, SBPH caused serious yield losses of wheat and rice

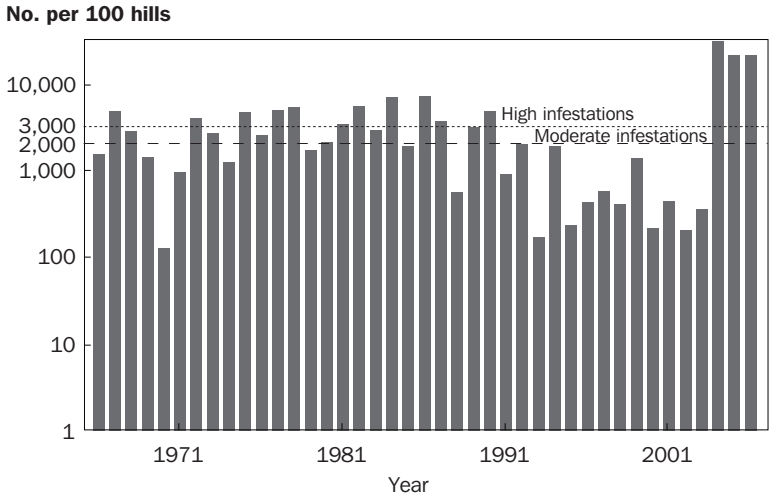

Fig. 1. Historical profile of rice planthoppers in Jiaxing, Zhejiang, China.

by transmitting virus diseases, WBPH caused hopperburn mainly in hybrid rice, and BPH caused hopperburn mainly in japonica rice.

To explore the real situation of rice planthoppers, historical data on the main population parameters of planthoppers were compared and the results revealed that new rice planthopper problems in recent years could be represented by the four most significant phenomena in planthopper history.

Highest initial population

The initial populations of BPH and WBPH in Jiaxing, Zhejiang Province, are immigrants from South China, but the initial population of SBPH is the local overwintering population. The main initial population of SBPH for paddy rice is the adults of the first generation around mid-May to early June. WBPH immigrants arrive in May and peak in late June to early July, but BPH immigrants arrive in June and the main immigration period lasts from late July to early September. Figure 2 shows the historical profile of main initial population sizes under light traps in these peak periods since 1979. The highest peak population sizes under light traps for SBPH, WBPH, and BPH were 93,192, 4,502, and 9,712, which occurred in 2006, 2003, and 2007, respectively. The highest peak population sizes for the three species are at least two times higher than those in the 1980s and 1990s.

Highest growth rate

The growth rate, the ratio between the peak size of the initial population and the peak size of the highest peak population, is a most important population parameter, which indicates species capacity for increasing as well as the suitability of environmental conditions to the species. BPH is a well-known pest species with a high growth rate. The growth rates and standard errors of BPH from immigration to peak population,

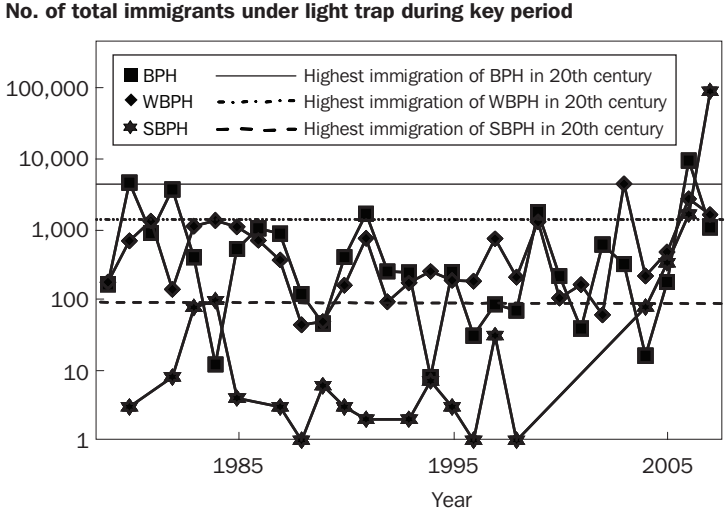

Fig. 2. Historical profile of initial population under a light trap in Jiaxing, China.

developing two generations after immigration, were 990.60 ± 193.48 in the second rice crop season during the 1970s and 1980s (Cheng 1996). Based on data from the same fields mentioned above, the growth rates and standard errors of SBPH and WBPH in the 1980s in the second rice crop season were 24.58 ± 12.72 and 283.95 ± 8.00. However, the growth rates from the initial population to the peak population for SBPH and BPH in the single rice crop season in the past three years were 1,335.25 ± 607.21 and 5,423.32 ± 1,739.33 in the same area. The results clearly indicate that average growth rates of BPH and SBPH in recent years were more than 4–8 times higher than those in the 20th century.

Highest peak population size

As Figure 1 showed, the peak population sizes fluctuated year to year and were more than 20,000 per 100 hills in the past 3 years, which clearly showed that the peak population sizes in the past 3 years were more than two times higher than the highest population size in the 20th century. Based on the historical data collected from these fields without any insecticide application, the highest peak densities for SBPH, BPH, and total planthoppers per 677 m^2 in the 20th century were less than 1 million, 2.36 million, and 2.42 million, respectively. But the average peak densities of the SBPH, BPH, and total planthoppers were 1.73 ± 0.57, 5.24 ± 0.86, and 6.52 ± 0.73 million in the past 3 years, which are also more than two times higher than the highest ones in the 20th century. SBPH could cause 10–20% yield losses by feeding on heads directly, which never happened in the 20th century (Wang et al 2007).

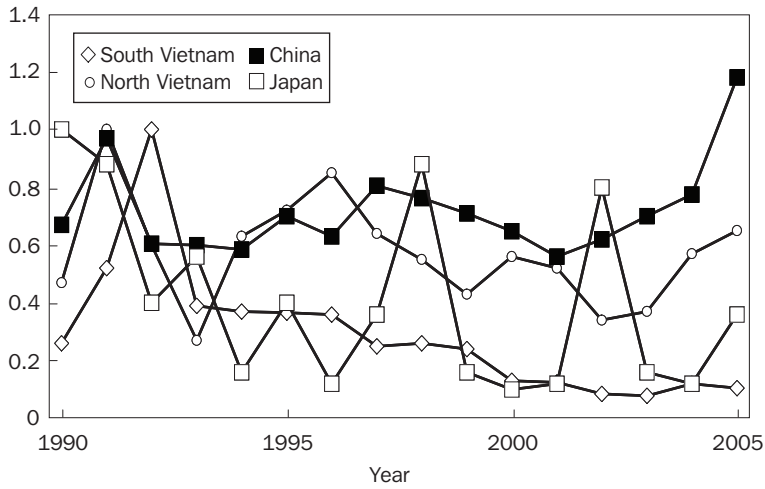

Fig. 3. Comparison of relative occurring areas of rice planthoppers among years in China, Japan, and Vietnam.

Highest outbreak frequency

Rice planthoppers, mainly BPH and WBPH, had outbreaks in the early 1990s and the occurring areas were considered as the largest in Vietnam, Japan, and China as shown in Figure 3. Rice planthoppers in 1991 in China occurred on 23.2 million ha (Tang et al 1995). However, the average annual occurring area in 2005-07 was about 26.7 million ha (Xia 2008). In 14 different years, peak population sizes were above 3,000 per 100 hills (outbreak) from 1967 to 2007. The outbreak years were separated individually before the mid-1970s, such as 1968, 1973, and 1976, and covered 2-year periods since the late 1970s, such as 1978-79, 1982-83, and 1987-88. But outbreaks continued for 3 years during 2005-07 since all three rice planthoppers had outbreaks.

Historical profile of main environmental factors

Rice planthoppers are secondary pests in high-yielding agricultural systems. Outbreaks of planthoppers have been triggered by misuse of insecticides, varieties with high nutrition, and other environmental factors related to cultural and climatic factors (Kiritani 1979, Kenmore et al 1984, Cheng 1995). These environmental factors, including cropping systems, variety, usage of chemical fertilizer and pesticide, and temperatures have been changing in the rice-growing areas of China.

Cropping systems

The change in area with a double-rice cropping system in China since the 1950s looks like a mountain peak. The area for double-rice cropping started increasing in the 1950s and reached a peak in the 1970s, then declined in the 1980s and 1990s (Huang 1997). The areas with a first rice crop system accounted for only about 20% in 1950, but about 40% of the total rice-growing area in 1980 in China. In general, areas with a second rice crop system are equal to the sum of the first rice crop area and the area used for seedling beds of a second rice crop. Therefore, the rice-growing area for the first and second rice crop was more than 80% of the total rice-growing area in China, and almost 100% in South China at the peak in the 1970s. However, the first rice crop area declined in the 1980s and reached about 20% of the total rice-growing area again in recent years (MOA 2006). Most of the double rice-cropping system is found in Guangdong, Guangxi, South Hunan, and Jiangxi and the single-rice cropping system accounts for more than 90% in the Yangtze Delta area, including Jiangsu, Shanghai, and Zhejiang (NBSC 2006). Figure 4A showed that areas growing a single-rice crop have been increasing dramatically as the areas growing a first crop declined in Zhejiang Province (ZPBS 2006).

In the meantime, areas growing winter crops have been changing. Areas growing wheat increased from 1980 to 1990 and declined after 1990 in both Jiangsu and Zhejiang provinces. The ratios between wheat fields and rice paddy in Jiangsu and Zhejiang in recent years were about 0.8 and 0.1, respectively (NBSC 2006). The high ratio in Jiangsu indicated that the cropping system was becoming mainly a wheat-rice system. In contrast, the ratio in Zhejiang was becoming lower and only about 40% of fields were used for winter crops, including barley, oil rape, and broad bean (Fig. 4A). More than half of the fields became fallow with graminaceous weeds and this means that these fields had only one rice crop per year, which was a pure single-rice crop. Both wheat fields and fallow fields are usually plowed in June after adults of the first generation of overwintering SBPH emerged and moved to the rice paddy.

Another important change in the rice farming systems in the Yangtze Delta area since the 1990s is the increase in area using the direct sowing technique for wheat and rice. Wheat is directly sowed in rice paddies before the rice harvest in Jiangsu and rice is directly sowed around late May in Shanghai and Northern Zhejiang. The rice-growing area using direct sowing has accounted for about 80% of the total rice-growing area in the Yangtze Delta in recent years.

Variety

The most important revolution for rice in the 20th century was probably the development of hybrid rice. Hybrid varieties started to be released widely in 1976 in China. It was reported that the yield of hybrid rice per hectare could be increased by about 1,500 kg compared with conventional rice. Therefore, hybrid rice growing area expanded rapidly and reached about 10 million hectares in about 10 years. In 1990, hybrid rice area exceeded 15 million hectares and accounted for about 50% of the total rice-growing area in China. Since then, the percentage of hybrid rice area has increased gradually to about 60% as shown in Figure 4B (Mao et al 2006). The main

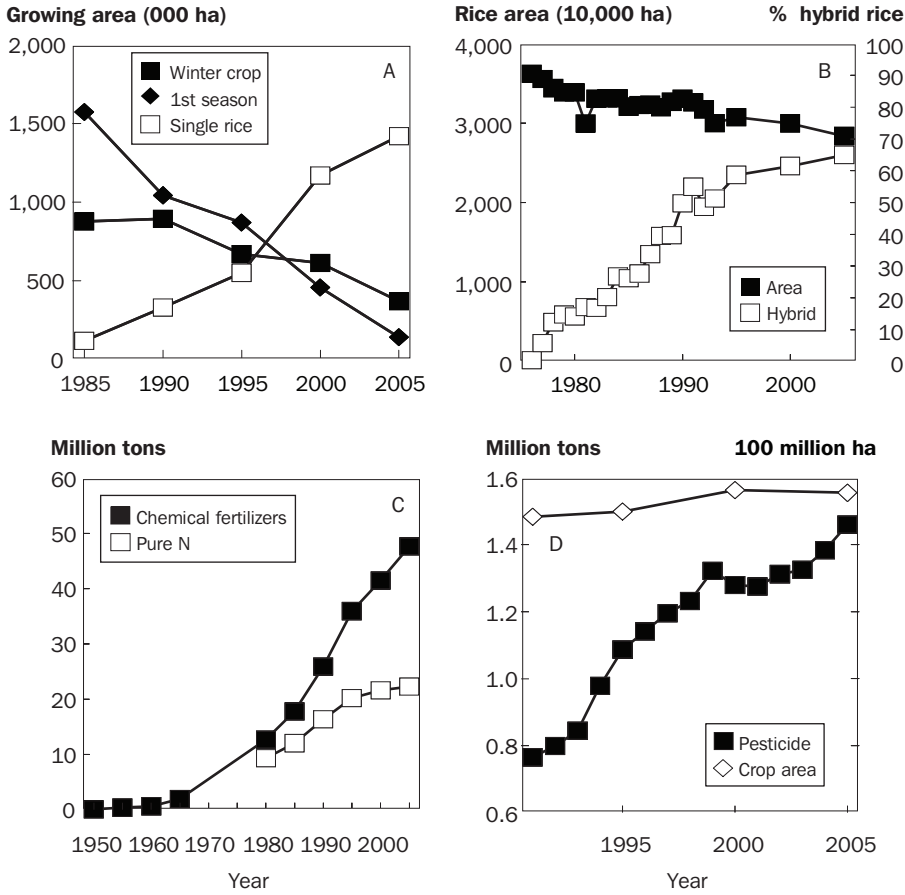

Fig. 4. Historical profiles of main agricultural practices in China. (A) Cropping systems in Zhejiang, (B) areas growing rice and hybrid rice, (C) chemical fertilizers, (D) chemical pesticides.

sterility system used for hybrid varieties comes from Minghui 63, which is susceptible to rice planthoppers, and the main mother parents used are IR36 and IR64, which are susceptible to WBPH, but resistant to Biotypes 1 and 2 of BPH. Therefore, the main varieties of hybrid rice, such as Shan-you, Wei-you, D-you, Gang-you, and Liang-you, are susceptible to WBPH, with some resistance to BPH (Mao et al 2006). Based on field testing, only about 12% of the newly developed varieties were ranked at grades 0–5 for the levels of resistance to BPH (Chen et al 2005).

Interactions between variety and BPH have been extensively studied, and some resistant varieties were developed and applied in small areas in China. For example, resistant varieties incorporating resistance genes from IR26, IR28, and IR54 started to be used in 1989, and then the area growing resistant varieties expanded quickly, reaching about 80% of the total rice-growing area in Jiaxing, Zhejiang Province, in

1991 (Cheng 1996). However, it is not an indispensable condition to have resistance genes for planthoppers in variety breeding programs. Many varieties resistant to planthoppers were developed and the proportion of area growing resistant varieties declined significantly to almost zero in the late 1990s, when the BPH problem was becoming less serious.

Chemical fertilizer and insecticide

Although the one child per family policy has been in place since the 1970s, the population still increased from about 1 billion to 1.3 billion in the past 25 years in China. To feed the increasing population with limited arable land, yield per unit area has to be raised by using modern technology. The yield of rice increased from 4.13 to 6.26 t $ha^{-1}$and the yield of food crops increased from 2.72 to 5.23 t ha^{-1} during the past 25 years. During the same period, the usage of total chemical fertilizers and nitrogen increased from 12.69 and 9.34 million tons to 47.66 and 22.29 million tons, respectively (MOA 2006).

The total usage of pesticides also kept increasing and almost doubled in the past 15 years. Total pesticide use was about 0.76 million tons in 1991 and about 1.46 million tons in 2005 (MOA 2006). During the same time period, striped stem borer started to be resistant to Shachongshang and triazophos, and methamidophos was banned because of its high toxicity. To replace these pesticides, new pesticides, including regent, imidacloprid, and pyrethrum, were widely applied. Although use of these new pesticides per unit area is much less than that of old pesticides, the total use of pesticides kept increasing (Yang 2007). The high control efficiency and cheap price of imidacloprid made farmers believe that this pesticide was the most popular "magic drug" and pesticide products containing imidacloprid, but with different names or formulas, were more than 400 in China. They were used in all the rice-growing areas in China and 3–5 applications, as a main component of a "cocktail pesticide," were made per crop season. In the meantime, imidacloprid was also widely used in Vietnam, South Korea, and Japan (Liang et al 2007).

Temperature

Temperature is the main climatic factor affecting development, fecundity, and mortality. Figure 5 shows the annual monthly average temperatures from 1954 to 2007 in Jiaxing, China, and the broken lines in each small figure are the average monthly temperatures during this period. The monthly average temperatures fluctuated, but they clearly showed that weather conditions were getting warmer, especially in winter and spring. The monthly average temperatures for most of the months in recent years were higher than, or at least close to, the average temperature during the 54 years. The highest or the second highest monthly average temperatures in most months occurred in recent years.

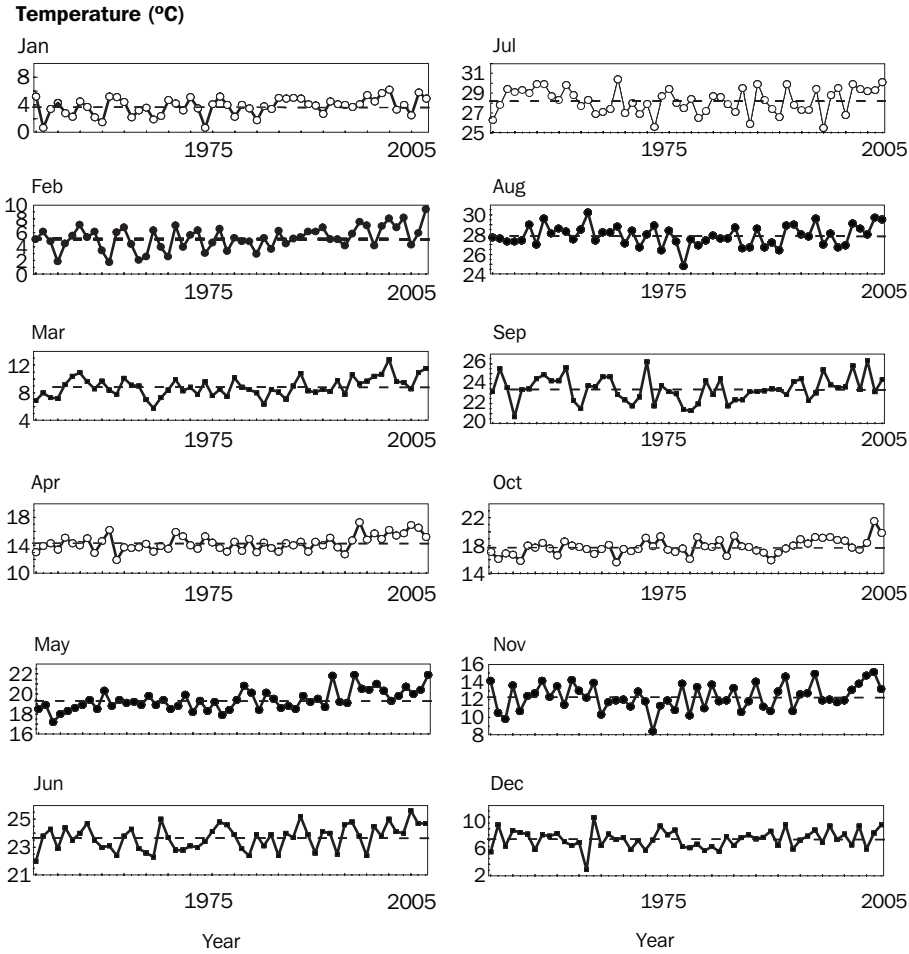

Fig. 5. Historical profile of monthly average temperature in Jiaxing, China.

Interactions between planthoppers and main environmental factors

Based on ecological principles, total population size of rice planthoppers (total N) could be described using the following equation:

$$\text{Total } N_t = \sum N_{i,t} = \sum N_{i,0} * R_{i,t} * (1 - P_{i,t}) \; (i = 1, 2, 3)$$

where N is population size, t is the number of generations, N_0 is initial population size and N_t is population size at generation t, i is number of species and there are three planthopper species, R is growth rate, and P is control efficiency of agricultural practices. The equation indicates that total population size is equal to the sum of population

sizes of the three rice planthopper species. All the environmental factors will affect total population size through their impact on the three parameters mentioned in the equation: initial population, growth rate, and control efficiency.

Impacts on initial population

The initial population is the population from source areas and fields and it is the seed population for the field we are dealing with. The population parameters related to initial population are mainly starting time (the time for earliest initial population arriving in the rice paddy), pattern (temporal distribution of initial population during the immigration period), and size (total population size moving into the rice paddy) (Cheng and Holt 1990). The cropping system could affect population development through its effect on the three parameters of initial population.

Earlier starting time. The earliest initial SBPH population is mainly from its local overwintering areas, but immigrants of BPH and WBPH are from their source regions. In general, the starting time of initial population depends on two factors, population development patterns in source areas and cropping systems in local areas. Figure 6 shows the population of three rice planthoppers under light traps in Jiaxing in the 1980s, 1990s, and the early 21st century, and the figure indicated that the starting time to catch three rice planthopper species under light traps was becoming earlier. One of the main reasons for the earlier starting time might be the warm winter and spring as shown in Figure 5, and all the monthly average temperatures from February to June increased about 1–2 °C since the 1980s. But the most important way to consider the starting time, the parameter related to arriving time in fields, could be the length of the period for planthopper development from arriving to peak of emigration in fields. In double-rice cropping, the initial populations of planthoppers move into fields growing a first rice crop transplanted around May and harvested in late July to early August or fields growing a second rice crop transplanted in late July to early August and harvested in November. There will be only about 1–2 months for population development from the time the initial population arrives to harvesting time in the first crop season and about 2–3 months in the second rice crop. The single-rice crop, however, is usually sown in late May to early June or transplanted in June and the harvesting time is in October to November. Therefore, rice planthoppers could develop 1 or 2, about 2, and 3–4 generations a season, respectively in the first-, the second-, and the single-rice crop seasons, respectively. This means that the time for initial populations to arrive in the single-rice crop season is much earlier than for the first- or second-rice crop season based on population development pattern (Fig.7C, D).

Longer immigration pattern. The temporal distribution of the immigration population is related to the population development pattern in the source area as well as crop season in the local area, and both the population development pattern in the source area and crop season in the local area are related to the cropping system. In general, macropterous adults increase after the heading stage and more macropterous planthoppers emigrate when rice is maturing because of poor food conditions (Cheng et al 1979). A change in cropping systems in source areas must affect crop stages, as

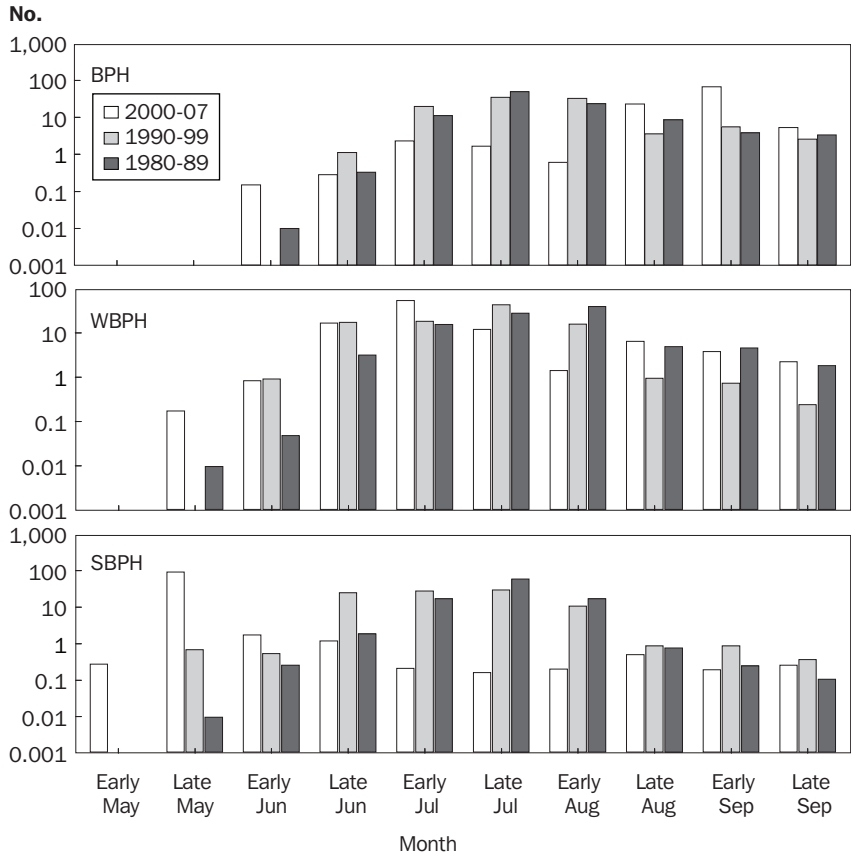

Fig. 6. Comparison of population development patterns of three rice planthoppers under light traps in 1980s, 1990s, and early 21st century in Jiaxing, China.

well as food conditions, in a specific calendar period. The source areas for Yangtze Delta areas are mainly around South Mountain areas, including Guangdong, Guangxi, Guizhou, Fujian, Hunan, and Jiangxi (Cheng et al 1979). There were mainly two immigration peaks of BPH, which were around late June to early July and late July to early August in the Yangtze Delta and the peak around late August was very low, when the rice cropping system was mainly a double-rice crop season there before the 1990s (Fig. 7A). However, the late immigration peak around late August to early September was very high in the single-rice cropping system in recent years (see Fig. 7B) because these immigrants were from single-rice crop fields and population sizes were already very high after developing two or three generations there.

Higher initial population size. Based on the historical profile of immigrants under light traps from 1979 to 2007, total immigrants in the main immigration periods, late May to early June for SBPH, late May to early July for WBPH, and late June to early

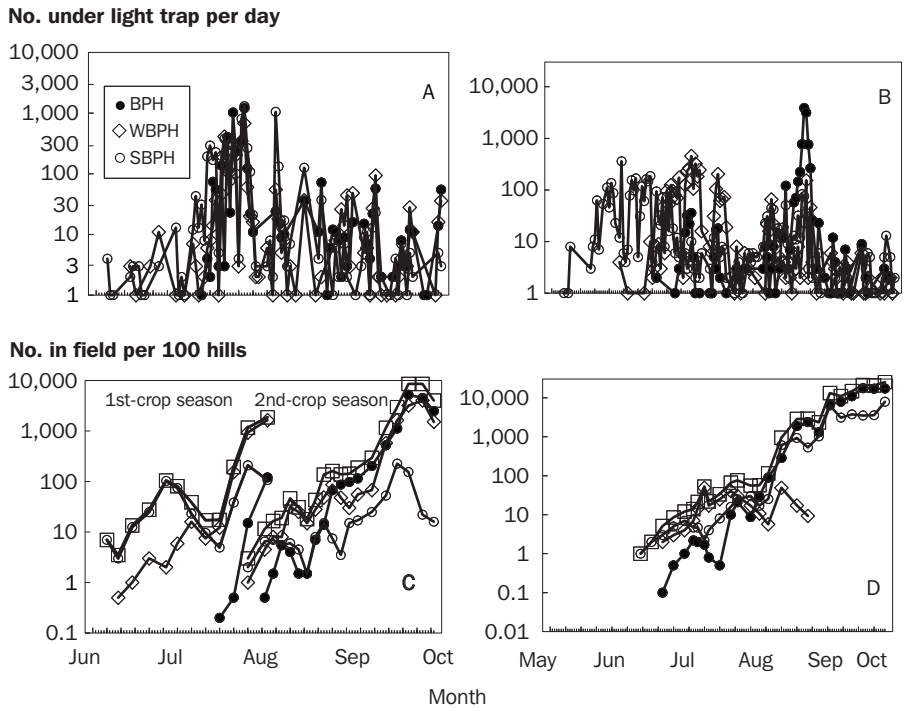

Fig. 7. Comparison of development patterns of populations under a light trap and in fields between the 1980s and 2000s. (A) Population under light trap in double-rice cropping system, (B) population under light trap in single-rice cropping system, (C) population in fields in double-rice cropping system, (D) population in fields in single-rice cropping system.

September for BPH, were 98 (1984), 1,359 (1984), and 4,707 (1980) in double-rice cropping systems, but 93,192 (2006), 4,502 (2003), and 9,712 (2007) in single-rice cropping systems (see Fig. 2). The initial populations in the single-rice cropping system are much higher than those in the double-rice cropping system because of the effects of cropping systems on the population development pattern in source areas. The higher initial population size of SBPH mainly resulted from the increase in wheat and fallow fields where an SBPH overwintering population could develop normally until the adults of the first generation emerged and dispersed to the rice paddy. The higher immigrants of BPH mainly resulted from the increase in area under a single-rice cropping season in source regions, where the BPH emigration population in late August to early September is much higher than in late July to early August from fields with a first-rice cropping season as mentioned above. The higher immigrants of WBPH mainly resulted from the expansion in hybrid rice growing area in source areas, including Vietnam and southern China.

Impacts on growth rates

Based on the data collected from fields in Jiaxing, Zhejiang, during 1976 to 2007, the growth rates of total planthoppers, including SBPH, BPH, and WBPH, from immigra-

tion to peak population, developing two generations after immigration, in fields with a second-rice crop season were about 1,000 in the 1980s and 1990s, but the growth rates in recent years have been more than 5,000 in fields with a single-rice crop season because of the following higher population parameters.

Higher fecundity. Rice planthoppers are r-strategic pests with high fecundity and high-yielding techniques that promote their capacity for increasing fast. Lu et al (2004) reported that high nitrogen could increase BPH fecundity by improving food nutrition. The wide use of hybrid varieties provides better nutrition for WBPH and experiments showed that fecundity of WBPH on hybrid varieties was 2–9.7 times higher than on other varieties (Huang et al 1994). Laboratory and field experiments showed that pyrethrum, triazophos, and chlorpyrifos could cause a resurgence of BPH by stimulating fecundity. A sublethal dose of triazophos could double female macropterous fecundity. The application of chlorpyrifos could increase BPH fecundity by 39.2–47.3% and population sizes of WBPH by 130–160% in fields (Heinrichs 1994, Wang et al 1994, Cheng et al 1995). Nonetheless, triazophos and chlorpyrifos were still recommended to replace methamidophos in rice pest management and pyrethrum became the main component in cocktail pesticides for leaffolder control after methamidophos was banned in 2004. Since the 1980s, herbicides have been widely used in rice-growing areas and herbicide usage doubled in the past 10 years. The proportion of herbicides to total pesticides is more than 30% in recent years. Wu et al (2001) reported that the commonly used herbicides, including butachlor, metoachlor, oxadiazon, and bentazon, could significantly stimulate BPH fecundity by increasing BPH feeding rate and reducing the resistance of rice plants. The fecundity of rice planthoppers is also affected by temperature and the optimum temperature for fecundity of BPH and WBPH is about 26–28 °C (Chen et al 1986, Feng et al 1985). September is the main developmental period for BPH due to the high proportion of short-wing-form females and better nutrition around heading stage, but the temperature starts to decline in September and average temperature is only 21.84 °C at in late September. Therefore, higher temperature in autumn could increase fecundity (Cheng et al 1992).

More generations. In general, rice planthoppers could develop more generations in fields with a single-rice crop because of the longer cropping period, but the number of generations they can develop in fields with a single-rice crop depends on the time when the field is transplanted as well as the temperature. The single-rice crop in the Yangtze Delta is transplanted around mid-June to early July, but sown around late May to early June. The earlier the single-rice crop is transplanted or sown, the more generations it can develop. Compared with the second-rice cropping system, planthoppers could develop one or two more generations in single-rice cropping because of the earlier arrival of planthoppers and longer growing period of rice (see Fig. 6). The average temperature in September 2005 was the highest since 1954 and it was 26.3 °C and 2.8 °C higher than the average, which made BPH develop an additional generation.

Lower mortality. As an r-strategic pest, rice planthoppers are subject to high mortality caused by natural control agents. Kenmore et al (1984) reported a preadult survivorship of only 4% in the Philippines and Gao et al (1988) reported a natural

control effect of 63% in the Yangtze Delta area. The major natural control agents are *Anagrus* spp., *Cyrtorhinus lividipennis*, and *Haplogonatopus* spp. Field investigations in Jiaxing showed that egg parasitic rates for rice planthopper eggs by *Anagrus* spp. were about 20–30% and the parasitic rates of planthopper nymphs and adults by *Haplogonatopus* spp. and nematodes were about 15–30% and 20% during the 1980s, respectively (Gao et al 1988). However, parasitic rates for eggs and two other development stages by these parasitoids are only about 10% each in recent years. The densities of various predators also declined significantly. Experiments showed that predatory capacities of *C. lividipennis* Reuter on BPH eggs and young nymphs were negatively related to the nitrogen contents of the host plants. The reduction in *C. lividipennis* natural control function could be one of the crucial factors inducing the outbreak of BPH populations in rice fields receiving excessive nitrogen fertilizer (Lu et al 2005).

Effects on control efficiency

Rice planthoppers have been managed mainly by using pesticides in China because of the lack of resistant varieties as well as the perception of farmers and technicians on pesticides. Extensive research on pesticide control strategy has been carried out and the key tactics for a control strategy are timing of application and type of pesticides to be used. Field experiments and a simulation study demonstrated that the best strategy is to apply pesticide with higher efficiency and a longer residual period at 30 days after transplanting based on the control threshold in the second-rice cropping season (Cheng et al 1990). However, the changes in population structure of rice planthoppers resulting from changes in ecological conditions made pesticide control become less efficient in reducing yield losses.

Changes in species structure. Species structure here refers to the composition of three rice planthopper species in various rice crop stages. The long evolutional development of the three planthopper species not only made them develop their specific niches to avoid competition in the rice ecosystem but also made them develop a strategy for mutualism among them. Serious yield losses were usually caused only by one planthopper species during the 1960s and 1970s and by two planthopper species in the 1980s and 1990s, but by three species in recent years. Therefore, species structure has become more diversified in recent years and three species co-occur in the same fields in most crop stages. Field investigations showed that species structure was closely related to cropping systems and varieties (see Fig. 8). In Yangtze Delta areas, the main planthopper species are SBPH and WBPH in the first-rice cropping season, but varied in the second-rice and single-rice cropping seasons depending on varieties. Mainly SBPH and WBPH occur in hybrid rice, SBPH and BPH in japonica rice, and the three species together in indica rice. Therefore, interactions among the three species become more important for population development. Laboratory experiments on the interspecific effects of BPH and WBPH indicated that interspecific interactions between BPH and WBPH provided positive effects for the two species at low and medium density, with less than 6 per seedling. Nymphal development duration, emergence rate, adult longevity, and fecundity of the two species reared in mixed

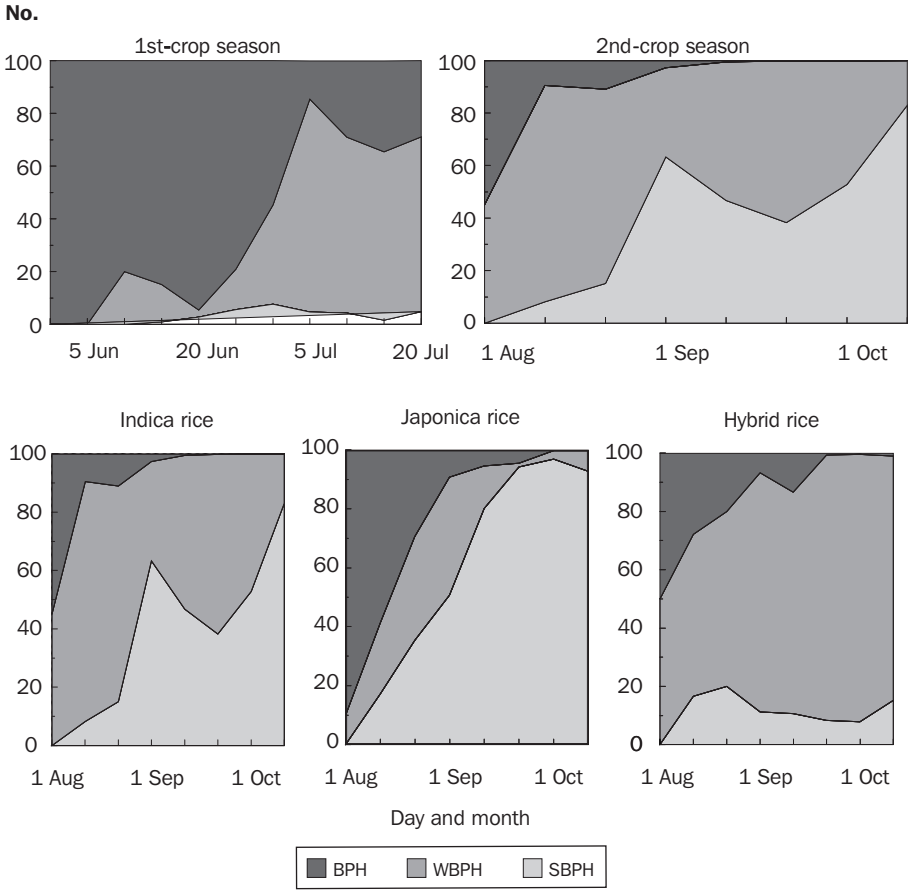

Fig. 8. Relationship of species structure to cropping system and varieties.

culture with other species were usually lower or higher than for those reared in pure culture. But the positive effects were also related to species and rice varieties. WBPH showed more positive effects under mixed culture conditions than BPH. The positive effects for both BPH and WBPH were higher on unsuitable varieties than on suitable varieties (Cheng et al 2001). The co-occurrence of planthopper species might also help them to escape from predation. Field investigation using monoclonal antibodies revealed that food shifting of spiders from one prey species to another in the field was mainly related to the proportions of density of these prey species to the density of total preys. *Pardosa pseudoannulata* mainly preys on midges when WBPH starts to migrate into paddy fields around June and on WBPH when BPH starts to migrate into paddy fields around July because densities of midges and WBPH at those times are much higher than those of WBPH and BPH, respectively (Zhao 2003). These two phenomena imply that the co-occurrence of these planthopper species benefits their

population development at the early stage. The variance in sensitivity of the three planthopper species to varieties and insecticides makes the choice of management programs more complex.

Changes in genetic structure. The excessive use of insecticide led to the development of insecticide resistance in rice planthoppers and SBPH was the earliest rice planthopper species being detected as resistant to malathion and other organophosphates, as well as BHC, in the rice ecosystem in the mid-1960s. Between 1967 and 1979, immigrants of BPH developed resistance to several insecticides, including carbaryl, MTMC, malathion, diazinon, and fenitrothion. Research revealed a distinct contrast in the rapidity of the development of insecticide resistance between migratory rice planthoppers (BPH and WBPH) and the less migratory planthopper (SBPH) and the development of resistance in BPH and WBPH had historically been rather slow when compared with SBPH (Heinrichs 1994). Although there were reports on various problems, pesticide resistance for yellow stem borer to BHC in the mid-1960s, rice green leafhopper to malathion and other organophosphates in the early 1970s, striped stem borer to Shachongshuang and triazophos in the 1990s, and rice planthoppers to organophosphates and carbamates (Long 2005), pesticides are still used extensively for rice planthopper control. The sudden occurrence of high resistance of BPH to imidacloprid indicated that the resistance problems of rice planthoppers were more serious than what we thought. Further experiments showed that resistance indices of BPH to imidacloprid were about 70–557 (Yang 2007) and control efficiencies of Applaud and imidacloprid for SBPH were only 22.9% and 36.5% (Wang et al 2007). Recent experiments also showed that resistance indices of WBPH to imidacloprid and Applaud were 12.2–23.1 and 28.0–35.0, respectively (Tang et al 2008). The high resistance to imidacloprid for BPH that occurred suddenly from Vietnam to Japan in the same year, 2005, revealed that the genetic change of migratory planthopper species could occur more quickly than what we expected because the same pesticide could be used in all the areas along migratory routes in the globalizing world. The composition of virulent populations in local areas is also affected by that in source areas (Li et al 1999).

Change of temporal structure. The temporal structure is the age structure of a planthopper population through a crop season. The most important structure related to population development is the proportion of immigrants to all adults during the crop season, which is related to the effects of immigrants on population development from outside of fields. The reasons for higher efficiency to take control action at 30 days after transplanting, around late August, in the second-rice crop season are the short immigration period and short development period for BPH populations in it. The main immigrants usually arrive in the second-rice crop season around late July and early August and the main immigration period is only about 10–20 days. The time period good for population development is about 2 months because the temperature around late September might be too low for population reproduction (Cheng et al 1992). Although the pesticides used could kill only adults and nymphs, but not eggs, adults developed from these eggs laid by immigrants in August may not be very effective for population development because it is already close to late September. However, there

might be three main immigration periods, late June to early July, late July to early August, and late August to early September in the new single-rice cropping systems now. Therefore, the immigration period could last about 3 months and one pesticide application is unable to cover the whole period in a single cropping season. The best control strategy used for a second-rice cropping season in the double cropping system is not able to get the same efficiency in a single-rice cropping system. Field investigations in 2006 showed that the immigration population arriving in early September was more than 2.6 macropterous adults and reached about 87.5 nymphs and adults per hill after one generation, and caused economic loss. This indicated that the effective immigration period could last from July to early September and yield losses could be caused by the generation produced directly by immigrants.

Developing new management programs

The new rice planthopper problems mentioned above revealed that planthopper outbreaks resulted from the high intrinsic capacity for a population increase in rice planthoppers and changes in environmental factors in their habitats in recent years, which provided favorable conditions for them to show this high capacity for increase. This verified three basic principles for rice planthopper management: it is impossible to obtain sustainable control for rice planthoppers by using pesticide only, even with a highly efficiency insecticide such as imidacloprid; a key strategy for planthopper control is to reduce their capacity for increase by managing the three key parameters mentioned in the earlier equation; and, it is better to design management programs on a large geographic scale for migratory pests.

Managing initial populations by modifying cropping systems

Field investigation and simulation study indicated that an early transplanting time (early starting time for immigration), an early immigration peak, and a high immigration rate all tended to favor BPH outbreaks (Cheng et al 1990). Expansion of the single-rice crop season in Yangtze Delta areas shifted transplanting time to around June, 1–2 months earlier than that for the second-rice crop season, as it did for starting time for immigrants. Expansion of the single-rice crop season in source areas extended the immigration period (late August to early September) and 1 more month increased the immigration rate. Field investigations in 2006 showed that earlier immigrants played a more important role. The earlier immigrants, 2.26 per 100 hills in early July, could develop 7,804 times and they reached 17,637 per 100 hills in late September. But late immigrants, 172 per 100 hills in early September, could develop only 33.7 times and reach 5,836 per 100 hills. This comparison clearly showed that small earlier immigrants could cause serious problems and the starting time for immigration was closely related to the cropping system. The starting time for immigration could be postponed if the transplanting time was postponed. Field experiments showed that plant infection rates of rice stripe virus disease and densities of BPH immigrants could be reduced by about 50% and 70%, respectively, if the time for sowing and transplanting could

be postponed from 15 May and 15 June to 29 May and 29 June. The yields in the two treatments had no significant difference.

Managing growth rate by building up system resistance

Based on historical data collected from fields without any insecticide applications, the average peak densities of immigration generations in most of the 14 outbreak years were about 3 macropterous adults per 100 hills and the growth rates after 2–3 generations in these years were more than 1,000. The high growth rates mainly resulted from high nutrition (susceptible varieties and high nitrogen input), low natural mortality (overuse of pesticides), high humidity (dense canopy), higher autumn temperature, and stimulative effects of pesticides on fecundity in high-yielding rice ecosystems. It is important to develop a management program that will harmonize high yield and system resistance to rice planthoppers. System resistance means the general capability of a rice ecosystem to reduce the growth rate of rice planthoppers. The basic approaches for building up system resistance could include the development of resistant varieties, enhancement of natural biological control, and improvement of nutritional management. Although virulence to resistant varieties could be developed, varietal resistance should still be considered as one of the basic components of planthopper management, especially for an ecosystem such as China, where natural biocontrol agents are weak due to the long history of pesticide overuse.

Managing yield losses by developing a new control strategy

The high growth rate and unusual high immigration in some years in subtropical and temperate regions make urgent control action an important component for a management program of rice planthoppers to reduce or avoid economic yield losses. The sudden occurrence of high resistance of BPH to imidacloprid on a large scale in 2005 after the unreasonable use of the pesticide revealed that the development of a scientific control strategy for using control measures wisely might be more important than the development of new control measures. Most control strategies developed before were mainly based on the population development pattern of one particular planthopper species and the differences in population development patterns and sensibility to varieties and pesticides among species could reduce the control efficiency of these traditional strategies. Therefore, a new control strategy should be developed with a view of the rice ecosystem, which should take the three rice planthoppers, as well as other pests, into consideration. To improve the traditional strategy relying on chemicals, new environment-friendly control measures should be developed.

Managing rice planthoppers through establishing international collaboration

As migratory pests, both BPH and WBPH migrate among South Asia, China, South Korea, and Japan and planthopper problems in one country will always be related to planthopper problems in other countries. The immigrants in one country/region are from another country/region and the starting time, pattern, rate, and genetic structure of the immigration population in one country must be related to the population in

another country. Since BPH and WBPH move from one country to another country every year, biological characteristics of the two planthopper populations in one country, especially for genetic structure, could be a mixture of the populations in many of the countries. The development of virulence to varieties and resistance to insecticides for BPH provided examples to demonstrate that a management program in the globalizing world should be designed on an international basis. International collaboration should not only include surveillance of population development patterns, virulence, and pesticide resistance for the development of management programs but also diversified techniques for high yield to be used for a delay of virulence and the development of resistance. In the meantime, cropping systems in both source and local areas could be designed based on population development pattern at a migratory scale to manage planthopper problems.

The increase in food requirements by the increasing population in the world will make high yield the first priority for rice production, but rice planthopper problems have been exacerbated by traditional high-yielding practices since the 1960s. A comparison of rice planthopper problems between tropical rice ecosystems and subtropical and temperate rice ecosystems revealed that the most important task would be to develop sustainable management programs for rice planthoppers by building up system resistance to reduce their initial population and capacity for increasing in subtropical and temperate rice ecosystems.

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Recent occurrences of long-distance migratory planthoppers and factors causing outbreaks in Japan

Tomonari Watanabe, Masaya Matsumura, and Akira Otuka

Serious outbreaks of *Nilaparvata lugens* were reported in 2005 on Kyushu Island, in the southern part of Japan. In order to improve planthopper management, we analyze the factors causing recent planthopper outbreaks: (1) fluctuations in the immigrant density and timing, and (2) the growth rate from the immigrant generation to the reproductive generation. It is considered that the increase in immigrant density was caused by the high planthopper density in the migration source and the development of suitable weather conditions, which can cause planthoppers to be displaced in early to mid-July. High temperature during summer to early autumn, high brachypterous ratio of females, and low *Sogatella furcifera*/*N. lugens* ratio may affect the growth rate from the immigrant to reproductive generation of *N. lugens*. Recent chemical control measures and their problems are described.

Population growth patterns of rice planthoppers, the brown planthopper (*Nilaparvata lugens*) and the whitebacked planthopper (*Sogatella furcifera*), have been studied in both tropical and temperate rice-growing areas since the 1960s (e.g., Cook and Perfect 1989, Kenmore 1980. Kisimoto 1965, Kuno 1968, Kuno and Dyck 1985, Sawada et al 1993, Wada and Nick 1992). Kuno (1968) and Kisimoto (1965) revealed the basic population dynamics of planthoppers in Japan.

In the late 1980s, the low population growth rate of *N. lugens* between successive generations occurred in some areas when the immigrant density was remarkably high (Noda 1988, Sogawa et al 1988). Watanabe et al (1994) analyzed a 40-year light trap record and found three different types of growth pattern for planthoppers: (1) low immigrant density and high population growth rate, (2) low immigrant density and low population growth rate, and (3) high immigrant density and low population growth rate. In the 1980s, immigrant density varied and population growth rates were lower than those in the other decades (Watanabe et al 1994). After the mid-1990s to early 2000, the immigrant densities of both planthopper species were lower than those in the 1980s (Matsumura 2000). Not only changes in population dynamics but also changes in genetic character were observed in the 1980s and 1990s. Major changes

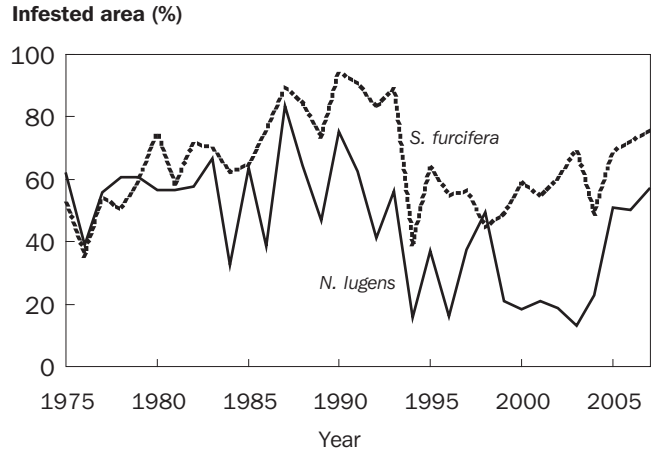

Fig. 1. Changes in the percentages of planthopper-infested area in Kyushu, southern part of Japan.

in the influence of *N. lugens* on resistant varieties occurred around 1988-90 (Sogawa 1992) and 1997 (Tanaka and Matsumura 2000).

In 2005, serious outbreaks of *N. lugens* were reported mainly on Kyushu Island, in the southern part of Japan (Fig. 1). That had not happened in 20 years. Similar outbreaks were reported in China and Korea. Immigration densities in 2006 and 2007 were also higher than those in the previous 10 years, and *N. lugens* outbreaks were again reported in 2007. In order to improve the management strategy for planthoppers, analysis of the factors causing yearly fluctuations in the occurrences of immigrant and reproductive generations is essential. In this paper, we describe the recent occurrences of planthoppers, especially *N. lugens* in Kyushu, and discuss the possible factors causing *N. lugens* outbreaks.

Insects and weather data

Data on daily catches from light traps, total infestation area, and total area of chemical control in paddy fields were downloaded from the database on JPP-NET, the Japan Plant Protection general information NETwork system, which accumulates nationwide statistical data on insect pests and diseases. Monthly mean temperature was downloaded from the climatic statistics of the Japan Meteorological Agency (www.jma.go.jp/jma/index.html). NCEP/NCAR re-analysis data were used for the analysis of upper-air currents.

Immigrant generation

Kuno (1968) revealed that, for both species, *N. lugens* and *S. furcifera*, more than 50% of the variance in the peak density of reproductive generations was due to that in the density of the immigrant generation. Therefore, we first analyzed

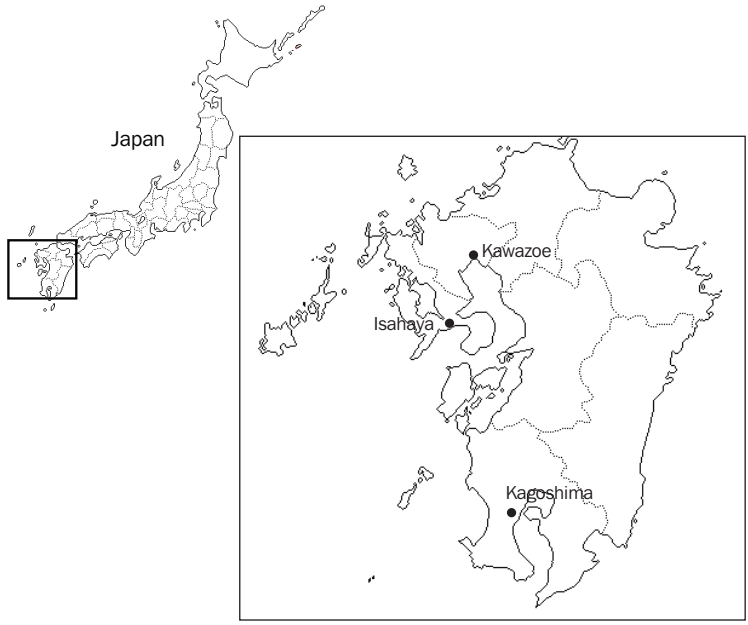

Fig. 2. Location of the monitoring sites.

the fluctuations in the immigrant density and period. Three locations of light trap monitoring sites on Kyushu Island, Isahaya (130.01′E, 32.49′N), Kawazoe (130.20′E, 33.10′N), and Kagoshima (130.47′E, 32.75′N), were selected for the analysis (Fig. 2). Total light trap catches in June and July were calculated.

Annual fluctuations in light trap catches during June and July (Fig. 3) are similar among the three monitoring sites and are also correlated with the annual trend of infested area in Kyushu (Fig. 1). Those relationships show the importance of immigrant density in the population dynamics of reproductive generations of rice planthoppers in Japan.

Fluctuations in the immigrant density of planthoppers are mainly dependent on two factors: planthopper density in the migration source area and weather factors that assist planthopper long-distance migration. The planthopper immigration is highly correlated with the development of the low-level jet stream (LLJ), which is the strong southwesterly upper-air current in the warm sector of a depression moving along the Bai-u (rainy season, June to July) front extending from continental China to Japan (Seino et al 1987, Watanabe et al 1991, Watanabe and Seino 1991). The total number of catches of planthoppers during June and July was also correlated with the cumulative days of the development of LLJ suitable for migration from China and Japan (Figs. 3 and 4).

Fluctuation in the cumulative days of LLJ was mainly due to the changes in the days of LLJ development during July (see annual changes in the June/June + July ratio in Fig. 4). During 1994 to 2004, when planthopper immigrant densities were low, few

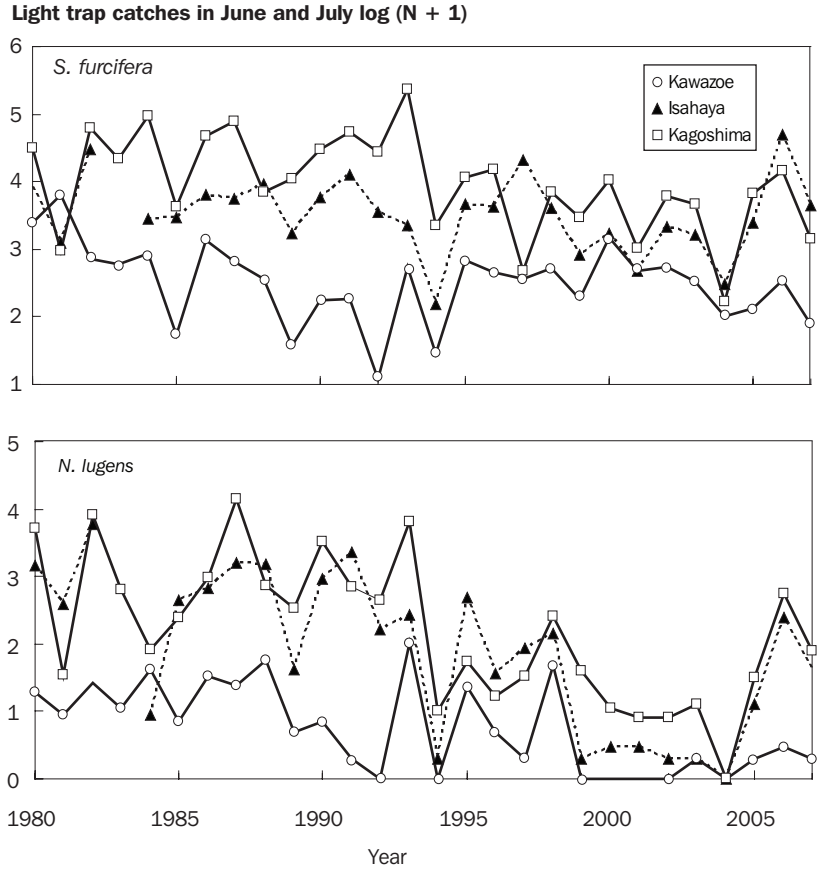

Fig. 3. Changes in the number of light trap catches of *S. furcifera* and *N. lugens* at three monitoring sites in Kyushu, Japan.

LLJ developments were observed during July. The cumulative days of LLJ in July have been increasing since 2005, but not to a high value compared with those during the mid-1980s to early 1990s (Fig. 4). Main immigration periods were observed in mid-July 2005 and early July in 2006 and 2007. Otuka et al (2007) reported planthopper outbreaks in Vietnam and southern China, the suspected migration source areas of the planthoppers. Therefore, the increases in the immigrant density of *N. lugens* in 2005, 2006, and 2007 were caused by the high planthopper density in the migration source area and the development of suitable weather conditions that can cause those planthoppers to be displaced in July.

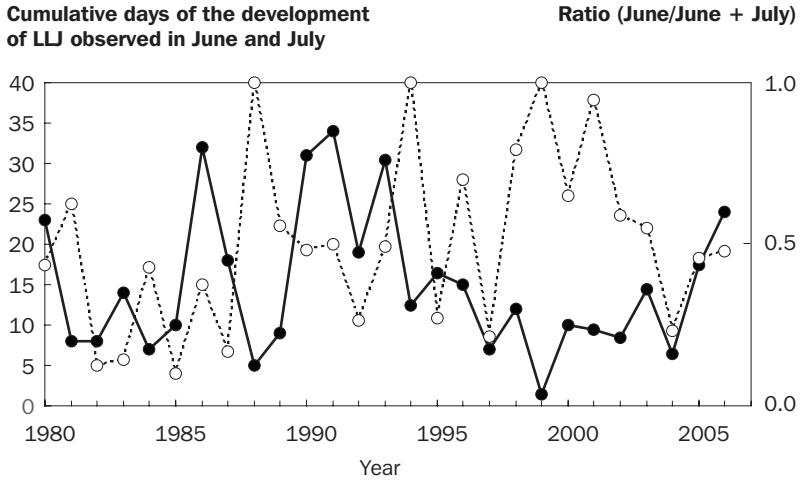

Fig. 4. Changes in the cumulative days of the development of low-level jet stream (LLJ, ●) observed in June and July, and the June ratio (June/July + July, ▯). Analysis results in 1980 to 1990 and 1996 to 1998 were obtained from Seino et al (1987), Sogawa (1995), and Syobu and Mikuriya (2000). LLJ development period in 1991 to 1995 and 1999 to 2006 was analyzed using NCEP/NCAR re-analysis data and JPP-NET information, respectively.

Population growth rate

Many factors that may affect population growth rate were reported: immigration period and density, female brachypterous ratio, summer temperature, etc. Watanabe et al (1994) analyzed a 40-year light trap record and showed that early immigrant period and high temperature in summer may increase the *N. lugens* population growth rate. Here, we analyzed the effect of each factor on the population dynamics of *N. lugens*.

In 2005, the main immigration period, mid-July, was not earlier than that in other years. Summer and autumn temperature, however, were considerably higher than the 30-year mean temperature. Recently, summer and early autumn temperature have usually been higher than the 30-year mean temperature (Fig. 5), and this is one of the possible factors that stimulate the high growth rate of *N. lugen*s during summer to autumn.

Wing dimorphism of planthoppers has been studied (e.g., Kisimoto 1956, Iwanaga et al 1985, Morooka et al 1988, Matsumura 1996). Iwanaga et al (1985) revealed various responses to density in the wing form (brachypterous and macropterous) ratio among the immigrant populations of *N. lugens*. Matsumura (2002 unpublished data) investigated the annual variation of density and wing-form relationship in the immigrant populations and showed a high ratio of brachypterous females in the 2005 population (Fig. 6).

In 2006, the immigrant density of *N. lugens* was higher than that in 2005 (Fig. 2), but the total percentage of *N. lugens* infested area was not higher than that in the

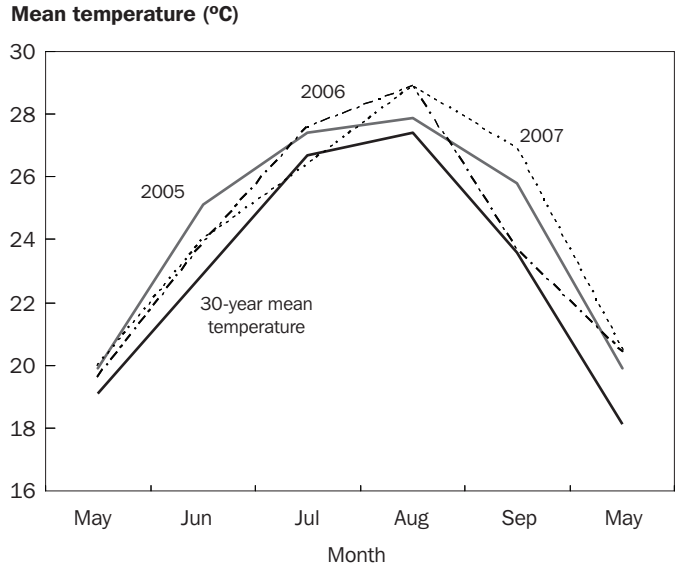

Fig. 5. Monthly mean temperature in Saga, Kyushu, Japan. Data from climatic statistics of the Japan Meteorological Agency.

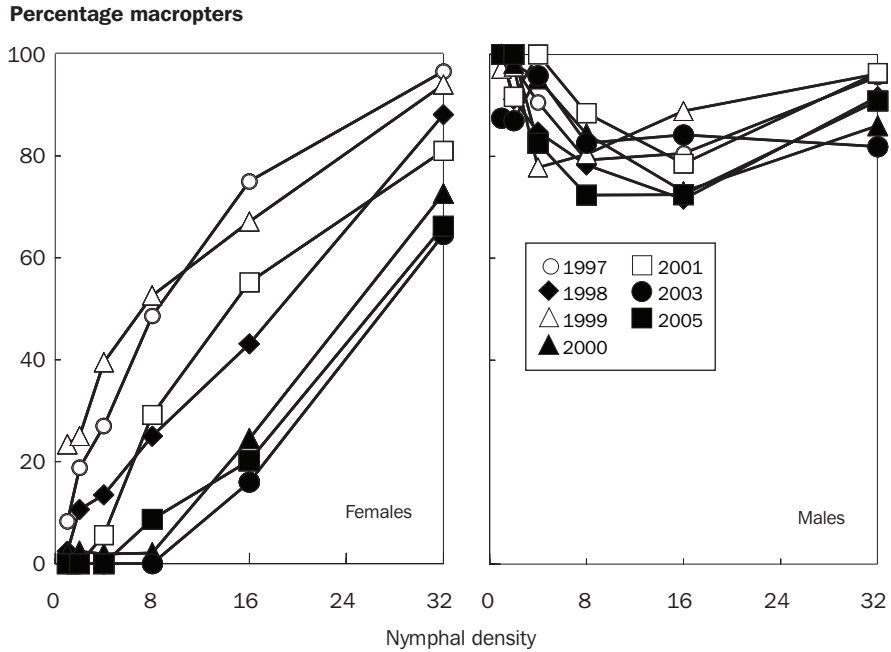

Fig. 6. Density and wing-form relationship in immigrant populations of *Nilaparvata lugens* in Japan (Matsumura 2002, unpublished data).

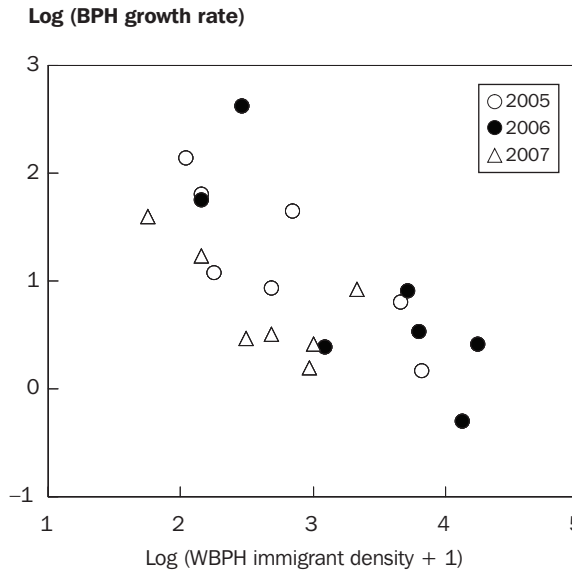

Fig. 7. Correlation between *S. furcifera* immigrant density and *N. lugens* growth rate from the immigrant generation to reproductive generation.

previous year (Fig. 1). The negative effect of *S. furcifera* on the population growth of *N. lugens* was suggested in laboratory experiments (Matsumura and Suzuki 2003). In order to analyze the effect of *S. furcifera* population on *N. lugens* growth in field conditions, population growth rates from the immigrant generation to reproductive generation were calculated using light trap data. Seven locations for light trap monitoring sites on Kyushu Island—Kawazoe, Koshi, Hondo, Miyakonojyo, Nobeoka, Kunitomi, and Kagoshima—were selected. The total number of trap catches from 20 June to 20 July represented population density of the immigrant generation, and from 21 July to 30 September represented population density of the reproductive generation. Negative correlation was observed between *S. furcifera* immigrant density and *N. lugens* growth rate (reproductive/immigrant) (Fig. 7). Average *S. furcifera/N. lugens* ratios of the immigrant generation varied among years: 42, 59, and 24 in 2005, 2006, and 2007, respectively. The high *S. furcifera* ratio in the immigrant generation may have caused the low growth rate of *N. lugens* in 2006.

Changes in insecticide application manner

Insecticide applications are a major control method against planthoppers in Japan. In the 1980s, total insecticide usage was more than 2–3 times per field. However, the total amount of chemical application decreased in the mid-1990s (Fig. 8). One major reason for that reduction in chemical usage was the introduction of persistent

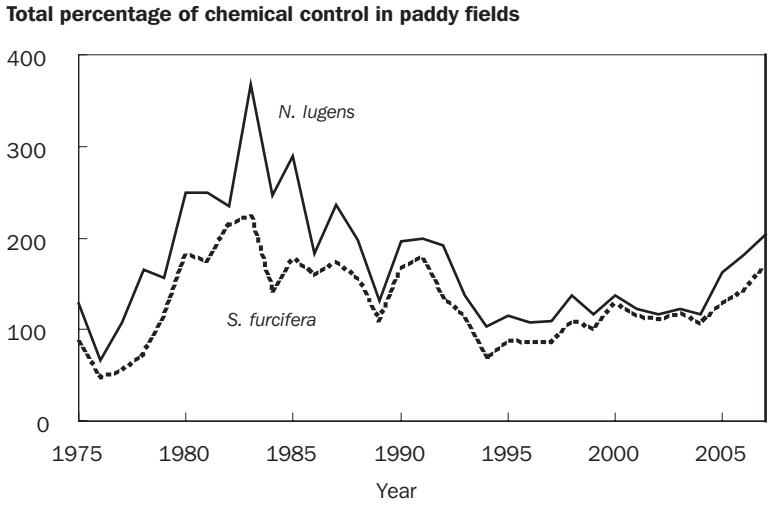

Fig. 8. Changes in the total percentages of chemical control in paddy fields against planthoppers in Kyushu, Japan.

systemic insecticides for nursery-box application. This method has been widely used in more than 60% of the rice fields in Japan for control of insect pests of early-stage rice plants. The *N. lugens* population growth rate from the immigrant generation to the first generation is higher than that in other generations (Fig. 9, Kuno 1979, Watanabe ad Tanaka, unpublished). Therefore, reducing the initial population growth rate using insecticide is an effective method for *N. lugens* in the temperate region.

The nursery-box application method can reduce labor and time for chemical treatment, and the total amount of chemical usage. But the chemicals are applied regardless of the pest density at transplanting time, earlier than planthopper immigration. Under such conditions, farmers may lose their concern about insect pest occurrences, and tend to miss a timing of an additional spray even when the forecasting of outbreaks is released. Many agricultural cooperative associations have introduced radio-controlled helicopters to spray additional chemicals in rice fields. The flight schedule of the helicopter is usually fixed before the rice-growing season and does not depend on pest incidence. In 2005, even with the forecasting information on *N. lugens* outbreaks, an additional spray of chemicals with appropriate timing was difficult for such reasons.

The development of insecticide resistance to some chemicals was reported in the planthopper population in 2005 (Matsumura et al 2007, Gyotoku and Kuchiki 2007). Insecticide resistance is one of the important population characteristics, as well as wing-form response to density and virulence to resistant varieties that we should know in more detail to improve the control strategy for planthoppers.

A high-precision and real-time migration prediction model was developed (Otuka et al 2005) and is now available on the Web (http://agri.narc.affrc.go.jp/). The combination of information on planthopper incidence in each area and a real-time

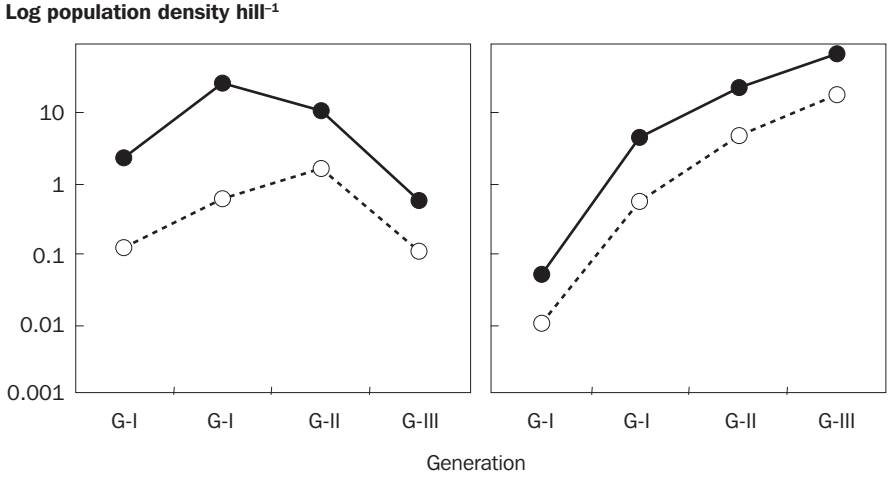

Fig. 9. Population growth of two planthopper species obtained by field census in Kyushu, Japan. 1961-68: Kuno (1979); 1987-91: Watanabe and Tanaka, unpublished.

prediction model makes it possible to improve wide-area planthopper management. Therefore, we should discuss Asia-wide planthopper management strategies.

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Situation of planthoppers in Asia

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The brown planthopper *Nilaparvata lugens* (Stål) and the whitebacked planthopper *Sogatella furcifera* (Horvath) are the two most important planthoppers in Asia. They cause plants to wilt, known as hopper burn. To know the current problems of planthoppers in Asia, questionnaires relating to the historical trends of distribution, damage to the rice crop, occurrence of insecticide resistance, management of planthoppers, and research activities from 1998 to 2007 were sent out to our Asian partners in China, India, Indonesia, Malaysia, the Philippines, Thailand, and Vietnam.

The results of the survey showed that the predominant management option of planthoppers in most countries today continues to rely solely on insecticides. Insecticide resistance to planthoppers was recorded in Thailand, China, and India. All our Asian partners focus more on insecticide evaluation research than on field resistance and ecology.

Planthoppers constitute a large group of phytophagous insects in the Order Hemiptera. Distributed worldwide, all members of this group are plant-feeders and some species are considered pests. In Asia, two planthoppers of economic importance are the brown planthopper (BPH), *Nilaparvata lugens* (Stål), and the whitebacked planthopper (WBPH), *Sogatella furcifera* (Horvath) of the Family Delphacidae. They damage plants directly by sucking the plant sap and by ovipositing in plant tissues, causing plant wilting or hopper burn. When conditions are unfavorable, especially when the crop is already dead, they migrate into a crop in large numbers. In China, both the brown planthopper and whitebacked planthopper migrate from the warmer, tropical regions of southern China to the Korean peninsula, as well as to Japan and central China, in the early summer of each year (Turner et al 1999). These regions are unable to sustain populations on the peninsula in the winter. The distance these migratory pests must travel is more than 1,000 km and much of it is over the ocean. It has been shown that favorable meteorological conditions of sustained strong southwest winds in the lower atmosphere, which are often associated with the "Bai" front, are necessary for successful migration. Simulation studies on migration suggest that the source region for early-season planthopper migrants to Korea is southeastern China

(south of 25°N and east of 115°E) (Zhu Min et al 2000). The results also indicate that planthoppers must have the ability to fly continuously for at least 30 and up to 48 hours, with much of the flight over the ocean, and that the altitude of flight may vary from 500 m to 1,500 m from one episode to another. If more remote source regions or circuitous migration routes are to be considered, much longer flight durations would have to be assumed in most cases.

Of the two planthoppers, the brown planthopper not only directly damages the rice crop but also transmits viral diseases of rice such as grassy stunt and ragged stunt (Reissig et al 1986). For many years, brown planthoppers have been a serious threat to rice production throughout Asia (IRRI 1979). In the 1970s, they caused extensive damage to the rice crop in Asia (Dyck and Thomas 1979). They were formerly only a minor pest in most tropical countries of Asia. Many regard the BPH as the number-one insect pest of rice in Asia today, primarily because of the unpredictability of the infestation and the dramatically severe damage it causes.

The whitebacked planthopper, though not a virus disease transmitter, occurs widely and can become sufficiently numerous to kill plants by hopper burn (Reissig et al 1986).

Shepard et al (1995) have shown that the populations of both the brown planthopper and whitebacked planthopper increase after insecticide applications. Because of widespread misuse of insecticides, outbreaks of BPH have occurred, thus killing natural enemies that normally play a key role in suppressing planthopper populations in rice (Kenmore et al 1984). Moreover, the promiscuous use of pesticides also promoted resurgence of the insect pest (Heinrichs and Mochida 1984). Likewise, it is believed that excessive use of urea as a nitrogenous fertilizer can also lead to outbreaks by increasing the fecundity of BPH (Preap et al 2002).

To learn more about planthopper problems in Asia, a questionnaire was distributed to our Asian partners in China, India, Indonesia, Malaysia, the Philippines, Thailand, and Vietnam. This paper summarizes the available data and other information on planthoppers in different Asian countries from 1998 to 2007.

Distribution

Nilaparvata lugens (Stål) is distributed in Asia, Australasia, and the Pacific Islands. In Asia, it is found in Bangladesh, Brunei, Burma (Myanmar), China, Hong Kong, India, Indonesia, Japan, Cambodia, Korea, Laos, Malaysia, Nepal, Pakistan, the Philippines, Singapore, Sri Lanka, Taiwan, Thailand, and Vietnam. In Australia and the Pacific Islands, it is found on the Caroline Islands, Fiji, Mariana Islands, Papua New Guinea, and Solomon Islands (Fig. 1) (Reissig et al 1986, CAB 1984). It is not found in America and Africa. The brown planthopper is mainly a pest of irrigated rice, but it can also be abundant in rainfed environments. It is rare in upland rice (Reissig et al 1986).

Sogatella furcifera (Horvath), or the whitebacked planthopper, is distributed in Asian countries, Australasia, and the Pacific Islands. In Asia, it is found in Bangladesh, Cambodia, China, Hong Kong, India, Indonesia, Japan, Korea, Laos, Malaysia, Myanmar, Nepal, Pakistan, the Philippines, Ryukyu Islands, Sri Lanka, Taiwan, Thailand,

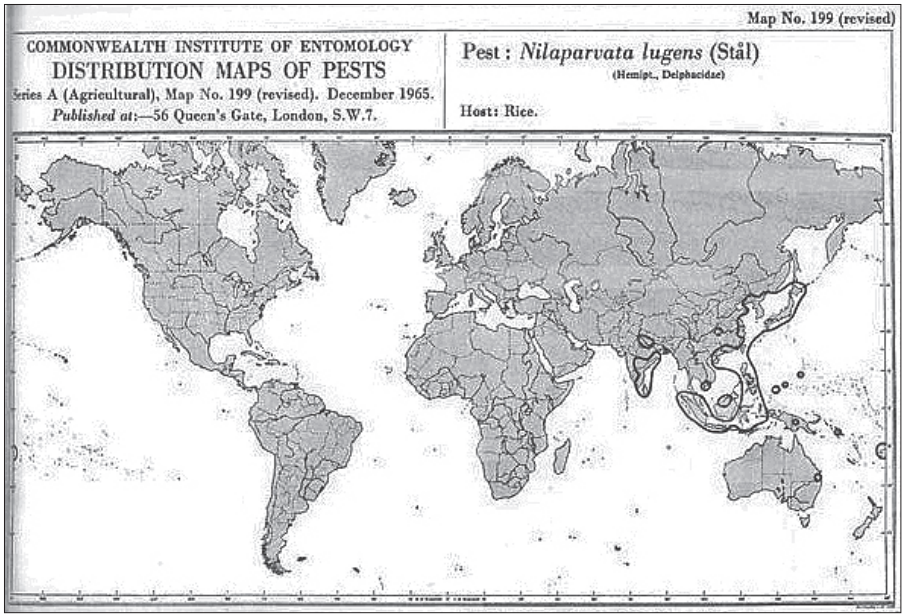

Fig. 1. Distribution map of *Nilaparvata lugens* (Stål) (shown by the black solid lines) (Reissig et al 1986). Reprinted with permission from CABI.

Vietnam, and in the former Soviet Union. In Australasia and the Pacific Islands, it is distributed in Australia, the Caroline Islands, Fiji, Irian Jaya, Marianas Islands, and Marshall Islands (Fig. 2) (Reissig et al 1986, CAB 1980). The whitebacked planthopper is also not found in America and Africa. It occurs in all rice environments (Reissig et al 1986).

Historical trends of distribution

Relative abundance of planthoppers

Light trap catches of BPH. Light trap catches of brown planthoppers from China, India, Indonesia, Malaysia, the Philippines, Thailand, and Vietnam have indicated strong fluctuation patterns over the last 10 years (Fig. 3, Table 1). Comparisons on the data between countries are not applicable since different countries show different trends.

In the five rice regions in China (Nantong City, Jinhua City, Yangtze River rice region, central China rice region, and southern China rice region), the general trend of light trap catches is toward increasing BPH populations over the last 10 years (Fig. 3). Starting from 1998 to 2003, the average of brown planthopper populations has risen and fallen. Within these periods, the lowest population of 1,791 BPH was recorded in 2002 and the highest population of 6,800 BPH was observed in 1999. Based on the highest catch of 1999, there were about 15% more brown planthoppers in 2006 and 2007. There were 103,211 BPH in 2006 and 102,084 in 2007 (Table 1).

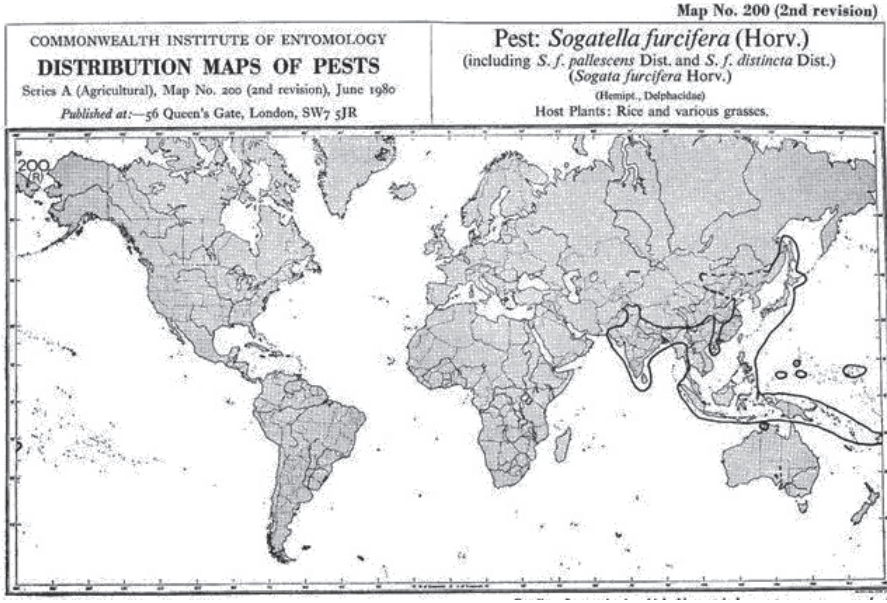

Fig. 2. Distribution map of *Sogatella furcifera* (Horvath) (shown by the black solid lines) (Reissig et al 1986). Reprinted with permission from CABI.

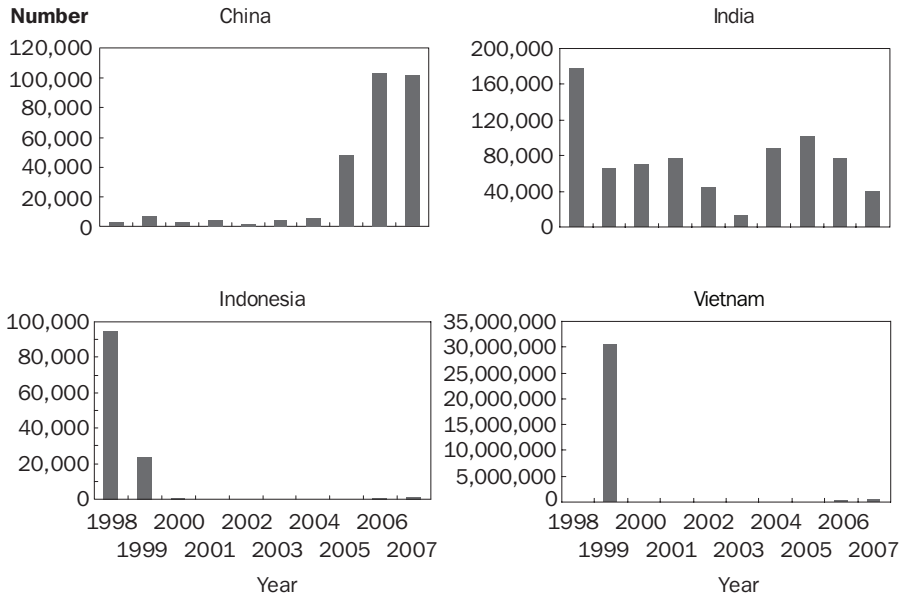

Fig. 3. Number of brown planthoppers from light trap catches in some Asian countries.

Table 1. Number of *Nilaparvata lugens* caught from yearly light trap catches in some Asian countries in 1998-2007.

Year	China	India	Indonesia	Malaysia	Philippines	Thailand	Vietnam
1998	2,207	177,283	94,562	No data	No data	No data	93,057
1999	6,800	65,561	23,617	No data	3,939	2,526,546	30,409,002
2000	2,785	69,989	350	No data	4,184	20,165	18,747
2001	3,734	76,514	9	No data	19,739	194,917	12,317
2002	1,791	44,774	48	No data	18,056	2,484,789	22,008
2003	3,750	12,973	60	No data	No data	No data	47,321
2004	6,063	88,469	24	No data	No data	No data	34,637
2005	47,800	100,689	49	No data	No data	No data	105,057
2006	103,211	75,672	362	No data	No data	297,047	158,356
2007	102,084	39,699	1,008	No data	1,322	194,155	512,141

In six cities in India (Aduthurai, Coimbatore, Maruteru, Sambalpur, Kaul, and Pattambi), the trend in BPH catches was of a decreasing nature during 1998 to 2003, while it was increasing from 2003 to 2005 (Fig. 3). From 2005 to 2007, the BPH population tended to decrease. There were more BPH observed in the 1990s than in the 2000s. The yearly catches decreased by 2.3% in 2006 and 4.5% in 2007. There were only 39,699 BPH trapped in 2007, which was the second lowest sample observed in the past 10 years (Table 1).

In Indonesia, especially in Sukamandi of the north coastal region of West Java, starting from a high population of 94,562 in 1998, the trend in light trap catches was decreasing until 2004 (Fig. 3, Table 1). The BPH population started to pick up from 2005 to 2007. Based on the catch in 1998, there was a 93% reduction in the BPH population in 2007.

In the Philippines, covering Muñoz, Isabela, and Agusan provinces, the BPH population was 5 to 4 times higher in 2001 (19,739 catches) and 2002 (18,056 catches) than in 1999 (3,939 catches) and 2000 (4,184 catches), respectively. In 2007, only one province was sampled; hence, a low population of BPH was recorded at 1,322 counts (Table 1).

In Thailand, the most BPH were observed in 1999 and 2002, when the population was 2.5 million (Table 1). No data on light trap catches were available from 2003 to 2005. The population declined heavily in 2006 and 2007 by more than 2.2 million and 2.3 million, respectively.

In Vietnam, an abnormal trend in BPH populations was observed in the last 10 years (Fig. 3, Table 1). Considering the very high catch in 1999 (30.4 million), the BPH population suddenly went down in 2000 to 2007. Although the BPH population was five times more in 2007 (512,141 individuals) than in 1998 (93,057 individuals), the trend is still toward an abnormal one.

Table 2. Number of *Sogatella furcifera* caught from yearly light trap catches in some Asian countries in 1998-2007.

Year	China	India	Indonesia	Malaysia	Philippines	Thailand	Vietnam
1998	9,139	No data	0	No data	No data	No data	No data
1999	13,318	10,418	0	No data	1,632	No data	No data
2000	16,867	29,350	4	No data	604	No data	No data
2001	12,023	10,057	1	No data	2,231	No data	No data
2002	12,619	14,065	0	No data	9,396	No data	No data
2003	27,852	5,652	22	No data	No data	No data	No data
2004	8,930	2,260	5	No data	No data	No data	No data
2005	59,998	8,020	7	No data	No data	No data	No data
2006	56,720	9,692	202	No data	No data	154	No data
2007	112,993	11,762	601	No data	1,138	237	No data

No data on light trap catches were available for Malaysia**.**

Light trap catches of WBPH. In the five rice regions in China (Nantong City, Jinhua City, Yangtze River, central China, and southern China), 112,993 WBPH were sampled in 2007, which was almost 13 times more than those obtained during 1998 (9,139 individuals) (Table 2). The lowest population of 8,930 WBPH was observed in 2004. The general trend in light trap catches of WBPH in China has been increasing for the last 10 years (Fig. 4).

In India (Aduthurai, Maruteru, Sambalpur, Kual, and Nawagam), the greatest number of WBPH was observed in 2000, with 29,350 in the light traps. In 2003, 5,652 WBPH were caught and this number declined by almost half in 2004. It gradually increased by 4% in 2005 to 6% in 2007, which is almost half of the WBPH sampled in 2000 (Table 2). The trend in catches was fluctuating (increasing from 1999 to 2000, decreasing from 2000 to 2001, increasing from 2001 to 2002, decreasing from 2002 to 2004, and finally increasing from 2004 to 2007) (Fig. 4).

Indonesia had more whitebacked planthoppers in 2007 (601 individuals) in susceptible varieties. However, the data on light trap catches for WBPH showed fewer catches for the past 10 years despite an increasing trend in the population (Table 2). Visual counts of WBPH in the field showed higher populations in susceptible varieties (Baehaki 2008).

In the three provinces in the Philippines, the most catches (9,396 WBPH) were recorded in 2002 and the least (604) in 2000 (Table 2). In one province, a catch of 1,138 was recorded in 2007.

Only two observations on light trap data were available in Thailand. Some 154 WBPH were caught in 2006, whereas 237 WBPH were trapped in 2007. A difference of 83 counts in the WBPH population was obtained in the two years, with 2007 having the highest count.

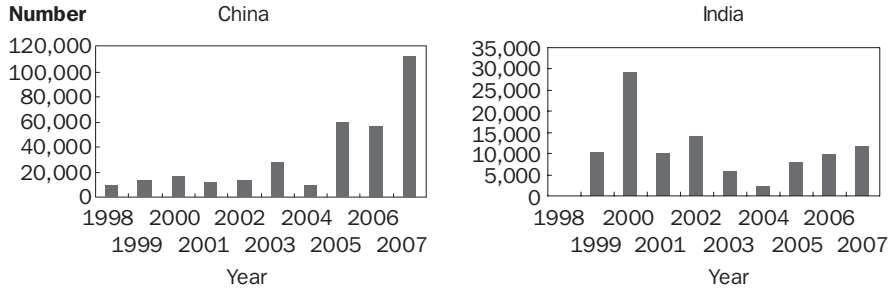

Fig. 4. Number of whitebacked planthoppers from light trap catches in some Asian countries.

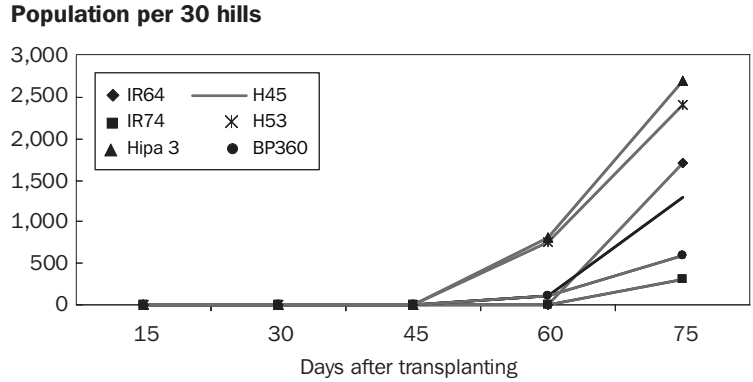

Fig. 5. Population of brown planthopper on hybrid and inbred rice, Subang, West Java, WS 2005.

No data on light trap catches were available for Malaysia and Vietnam.

Other sampling data for planthoppers. In Indonesia, during the wet season in 2005, the brown planthopper was observed to develop more on hybrid rice than on inbred rice (Fig. 5). At 60 and 75 days after transplanting, there were more BPH on hybrids (Hipa 3, H53, and line H45) than on inbreds (IR64, IR74, and line BP360). The same results were recorded for whitebacked planthopper during the dry season of 2004 (Fig. 6). More WBPH were found to develop on hybrid rice (Rokan, Hipa 3, and Hipa 4) than on inbred rice (IR64 and BP360E) from 2 to 7 weeks after transplanting.

In the Philippines, during the 2006 and 2007 DS and WS, planthoppers were collected in Central Luzon, using four sampling devices—visual count, yellow pan trap, window trap, and yellow board trap (Figs. 7 and 8). Most of the time, there were more WBPH than BPH collected from the four sampling devices. The trend was noticeable during the four cropping seasons. There were more BPH (37 individuals) and WBPH (81 individuals) caught in yellow board traps at 52 and 45 DAT, respectively,

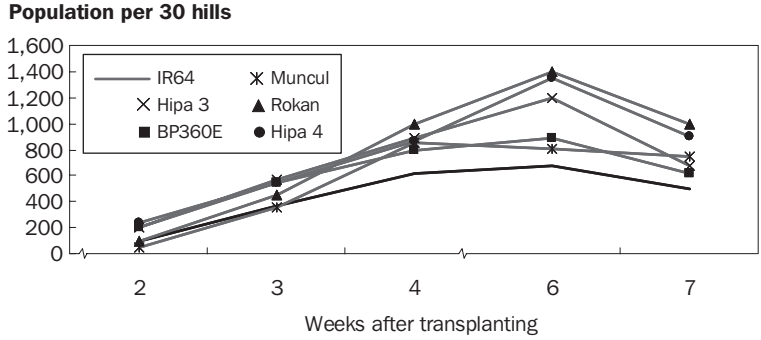

Fig. 6. Population of whitebacked planthopper on hybrid rice, Karawang, West Java, DS 2004.

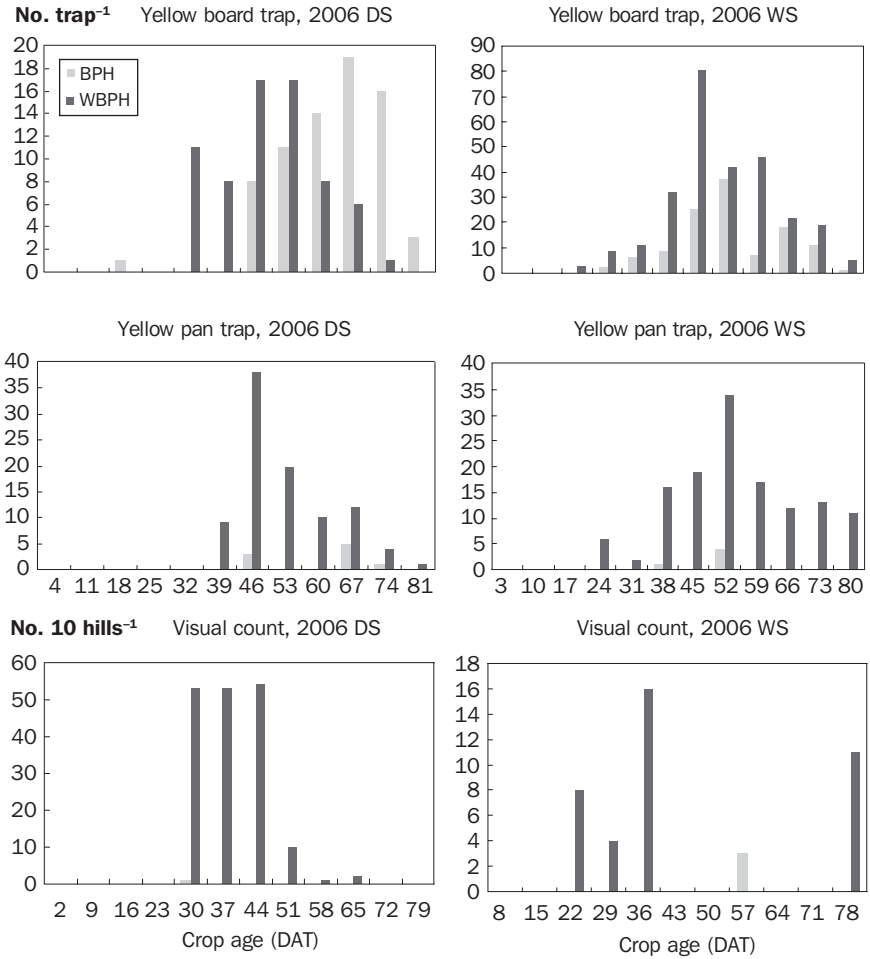

Fig. 7. Observations on planthoppers in 2006 DS and WS, Philippines, using different sampling techniques.

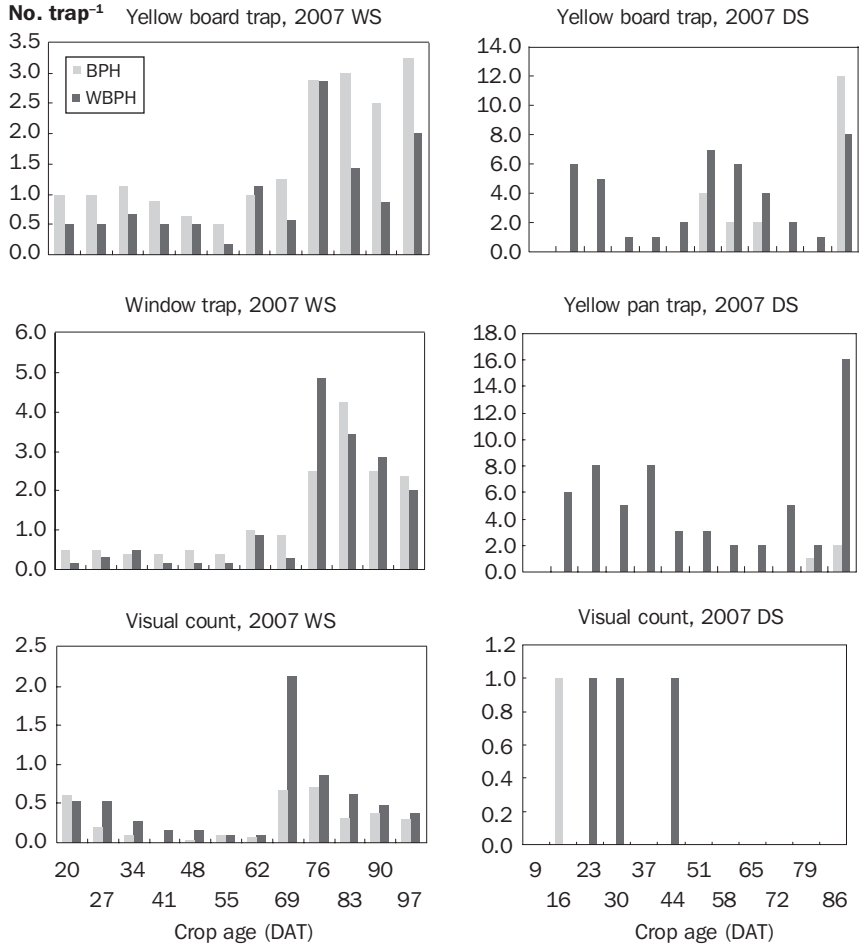

Fig. 8. Observations on planthoppers in 2007 DS and WS, Philippines, using different sampling techniques.

than on the yellow pan trap (4 BPH, 19 WBPH) during the 2006 WS (Figs. 7). In the same season, there were 16 WBPH and 3 BPH per 10 hills counted visually at 36 and 57 DAT, respectively. In the 2006 DS, only 1 BPH was visually collected at 30 DAT with 0 BPH at all the other sampling times and 54 WBPH at 44 DAT (Fig. 6). More WBPH (38 individuals) were collected in yellow pan traps at 46 DAT than on yellow board traps. However, there were more BPH (19) collected on yellow board traps at 67 DAT than on yellow board traps (Fig. 7). In the 2007 WS, considering the total number of planthoppers collected, there were more planthoppers in the window trap sampling device than on the yellow board trap (Fig. 8). There were more WBPH (16) on yellow pan traps at 86 DAT, but more BPH (12) on yellow board traps at 86 DAT in the 2007 DS. Visually, only 1 BPH was recorded at 16 DAT and 1 WBPH at

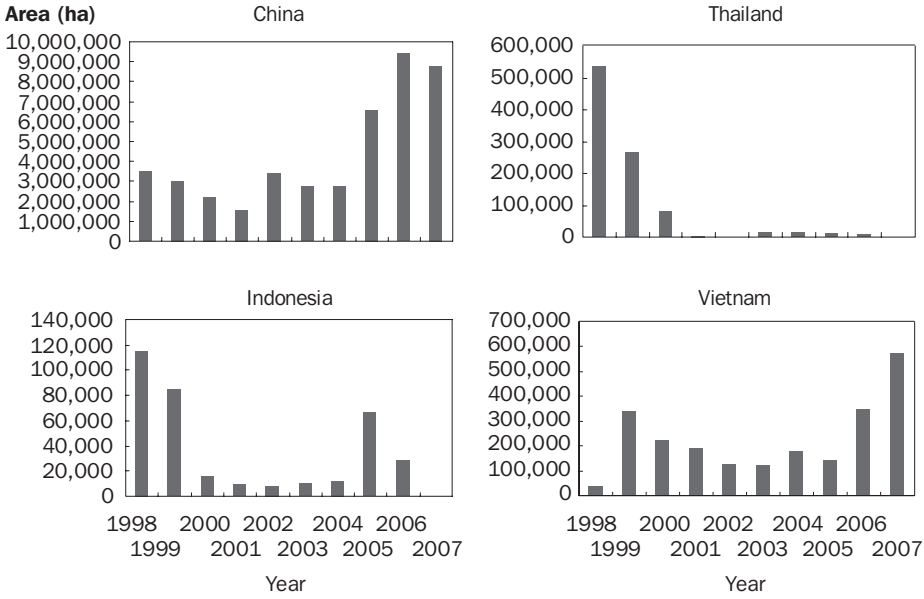

Fig. 9. Damage (in hectares) in rice fields caused by brown planthoppers.

23, 30, and 44 DAT. During the 2007 WS, there were more WBPH counted visually at 69 DAT, and 4.86 were collected on window traps at 76 DAT. Using the yellow board trap, more BPH (3.25) were trapped than WBPH (Fig. 8).

Damage to the rice crop

Planthoppers cause plants to wilt, a symptom called hopper burn. The damage from hopper burn that they caused was documented in some Asian countries from 1998 to 2007 (Fig. 9, Tables 3 and 4). Different trends of damage were observed in different countries.

Damage by BPH. In China, millions of hectares of rice fields were observed with BPH damage every year for the last 10 years (Fig. 9, Table 3). The biggest damage of 9.4 million hectares and 8.7 million hectares was observed in 2006 and 2007, respectively. The general damage trend is increasing.

In Indonesia, BPH damage decreased from 1998 to 2004, but it suddenly increased in 2005, but decreased in 2006 (Fig. 9). The least and maximum areas with hopper-burn damage were 8,573 ha in 2002 and 115,484 ha in 1998. In 2006, there were 28,421 ha of damage recorded, which was 13% less than the observed damage in 1998 (Table 3).

In Malaysia, there was not much difference in the damage area caused by BPH per year. The greatest damage observed was 7,259 ha in 2002 and the least was 3,708 ha in 1999 (Table 3). There were no data on damage from 2003 to 2007.

Beginning in 1998, the highest damage of 535,190 ha was recorded in Thailand (Table 3). Surprisingly, this declined heavily in 2007, when the damage area was only

Table 3. Area (ha) damage to the rice crop by brown planthoppers in some Asian countries in 1998-2007.

Year	China	India	Indonesia	Malaysia	Philippines	Thailand	Vietnam
1998	3,487,850	No data	115,484	4,964	No data	535,190	35,358
1999	3,030,300	No data	84,491	3,708	No data	263,725	341,994
2000	2,196,600	No data	15,910	4,193	No data	81,028	224,411
2001	1,594,550	No data	8,949	5,541	No data	3,328	189,574
2002	3,412,700	No data	8,573	7,259	No data	1,346	128,221
2003	2,725,000	No data	10,350	No data	No data	15,004	120,072
2004	2,735,100	No data	11,844	No data	No data	14,376	176,257
2005	6,588,500	No data	65,908	No data	No data	9,881	145,833
2006	9,418,650	No data	28,421	No data	No data	7,904	348,927
2007	8,751,500	No data	No data	No data	No data	64	572,419

Table 4. Area (ha) damage to the rice crop by the whitebacked planthopper in some Asian countries in 1998-2007.

Year	China	India	Indonesia	Malaysia	Philippines	Thailand	Vietnam
1998	6,903,500	No data	No data	0	No data	No data	No data
1999	6,850,500	No data	No data	1,256	No data	14,905	No data
2000	6,728,100	No data	No data	1,235	No data	No data	No data
2001	6,093,250	No data	No data	541	No data	1	No data
2002	5,134,350	No data	No data	1,068	No data	No data	No data
2003	6,661,450	No data	No data	No data	No data	No data	No data
2004	7,956,600	No data	No data	No data	No data	No data	No data
2005	7,679,400	No data	No data	No data	No data	No data	No data
2006	8,584,900	No data	No data	No data	No data	No data	No data
2007	1,500,000	No data	No data	No data	No data	No data	No data

64 ha, the least recorded in Thailand. The general trend of damage was decreasing.

In Vietnam, the highest damage was 348,927 ha in 2006 and 572,419 ha in 2007 (Table 3). The general trend in damage is sloping. There was a decreasing trend from 1999 to 2003 and an increasing trend from 2003 to 2007 (Fig. 9).

No data on area damage in hectares were available for India and the Philippines.

Damage by WBPH. In terms of the damage caused by whitebacked planthoppers, some data were gathered from China, Malaysia, and Thailand (Table 4). In China,

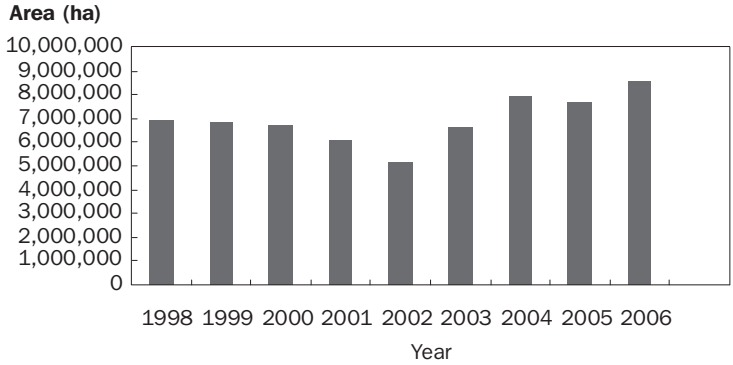

Fig. 10. Damage (in hectares) in rice fields caused by whitebacked planthoppers in China.

millions of hectares of rice area were damaged by WBPH every year for the past 10 years. For example, covering five regions in China, 5.1 million ha were the least observed damage (in 2002), with 8.5 million ha being the greatest observed damage (in 2006). In 2007, 1.5 million ha of damage covered only one province. The general trend is increasing (Fig. 10).

In Malaysia, the lowest area damage was 541 ha in 2001, with 1,256 ha being the largest area damage in 1999 (Table 4). There were no available data from 2003 to 2007.

Thailand provided only limited data on the damage caused by WBPH (14,905 ha in 1999 and 1 hectare in 2001).

No data were available on area damaged by whitebacked planthoppers in India, Indonesia, the Philippines, and Vietnam.

Comparison of the damage by the two planthoppers in China showed that whitebacked planthoppers damaged more area than brown planthoppers for the last 10 years (Tables 3 and 4).

Occurrence of insecticide resistance

The excessive use of insecticides led to the development of insecticide resistance to brown planthopper and whitebacked planthopper in the tropics and in temperate Asian countries (Heinrichs 1994). China, India, Indonesia, and Thailand had reports of rice planthopper resistance to insecticide (Fig. 11, Table 5).

In China, planthoppers exhibited 28.8-fold and 79.1- to 81.1-fold resistance to buprofezin and imidacloprid, respectively, in 2004 and 2005 to 2006.

In India, common organophosphates were tested against planthoppers in 1998. However, the planthoppers did not show any significant resistance to the chemical. Other tests in 2006 took place that showed planthopper resistance by 35.13-, 10.78-, and 4.98-fold to imidacloprid, thiamethoxam, and clothianidin, respectively.

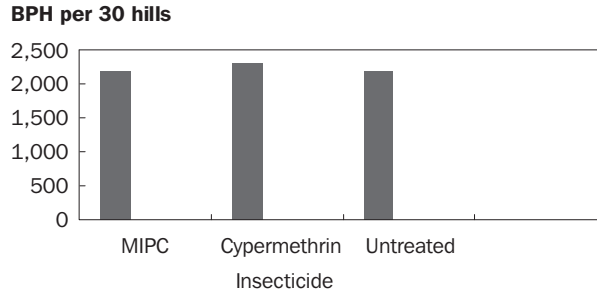

Fig. 11. Effectiveness of insecticides for brown planthopper, Karawang, West Java, 2001.

Table 5. Rice insecticide use in Asian countries showing resistance to planthoppers.

Year	Country	Chemical(s)	Description	References
1998	India	Common organophosphates	No significant resistance	Sarupa et al (1998)
2002	Thailand	Fenobucarb	3–5.6 times resistance	
2004	China	Buprofezin	28.8-fold resistance	Li et al (2008)
2005-06	China	Imidacloprid	79.1–81.1-fold resistance	Wang et al (2008), Liu and Han (2006)
2006	India	Imidacloprid	35.13-fold resistance	Krishnaiah et al (2006), IRC poster presented.
		Thiamethoxam	10.78-fold resistance	
		Clothianidin	4.98-fold resistance	
	Thailand	Imidacloprid	3–4.1 times resistance	

In Indonesia, MIPC and cypermethrin were tested for the brown planthopper. The insect population increased more than the control when cypermethrin was sprayed (Fig. 11).

In Thailand, planthoppers were 3 to 5.6 times more resistant to fenobucarb and 3 to 4.1 times more resistant to imidacloprid when tested in 2002 and 2006, respectively.

Imidacloprid is the common insecticide in China, India, and Thailand against which planthoppers have developed resistance. No data on insecticide resistance were available in Malaysia, the Philippines, and Vietnam.

Table 6. Planthopper management options in some Asian countries.

Country	Management options
China	Insecticides (buprofezin, Imidacloprid, fipronil, chlorpyrifos, DDVP) Rearing and releasing ducks in paddy Rice-fish double-culture systems Adjusting planting date Using insect-net proofs in nursery Light trapping Management of BPH resistance to imidacloprid
India	Summer plowing Clipping leaf tips of seedlings before transplanting Optimum dose of N application Leaving alleyways at 5-meter intervals Avoiding broad-spectrum insecticides Draining water during mid-season Wider spacing Resistant varieties Need-based insecticides
Indonesia	Monitoring Resistant varietes (IR64, IR74, Ciherang, Digul, Fatmawati, Membramo, and Mekongga) Use of economic threshold Insecticides (industrial or company and botanical) Manipulation of natural enemies Cultural practices (intermittent irrigation, weeding, varietal rotation, and fertilizer management)
Malaysia	Monitoring Use of insecticides
Thailand	Resistant varieties (Pathum Thani 1, Suphanburi 1, Suphanburi 2, Suphanburi 90, Chainat 1, Chainat 2, and Phisanuloke 2) Recommended insecticides (imidacloprid, dinotefuran, thiamitozam, buprofezin, carbosulfan, and isoprocarb) Surveillance and survey sampling of BPH and rice ragged stunt diseases Eradication and destruction of rice ragged stunt plants and their platoon Eradication of weeds that are hosts of rice ragged stunt virus

Management of planthoppers

A list of management options for planthoppers was provided by China, India, Indonesia, and Thailand (Table 6). The predominant management option for planthoppers today in most countries continues to rely solely on insecticide.

Except for China, the use of resistant varieties is common to India, Indonesia, and Thailand. It is only in Indonesia that natural enemies are used as part of the management program for planthoppers.

Research activities

Studies on planthoppers are conducted continuously in Asian countries because of the threat they pose to rice production (Tables 7 and 8). Most of the research activities on BPH and WBPH focus on insecticide screening and varietal screening. Comparing the number of research activities between the two hopper species, more work is conducted on BPH than on WBPH.

In order of publications, more works were published on insecticide screening, followed by varietal screening, virulence, biotypes, ecological fitness, pest management, nutrient management, and modeling of planthopper damage (Table 9).

Table 7. List of research activities conducted on brown planthopper or its associated viruses in some Asian countries in 1998-2007.

Country	Years	Research activity
China	1996-2007	Forewarning system for catastrophes of the main rice diseases and pests Forewarning parameters for catastrophes of migratory pests and on national catastrophes Forewarning and decision support system for pernicious living beings Development on monitoring and forewarning techniques for major diseases and pests Fundamental research on catastrophe forewarning, ecological adjustment, and control of diseases and pests Fundamental research on rampant endangering mechanisms of major agricultural pests and their sustainable control Study on atmospheric dynamical mechanisms for catastrophic immigrations of brown planthoppers Monitoring the virulence shift of BPH to rice varieties with different resistance genes Screening resistance to BPH of rice varieties (lines) in both greenhouse and fields Relationship between planthoppers and biodiversity around paddy field The role of endosymbiosis of BPH in its adaptation to resistant rice varieties The interaction of nitrogen fertilizer and high temperature on ecological fitness of BPH
India	1998-2007	Screening rice germplasm accessions and breeding lines for resistance Identifying effective insecticides Biocontrol agents IPM Evaluating transgenic lines with GNA gene Genetics of resistance

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Table 7 continued.

Country	Years	Research activity
Indonesia	1998-2007	Damage level of planthopper and rice stem borer attacks on transplanted and direct-seeded rice Identification of BPH biotypes and rice damage on upland rice area Impact of nutrient management on pest and yield losses of different rice varieties Augmentation technique for raising efficacy of *Metarhizium anisopliae* with additive material Efficacy of *Beauveria bassiana* RIRCC2 on adjuvant material to BPH in the laboratory Assessment on decreasing yield losses based on scoring damage by BPH and WBPH Virulence and assessment of BPH biotypes from central Java Distribution of BPH biotypes on some central rice production areas Evaluation of components of resistance on lines and varieties to BPH biotypes 3 and through filtering test and population buildup
Malaysia	1990-2003	Population dynamics of *Nilaparvata lugens* in rice The role of spatial heterogeneity on population dynamics of major rice pests
Thailand	1998-2004	Development of resistance to carbofuran, BPMC, etofenprox, and buprofezin in brown planthopper Effect of recommended granular insecticides for controlling stem borers, leaffolder, and brown planthopper on different resistant rice varieties Study on appropriate dosage of recommended insecticides for controlling resistant strains of BPH Effect of recommended granular insecticides for controlling stem borers, leaffolder, and brown planthopper on Pathum Thani 1, Chai Nat 1, Suphanburi 1, and Khao' Jow Hawm Suphan Buri rice varieties Application technique of recommended foliar spray insecticide to retard insecticide resistance developing in BPH Study of BPH biotypes for improving resistant rice varieties Biology of viruliferous rice ragged stunt, brown planthopper, and healthy brown planthopper Improvement of dot immuno binding assay for rapid detection Relationship among RRSV viruliferous insects Screening of some rice varieties' reaction for RRSV resistance genetic source in rice breeding program
	2005-06	Purification of rice ragged stunt virus and antiserum production

Table 8. List of research activities conducted on whitebacked planthoppers in some Asian countries in 1998-2007.

Country	Years	Research activity
China	2004	The effect of nitrogen on ecological fitness of WBPH
India	1998-2007	Screening rice germplasm accessions and breeding lines for resistance
		Evaluating transgenic lines with GNA gene
Indonesia	2002	Competition of BPH and WBPH in the same niche
Thailand	1998, 2004	Monitoring and determining insecticide resistance of WBPH collected from rice-planting areas
		Study of WBPH biotypes for improving resistant rice varieties

Table 9. List of publications on planthoppers in some Asian countries in 1998-2007.

Country	Year and title
China	1998. The virulence characteristics of various populations of brown planthopper. J. Southwest Agric. Univ. 20(5):446-449.
	1997. Variation in virulence of the brown planthopper to resistant rice varieties and its relation to the changes in the activities of endogenous enzymes. Entomol. Sin. (Suppl.)40:122-127.
	1999. On the brown planthopper resistance in introgressive lines from wild rice. Acta Phytophyl. Sin. 26(3):197-202.
	1999. Study on brown planthopper control tactic in the middle-late non-glutinous rice zone. J. Nanjing Agric. Univ. 22(1):42-45.
	1999. Study on resistance to brown planthopper *Nilaparvata lugens* (Stål) in indica hybrid rice. Acta Agric. Zhejiangensis 11(4):163-166.
	1999. The second male vibrational signal of brown planthopper *Nilaparvata lugens* (Stål) and its significance in competitive reproductive behaviour. Acta Entomol. Sin. 42(1):1-6.
	1999. The tolerance differences of brown planthopper biotypes to adverse environmental factors. Acta Agric. Zhejiangensis 11(6):301-305.
	1999. The different feeding and oviposition behavior among brown planthopper biotypes. Acta Phytophyl. Sin. 203-207.
	1999. Virulence to resistant rice varieties of brown planthopper populations from fields and greenhouse. Chinese J. Rice Sci. 13(1):46-48.
	1999. The virulence changes and damage characteristics of different geographic populations of brown planthopper. Entomol. Sin. 6(2):146-154.
	2000. Effects of high temperature on juvenile hormone esterase activity in brown planthopper, *Nilaparvata lugens* (Stål). J. Nanjing Agric. Univ. 23(2):114-115.
	2000. Tolerence of various geographic populations of brown planthopper to adverse environmental stresses. Chinese J. Appl. Ecol. 11(5):745-748.

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Table 9 continued.

Country	Year and title
	2000. The effect of submerging rice plants on the survival and fecundity of brown planthopper at different temperatures. Acta Ecol. Sin. 20(4):624-628.
	2001. Chaos and predictable time-scale of the brown planthopper *Nilaparvata lugens* (Stål) occurrence. Syst. J. Asia-Pacific Entomol. 4(1):67-74.
	2001. Intra- and inter-specific effects of the brown planthopper and whitebacked planthopper on their population performance. J. Asia-Pacific Entomol. 4(1):85-92.
	2001. The differentiation of amino acid requirements in three host related populations of the brown planthopper, *Nilaparvata lugens* (Stål). Acta Entomol. Sin. 8(4):361-369.
	2002. Resistance of rice varieties to brown planthopper *Nilaparvata lugens* Stål. Sci. Agric. Sin. 35(2):225-229.
	2001. The population dynamics of endosymbionts in body of brown planthopper from different geographic fields and adapted to different resistant rice varieties. Entomol. J. East China 10(1):44-49.
	2001. Effects of endosymbiont on feeding, development, and reproduction of brown planthopper, *Nilaparvata lugens* Stål. Chinese Rice Res. Newsl. 9(2):11-12.
	2001. Bionomics of brown planthopper biotype 2 collected in field and greenhouse. Chinese Rice Res. Newsl. 9(4):9.
	2001. The effect of endosymbiont on the development and reproduction of brown planthopper, *Nilaparvata lugens* Stål. Acta Phytophyl. Sin. 28(3):193-197.
	2001. The role of endosymbiont in virulent shift of brown planthopper. Acta Ecol. Sin. 44(2):197-204.
	2002. Behavioral responses of brown planthopper and white-backed planthopper to BPH-resistant rice varieties. Acta Phytophyl. Sin. 29(2):145-152.
	2002. The biological characteristics of biotype 2 of brown planthopper populations from greenhouse and paddy fields. Chinese J. Rice Sci. 16(1):89-92.
	2002. Evaluation for resistance levels of newly-bred rice varieties (lines) to brown planthopper *Nilaparvata lugens* Stål in China. Agric. Sci. China 1(3):323-327.
	2004. Effects of temperature on population growth of susceptible and resistant strains of *Nilaparvata lugens* to imidacloprid. Entomol. Knowl. 41(1):47-50.
	2004. Predatory behavior of mirid bug, *Cyrtorhinus lividipennis,* on rice plants with different nitrogen regimes. Int. Rice Res. Notes 29(2):32-34.
	2004. Effect of nitrogen nutrient on the ecological fitness of brown planthopper, *Nilaparvata lugens* Stål, on rice cultivar IR64. In: Plant protection towards the 21st century. Proceedings of the 15th International Plant Protection Congress, Beijing, China, 11-16 May 2004. p 315.

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Table 9 continued.

Country	Year and title
	2004. Dynamics of yeast-like symbionte and its relationship with the virulence of brown planthopper, *Nilaparvata lugens* Stål, to resistant rice varieties. J. Asia-Pacific Entomol. 7(3):317-323.
	2004. Effect of nitrogen on water content, sap flow of rice plants in association with tolerance of brown planthopper. Chinese J. Rice Sci. 18(2):105-111.
	2004. Effects of plant nitrogen on ecological fitness of the brown planthopper, *Nilaparvata lugens* Stål, in rice. J. Asia-Pacific Entomol. 7(1):97-104.
	2004. Effect of nitrogen on water content, sap flow, and tolerance of rice plants to brown planthopper, *Nilaparvata lugens*. Rice Sci. 11(3):129-134.
	2005. Planthopper damage to rice and the resurgence mechanism. Chinese Bull. Entomol. 2(6):612-615.
	2005. Progress in the histological studies of the intracellular yeast-like symbiotes in rice planthoppers. Chinese Bull. Entomol. 42(6):607-611.
	2005. Effects of nitrogen on the tolerance of brown planthopper, *Nilaparvata lugens*, to adverse environmental factors. The 5th Asia-Pacific Congress Entomology—Insects, Nature, and Humans, Jeju, Korea.
	2005. Effects of nitrogen on the tolerance of brown planthopper, *Nilaparvata lugens,* to adverse environmental factors. Insect Sci. 12:121-128.
	2005. Effects of nitrogen content in rice plants and densities on the survival, development and reproduction of brown planthopper. Acta Ecol. Sin. 25(8):1838-1843.
	2005. Effect of nitrogen fertilizer in rice fields on the predatory function of *Cyrtorhinus lividipennis* to brown planthopper. Acta Entomol. Sin. 48(1):48-56.
	2005. Effect of nitrogen nutrient on the behavior of feeding and oviposition of brown planthopper on IR64. J. Zhejiang Univ. (Agric. & Life Sci.) 31(1):62-70.
	2006. Occurrence and ovipositing characterstics of *Nilaparvata lugens* on scented rice. Chinese Bull. Entomol. 43(4):466-469.
	2006. Biodiversity and dynamics of planthoppers and their natural enemies in rice fields with different nitrogen regimes. Rice Sci. 3(3): 218-226.
	2006. Impact of nitrogen fertilizer on natural control capacities of invertebrate predators and parasitoids and its demonstration in rice-based ecosystem. Acta Agric. Zhejiangensis 18(2):128-132.
	2006. Dynamics of predators in rice canopy and capacity of natural control on insect pests in paddy fields with different nitrogen regimes, Acta Phytophyl. Sin. 33(3):225-229.
	2007. Effect of nitrogen fertilizer in rice fields on the predatory function of *Cyrtorhinus lividipennis* to brown planthopper. Proc. China Assoc. Sci. Tech. 4(1):571-577.
	2007. Effect of nitrogen fertilizer on herbivores and its stimulation to major insect pests in rice. Rice Sci. 14(1):56-66.

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Table 9 continued.

Country	Year and title
India	1998-2007. Progress report of AICRIP, v. 2.
Indonesia	1998. Damage level of planthopper and rice stem borer attacks on transplanted and direct seeded rice (Tingkat serangan Hama wereng dan Penggerek padi pada Tapin dan Tabela di dua golongan air pengairan). Prosiding Seminar Peningkatan Produksi Padi Nasional melalui sitem tabela padi sawah dan pemanfaatan lahan kurang produktif. p 122-127 (with English summary).
	2001. Identification of BPH biotype and rice damage on upland rice area (Identifikasi Biotipe Wereng Coklat dan Kerusakan Padi pada Tanaman Tumpangsari di Lahan Padi Gogo). Implementasi Kebijakan Strategis untuk Peningkatan Produksi Padi Berwawasan Agribisnis dan Lingkungan. Indonesian Center for Food Crops Seminar. p 149-154.
	2001. Impact of nutrient management on pest and yield losses of different rice varieties. Workshop and Data Analysis and Synthesis Relationship between Multiple Pests and Yields. Zhejiang University, Hangzhou, China. 10 p.
	2002. Level of eggs BPH parasitizing by *Anagrus* and *Oligosita* on two varieties and different pattern system (Tingkat Parasitasi Telur Wereng Coklat oleh Anagrus dan Oligosita pada dua Varietas dan Sistem tanam yang Berbeda). Prosiding Seminar Nasional Biologi XVI dalam rangka Kongres Nasional Biologi XII. Perhimpunan Biologi Indonesia. p 262-265.
	2002. Daya Kompetisi Wereng Coklat dengan Wereng Punggung Putih pada Relung Ekologi yang Sama. Penelitian Pertanian Tanaman Pangan 21(3):41-53 (with English summary).
	2002. Augmentation technique for raising efficacy of *Metarhizium anisopliae* with additive material (Teknik Augmentasi Peningkatan Efikasi Metarhizium anisopliae dengan Berbagai Zat Aditif Terhadap Wereng Coklat). Report of Indonesian Center for Rice Research.
	2003. Efficacy of *Beauveria bassiana* RIRCC2 on adjuvant material to BPH in the laboratory (Efikasi Beauveria bassiana RIRCC2 terhadap wereng coklat dengan penambahan zat perekat dan ajuvant di Laboratorium). Report of Indonesian Center for Rice Research.
	2004. Simulation of mosaic rice varieties as a management to reduce BPH development (Simulasi Sistem Pertanaman Padi Multi Varietas Sebagai Alternatif Teknik Mengendalikan Wereng Coklat Serta Profil Varietas Padi Di Lapangan). Seminar of National Rice Week II.
	2005. Assessment decreasing yield losses based on scoring damage by BPH and WBPH (Penilaian Penurunan Hasil Berdasar Skor Kerusakan Akibat Wereng Coklat Dan Wereng Punggung Putih). Prosiding Seminar Nasional dan Kongres Biologi XIII. Yogyakarta. p 351-357.
	2005. Virulent and assessment biotype of BPH from central Java. Keganasan dan penentuan biotipe wereng coklat Jawa Tengah (kasus pati dan demak) terhadap varietas padi yang dilepas. Prosiding Seminar Nasional dan Kongres Biologi XIII. Yogyakarta, 16-17 September 2005. p 726-731.

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Table 9 continued.

Country	Year and title
	2005. Characteristic development of brown planthopper in The North Coastal of West Java on popular rice varieties. Presented at the 1st International Conference of Crop Security 2005. Brawijaya University, Malang, Indonesia. 16 p.
	2007. Distribution of BPH biotype on some central rice production area (Sebaran Biotipe Wereng Coklat Di Beberapa Sentra Produksi Padi). CRIFC Seminar, Bogor, 15 February 2007.
	2007. Evaluation of resistance components on lines and varieties to BPH biotype 3 and through filtering test and population buildup (Evaluasi Komponen Ketahanan Galur Padi Terhadap Wereng Coklat Biotipe 3 Melalui Uji Penapisan Dan Population Buildup). Seminar Apresiasi Hasil Penelitian. p 14. (With English summary.)
	2007. The effect of multiple pests on yield losses in an intensive rice system in Indonesia. Rice industry, culture and environment. Indonesia Center for Rice Research (ICRR). 16 p.
Malaysia	1999. Towards site-specific agriculture of pest management in rice ecosystem. MCB-MAPPS Plant Protection Conference 99. Malaysian Cocoa Board and Malaysian Plant Protection Society. 11-12 November 1999, Kota Kinabalu, Malaysia. p 42-45.
	1995. Modelling planthopper damage mechanism on rice. Paper presented at SARP and SAAD II Symposium. December 1995.
	2000. Quantifying the impact of insecticide application on arthropod diversity in the rice ecosystem. Malaysian Plant Protection Society, 23-24 November 2000. Kuching, Malaysia. p 141-144.
	2000. Precision farming: Can it be applied to manage BPH population in rice ecosystem? Poster presented at MARDI Senior Staff Conference 2000. MARDI and PKKM, 18-19 September 2000, Genting Highland, Malaysia.
	2001. Simulation of brown planthopper damage mechanism on rice. J. Trop. Agric. Food Sci. 29(1):39-51.
	2001. Spatio-temporal distribution of brown planthopper in relation to distribution of their predator *Cyrtorhinus lividipennis* in two rice granary areas in Malaysia. International Rice Research Conference. MARDI, Alor Star.
	2005. Precision agriculture in integrated pest and disease management. Proceedings National Conference on AgrICT 2005: Revolutionizing Agriculture through ICT, 27-28 September 2005, MARDI, Kuala Lumpur. p 242-249.
	2006. Spatio-temporal distribution of planthopper and predator mirid bug for two rice granary areas in Malaysia. J. Trop. Agric. Food Sci. 33(2):405-416.
Thailand	1998. Development of resistance to carbofuran, BPMC, etofenprox, and buprofezin in the brown planthopper. In: Annual Report of Entomology and Zoology Division. 1998. Division of Entomology and Zoology, Department of Agriculture, Bangkok, Thailand. p 65-77.

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Table 9 continued.

Country	Year and title
	1999. Resistance level to insecticides of whitebacked planthopper, *Sogatella furcifera* (Horvath). Entomol. Zool. Gazette. 21(1):3-12.
	1999. Resistance level of the mirid bug, *Cyrtorhinus lividipennis* (Reuter) to recommended insecticides. In: Annual Report of Entomology and Zoology Division, Division of Entomology and Zoology, Department of Agriculture, Bangkok, Thailand. p 118-125.
	2002. Effect of recommended granular insecticides for controlling stem borers, leaffolder, and brown planthopper on Pathum Thani 1, Chai Nat 1, Suphanburi 1 and Khao' Jow Hawm Suphan Buri rice varieties. Entomol. Zool. Gazette. 24(1):17-38.
	2002. Study on appropriate dosage of recommended insecticides for controlling resistance strain BPH. In: Proceedings of Rice Research Conference 2002. Pathum Thani Rice Research Center, Thanyaburi, Pathum Thani, 29 Feb.-1 Mar., Thailand. p 179-200.
	2006. Adaptation to breaking resistant varieties of different populations of brown planthopper from Central and Northern Provinces. In: Proceedings of Rice Research Conference 2006. Rice Research Institute, 28-29 Mar., Cha-um, Petchaburi, Thailand. p 119-128.
	2006. Situation and management of brown planthopper (BPH) in Thailand. In: International Workshop on Ecology and Management of Rice Planthoppers (abstract), Huajiachi Campus, Hangzhou, Zhejiang, China, 16-19 May 2006. p 9-13.
	2006. Production of antiserum for rice ragged stunt virus detection. In: Proceedings of Rice Research Conference 2006. Rice Research Institute, 28-29 Mar., Cha-um, Petchaburi, Thailand. p 95-99.
	2007. Resistance situation of brown planthopper in Thailand. In: International Workshop on Forecasting and Management of Rice Planthoppers in East Asia: Their Ecology and Genetics, 4-5 December 2007. National Agriculture Research Center for Khushu Okinawa Region, Kumamoto, Japan. p 20-26.

A list of current activities on brown planthopper and whitebacked planthopper was provided by China, India, Indonesia, Malaysia, and Thailand (Table 10). The most common activities involve insecticide screening, varietal screening, and biotypes.

Discussion

Nilaparvata lugens and *Sogatella furcifera* have only within the past few decades emerged as important economic pests in Asia (Heinrichs 1994). Asian countries that continue to rely on insecticide for control of the two planthoppers have experienced a reflective increase in the numbers in light trap catches for the last 10 years. Unnecessary insecticide sprays often disrupt the ecological balance in a rice ecosystem,

Table 10. Current research activities in some Asian countries.

Planthopper	Country	Research activity
BPH	China	Insecticide resistance detection and monitoring in brown planthopper Cross-resistance of imidacloprid resistance in brown planthopper Assessment of biological activity of pymetrozine against brown planthopper Mechanism for imidacloprid resistance in brown planthopper Genetics of imidacloprid resistance in brown planthopper Laboratory screening of alternative insecticides for replacing highly-toxic five-phosphorus insecticides (such as methamidophos, parathion, methyl-parathion, monocrotophos, phosphamidon) for controlling brown planthopper The molecular mechanism in the role of endosymbiosis in adaptation of BPH to resistant rice varieties The impact of global warming on the relationship between planthoppers and their natural enemies Field demonstration of rice varieties resistant to planthoppers and ecological control in insecticide reduction in Jinhua Exploring intercropping plants to enhance parasitoids of planthoppers for insecticide reduction Monitoring for BPH resistance to insecticides
	India	Screening for resistance Genetics of resistance and QTL mapping MAS for gene pyramiding for high resistance Evaluation of transgenics with GNA and VIP genes
	Indonesia	Screening lines and rescreening varieties for BPH biotypes 3 and 4 BPH development on new hybrids and new plant type in the field Assessment of BPH resistance to insecticides Mapping BPH
	Malaysia	Monitoring of rice arthropod diversity in the rice ecosystem
	Philippines	Varietal screening
	Thailand	BPH biotypes for improving resistant rice varieties Monitoring and prediction of BPH outbreaks in Central Region Efficacy of insecticides for controlling BPH
WBPH	China	Assessment of risk of resistance to imidacloprid and buprofezin in whitebacked planthopper Laboratory screening of alternative insecticides for replacing highly-toxic five-phosphorus insecticides for controlling whitebacked planthopper
	India	Screening for resistance Genetics of resistance and QTL mapping MAS for gene pyramiding for high resistance Evaluation of transgenics with GNA and VIP genes
	Indonesia	WBPH development on new hybrids and new plant type in the field Assessment of WBPH resistance to insecticides Study on changed WBPH biotype
	Malaysia	Monitor rice arthropod diversity in the rice ecosystem
	Thailand	WBPH biotypes for improving resistant rice varieties

favoring the development of planthoppers. Observations on the population abundance of planthoppers also reflect the area of hopper burn created. Hopper burn was greatest in China.

In sprayed fields like those in China, an increasing trend in planthopper populations was observed for the last 10 years. In Zhejiang Province, farmers constantly use chemicals such as imidacloprid, buprofezin, chlorpyrifos, and fipronil to spray their rice fields. This practice started in Zhejiang in 1998. Imidacloprid, being one of the popular insecticides in China, has been widely used in other rice-growing areas in Vietnam, South Korea, and Japan since the early 1990s (Liang et al 2007). Because of the high control efficiency and cheaper price of insecticides, Chinese farmers were lulled into using 3–5 applications as a main component of a "cocktail insecticide" for every crop. In 2005, the excessive use of this insecticide caused a serious outbreak of BPH because of the development of insecticide resistance in rice planthoppers (Cheng and Zhu 2006). A resurgence of BPH had stimulated its population growth. Although there were some reports on various pesticide resistance problems for rice planthoppers with organophosphates and carbamates (Long 2005), insecticides are still being used in China because of a lack of resistant varieties as well as the perceptions of farmers and technicians on pesticides with regard to timing of application and type of pesticide to be used (Cheng et al 1995). Moreover, field experiments and simulation studies demonstrated that the best strategy is to apply insecticide with higher efficiency and a longer residual period at 30 days after transplanting based on a control threshold in the second rice-cropping season. Another factor causing the increase in the planthopper population in China is the wide adoption of high-yielding hybrid rice since 1976 (Sogawa 2004). Chinese hybrid rice has caused a new pest problem, the whitebacked planthopper. Outbreaks of WBPH were observed because of the high susceptibility of hybrids to *S. furcifera* (Sogawa 2004). Furthermore, the subsequent increase in insecticide applications against WBPH resulted in the development of resistance of this insect pest to pesticide and increased the risk of pest resurgence due to the destruction of natural enemies in paddy fields.

In India, planthopper populations were fluctuating for the last 10 years. Brown planthopper was contained during the mid-1990s through advocating IPM involving the adoption of resistant rice varieties, wider spacing between plants or leaving alleyways every 1–2 meters, optimum nitrogenous fertilizers, and strictly need-based insecticide application. However, the recent increase in their population has been brought about by the different neonicotinoid insecticides that were introduced, which helped growers to successfully manage the BPH (IRAC 2007). But, because of the continuous and indiscriminate use of neonicotinoids over the past few years, frequent control failures by this class of insecticide became evident in the past 2 years, especially in the southern Indian states of Andhra Pradesh and Karnataka. It is possible that BPH has evolved resistance to neonicotinoid chemistry. Other factors that contributed to the BPH outbreaks in rice are the continuous cultivation of susceptible rice varieties such as BPT and Swarna, the high use and even four times the recommended dose of nitrogenous fertilizers, favorable microclimate, favorable conditions for the development of winged black-colored macropterous forms, widespread migration in

endemic areas and new areas, closer planting, and an imbalance between the use of N and K fertilizers (Gudem 2006). Fresh reports on BPH during 2007-08 came from the states of Haryana, Punjab, and Delhi. Popular rice hybrids have shown greater damage. Likewise, WBPH outbreaks were reported prior to 1980 in the northern states and again during 2007-08 pest outbreaks were reported from Himachal Pradesh and Punjab. However, so far, no major reports of virus diseases associated with BPH are on record.

In countries where planthopper outbreaks were minimal or negligible, there is a significant reduction in insecticide use (Huan et al 1999). For example, in Indonesia, there was a relatively low density of planthoppers from light trap catches from 2000 to 2007. The reason may be Presidential Decree 3/86 by President Suharto in 1986 banning most pesticides. This decree also provided the framework and support necessary for farmers to understand and conserve natural enemies. Because of this, it has helped keep rice fields in Indonesia relatively free from brown planthoppers over the past 10 years. Since Indonesia adopted an IPM program in 1986, pesticide production has dropped by more than 50% and the country banned the use of 57 trade formulations of insecticides. Among the Asian partners, Indonesia is the only one using natural enemies as part of its management program for planthoppers. Moreover, an extensive program to educate farmers based on a farmer field school model was implemented (Gallagher et al 2002).

The brown planthopper problem in Malaysia seems to be very small compared with other Asian countries. Nevertheless, it remains an important pest of rice. In the past, devastating outbreaks of planthoppers led to the establishment of a surveillance system in the major rice-growing regions in Malaysia (Ooi 1988). The surveillance system also directed the development of rice planthopper control stategies as well as providing information on optimum time for application of insecticides. Furthermore, when IPM was introduced in Malaysia, it was widely promoted for rice paddies and resulted in a reduction in incidence of pest population explosions, especially severe outbreaks of brown planthoppers and whitebacked planthoppers (Taylor et al 2003). Lately, IPM practices have seemed to slow down. Farmers tend to return to insecticide sprays to "protect" their rice fields from brown planthopper outbreaks. A survey carried out by Normiyah in 1995 showed that 47% of farmers in the Muda area sprayed their fields during the first 30 days after sowing.

In the Philippines, in 2002, there was a report of brown planthopper infestation in Camarines Sur accounting for 173.5 affected hectares (Umasenso 2002). Since then, no other heavy infestations caused by planthoppers were reported. This may be due to the low insecticide use in the Philippines. There are two main factors for this low insecticide use—the education campaign based on research findings from entomologists at UPLB, PhilRice, IRRI, and other organizations have convinced farmers of the dangers of pesticide use, and insecticide prices are relatively high in the Philippines unlike the two to six times higher prices in Thailand, Vietnam, India, and China (Dawe 2002). Likewise, the government of the Philippines actively encouraged farmers to give up the wholesale use of pesticides and to follow a system of integrated pest management that included growing resistant strains of rice, maintaining a pool of

natural predators, and resorting to chemicals only when pests reached a certain level. With pesticide reduction, agricultural biodiversity is enriched due to the increase in beneficial insect populations. This provides an ecological balance that is conducive to sustainable farming (The Philippines 1996).

Though a relatively low population of planthoppers has been observed on light trap catches in Thailand for the last 10 years, this country also practiced the use of insecticides for planthopper management. Among the insecticides that are common in Thailand, the brown planthopper was found to be resistant to imidacloprid in 2003 (Harris 2006). In a survey conducted by Meenakanit et al (in 1997), most of the women farmers that they interviewed used pesticides for brown planthopper and applied their first spray within the first 30 days after planting. Pesticide application frequencies ranged from 1 to 10 per season, with 1–3 times as the most common. Furthermore, approximately one-half of Thai farmers apply higher than recommended concentrations, do not pay attention to labels, wear no protective clothing, and do not observe recommended intervals between spraying and harvest (Jungbluth 1996). Although there are no direct subsidies on pesticides in Thailand, several factors encourage pesticide use: low import taxes have helped keep prices down, there is little independent information or training and the extension service focuses primarily on pesticide-based pest management, and the government keeps a budget for emergency outbreaks of pests, generally using pesticides to contain the problem (Jungbluth 1996).

In Vietnam, the population of brown planthoppers declined over the last 10 years mainly because of unfavorable weather conditions such as typhoons and floods in September and October in 1999-2003 and the diversification of the genetic background for resistance to BPH in rice varieties (Chau 2007). Despite the low population density of the brown planthopper, its hopper-burn damage increased in 2006 and 2007. This may have been due to abnormal weather in the Mekong Delta; a simple gene source of resistance to BPH; the development of BPH on susceptible aromatic rice varieties; farmers kept the habit of high seed rates, more nitrogen application, and misuse of insecticides; and the development of BPH virulence. It was also observed that several insecticides, such as imidacloprid and fenobucarb, have developed resistance to brown planthopper (Chau 2007). In 2005-06, BPH and the resulting ragged stunt rice disease damaged four consecutive rice crops (Vietnam News 2006). The disease spread over 485,000 hectares of rice fields, resulting in the loss of 828,000 tons of rice. Funds for pesticides had been provided to farmers to counteract this menace.

In general, the brown planthopper and whitebacked planthopper are secondary pests brought about by an overuse of insecticides. Many research studies were conducted to prove this claim. For example, in an experiment in Thailand, rice plots treated with insecticide supported high planthopper populations because of their eggs and nymphs, whereas planthopper populations in plots not receiving an insecticide treatment did not increase (Kenmore 1991). Likewise, in a study by Heong and Schoenly (1998), insecticides that had been tested in field plot experiments favored the development of planthoppers and destroyed natural enemies. When brown planthoppers were introduced to treated resistant rice varieties, the resistant varieties lost their effectiveness, causing a density increase in the BPH population (Gallagher et al

1994). On some occasions when insecticides were suddenly stopped, rice crops suffered high BPH attacks mainly from recruitments from neighboring fields (Way and Heong 1994). In a study on some organophosphate and pyrethroid pesticides, these caused increased fecundity of BPH, thus further increasing the probability of outbreak (Heinrichs and Mochida 1984). The indiscriminate use of insecticides not only caused outbreaks of planthoppers but also killed the natural enemies present in the rice field (Kenmore et al 1984). When broad-spectrum pesticides are applied, natural enemies can be selectively destroyed, allowing populations of *N. lugens* to increase 1,000 times compared with densities when pesticides are not used (Kenmore 1980, Ooi 1988). This promoted resurgence of the insect pest (Heinrichs and Mochida 1984). Brown planthoppers that were reared on high-nitrogen applications have significantly higher ecological fitness (Cook and Denno 1994). Furthermore, most of the fitness variables of BPH increased in successive generations in high-nitrogen regimes (Lu et al 2004). In the 1970s and '80s, nitrogen fertilization was implicated as a cause of BPH outbreaks and a threat to the rice industry (Dyck et al 1979, Heinrichs and Mochida 1984). This implication was based on experiments in greenhouses without natural enemies or in fields where insecticides were heavily used.

Conclusions

The brown planthopper and the whitebacked planthopper are problem pests in China and Vietnam, two of the Asian countries involved in this report. Continuous research studies are being conducted to overcome the problems that they cause to rice production. The rice planthopper problem in these two Asian countries is due to their continuous use of insecticides, their most common measure for planthopper management. When the use of insecticides declines, problems in rice fields brought about by planthoppers will decline. Using insecticides judiciously will lead to the conservation of natural enemies that will help check not only the population increase of planthoppers but other insect pests as well. It will also solve the problem of insecticide resistance, which will prevent secondary pest outbreaks and resurgence of targeted insect pests.

China and Vietnam, along with the other Asian countries, focus their research on insecticide evaluation, screening of varieties, and some laboratory studies. Limited research is being done on developing field resistance and ecology. Considering the known harmful effect of insecticides, Asian countries should identify other research studies and issues related to the management of planthoppers.

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Are planthopper problems caused by a breakdown in ecosystem services?

K.L. Heong

An insect outbreak is an explosive increase in abundance that occurs over a short period. Such outbreaks of rice planthoppers often have devastating economic impacts when crops are completed destroyed. Outbreaks are rare and occur when the natural control ecosystem services are compromised, either by natural events such as floods and drought or agronomic practices, such as excess use of fertilizers and pesticides. Planthoppers are monophagous insects moving from rice fields to invade other fields and, in fields that are vulnerable, they increase exponentially to outbreak proportions. Thus, when outbreaks occur frequently, it is a sign of instability in the production environment. Another sign is the rapid development of insecticide resistance caused by pesticide abuse. High ecosystem services in rice fields are derived from sufficient arthropod biodiversity, especially in the species richness of predators and parasitoids. On the IRRI farm when insecticide use decreased by 95%, arthropod biodiversity was restored and planthopper outbreaks became negligible. Since planthoppers are r-strategists, which have high migratory ability, high reproductive capacity, and a short life span, their populations would be more effectively managed at the regional scale. Ecological engineering techniques can be used to enhance local biodiversity to increase ecosystem services.

Pest outbreaks are a sudden explosive increase in a pest population, often associated with changes in the ecosystem brought about by external environmental disturbances. These disturbances include warm or dry weather, elevated temperatures, floods, gales, and pesticide sprays. Outbreaks are generally rare and may be considered abnormal since most fields do not always experience them (Barbosa and Schultz 1987). However, pest outbreaks often receive a great deal of attention because of their sudden and devastating effects. Ecologists have been concerned about the diversity of life strategies and Mac Arthur and Wilson (1967) coined the r-K continuum, a rather simplified way, but still very useful, of providing some insights into population characteristics of pests. The r-strategists are opportunists, selected for their characteristic of maximizing food intake and exploiting their ephemeral habitats. The K-strategists, on the other hand, are selected for their efficient food-harvesting behavior and their populations are regulated

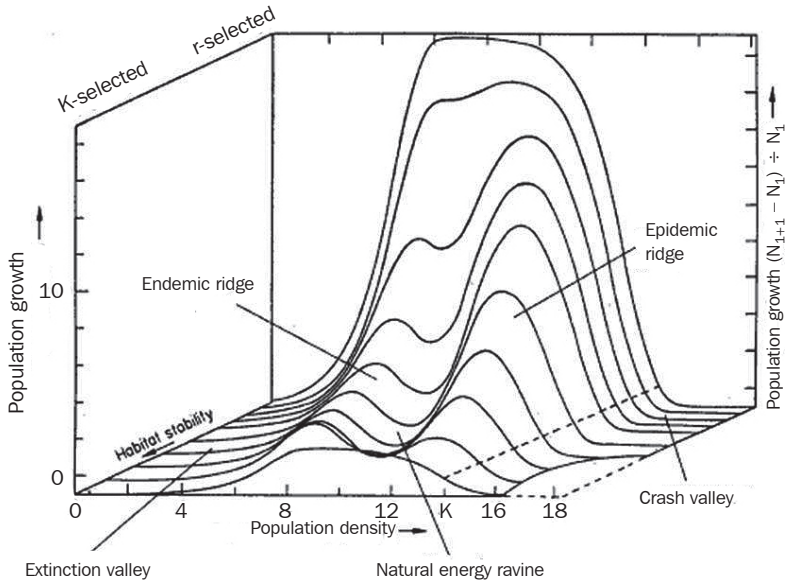

Fig. 1. The landscape of the sypnotic model of population growth.

to near the carrying capacity of the habitat. Southwood and Comins (1976) developed a synoptic model (Fig. 1) to describe the associated spectra of biological strategies and habitat characteristics, which can be used to evaluate pest management.

The r-strategists often become pests and a common characteristic feature is a high migratory tendency, which is essential for movement from the "dying habitat" to a new one. They are exogenous invaders to a particular crop. Thus, because of the ephemeral nature of the crop, it is more useful to consider managing their population on a regional scale (Southwood 1977). The brown planthopper (BPH) and the whitebacked planthopper (WBPH) are typically r-pests, which feed primarily on rice. They are normally not pests under low densities but can occasionally increase exponentially, causing huge losses from "hopper burn," a symptom from the heavy removal of phloem sap and the virus diseases they carry (Pathak and Khan 1994). Records of rice planthopper outbreaks date back to A.D. 18 and rice shortages and even famines were attributed to planthopper destruction in Japan (Heinrichs 1994). There are several hypotheses for outbreak causation, but what are the factors that trigger planthopper outbreaks in rice? Are planthopper outbreaks caused by deteriorated ecosystem services? Are frequent planthopper outbreaks signs of unsustainable practices? What are the root causes of planthopper outbreaks and how can they be prevented or reduced? A better understanding of the underlining ecological processes that create such population abnormalities is important for developing sustainable management strategies. This paper explores the use of an ecosystem services framework to consider planthopper outbreaks and their management.

Provisioning Products from the ecosystems	**Regulating** Benefits from regulation of ecosystem processes	**Cultural** Nonmaterial benefits from ecosystems
In most lowland rice		
• Nitrogen fixing • Food production	• Water regulation Flood storage • Climate regulation Raise local humidity Anaerobic soils store C	• Spiritual and religious values • Cultural heritage
Lowland under specific management		
• Food production, nonrice crops, fish • Wood and straw for fuel • Genetic resources, wild rice	• Water regulation Soil salinity management • Climate regulation • Purification of polluted water • Soil organic matter maintenance • Biological control—pest and disease regulation • Pest invasion resistance	• Aesthetic • Inspirational • Educational • Recreation and ecotourism
Supporting services Services necessary for the production of all other ecosystem services, including soil formation, nutrient cycling, and primary production. These services depend heavily on connectivity/flows between rice fields and surrounding habitats.		

Fig. 2. Ecosystem services of lowland rice (after IRRI 2006).

Ecosystem services

Ecosystem services (ES) are broadly defined as "benefits that people obtain from ecosystems" (MA 2005) and they include services related to provisioning, regulating, supporting, and cultural functions (Fig. 2). First proposed by Daily (1997), the ES concept has gained considerable following and "ecological engineering" has emerged as a new direction for agricultural pest management (Gurr et al 2004). Provisioning services include production of food, fresh water, fuel, wood, and fiber. The supporting services basically provide maintenance to the resource base and include nutrient cycling, soil formation, and primary production. Cultural services provide humans with aesthetic and spiritual values, education, and recreation, and regulating services include water purification and climate and flood regulation. Regulating services relating directly to sustainable agriculture are pollination, pest invasion resistance, natural biological control, and pest and disease regulation. Biodiversity is the foundation of ES contributing to food provisioning through crop and genetic biodiversity (Fig. 3). In addition, biodiversity through ecological functions contributes to regulating services, such as pollination, invasion resistance, natural biological control, and pest and disease regulation. For instance, loss in species richness of bees and syrphids is directly linked to loss in pollination service (Beismeijer et al 2006). In pest management, the two ecological functions of importance are predation and parasitization and they are linked to the biodiversity of predators and parasitoids. The ES concept has

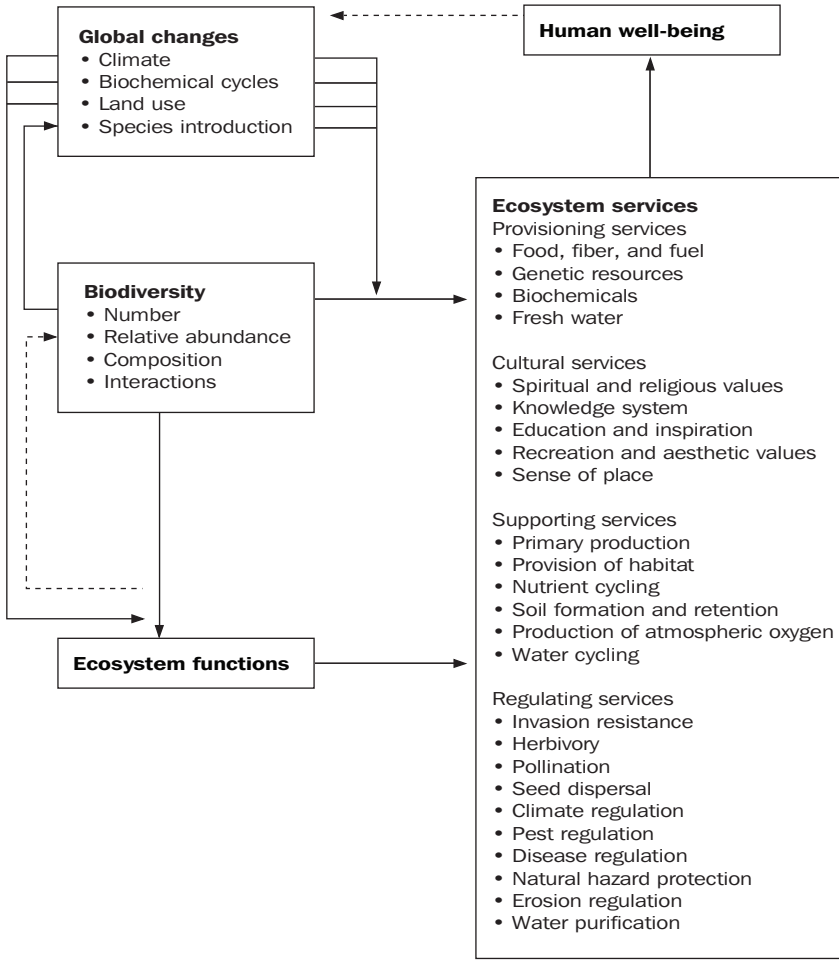

Fig. 3. Biodiversity, ecosystem functioning, and ecosystem services (after MA 2005).

been adopted as an integrative framework for natural resource management research as it can integrate ecological, social, and economic dimensions and can also include food production as well as conservation objectives.

Planthoppers are secondary pests

Natural biological control is linked to the ecosystem services pest regulation and invasion resistance and its importance was strongly emphasized more than 30 years ago by Bosch et al (1973). The important role of biodiversity in rice had also been discussed by Way and Heong (1994). As pointed out by Bosch et al (1973), chemical-based pest management has three ecological backlashes: target pest resurgence, secondary pest

outbreaks, and pesticide resistance. In rice, insecticide sprays at the community level were found to disorganize predator-prey relationships and the food web structure, thus favoring r-strategist pests, such as planthoppers (Heong and Schoenly 1998). Very often, insecticides in the early crop stages are either applied as prophylactics or are directed at leaf feeders, such as leaffolders. These sprays tend to favor the development of secondary pests, such as planthoppers. Secondary pest outbreaks occur when insecticides applied to control target pests, such as the leaffolder, destroy biodiversity and natural control services, thus making the ecosystem vulnerable to pest invasions. The ecological fitness of the pest species increases due to "release from natural enemies" (Southwood and Comins 1976). Ecological fitness of secondary pests is further enhanced if the crops are enriched with high nitrogen applications (Lu et al 2004). In a computer simulation study, when N inputs were increased 4-fold from 100 to 400 kg ha^{-1}, BPH populations increased by 40-fold (Fig. 4) when predation was negligible. Thus, intensive rice production systems that are homogeneous and have high N inputs tend to be vulnerable to pest invasions and vulnerability is further enhanced if these fields are sprayed in the early crop stages.

Development of insecticide resistance

Another backlash is the development of insecticide resistance. Work done by Matsumura et al (2007) showed that some WBPH populations in China, Taiwan, Vietnam, and the Philippines are 40 to 100 times more resistant to fipronil. This has been attributed to the high use of fipronil to control leaffolders and stem borers. Resistance to imidacloprid is also extremely high in BPH populations of China, Vietnam, and Japan. For instance, BPH populations in the Mekong Delta are at least 200 times more tolerant than populations in the Philippines (Fig. 4). Resistance to buprofezin has also been recently recorded in BPH. Secondary pest outbreaks in turn contribute directly to an increase in insecticide resistance because outbreaks often bring on heavier and more frequent treatments that will speed up genetic selection for resistance.

Many examples of such "pesticide addiction" situations were illustrated in the 1970s (Huffaker 1971). The spider mite problem worldwide was a clear example of a secondary pest becoming a serious one (Bosch et al 1973). Similar experiences were recorded in cotton in northeastern Mexico, California's Imperial Valley, Cañete and several places in Peru, Colombia, and Central America (Bottrell and Adkisson 1977) and more recently in Thailand (Castella et al 1999). In fact, these experiences in pesticide addiction in which ecosystem services had been so badly deteriorated triggered the development of integrated pest management (IPM) (Huffaker 1980). The IPM approach to rationalize and use pesticide only as a last resort is primarily aimed at conserving natural biological control, which is the foundation of sustainable pest management.

The rice planthopper problem in Asia has similar characteristics of pesticide addiction and, when insecticide stresses were removed, planthopper problems decreased. In the 1970s and 1980s, planthoppers had been a serious threat (IRRI 1979, Heinrichs and Mochida 1984), but now, in several Southeast Asian countries, where

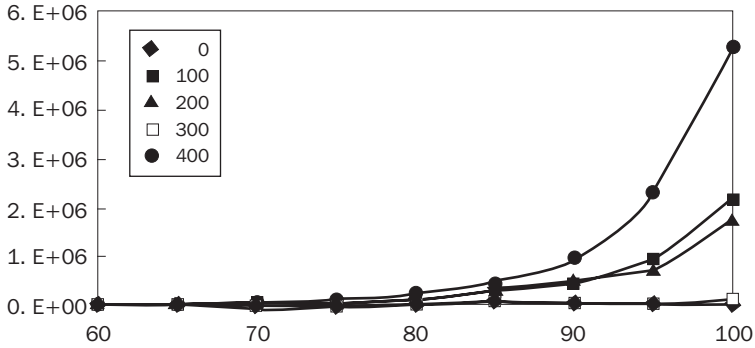

Fig. 4. Simulations of brown planthopper density increases in scenarios of nitrogen enrichment ranging from 0 N to 400 N.

IPM has been implemented and insecticide use reduced, either through training or media campaigns, planthopper problems have been insignificant (Matteson 2000, Matteson et al 1994, Rombach and Gallagher 1994, Escalada et al 1999). Planthopper problems are not serious pests in most of these areas and, wherever they become problematic, there have been close links to an increase in unnecessary insecticide usage. Field plot experiments have shown that insecticide sprays destroyed natural enemies (Heinrichs 1994), destroyed detritivores (Settle et al 1996), disorganized predator-prey relationships and food chain linkages (Cohen et al 1994), and favored the development of r-pests, such as the planthoppers (Heinrichs and Mochida 1984, Heong and Schoenly 1998). Even brown planthopper–resistant varieties treated with insecticides have increased BPH densities (Gallagher et al 1994). Clearly, current planthopper problems require a broader ecological approach. In northern China, Korea, and Japan, where brown planthoppers do not overwinter, populations may be started by initial immigrants carried by wind. Thus, rice crops with sufficient "invasion resistance," a regulating ecosystem service, may be less vulnerable to population buildups and outbreaks. Planthopper outbreaks in temperate regions may in fact be due to local deterioration of these services as a result of habitat biodiversity loss and pesticide addiction.

Arthropod biodiversity

Arthropod biodiversity in rice ecosystems has inherent resilience and capacity to increase when the suppressing factors are removed. At the IRRI farm, insecticide use declined by more than 95% from 1994 to 2007 because of strict implementation of IPM (Fig. 5). As a result, arthropod biodiversity increased significantly (Table 1 and Fig. 6) (Heong et al 2007). Predator species richness after rarefaction increased from 38 to 65, and parasitoid species richness increased from 17 to 38. Species richness of detritivores increased 5-fold, probably because insecticides had the most devastating effects on these mostly aquatic species. Herbivores also increased in biodiversity from

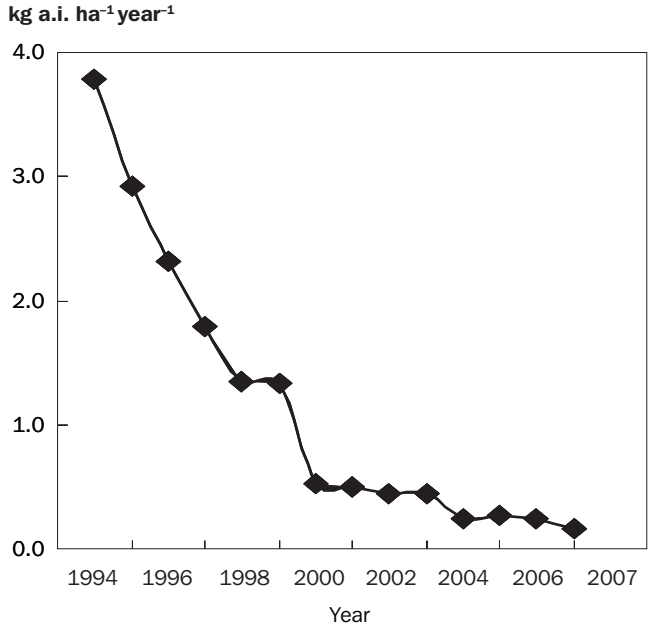

Fig. 5. Decrease in insecticide usage from 1994 to 2007 on IRRI farm.

14 to 36, but most "new" species were minor pests such as thrips, plant lice, beetles, and leafhoppers. Planthoppers remained at low densities of < 5 hoppers per hill.

Based on research results, both experimental and field, and related literature, it is evident that planthopper outbreaks are secondary pest problems because of the deterioration of important ecosystem services, such as natural biological control and invasion resistance. These services can be affected by several system perturbations, such as droughts, floods, extreme weather changes, and pesticide applications, working singly or in combination. Among these factors, perhaps pesticide applications are the most common and within people's control. In Vietnam, through mass media campaigns, farmers in the Mekong Delta reduced their insecticide sprays by 53% and sustained the reduction for more than 10 years and, during this period, yields increased slightly and planthopper outbreaks were negligible (Escalada et al 1999). Thousands of farmers trained through farmer field schools had similar experiences (Matteson 2000). Besides reducing pesticides, ecosystem services in rice production can be further enhanced through habitat manipulation or ecological engineering strategies (Gurr, this volume) that will increase invasion resistance and natural biological control. However, for the positive benefits of ecological engineering to work, there is a need for a corresponding reduction in negative and ecologically destructive forces, such as unnecessary pesticide use.

Table 1. Comparison of arthropod biodiversity on the IRRI farm in 1989 and 2005.

Guilds	Biodiversity parameters	1989	2005
Herbivores	% abundance	46.2	11.6
	Species richness, S or E_{sn} (rarefaction)	13.6	36.0
	Log series index α	3.10	8.97
	Reciprocal Simpson's (1/D)	2.25	2.56
	Exp Shannon or Hill N_1	3.46	5.75
Predators	% abundance	40.0	58.0
	Species richness, S or E_{sn} (rarefaction)	37.6	65.0
	Log series index α	6.38	12.28
	Reciprocal Simpson's (1/D)	5.12	6.50
	Exp Shannon or Hill N_1	8.25	11.70
Parasitoids	% abundance	5.6	4.3
	Species richness, S or E_{sn} (rarefaction)	17.1	38.0
	Log series index α	5.41	14.67
	Reciprocal Simpson's (1/D)	2.57	13.25
	Exp Shannon or Hill N_1	5.37	20.91
Detritivores	% abundance	8.1	26.1
	Species richness, S or E_{sn} (rarefaction)	5.6	30.0
	Log series index α	0.88	5.70
	Reciprocal Simpson's (1/D)	1.19	8.02
	Exp Shannon or Hill N_1	1.46	10.80

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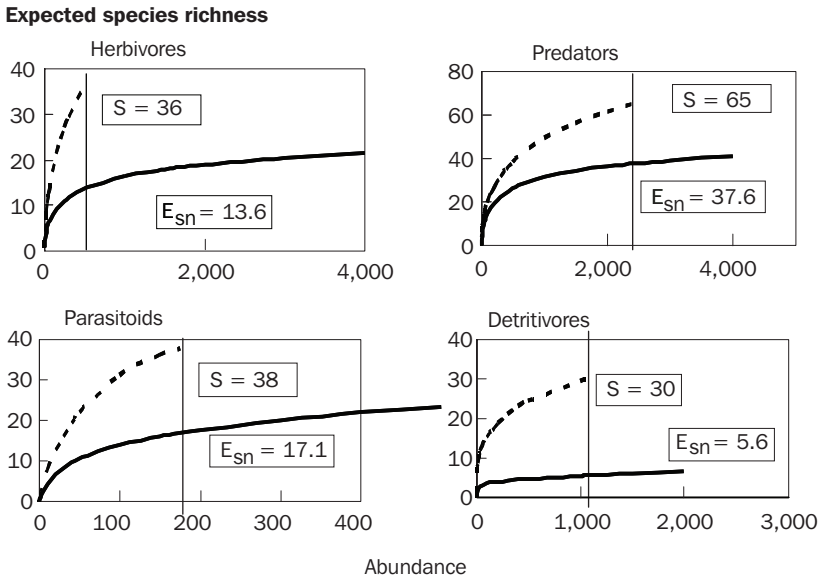

Fig. 6. Rarefaction curves of arthropod guild of samples collected in 1989 and 2005. Rarefaction estimates (E_{sn}) were computed using ECOSIM (Gotelli and Entsminger 2005).

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Current status of insecticide resistance in rice planthoppers in Asia

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In 2003, the development of insecticide resistance against neonicotinoids (mainly imidacloprid) in the brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), was first observed in Thailand and has since been found in other Asian countries such as Vietnam, China, and Japan. However, the LD_{50}-values of BPH and the whitebacked planthopper (WBPH), *Sogatella furcifera* (Horváth), against both neonicotinoid and phenylpyrazole insecticides have been poorly reported in many Asian countries. We thus determined and compared the insecticide susceptibility (topical LD_{50}s) of BPH and WBPH that were collected in Japan from 2005 to 2007 and from East and Southeast Asian countries in 2006. Species-specific changes in insecticide susceptibility were found in Asian rice planthoppers (i.e., BPH for imidacloprid and WBPH for fipronil). The topical LD_{50}-values for imidacloprid in the BPH populations collected from East Asia (Japan, China, Taiwan) and Vietnam in 2006 were significantly higher than in those collected from the Philippines, suggesting that insecticide resistance in BPH against imidacloprid occurred in East Asia and Indochina, but not in the Philippines. The BPH populations indicated a positive cross-resistance between imidacloprid and thiamethoxam. Almost all the WBPH populations from Japan, Taiwan, China, Vietnam, and the Philippines had extremely large LD_{50}-values for fipronil, suggesting that insecticide resistance in WBPH against fipronil occurred widely in East and Southeast Asia.

Keywords: *Nilaparvata lugens*, *Sogatella furcifera*, topical application, imidaclopirid, fipronil

The brown planthopper (BPH), *Nilaparvata lugens* (Stål), and the whitebacked planthopper (WBPH), *Sogatella furcifera* (Horváth) (Homoptera: Delphacidae), are two serious pests of rice throughout Asia. The northern limit of breeding area for these species is around the Red River Delta of Vietnam, where rice (*Oryza sativa*, their only host plant) is cultivated year-round. Neither of these species is able to overwinter successfully in temperate areas (Japan, Korea, and most areas of China), and

colonization occurs annually following long-distance migration from overwintering area (Kisimoto 1976).

To control these planthoppers, neonicotinoid and phenylpyrazole insecticides such as imidacloprid and fipronil have been used since the mid-1990s in many East Asian countries and Indochina. Treatment methods of these insecticides vary among countries. In Japan, imidacloprid and fipronil are used exclusively for seedling-box treatment to control rice planthoppers. In Vietnam and China, in contrast, these insecticides are usually sprayed on rice fields. In any event, the population densities of BPH and WBPH had been relatively low since the mid-1990s when these insecticides began to be used.

In 2003, however, the development of insecticide resistance against neonicotinoids (mainly imidacloprid) in BPH was first observed in Thailand and has since been found in other neighboring countries such as Vietnam, India, and China (Harris 2006). However, until now, the LD_{50}-values of BPH and WBPH against both neonicotinoid and phenylpyrazole insecticides tested by highly accurate methods such as the topical application method (Fukuda and Nagata 1969) have been poorly reported in many Asian countries. Therefore, we determined and compared the insecticide susceptibility of BPH and WBPH that were collected (1) in Japan from 2005 to 2007 and (2) from East and Southeast Asian countries in 2006.

Insecticide susceptibility of BPH and WBPH immigrating into Japan

Immigrant adults of BPH and WBPH were collected in early July from 2005 to 2007 in Kumamoto (in 2005 and 2007) and Kagoshima (in 2006), Japan. The collected populations were derived from more than 50 pairs of adults. These populations were maintained in the laboratory for 2–5 generations prior to the test using rice seedlings (var. Reihou) at a daylength of 16 h and a temperature of 25 °C.

The insecticide susceptibility of these populations was monitored by a standard topical application method (Fukuda and Nagata 1969). Altogether, ten insecticides (malathion, fenitrothion, MIPC, BPMC, carbaryl, etofenprox, imidacloprid, fipronil, dinotefuran, and thiamethoxam) were tested.

The long-winged female adults within 7 days after emergence were anaesthetized with carbon dioxide for about 5 s prior to treatment. A 0.08 μL droplet of acetone solution was applied topically on the dorsal surface of the thorax with a hand microapplicator (Burkard Manufacturing Company Ltd.). The treated insects were kept at a daylength of 16 h and a temperature of 25 °C, with rice seedlings in a transparent plastic box (5 cm in diameter, 10 cm high). Mortality was determined 24 hours after treatment for all insecticides. All the tests were conducted on 2–5 generations after collection. More than 45 females were used for each concentration. Tests were carried out on 5–6 concentrations. The LD_{50}-value, 95% confidence interval, and slope of regression line were calculated by Bliss's probit method (Bliss 1935). Control mortality was corrected for by using Abbott's formula for each probit analysis. A chi-square test was used to test for heterogeneity ($P = 0.05$).

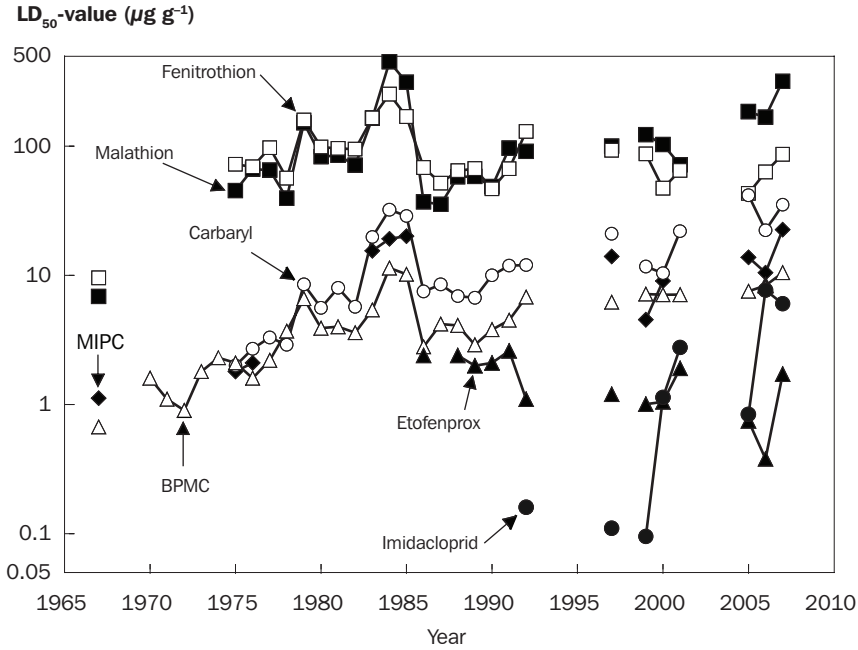

Fig. 1. Annual changes in topical LD_{50}-values of *Nilaparvata lugens* collected in Japan. (1967: Fukuda and Nagata 1969; 1970-91: Hosoda 1983 and unpublished; 1992: Endo and Tsurumachi 2001; 1997: Ping et al 2001; 1999-2000: Nagata et al 2002; 2001: Nagata and Kamimuro 2002; 2005-07: Matsumura et al unpublished.)

The LD_{50}-values for the BPH and WBPH strains collected from 2005 to 2007 in Japan for the seven insecticides (malathion, fenitrothion, MIPC, BPMC, carbaryl, etofenprox, and imidacloprid) were compared with those obtained before 2001 in Japan (Figs. 1 and 2). In general, no significant changes were observed except an increase in LD_{50}-values for imidacloprid in BPH from 1990 to 2007 (Fig. 1). The LD_{50}-value for imidacloprid for the 2000 population was 10 times larger than the 1999 population (Nagata et al 2002), and this trend continued up to 2005. From 2006, a significant increase in LD_{50}-value was observed again for imidacloprid. In contrast to BPH, the LD_{50}-values in WBPH were still low until 2007 (Fig. 2).

Although no previous baseline data have been reported for dinotefuran, fipronil, and thiamethoxam against BPH and WBPH, the LD_{50}-values in WBPH against fipronil and those in BPH against thiamethoxam increased about tenfold during 2005 to 2007, indicating that the insecticide susceptibility has been decreasing (Fig. 3). Dinotefuran is the same neonicotinoid group as imidacloprid, but the LD_{50}-values in BPH in 2005 to 2007 were lower than those against imidacloprid, indicating no cross-resistance between imidacloprid and dinotefuran (Fig. 3).

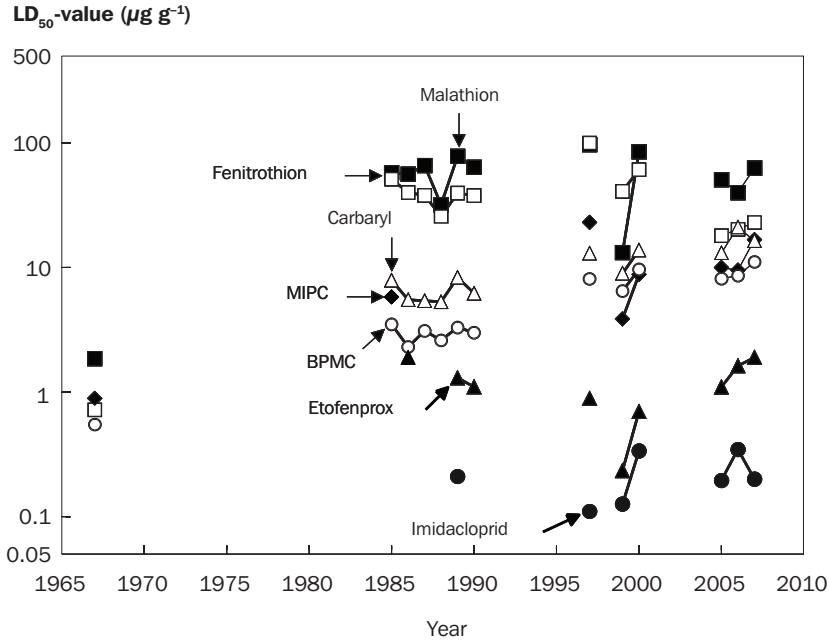

Fig. 2. Annual changes in topical LD_{50}-values of *Sogatella furcifera* collected in Japan. (1967: Fukuda and Nagata 1969; 1985-90: Hosoda 1989, and unpublished; 1997: Ping et al 2001; 1999-2000: Nagata et al 2002; 2005-07: Matsumura et al unpublished.)

Insecticide susceptibility in East and Southeast Asia

The 16 and 17 populations for BPH and WBPH, respectively, were collected from East Asia (Japan, China, Taiwan), Indochina (Vietnam), and Southeast Asia (Philippines) in 2006. The collected populations were derived from more than 50 pairs of adults except for three Philippine populations in 2006. These populations were maintained in the laboratory for 2–5 generations prior to the test using rice seedlings (var. Reihou) at a daylength of 16 h and a temperature of 25 °C. The insecticide susceptibility of these populations was monitored by a standard topical application method (Fukuda and Nagata 1969). Four insecticides (imidaclopirid, thiamethoxam, fipronil, and BPMC) were tested.

In the case of imidaclopirid, the LD_{50}-values for the BPH populations collected from East Asia (Japan, China, Taiwan) and Vietnam were 4.3–24.2 μg g^{-1} and were remarkably larger than for populations collected from the Philippines (0.18–0.35 μg g^{-1}) ($P<0.01$, Mann-Whitney U test) (Fig. 4). The East Asian and Vietnamese populations had significantly larger LD_{50}-values (0.27–2.16 μg g^{-1}) for thiamethoxam than the Philippine ones (0.41–0.62) ($P<0.05$, Mann-Whitney U test). There was a significant

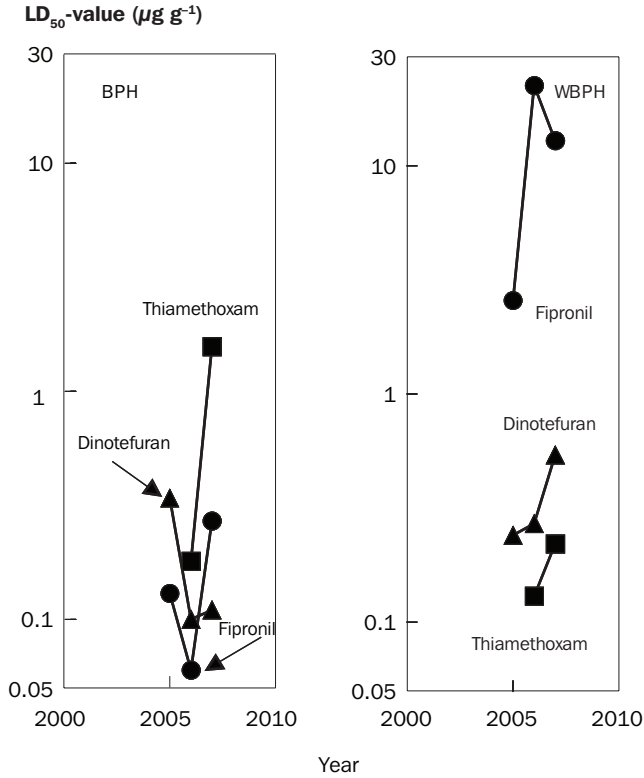

Fig. 3. LD_{50}-values of *Nilaparvata lugens* (left) and *Sogatella furcifera* (right) collected in 2005-07 in Japan (Matsumura et al, unpublished.)

positive relationship between the LD_{50}-values of imidacloprid and thiamethoxam in all the Asian populations (r = 0.72, $P<0.01$) (Fig. 5).

In contrast to the two neonicotinoids, all the Asian BPH populations had much smaller LD_{50}-values (0.06–0.65 μg g^{-1}) for fipronil and no difference was found among locations ($P>0.05$, Mann-Whitney U test) (Fig. 4). In BPMC, the LD_{50}-values were larger (>30 μg/g) in several Vietnamese and Philippine populations than those in other populations, but there was no significant difference among countries ($P>0.05$, Mann-Whitney U test) (Fig. 4).

In WBPH, almost all the populations collected from Japan, Taiwan, China, Vietnam, and the Philippines had much larger LD_{50}-values (19.7–239 μg g^{-1} or more for 24 h after treatment) for fipronil except for several populations from the Philippines (0.3–5.9 μg g^{-1}) and China (3.0 μg g^{-1}) (Fig. 6).

In the case of imidaclopirid, all the WBPH populations had small LD_{50}-values (0.11–0.34 μg g^{-1}). In the case of BPMC, the LD_{50}-values for WBPH ranged from 6.1 to 26.6 μg g^{-1}. There were no significant differences in LD_{50}-values for all three

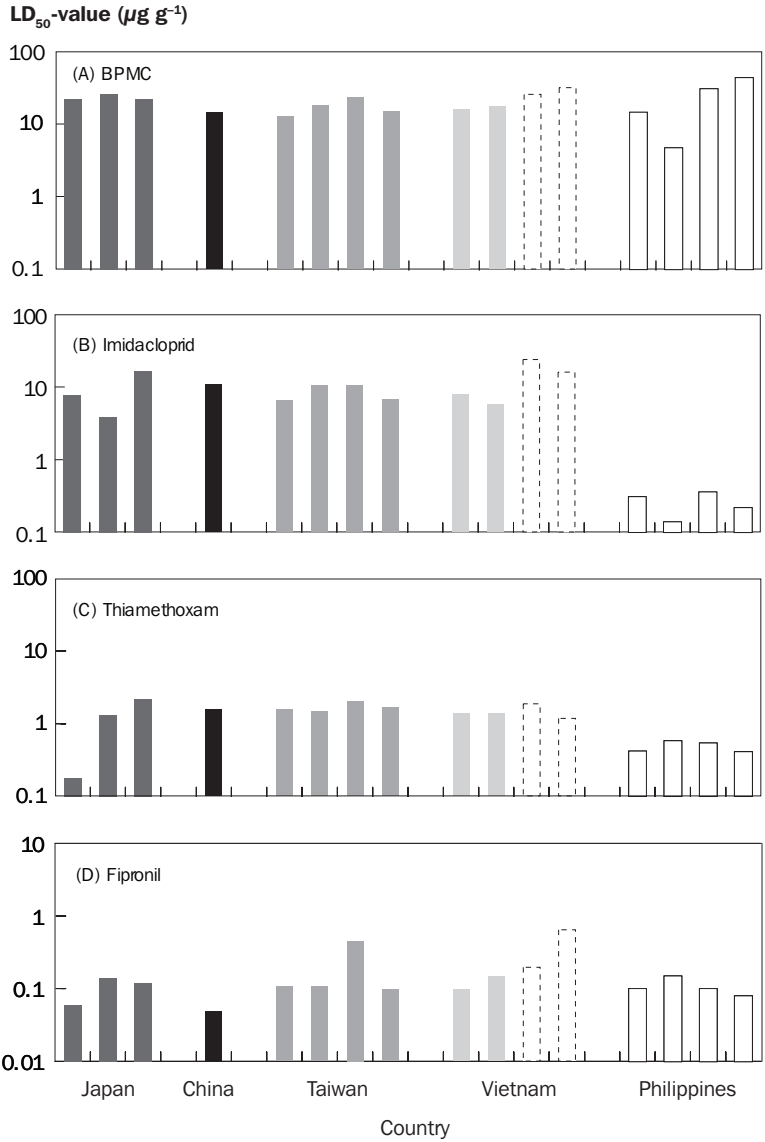

Fig. 4. LD_{50}-values of *Nilaparvata lugens* strains collected in East and Southeast Asia in 2006 (Matsumura et al 2008).

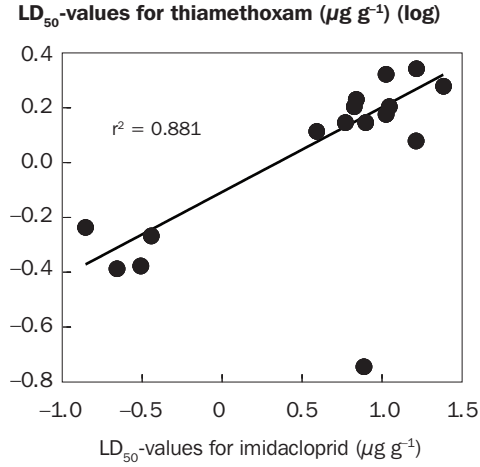

Fig. 5. Relationship between LD_{50}-values for imidacloprid and thiamethoxam in *Nilaparvata lugens* collected in Asia in 2006 (Matsumura et al 2008).

insecticides between East Asian and Southeast Asian WBPH populations (P>0.05, Mann-Whitney U test).

Discussion

Imidacloprid has been used widely to control rice planthoppers since the early 1990s in East Asia and Indochina. The topical LD_{50}-values of imidacloprid for BPH were in the range of 0.09–2 μg g^{-1} from 1992 to 2003 in Vietnam, China, and Japan (Endo and Tsurumachi 2001, Ping et al 2001, Nagata et al 2002, Nagata and Kamimuro 2002, Liu et al 2003a,b). In our study, however, the East Asian and Vietnamese BPH populations in 2006 had remarkably higher LD_{50}-values than those before 2003. In contrast, the BPH populations collected in the Philippines in 2006 had similar LD_{50}-values for imidacloprid vis-à-vis those in the East Asian populations before 2003 (Endo and Tsurumachi 2001, Ping et al 2001, Nagata et al 2002, Nagata and Kamimuro 2002, Liu et al 2003a,b). These results suggest that insecticide resistance against imidacloprid occurred only in East Asia and Indochina but not in the Philippines.

In contrast to BPH, no significant differences in LD_{50}-values for imidacloprid were found among Asian WBPH populations except for one Japanese population. The LD_{50}-values in 2006 were similar to those in Japanese and Chinese populations collected in 1992-2001 (0.02–0.33 μg g^{-1}) (Ping et al 2001, Liu et al 2003b). These results suggest that no insecticide resistance against imidacloprid occurred in WBPH in Asia.

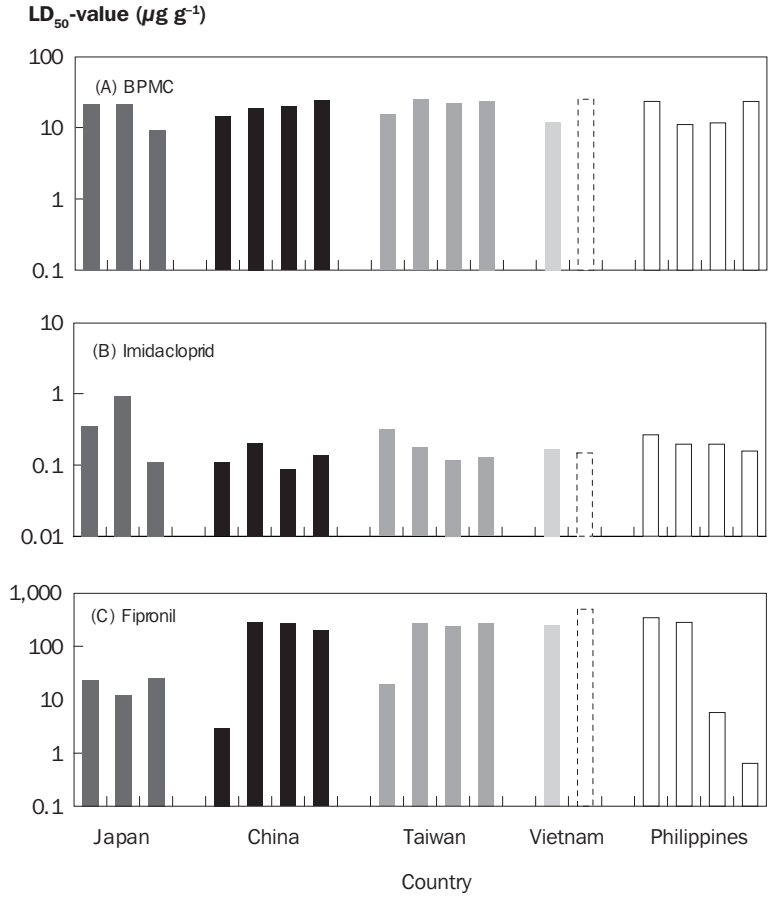

Fig. 6. LD_{50}-values of *Sogatella furcifera* strains collected in East and Southeast Asia in 2006 (Matsumura et al 2008).

Although the LD_{50}-values for thiamethoxam were not so large, the BPH populations indicated a positive cross-resistance between imidacloprid and thiamethoxam. In the case of dinotefuran, another neonicotinoid insecticide, the BPH populations collected in 2005-07 in Japan showed no insecticide resistance. Thus, the cross-resistance with imidacloprid might not occur in all the neonicotinoid insecticides.

Almost all the Asian WBPH populations collected in 2006 had large LD_{50}-values for fipronil at 24 h after treatment. Although no topical LD_{50}-values for fipronil in the field for WBPH populations have been published previously, these results suggest that insecticide resistance of WBPH against fipronil occurred widely in East and Southeast Asian countries.

On the other hand, all the Asian BPH populations had much smaller LD_{50}-values for fipronil, suggesting that no insecticide resistance against fipronil occurred in BPH

in Asia. However, the LD_{50}-values of these two populations are slightly higher than others. Thus, the monitoring of insecticide susceptibility to fipronil in BPH should be continued in this region.

In the case of BPMC, the LD_{50}-values of BPH and WBPH in 2006 were similar to those in Japan, China, and Vietnam in 1992-2001 (8.8–26 μg g^{-1} for BPH and 5.1–28 μg g^{-1} for WBPH) (Endo and Tsurumachi 2001, Ping et al 2001, Nagata et al 2002, Liu et al 2003b). No significant differences were detected among countries.

Our study revealed a species-specific change in insecticide susceptibility in Asian rice planthoppers (i.e., BPH for imidaclopirid and WBPH for fipronil). Imidacloprid has been used commonly to control BPH in the latter stage of rice in Vietnam and China (around May to early June in winter-spring rice cropping in northern Vietnam). Fipronil has been used commonly to control the rice leaffolder, *Cnaphalocrocis medinalis* (Guenée), and rice stem borers in the early stage of rice in Vietnam and China (around early April in winter-spring rice cropping in northern Vietnam). Spraying fipronil in the early season could also be more effective on WBPH than on BPH because WBPH increases earlier than BPH in the rice-growing season. This could be a possible reason insecticide resistance against fipronil occurred only on WBPH species. The overuse of insecticides is often the precursor to the development of insecticide resistance and many Asian countries rely heavily on a limited number of compounds for planthopper control (Nagata et al 2002, Sun et al 1996).

Our study suggests that the insecticide resistance of BPH against imidacloprid did not occur in the Philippines. This is because BPH outbreaks have not occurred recently and imidacloprid has not been used commonly in the Philippines. In contrast, fipronil has been used commonly to control rice stem borers in the Philippines. For this reason, the insecticide susceptibility of WBPH against fipronil in the Philippines was as low as that in East Asia and Vietnam.

The species-specific insecticide resistance against different insecticides might have also occurred by the difference in mode of action of insecticides. Liu et al (2005) found that a nicotinic acetylcholine receptor (nAChR) mutation confers target-site resistance to imidacloprid in BPH. However, this target-site resistance in BPH was selected only in the laboratory and was never found in a field strain. Although the target site of fipronil (GABA receptors) is different from that of imidacloprid (see review of Raymond-Delpech et al 2005), no detailed information is available for the mechanism of resistance to fipronil in WBPH. Further comparative studies on the mode of action of neonicotinoid and phenylpyrazole insecticides against BPH and WBPH are needed to explain the species-specific development of insecticide resistance against neonicotinoid and phenylpyrazole insecticides as well.

In the Mekong Delta of southern Vietnam, outbreaks of the two BPH-transmitted virus diseases, rice ragged stunt virus (RRSV) and rice grassy stunt virus (RGSV), have occurred since 2005 (Chien et al 2007), resulting in a heavy use of insecticides to control BPH. Our study showed that the LD_{50}-values in two southern Vietnamese BPH populations tended to be higher than those in the other locations for BPMC, imidacloprid, and fipronil. Thus, it is important to continue to carefully monitor the

status of insecticide susceptibility in BPH against these insecticides in southern Vietnam and neighboring countries such as Thailand.

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Host-plant relationships

Effects of nitrogen-enriched rice plants on ecological fitness of planthoppers

Zhongxian Lu and K.L. Heong

Planthoppers are known to prefer nitrogen-enriched rice plants. When reared on high-nitrogen plants, they have higher feeding rates and honeydew secretion, probe less, and lay more eggs. These ecological fitness characters are quantified and their relationships with tissue nitrogen content were found to be linear. The linear models were coupled with a transfer function population model and simulation studies showed that planthopper densities increased 40-fold for every fold increase in nitrogen content. Crops with nitrogen-enriched plants tend to favor planthopper population development and the implications for nitrogen use and sustainable management of planthoppers are discussed.

The Green Revolution that began in the mid-1960s was characterized by the breeding and widespread adoption of new high-yielding varieties (HYVs), pesticides, and nitrogenous fertilizers. Food production, especially of rice, wheat, and maize, increased markedly. In the next three decades, excessive inputs of pesticides and fertilizers resulted in negative environmental effects, which Conway and Pretty (1991) called the "unwelcome harvest." In the last 45 years, world consumption of nitrogenous fertilizer increased by 30-fold (Fig. 1), whereas rice yields increased by only 2.2-fold (FAOSTAT 2008), suggesting that the use of nitrogen is excessive. Since 1960, flows of biologically available nitrogen doubled and those of phosphorus tripled. The use of synthetic nitrogenous fertilizer escalated; 50% of all that had been produced was used since 1985. The recovery efficiency of applied nitrogen in most cases is less than 50% and for rice less than 35% (Witt 2003). The differences in nitrogen content between animal and plant tissues may be an important reason why most herbivores have an ability to seek out host plants with high nitrogen content (Southwood 1973). Heavy applications of nitrogenous fertilizer may not affect insect biology directly, but they bring about changes in host-plant morphology, biochemistry, and physiology, which can improve nutritional conditions for herbivores (Bernays 1990, Simpson and Simpson 1990), thus playing a key role in modifying and reducing host resistance to herbivores (Barbour et al 1991). Rice crops with high nitrogenous fertilization become favorable habitats to more than 200 species of insect herbivores, some of which are important pests. The excessive use of nitrogen fertilizer promoted by the Green Revolution had been

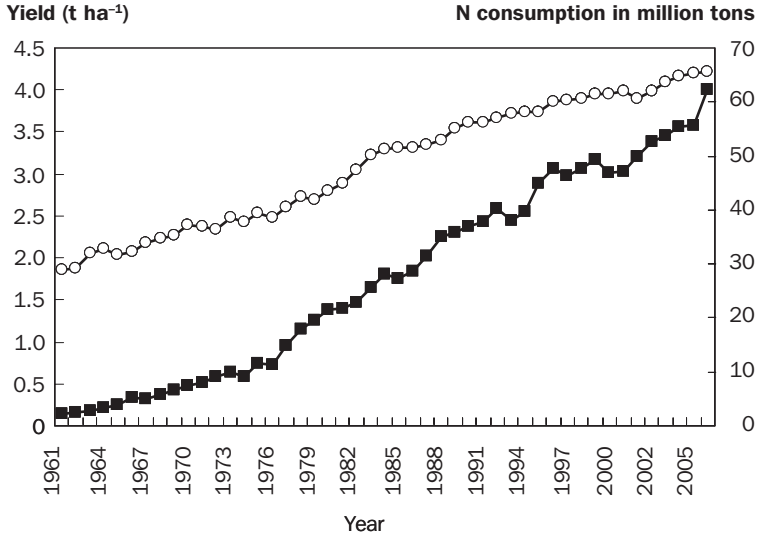

Fig. 1. World trends in nitrogen consumption (■) (million tons) and rice yields (○) (t ha^{-1}) between 1961 and 2006.

considered a key driver in the shift of brown planthopper (BPH) *Nilaparvata lugens* from a minor to a major insect pest in the 1970s (Dyck et al 1979). In this chapter, we provide further evidence and quantification of the effects of nitrogen-enriched rice plants on various planthopper ecological fitness characters.

The two important planthopper species in tropical Asia are the BPH and the whitebacked planthopper (WBPH) *Sogatella furcifera*. They are monophagous phloem feeders that invade maturing rice crops from other rice areas, sometimes being displaced by wind over long distances (see Otuka et al, this volume). Since phloem is poor in nutrients, the planthoppers need to filter large quantities of phloem sap and thus have low efficacy of conversion rates of only 5% to 7% compared with other herbivores' conversion rates of 40% to 90% (Slansky and Scriber 1985).

Planthoppers' preference for nitrogen-enriched rice plants has been documented (Cheng 1971, Lu et al 2005, Wang and Wu 1991) and BPH on high-nitrogen plants had been found to have higher feeding rates and honeydew excretion (Cheng 1971, Sogawa 1970). Planthoppers also probe less (Lu et al 2005, Sogawa 1970), have higher survival rates, and have greater population buildup (Cheng 1971, Preap et al 2001). They also produce more eggs (Preap et al 2001, Wang and Wu 1991) and have a higher tendency for outbreaks (Hosamani et al 1986, Li et al 1996, Uhm et al 1985). Kanno et al (1977) found that BPH on nitrogen-enriched plants consumed 3–7 times more, excreted 7 times more honeydew, and had 2–3 times higher body nitrogen. Both water content (WC) and relative water content (RWC) of BPH on high-nitrogen plants increased significantly (Lu et al 2004a). Similar responses to nitrogen fertilization were found in WBPH (Hu et al 1986, Ma and Lee 1996, Wu and Zhu 1994). Nitrogen enrichment

in plants can alter BPH on some resistant varieties. For instance, on resistant varieties IR26 and Utri Rajapan, BPH growth rates increased proportionately with nitrogen applied (Cheng 1971, Heinrichs and Medrano 1985). In these experiments, applied nitrogen was used as a treatment and tissue nitrogen was not measured.

Effects of plant tissue nitrogen on ecological fitness characters of planthoppers

Ecological fitness is the measure of how well an individual or a population adapts to a specific niche.[1] The characters used for measurement are survival rates, longevity, and fecundity under the different nitrogen enrichment regimes of rice variety IR64, which has the *Bph1* resistance gene and several QTLs rendering field resistance to BPH (Cohen et al 1997). Plant tissue nitrogen content was determined by converting chlorophyll meter readings using a calibration model (Lu et al 2004b). Planthopper nymphal survival rates were positively related to nitrogen content, whereas nymphal duration decreased with an increase in nitrogen content (Fig. 2A and B). Female progenies were heavier, lived longer, and laid more eggs (Fig. 2C, D, and E). The increase in prey size can have negative effects on predation as it can affect predator handling time. Egg hatchability also increased with nitrogen content (Fig. 2F), resulting in more hoppers produced and higher dry weights (Fig. 2G and H). Between generations, BPH reared on plants receiving 200 kg N ha^{-1} lived 3 times longer and produced 10 times more eggs than those plants reared with no nitrogen applied. Using a transfer function population model coupled with the predicted parameters from the linear equations in Figure 2, simulations of population densities for nitrogen application rates of 100 to 400 kg ha^{-1} showed that, for every fold increase in nitrogen application, planthopper densities can increase by 40-fold (Fig. 3).

WBPH were reared on Shanyou 63 (hybrid), Xiushui 63 (japonica), and Zhe 733 (indica) plants with low (0 N input) and high nitrogen (200 kg N ha^{-1} input) over three generations. Females reared on low nitrogen over three generations had decreasing trends in dry weight and egg oviposition (Fig. 4). On high-nitrogen plants, dry weights and oviposition increased with generations. Similarly, in BPH, fitness variables gradually increased when BPH were fed successively on high-nitrogen regimes, whereas, with successive low-nitrogen regimes, the variables gradually declined (Lu et al 2004a). The increase in eggs laid by WBPH females in low- and high-nitrogen plants was 267%, 163%, and 158% for Shanyou 63, Xuishui 63, and Zhe 733, respectively. This provides further support to reported population shifts in planthoppers. WBPH in China in the 1980s and 1990s had shifted due to the abnormal susceptibility of the Chinese hybrids to WBPH compared with japonica varieties (Sogawa et al 2003). However, for indica variety Zhe 733, the two fitness parameters were higher, indicating that this variety was more susceptible.

Populations of planthopper are known to have high fecundity of more than 1,000 eggs per female (Li et al 1996) and a rapid increase of about 500 times in three

[1]Further discussions on ecological fitness can be found in *The Standard Encyclopedia of Philosophy*, http://plato.stanford.edu/entries/fitness/.

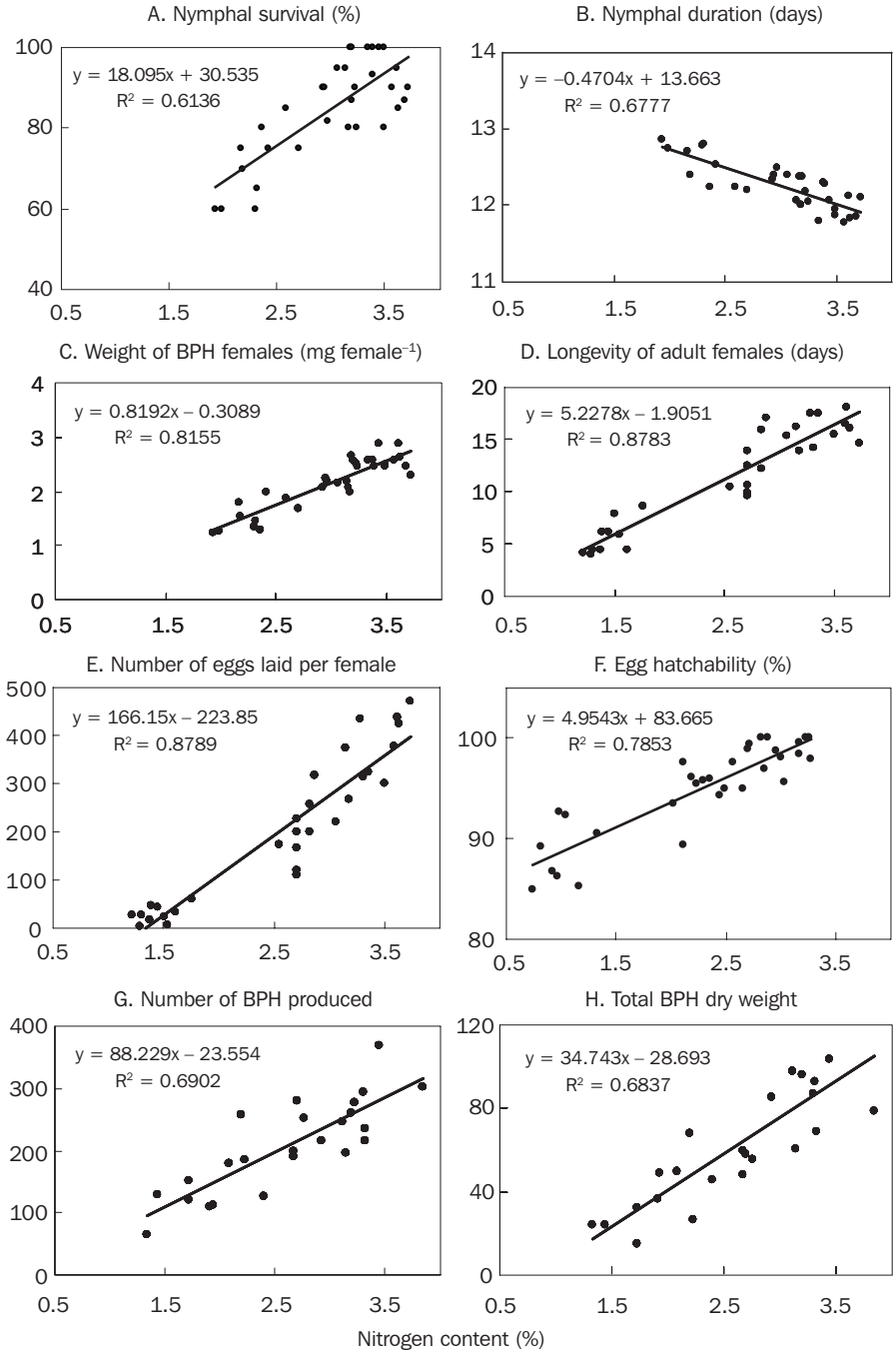

Fig. 2. Relationships between fitness variables of the brown planthopper and nitrogen content (%).

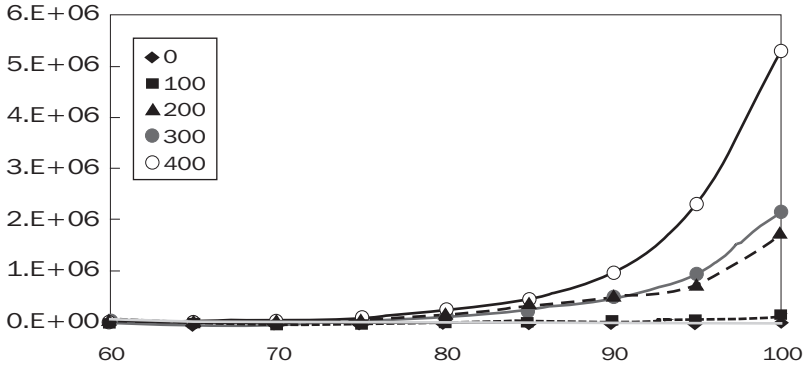

Fig. 3. Simulation of population development from 5 pairs of brown planthoppers using a transfer function population model (Heong 1988) and fitness parameters at nitrogen regimes of 0, 100, 200, 300, and 400 kg ha^{-1}.

generations (Kuno 1984), from a low initial density of less than 0.001 per hill. This is true in temperate regions or in environments with low naturally occurring biological control. In the tropics, such high increases were reported in fields sprayed with insecticides. Most of these studies also relied on data collected from the immediate generation after recruitment. When exposed to successive generations of nitrogen-enriched plants, the cumulative planthopper populations might even be fitter.

On nitrogen-enriched plants, planthoppers tend to increase their feeding rates. This may be because of the increase in host phloem amino acids such as aspartic and glutamic acids, which are feeding stimulants (Sogawa 1982). Planthoppers also tend to select nitrogen-rich over nitrogen-poor plants (Sogawa 1970, Lu et al 2005). The combined effects of increased colonization, increased stimulation for feeding, and increased fitness generally result in rapid population growth.

Plant injury and yield loss caused by BPH populations in paddy fields in temperate regions are dependent on the initial immigrant and high population parameters (Li et al 1996). BPH recruitments in these areas are apparently displaced by Asian monsoon winds from Southeast Asian areas where BPH reproduce around the year (Sogawa 1995). In the tropics, however, initial recruitments are lower (Yu et al 1997) and population suppression by natural enemies (Heong et al 1992, Way and Heong 1994) is high. Thus, high fitness potentials may be neutralized by strong natural biological mechanisms. In temperate rice, however, population abundances may be more dependent on fitness components and coupled with high nitrogen, high pesticide applications, and low natural biological control, which make these areas more vulnerable to BPH outbreaks.

It is clear that planthoppers in high-nitrogen application regimes have significantly higher fitness, as discussed by other authors (e.g., Cook and Denno 1994). And, after successive generations of high-nitrogen regimes, population increases might even be greater. Although ecological fitness is increased in high-nitrogen regimes, it does not completely explain the low planthopper outbreaks in many rice-growing

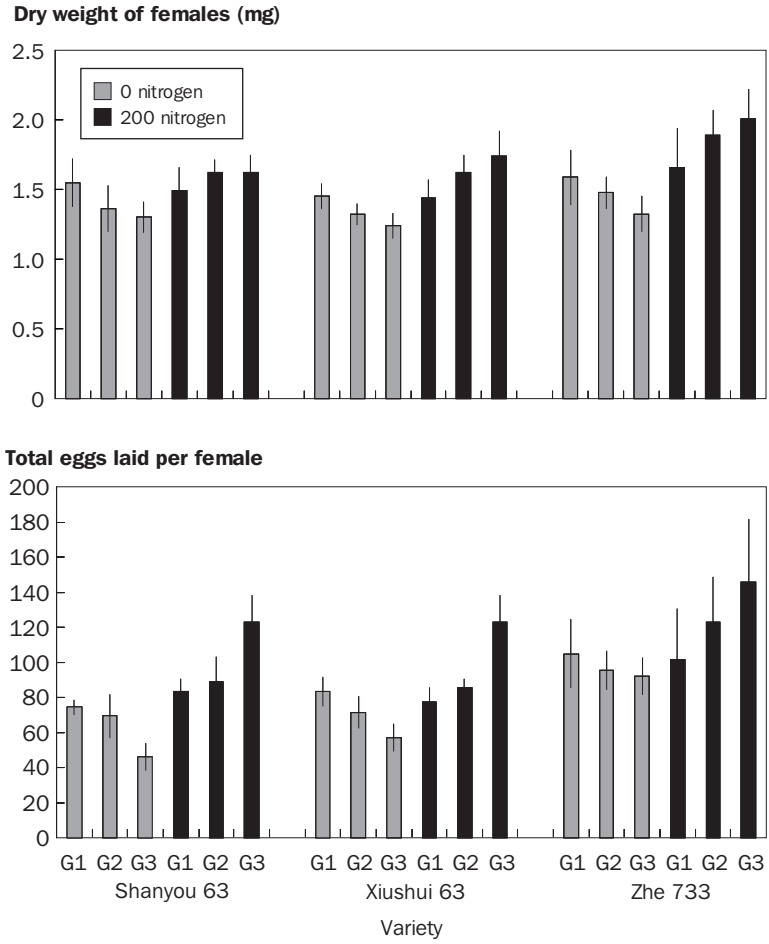

Fig. 4. Female weights and eggs laid per female of whitebacked planthoppers reared successively for 3 generations in 0 N and 200 kg N ha^{-1} regimes.

areas and fields, in both tropical and temperate regions, with high nitrogen use. Way and Heong (1994) attributed the stability of pest populations in tropical rice to natural biological control. It has been argued that the diversity and effectiveness of natural biological control in the temperate region are relatively low due perhaps to weather conditions coupled with high insecticide use. On some occasions when insecticides were suddenly stopped, crops suffered high BPH attacks mainly from recruitments from neighboring fields. Thus, in intensive areas with nitrogen applications, sudden stoppage of insecticide may render higher risks of BPH outbreaks. A gradual reduction in unnecessary sprays followed by a gradual spread of such practices may thus be a more practical and acceptable way to reduce insecticide use in these areas, as was done in Vietnam (Heong et al 1998).

Implications for fertilizer and planthopper management

Nitrogenous fertilizer is important to sustain and meet the world's food demand and food security in the foreseeable future. The world needs an additional 50 million tons of rice annually or 9% of current production to meet demand in the near future (IRRI 2006). However, fertilizer management in irrigated rice in Asia is characterized by inefficient and unbalanced use of inorganic fertilizers and the amount of grain yield produced per unit fertilizer N applied is low (Witt 2003). In addition, the excess N in plant tissues contributes significantly to pest and disease problems. Nutrient management methods that will improve efficiency (Witt et al 2005) will also improve the management of planthoppers. Excess nitrogen in rice generally causes excess vegetative growth, lower harvest index, proneness to lodging, and susceptibility to disease and insect pests and often results in an asymptotic or parabolic relationship between crop yield and nitrogen dose (Sinclair 1998, Srivastava and Singh 1999). In a 5-year test at the Missouri Rice Farm at Glennonville, rice yields were greatest when the recommended N fertilizer rate was applied, and yields decreased when N fertilizer was applied at 150% of the recommended amount.

Rice production must increase by about 65% more than today to meet the demand projected for 2025. If the technologies that affect nutrient use by the rice crop remain unchanged, that production increase will require almost 300% more than the present application rate of N alone in irrigated environments. This is an undesirable amount economically and environmentally. It is obvious that nutrient-use efficiency needs to be improved, along with the yield potential of new rice cultivars (Fischer 1998). In China, the consumption of nitrogen increased by 44-fold in the past 40 years, an average yearly increase of 10.5%. In 1998, China consumed three times more nitrogen than the rest of the world, 181 kg nitrogen per ha compared with the world's consumption of 60 kg per ha (Zhu and Chen 2002). High rice yields might be attributed to the high average nitrogen rate of 180 kg per ha. However, the partial factor productivity (PFP) of nitrogen fertilizer is much lower, implying low nitrogen fertilizer-use efficiency. The excessive use of nitrogenous fertilization may be due to low prices, high seed costs, and farmers' attitude of maximizing tillers and labor (Peng et al 2002). These practices, coupled with prophylactic spraying regimes of 5 to 10 sprays of multiple active ingredients of insecticides, might be the main causes of unstable planthopper populations and frequent outbreaks. Heavy insecticide use is not only masking the effects of natural biological control but is stimulating the development of insecticide resistance (see Matsumura et al, this volume). Thus, management of planthoppers will need to focus on reducing prophylactic insecticide applications, especially in the early crop period, and improving fertilizer efficiency.

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Notes

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Prevalence of whitebacked planthoppers in Chinese hybrid rice and whitebacked planthopper resistance in Chinese japonica rice

Kazushige Sogawa, Guangjie Liu, and Qiang Qiang

The whitebacked planthopper (WBPH), *Sogatella furcifera*, was only a secondary insect pest of rice before the 1970s in China. However, WBPH increased significantly and became the most predominant insect pest, replacing the brown planthopper (BPH), *Nilaparvata lugens*, in rice areas planted with indica hybrid rice in China in the 1980s. WBPH also became an important economic insect pest of japonica rice in Central China because of its massive displacements from the hybrid rice areas in South China. Eventually, devastating outbreaks of WBPH, as well as BPH, broke out over the entire rice area of China in 1987 and 1991, when hybrid rice had extended to almost half of the total rice area in China. Chinese hybrid rice introduced to Vietnam caused a historical outbreak of WBPH in the Red River Delta in 2000. High susceptibility to WBPH in a Chinese hybrid rice, Shunyou 63 (SY-63), is primarily inherited from the WA-CMS line, which is extremely vulnerable to WBPH infestation. In addition, greater tolerance of WBPH infestations in SY-63 due to vigorous growth is further attributed to the unusual upsurge of WBPH populations.

A Chinese japonica rice, Chenjiang 06 (CJ-06), was found to be highly resistant to WBPH. The WBPH resistance in CJ-06 is mediated by both the sucking inhibition and ovicidal reaction of the host plant. The sucking inhibitory and ovicidal traits are independently conferred by monogenic dominant genes, which are located on chromosomes 4 and 6, respectively. The sucking inhibitory trait exerts a distinct antixenosis, which disrupts host-plant selection by the macropterous females of WBPH immigrated into the paddy fields. The ovicidal trait causes a high mortality of WBPH eggs deposited onto CJ-06. By means of both antixenotic and antibiotic resistance, WBPH populations are constantly suppressed below the economic threshold level in CJ-06. These dual mechanisms could provide this Chinese japonica rice with durable resistance to WBPH. Field trials in WBPH epidemic areas in China demonstrated that the insecticide-free or reduced cultivation of WBPH-resistant japonica rice was more profitable than the insecticide-dependent cultivation of hybrid rice SY-63.

Keywords: Whitebacked planthopper, outbreak, Chinese hybrid rice, Chinese japonica rice, varietal resistance, sucking inhibitory resistance, ovicidal resistance

The brown planthopper (BPH), *Nilaparvata lugens*, and the whitebacked planthopper (WBPH), *Sogatella furcifera*, are herbivores restricted to the rice plant, *Oryza sativa* (Sogawa 1982). Because of their rice-monophagy and *r*-strategic ecology, rice varieties as major food resources and the environment of the paddy ecosystem as a breeding habitat directly influence the pest status of BPH and WBPH. Technical innovations through the introduction of high-yielding varieties (HYVs) and synthetic fertilizers and pesticides caused dynamic changes in the pest status of these rice planthoppers. From 1979 and into the 1980s, BPH and WBPH became epidemic in South and Southeast Asia, where traditional rice varieties were markedly replaced by modern HYVs to bring about the Green Revolution in rice agriculture (Dyck and Thomas 1979, Heinrichs and Mochida 1984, Dhaliwal et al 1985, Gallagher et al 1994, Rombach and Gallagher 1994). It has also been well documented that the simultaneous introduction of broad-spectrum insecticides induced a serious resurgence of planthopper populations (Ressing et al 1982a, Kenmore et al 1984). Resistant HYVs were promptly defeated by the adaptive genetic makeup of planthopper populations, the so-called biotypes. The uncontrollable outbreaks of rice planthoppers led to the crisis of paddy ecosystems, and brought about a paradigm shift in the management of rice insect pests in tropical rice areas (Heong and Sogawa 1994). In this regard, it is possible to say that BPH and WBPH are the sensitive barometers of mismanagement of tritrophic interactions among rice plants, planthoppers, and natural enemies in paddy ecosystems.

Rice agriculture in China is characterized by the wide adoption of high-yielding F_1 hybrids of rice. Since its introduction in 1976, hybrid rice spread rapidly to about half of the total rice area in China by 1990. Reportedly, a significant increase in rice production in the 1980s largely depended upon hybrid rice. However, it is also pointed out that the frequency of outbreaks of BPH and WBPH increased correspondingly with the spread of hybrid rice area in the 1980-90s in South China (Hu et al 1992, Tang et al 1998). Particularly, WBPH increased unusually and became the most predominant insect pest of hybrid rice (Liu et al 2002, Sogawa et al 2003b). The BPH biotype shift also possibly became accelerated in Chinese hybrid rice when hybrid rice with the *Bph1* gene for BPH resistance from IR varieties spread over the insect migration zone in South and Central China. After 1990, previously BPH-resistant hybrid rice became highly susceptible to BPH. WBPH generated in hybrid rice areas migrated massively to the japonica rice areas in Central China, and caused economic damage to japonica rice. Intensive insecticide applications to rice plants at the early tillering stage became inevitable to protect the plants from WBPH infestations. Eventually, devastating outbreaks of WBPH and BPH occured over the entire rice area in China in 1987 and 1991. Simultaneously, overseas invasions of these rice planthoppers into Japan increased significantly since the mid-1980s. Similar evidence was also recorded in Taiwan (Cheng and Huang 2004). As a result of intensive insecticide applications for controlling WBPH on hybrid rice and japonica rice in China, pesticide-resistant WBPH populations immigrated to Japan (Endo et al 1988).

An upsurge of rice planthopper infestations and the subsequent increase in insecticide investment in paddy ecosystems heighten the risk of pest resurgence due to

the destruction of natural enemies, the development of insecticide resistance in insect pests, and toxic pollution of environments and agro-products (Heong and Schoenly 1998). Particularly, the insecticide pollution of agro-products is a serious social problem in China. Therefore, pesticide-dependent high-yielding hybrid rice technologies are not friendly to paddy ecosystems and the environment for sustainable and safe rice production. Growing pest and pesticide problems in rice agriculture in China turned our attention to using the varietal resistance to rice planthoppers inherent in japonica rice germplasm in China. Insect pest resistance in rice plants is an alternative approach to reduce pesticide dependence in the management of insect pests in paddy fields.

This report deals with the field evidence and possible mechanism of WBPH resistance prevalent in Chinese hybrid rice in the earlier chapters and the WBPH resistance in Chinese japonica rice in the latter chapters of this publication.

Prevalence of whitebacked planthopper in Chinese hybrid rice

WBPH was only a secondary insect pest of rice before the 1970s in China. However, immediately after the release of hybrid rice in 1976, the first WBPH outbreak occurred on a hybrid rice, Nanyou 2, in Hunan Province in 1977 (Tan 1987). In 1982, about 1,600 ha of Shanyou 6 fields were severely infested with WBPH, and 80 ha were completely destroyed in hybrid rice pilot areas in Guangdong Province, South China, where Shanyou 2, Shanyou 6, and Weiyou 6 were introduced deliberately (Feng and Huang 1983). The field density of WBPH in Fujiang Province increased significantly from 1978 to 1988. Before 1980, the average field density was below 5 insects per hill, but this increased to 40 insects per hill in 1987 (Lin 1989) (Fig. 1). The frequency of WBPH outbreaks was positively correlated with the expansion of hybrid rice area from 1980 to 1990 in Guangdong Province and similarly in Hunan and Guangxi provinces. Light-trap catches of WBPH exceeded those of BPH at Shantou, Guangdong Province, by 1985, and WBPH became the most predominat insect pest (Lin 1994).

In Central China, an unusually high density of WBPH was first found in hybrid rice Shanyou 6 in Zhejiang Province in 1979. Observations in farmers' fields for 3 years from 1980 to 1982 showed that the population density of WBPH was 8 to 38 times higher than that in inbred rice (Ruan 1983). After that, it was demonstrated that the rate of WBPH reproduction in Shanyou-6 was 2.6–3.9 times higher than that in three inbred rice varieties (Huang et al 1985). Higher fecundity of WBPH on hybrid rice such as Shanyou 6, Shanyou 63, and Weiyou 35 was also recorded (Yu et al 1991, Shi and Lei 1992). This field evidence and these observations showed that WBPH is much more reproductive in Chinese hybrid rice than in inbred rice.

WBPH has been only a minor insect pest of monsoon rice in the Red River Delta (RRD) in Vietnam. However, WBPH had a historical outbreak on about 153,000 ha of winter-spring rice planted with Chinese hybrid rice in the RRD in 2000 (Thanh et al 2001). Since then, WBPH has steadily increased as a new important economic insect pest of rice in the rice granary (Thanh et al 2007). Chinese hybrid rice was first introduced to Vietnam in the early 1990s, and it quickly extended to cover 70–80% of

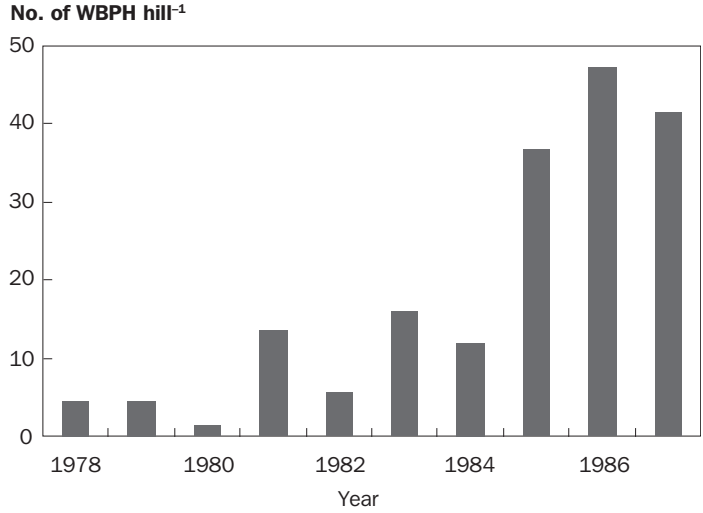

Fig. 1. Significant increase in average density of WBPH per hill of rice plants in Ningde District, Fujian Province, China (from Lin 1989).

the rice area in the RRD. Subsequent intensive investment in insecticides is spoiling the previous great efforts for integrated pest management (IPM), and inducing a paddy ecosystem crisis.

Population trends of WBPH in hybrid rice SY-63 and its parents

Shanyou 63 (SY-63) was one of the most popular Chinese indica hybrid rice varieties in the 1990s, when about 40% of the total hybrid rice area was covered only by SY-63. SY-63 is an F_1 hybrid between CMS line Zhenshan 97A (ZS-97A) carrying the wild abortive-CMS trait and restorer line Minghui 63 (MH-63) carrying the *Bph1* gene for BPH resistance from IR30. SY-63 and its parental lines are all susceptible to WBPH. WBPH can establish populations on them. However, there are considerable differences in the reproductive performance of WBPH among them.

The population trends of WBPH in SY-63 and its parental lines, ZS-97A and MH-63, were examined comparatively in field experiments. The density of macropterous immigrants was apparently higher in SY-63 and ZS-97A than in MH-63. The highest nymphal population developed on ZS-97A, and caused complete hopper burn (Sogawa et al 2003e) (Fig. 2). WBPH also established a high density of nymphal population on SY-63. Because of greater tolerance of WBPH infestations, WBPH continuously reproduced progenies in SY-63 even after ZS-97A plants collapsed completely because of hopper burn. In a separate field trial, maintenance line Zhenshan 97B (ZS-97B) and CMS line ZS-97A were found to be equally susceptible to WBPH, and suffered hopper-burn damage by the first-generation progeny. On the other hand, the WBPH population density was the lowest in the MH-63 field, where no visible damage appeared. Dry weights of newly emerged WBPH adults sampled by a sweeping method in ZS-97A,

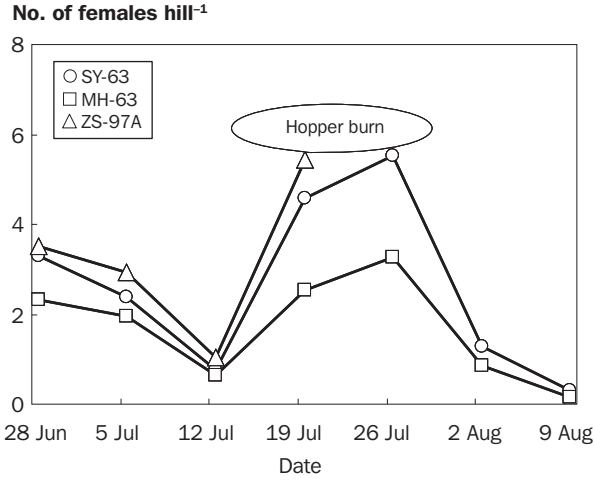

Fig. 2. Density fluctuations of WBPH adult females in SY-63 and its parental lines (CNRRI 1999).

SY-63, and MH-63 fields were 68.1 ± 18.4 mg, 50.1 ± 9.0 mg, and 28.8 ± 13.7 mg, respectively.

Biomass interactions between WBPH and hybrid rice

Average amounts of honeydew excreted by a single female adult of WBPH were 14.8, 11.8, and 6.9 mg per day on ZS-97A, SY-63, and MH-63, respectively (Sogawa et al 2003e). Different amounts of honeydew excretion show that ZS-97A and SY-63 are apparently more susceptible than MH-63. The sucking rate of WBPH is influenced by the quality of the phloem sap of host plants. Total free amino acid concentrations were 9.2%, 2.7%, and 2.4% in the phloem saps collected from ZS-97A, SY-63, and MH-63 plants, respectively. The highest sucking rate in ZS-97A may be related to the highest concentration of free amino acids in its phloem sap.

Average dry weight of the progeny reproduced by six WBPH females per plant was about 250 mg and 243 mg on SY-63 and ZS-97A, respectively, which is significantly higher than the 74 mg on MH-63. When eight females were introduced to each plant, WBPH dry biomass production increased significantly up to 321 mg on SY-63, but it was only 249 mg on ZS-97A. This different WBPH biomass productivity indicates that SY-63 has a much larger carrying capacity for the WBPH progeny load than ZS-97A. WBPH biomass production on MH-63 was suppressed to less than half that on SY-63 and ZS-97A.

The plant biomass of SY-63 and ZS-97A was more efficiently converted to WBPH biomass than was MH-63 biomass. Functional biomass losses (mg of dry plant biomass lost per mg of dry WBPH biomass produced) were about 10 mg and 12 mg in SY-63 and ZS-97A, respectively, whereas the loss was 32 mg in MH-63 (Fig. 3A). Likewise, daily plant biomass production by SY-63, ZS-97A, and MH-63

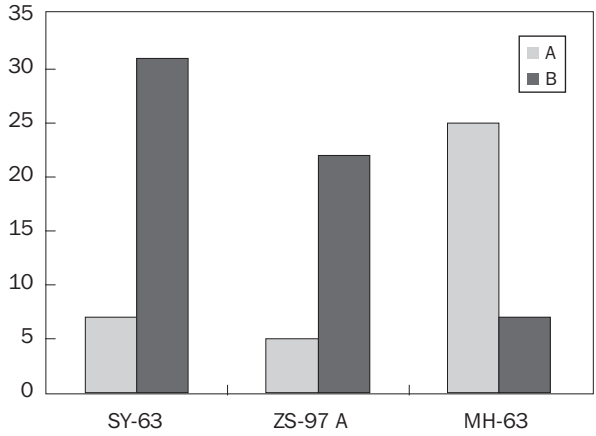

Fig. 3. Biomass interactions between WBPH and host plants, SY-63 and its parental lines. (A) Plant biomass loss (mg, dry weight) equivalent to 1 mg WBPH biomass production. (B) Potential daily WBPH biomass productivity (mg, dry weight per day), where average daily biomass production of host plants is converted to WBPH biomass.

was estimated to be equivalent to about 32 mg, 23 mg, and 9 mg WBPH biomass production, respectively (Fig. 3B). Based on these biomass interactions between WBPH and host rice plants, SY-63 and ZS-97A are found to be highly susceptible to WBPH, and equally suitable as food sources (Sogawa et al 2003e). On the other hand, SY-63 has a greater carrying capacity for WBPH load due to its greater rates of daily biomass productivity than ZS-97A. Greater ability of biomass production by SY-63 could be responsible for F_1 hybrid vigor.

Susceptibility to and tolerance of WBPH in hybrid rice

It is apparent by field performance that ZS-97A is unusually vulnerable to WBPH infestations, probably because of the complete lack of field resistance and tolerance of WBPH during the process of breeding. However, WBPH susceptibility is not related to the CMS trait in ZS-97A because ZS-97A and its maintainer line, ZS-97B, are equally susceptible to WBPH. Therefore, karyoplasmic genes confer susceptibility to WBPH in ZS-97A. The high WBPH susceptibility in ZS-97A is inherited by SY-63. However, greater tolerance of WBPH infestation conceals the susceptibility to WBPH in SY-63 in the field. Because of the greater tolerance due to a greater ability of biomass production in SY-63, SY-63 can persist under such a heavy WBPH infestation that could collapse ZS-97A plants completely. F_1 hybrid vigor provides SY-63 with a greater carrying capacity for WBPH load due to its greater daily biomass productivity than ZS-97A. It is also evident, however, that susceptibility to WBPH in SY-63 does not exceed the level in ZS-97A. Thus, neither heterosis nor heterobeltiosis are involved in the high susceptibility to WBPH in the F_1 hybrid SY-63.

Both ZS-97A and MH-63, the parents of SY-63, are susceptible to WBPH. However, there is a significant difference in the level of susceptibility to WBPH in terms of population growth, honeydew excretion, and biomass response to WBPH infestation between them. MH-63 is apparently less susceptible than ZS-97A. Less susceptibility to WBPH in MH-63 could be inherited from IR30, the precursor of MH-63, which is susceptible to WBPH in the standardized seedbox screening test (SSST), but moderately resistant in the modified seedbox screening test (MSST).

In addition to the susceptibility, WBPH abundance in SY-63 is also attributed to its greater tolerance due to a possible F_1 heterosis for vigorous vegetative growth, which gives a greater carrying capacity for a heavier WBPH population load. In the case of SY-63, tolerance does not work as a mechanism of varietal resistance. Basically susceptible but tolerant hybrid rice such as SY-63 will offer more favorable and durable breeding habitats to WBPH than simply susceptible inbred rice. Therefore, WBPH reproduces many more progeny on SY-63 than on the equally susceptible inbred rice. Tolerance because of F_1 hybrid vigor in susceptible hybrid rice only magnifies the host-plant capacity for planthopper load, and contributes to heighten pest density. Improvement of field resistance in CMS lines will be a practical approach to prevent WBPH prevalence on hybrid rice, as well as the introduction of dominant WBPH resistance genes to the restorer lines. If combined with field resistance in hybrid rice, tolerance will exert itself as an efficient trait to reduce plant damage.

Resistance to the whitebacked planthopper in Chinese japonica rice

WBPH resistance in a Chinese japonica rice, Chenjiang 06

We discovered a distinct resistance to WBPH in a Chinese japonica rice, Chenjiang 06 (CJ-06). Mechanisms of varietal resistance to WBPH in CJ-06 were investigated in comparison with a susceptible hybrid rice, SY-63. Field experiments revealed that WBPH immigrants exhibited nonpreference for CJ-06 and failed to establish a population on it, whereas the immigrants preferred to settle and reproduce on SY-63. Also, significantly less honeydew excretion by WBPH females on CJ-06 than on SY-63 indicated suppressed sucking on CJ-06 (Sogawa et al 2003c). A single WBPH female usually excretes more than 10 mg of honeydew per day on susceptible rice varieties, but less than 5 mg on CJ-06. This type of WBPH resistance in CJ-06 is described as "sucking inhibitory resistance."

WBPH eggs suffered high mortality in induced watery lesions at oviposition sites of CJ-06 plants (Fig. 4). The watery lesions rapidly led to the formation of conspicuous necrotic ovicidal symptoms before the eggs hatched. Egg mortality in the watery lesions occurred within 1–2 days after oviposition. WBPH resistance due to ovicidal response is called "ovicidal resistance" (Sogawa et al 2003c). Such watery lesions seldom occurred in SY-63, in which egg hatchability was very high.

Both fecundity and egg hatchability were markedly reduced on CJ-06 compared with those on SY-63 when newly emerged females were fed on CJ-06. The fertility of WBPH on CJ-6 was only about one-tenth of that on SY-63 (Fig. 5). Based on this finding, we concluded that sucking suppression and ovicidal reaction are the

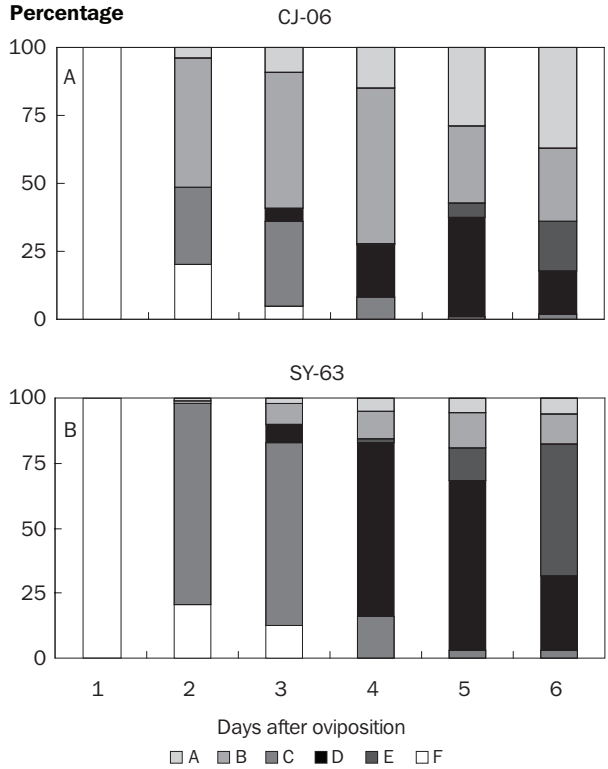

Fig. 4. Comparison of embryonic development of WBPH eggs deposited to CJ-11 (A) and SY-63 (B). A = dead eggs (brown), B = dead eggs (white), C = hatched eggs, D = eggs with eye-spots, E = eggs with yellow spot, F = fresh eggs.

major components for WBPH resistance in CJ-06, which is expressed not only as an antixenosis against WBPH immigrants but also as an antibiosis to reduce fecundity and egg hatchability against WBPH inhabitants, respectively. Such dual mechanisms of varietal resistance, namely, the sucking inhibitory and ovicidal resistance, could confer a stable and durable resistance to WBPH in CJ-06 in paddy fields (Sogawa et al 2003c).

Performance of ovicidal and sucking inhibitory resistance

Field expression of sucking inhibitory and ovicidal resistance in CJ-06 and its family varieties was evaluated by exposing them to natural infestations with WBPH under field conditions. It was found that there were significant differences in population performance of WBPH in varieties with a different genetic background for WBPH resistance (Sogawa et al 2003a). WBPH could not establish populations in CJ-06, Nonghu 6 (NH-6), and Dan 209 (D-209) that had both sucking inhibitory and ovicidal resistance because of distinct antixenosis against the immigrant females. Ovicidal resistance in

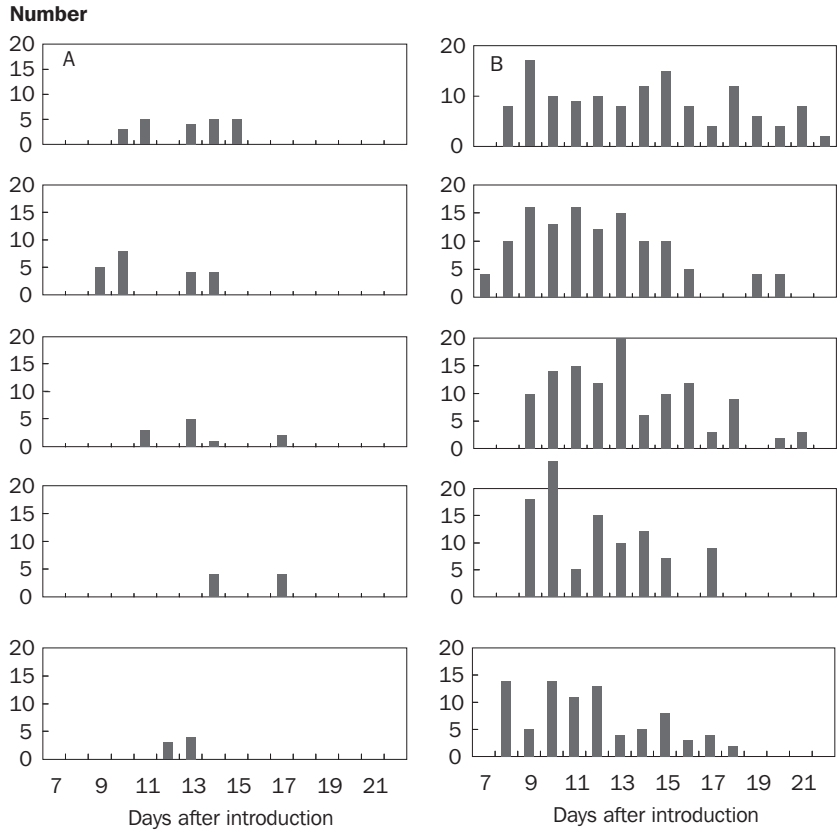

Fig. 5. Daily emergence of WBPH nymphs on five plants of CJ-11 (A) and SY-63 (B) at early tillering stage, on which a pair of newly emerged WBPH adults was introduced.

these varieties had almost no opportunity to act as a resistance mechanism against WBPH. Likewise, WBPH populations could not develop in varieties that had only sucking inhibitory resistance such as Funong 709 (FN-709) and Xiushui 04 (XS-04) due to antixenosis to the immigrant females. WBPH density declined as generations progressed on these varieties.

On the other hand, host selection response and oviposition by WBPH females and development of nymphs were not prevented in varieties Nongken 58 (NK-58), Ce 21 (C-21), Xianhu 24 (XH-24), and Belila (BLL). These varieties have ovicidal resistance but no sucking inhibitory resistance. These ovicidal varieties did not disrupt the settlement of WBPH immigrants, and allowed them to lay eggs. However, subsequent progeny density was kept low due to high mortality of the eggs deposited on these varieties. Early vegetative growth was deterred slightly in the ovicidal varieties because of necrotic symptoms due to the intensive oviposition and ovicidal response as well as sucking by a small number of nymphs that emerged escaping ovicidal

response. However, such early slight infestations were completely compensated for by later vegetative growth. On the contrary, WBPH reproduced exponentially for two consecutive generations, causing serious damage to Laohudao (LHD), a Chinese japonica landrace, which has no traits of resistance to WBPH.

Distribution of ovicidal and sucking inhibitory resistance in rice germplasm

Ovicidal and sucking inhibitory resistance to WBPH in japonica, indica, F_1 hybrid, and tropical japonica rice varieties were evaluated. The ovicidal phenomenon was originally discovered in japonica rice varieties in Japan (Sogawa 1991, Seino et al 1996, Suzuki et al 1996). It was confirmed that ovicidal varieties were found only among japonica rice (Sogawa et al 2003g). No ovicidal varieties were involved in indica, hybrid, and tropical japonica varieties. In addition, 42 japonica and 43 indica varieties from different provinces in China were reevaluated for WBPH resistance. Ten japonica varieties (about 24%) had ovicidal resistance, causing 53% to 100% egg mortality. In more than 95% of the indica varieties, WBPH egg mortality was below 30%. Only four japonica varieties from Zhejiang Province significantly suppressed honeydew excretion by WBPH, indicating sucking inhibitory resistance. Moreover, among 21 japonica landraces in Zhejiang Province, ovicidal and sucking inhibitory response of WBPH showed independent and continuous variations (Sogawa et al 2003g). Sanqianhuang (SQH), Changhongdao (CHD), and Aigandao (AGD) had ovicidal resistance. Jijiaofuang (JJH) and Maqueqing (MQQ) inhibited WBPH sucking. No landrace was found to carry both resistance traits together. These findings indicated that WBPH resistance traits have been retained in the japonica landraces in China (Sogawa et al 2003g).

It was found that a perennial Chinese wild rice (*O. rufipogon*, Dongxiang wild rice), a possible ancestor of japonica rice, shows ovicidal response against WBPH eggs, but a strain of annual tropical wild rice, *O. nivara*, a possible ancestor of indica rice, did not have the ovicidal trait. It is therefore considered that the ovicidal trait in japonica rice has originated in its possible ancestral wild rice.

Inheritance of ovicidal and sucking inhibitory resistance

Modes of inheritance of both sucking inhibitory and ovicidal resistance to WBPH in CJ-06 were analyzed by preparing F_1, F_2, and F_3 progenies from reciprocal crosses between CJ-06 and a susceptible indica variety, TN1. All the F_1 progeny were resistant, having both resistance traits. The sucking inhibitory and ovicidal resistance in F_2 segregated independently at a ratio of 3 (resistant):1 (susceptible). Four phenotypes with different combinations of sucking inhibitory and ovicidal traits segregated into a ratio of 9:3:3:1. The F_3 progenies that were established from individual F_2 plants showed very complicated expressions of WBPH resistance, mixing up the homozygotes and heterozygotes of sucking inhibitory and ovicidal traits. It was too difficult to discriminate homozygous and heterozygous groups for each resistance trait; F_3 batches that include resistant individual plants were all recorded as the progeny from resistant F_2 plants. Segregation ratios for each resistance trait in F_3 plants were 3 (homozygotes

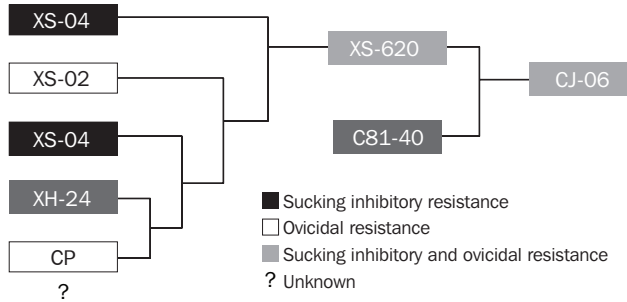

Fig. 6. WBPH resistance in the intermediate maternal varieties of CJ-11.

and heterozygous-resistant):1 (homozygous-susceptible). Segregation ratios for the combined resistance traits were 9:3:3:1. These results proved that two dominant genes independently conferred sucking inhibitory and ovicidal resistance to WBPH in CJ-06 (Sogawa et al 2003d). Preliminary crossings showed that the sucking inhibitory trait in CJ-06 is easily introduced into Japanese japonica rice.

Genealogical analysis of WBPH resistance in CJ-06

Genealogical analysis indicated that both the sucking inhibitory and ovicidal resistance to WBPH in CJ-06 were inherited together from Xiushui 620 (XS-620) (Fig. 6). Ovicidal resistance is a characteristic defense mechanism against WBPH infestations common in japonica rice. Thus, the japonica varieties involved in the pedigree of CJ-06 commonly retained ovicidal resistance. NK-58, a japonica rice introduced from Japan in the 1960s, was apparently one of the original donors of the ovicidal resistance trait (Sogawa et al 2003a). A distinct ovicidal response was also detected in XH-24 (Fig. 7).

Among the intermediate parental varieties of XS-620, only XS-04 had a strong sucking inhibitory resistance, but it had no ovicidal resistance. Of three parental lines of XS-04, only D-209 and FN-709 were sucking inhibitory. NH-6, a common parent of D-209 and FN-709, also inhibited WBPH sucking. It was confirmed that NH-6, D-209, FN-709, and XS-04 expressed distinct sucking inhibitory resistance (Sogawa et al 2003a) (Fig. 8). However, the parents of NH-6, NK-58, and LHD had no sucking inhibitory resistance, and were susceptible to WBPH. Thus, the real origin of sucking inhibitory resistance in NH-6 remained obscure. Two indica varieties, IR26 and IR28, which were used to introduce the *Bph1* gene for BPH resistance to CJ-06, were highly susceptible to WBPH, and had neither sucking inhibitory nor ovicidal resistance.

QTLs for ovicidal resistance

Quantitative trait loci (QTLs) associated with ovicidal resistance to WBPH in Zaiyeqing 8 (ZYQ-8, indica)/Jingxi 17 (JX-17, japonica) doubled-haploid (DH) lines were analyzed. The japonica parent JX-17 had ovicidal resistance to WBPH. The ovicidal trait in the DH lines was phenotyped based on the necrotic symptoms on the

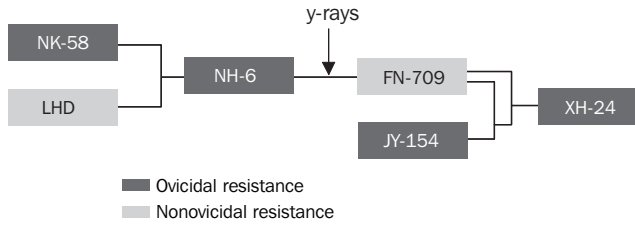

Fig. 7. Ovicidal resistance in the pedigree of XH-24.

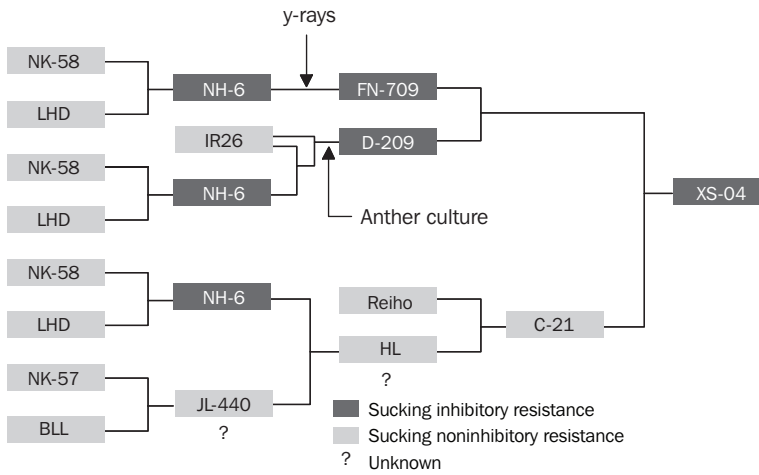

Fig. 8. Sucking inhibitory resistance in the pedigree of XS-04.

leaf sheaths due to ovicidal response at three different growth stages. Four ovicidal QTLs were detected on japonica segments of chromosomes 1, 2, 6, and 8 in the DH lines at early and mid-tillering stages. One more QTL appeared at the mid-tillering stage, which was located on an indica segment of chromosome 9. The ovicidal loci decreased to two at the maximum tillering to booting stages. The QTL (qOVC-6b) flanked by RFLP markers CT115 and CT506 on chromosome 6 explained 27.2% of the phenotypic variance, with an LOD score of 6.63 (Table 1). The analysis was based on the maximum score of ovicidal symptoms for each DH line throughout the experimental period, which revealed three QTLs on chromosomes 6 and 9. Two major QTLs (qOVC-6a and qOVC-6b) were located on the two closely adjacent segments of CT201-RZ450 and CT115-CT506 on the short arm of chromosome 6, which account for 25.7% and 29.6% of the phenotypic variance, with an LOD score of 7.00 and 7.31, respectively (Sogawa et al 2003f) (Table 1, Fig. 9). It is interesting that one of the minor QTLs (qOVC-9) on chromosome 9 comes from indica parent ZYQ-8, which has no ovicidal response. Detailed QTL-based analysis for the ovicidal response in

Table 1. QTLs associated with ovicidal symptoms due to WBPH oviposition.

Growth stage[a]	QTL	Chromosome	Marker interval	Peak LOD	Variance explained	Addivity
Early tillering (22)	qOVC-1b	1	GA594–CT380A	2.32	10.0	0.52
	qOVC-2b	2	G357–GA120	2.09	9.5	0.51
	qOVC-6c	6	G200–C235	2.29	9.2	0.52
	qOVC-8	8	BP127A–RZ617	2.60	9.5	0.52
Mid-tillering (32)	qOVC-1a	1	CT158–CT550	2.27	11.7	0.71
	qOVC-2c	2	GA120–GA43	2.29	8.8	0.61
	qOVC-6b	6	CT115–CT506	3.38	12.1	0.72
	qOVC-8	8	BP127A–RZ617	2.54	9.3	0.65
	qOVC-9	9	G103–G93F	2.52	13.4	–0.75
Max. tillering (54)	qOVC-2a	2	G1327–C132	2.38	9.6	0.81
	qOVC-2c	2	GA120–GA43	2.22	8.7	0.71
	qOVC-6b	6	CT115–CT506	6.63	27.3	1.39
Tillering (22–54)	qOVC-6a	6	CT201–RZ450	7.00	25.7	1.24
	qOVC-6b	6	CT115–CT506	7.31	29.6	1.33
	qOVC-9	9	G103–G93F	2.30	12.4	–0.84

[a]Numbers in parentheses indicate days after transplanting.

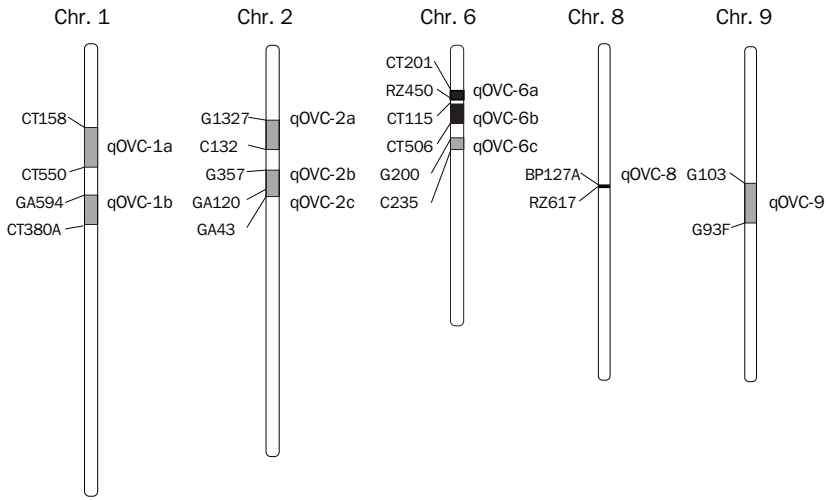

Fig. 9. Location of ovicidal QTLs on rice chromosomes. The markers flanking each QTL are shown to the left of each chromosome.

Japanese japonica rice Asominori has also demonstrated that a dominant ovicidal gene, *OVC*, is located on the short arm of chromosome 6, and R1954 is a target marker for marker-assisted selection (MAS) of the ovicidal gene (Yamasaki et al 1999, 2003).

QTLs for sucking inhibitory resistance

In order to analyze QTLs for sucking inhibitory resistance to WBPH, a new DH population consisting of about 180 lines was established from a cross between the WBPH-resistant japonica CJ-06 and susceptible indica TN1 by the anther culture method (Sogawa et al 2004). Both the sucking inhibitory and ovicidal resistance traits showed approximately 1 (resistant):1 (susceptible) segregations in the DH population.

Sucking inhibitory resistance was evaluated by the amount of honeydew excreted by the female adults of WBPH. Sucking inhibitory resistance is also evaluated by the density of macropterous females of WBPH immigrated and number of eggs deposited by them on each DH line in the paddy fields. WBPH females excreted only 1.7 mg of honeydew per day on J-06 on average, whereas 24.8 mg of honeydew was excreted on TN1. The amount of honeydew excretion varied from 0 to 34.4 mg per day among 109 DH lines tested beyond the parental range. On 53 DH lines (48.6%), WBPH females excreted less than 5 mg of honeydew per day. Those DH lines have sucking inhibitory resistance. There was a close positive correlation ($r = 0.80^{**}$) between the amount of honeydew excretion by WBPH females and field density of WBPH immigrant females in each DH line. Also, a significant positive correlation ($r = 0.72^{**}$) was found between honeydew excretion and egg density (Sogawa et al 2005a).

The most effective QTLs for honeydew excretion (qHND-4), immigrant density (qIMG-4), and number of eggs deposited (qEGN-4) were mapped on the identical CJ-06 segment flanked by the SSR markers RM401 and RM335 on chromosome 4 (Sogawa 2007) (Table 2, Fig. 10). These QTLs accounted for 71.7%, 78.4%, and 58.7% of the respective phenotypic variances, with LOD scores of 15.6, 21.8, and 15.3. This finding indicated that a single gene for sucking inhibition was located at the above QTL region. In addition, four minor QTLs related to sucking inhibitory resistance were mapped on chromosomes 2, 3, and 11.

QTLs for nymphal density and plant damage

Relative density of the first-generation progeny varied widely among the DH lines. The progeny density in the sucking inhibitory lines was significantly lower than in the nonsucking inhibitory lines (Tables 3 and 4). Also, among the nonsucking inhibitory lines, the density was significantly lower in the ovicidal lines than in the nonovicidal ones (Tables 3 and 4). Reproduction of progeny was suppressed primarily by the sucking inhibitory trait, and also by the ovicidal resistance to a lesser extent (Sogawa et al 2005a). Three QTLs related to progeny density were located on chromosomes 4 and 6. The most effective QTL was mapped at the same position of chromosome 4, where the sucking inhibitory gene is localized (Sogawa 2007) (Fig. 10). Another

Table 2. QTLs associated with sucking inhibitory resistance.

Data	QTL	Chromosome	Marker interval	Peak LOD	Variance explained	Additivity
Immigrant density	qIMG-2	2	RM341–RM263	3.07	14.6	–21.4
	qIMG-3	3	RM426–RM520	2.63	16.4	24.5
	qIMG-4	**4**	**RM401–RM335**	**21.76**	**78.4**	**56.1**
	qIMG-11	11	RM209–RM202	3.87	21.5	28.1
Amount of honeydew excreted	qHND-2a	2	RM341–RM263	2.84	30.4	–6.8
	qHND-2b	2	RM318–RM240	2.91	21.3	–8.2
	qHND-3a	3	RM251–RM16	2.61	28.6	6.3
	qHND-3b	3	RM426–RM520	2.40	16.5	7.8
	qHND-4	**4**	**RM401–RM335**	**15.56**	**71.7**	**15.0**
No. of eggs deposited	qEGN-2	2	RM341–RM263	2.53	45.1	–51.5
	qEGN-3a	3	RM251–RM16	2.81	26.4	35.5
	qEGN-3b	3	RM426–RM520	3.42	18.4	34.9
	qEGN-4	**4**	**RM401–RM335**	**15.34**	**58.7**	**66.8**

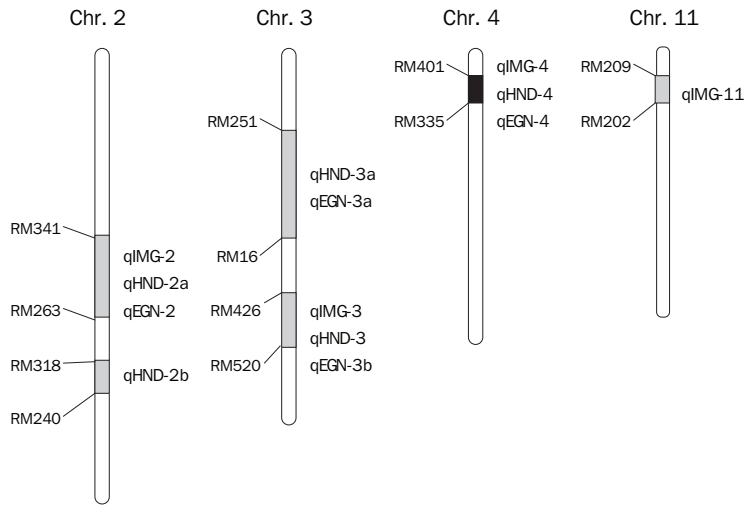

Fig. 10. Location of sucking inhibitory QTLs on rice chromosomes. The markers flanking each QTL are shown to the left of each chromosome.

QTL was found at the region near the ovicidal QTL on chromosome 6 (Fig. 9). These QTLs indicate that low nymphal density is strongly attributed to sucking inhibitory and ovicidal resistance to WBPH.

Of 151 DH lines tested, 65 lines (43.0%) did not suffer any visible damage by WBPH infestation, which all belonged to the sucking inhibitory lines. Five DH lines (3.3%) were completely killed by the heavy density of WBPH populations, which were all nonsucking inhibitory DH lines. This evidence indicated that final plant damage is also primarily influenced by the sucking inhibitory trait (Table 5). Two QTLs for

Table 3. Relative densities of immigrants and progeny in CJ-11/TN1 DH lines with different phenotypes of WBPH resistance in 2003.

Phenotype[a]	No. of lines	Immigrant	G1 progeny
R/R	36	1.2 ± 0.7 a	66 ± 87 a
R/S	43	1.1 ± 0.1 a	126 ± 55 a
S/R	41	6.5 ± 0.3 b	408 ± 45 b
S/S	31	6.7 ± 0.4 b	827 ± 95 c
CJ-11		0.3	7
TN1		5.6	681

[a]Phenotype: R/R = sucking inhibitory/ovicidal; R/S = sucking inhibitory/nonovicidal; S/R = nonsucking inhibitory/ovicidal; S/S = nonsucking inhibitory/nonovicidal. Immigrant: density of macropterous females per hill. G1 progeny: number of first-generation progeny (nymphs and adults) tapped down into a tray (29 cm × 41 cm) from 2 hills. In each column, means followed by the same letter are not significantly different in the Kruskal-Wallis test.

Table 4. Relative densities of immigrants and progeny in CJ-11/TN1 DH lines with different phenotypes of WBPH resistance in 2004.

Phenotype	No. of lines	Immigrant	G1 progeny	B female	G2 progeny
R/R	19	0.5 ± 0.4 a	17 ± 13 a	0.2 ± 0.2 a	8 ± 8 a
R/S	42	0.7 ± 0.5 a	21 ± 15 a	0.2 ± 0.2 a	11 ± 12 a
S/R	18	1.7 ± 0.6 b	31 ± 15 a	0.7 ± 0.6 b	16 ± 21 a
S/S	20	1.8 ± 0.8 b	69 ± 31 b	0.7 ± 0.6 b	33 ± 19 b
CJ-11		0.2	21	0	2
TN1		0.2	165	1.4	124

Phenotype: same as Table 3. Immigrant: same as Table 3. B female: density of brachypterous adult females per hill, which emerged from the G1 progeny. G1 and G2 progeny: number of first- and second-generation progeny sampled by tapping method. In each column, means followed by the same letter are not significantly different in the Kruskal-Wallis test.

Table 5. Scores of plant damage caused by WBPH infestation in CJ-11/TN1 DH lines with different resistance phenotypes.

Phenotype[a]	No. of lines	Damage score					Mean ± SD
		0	1	2	3	4	
R/R	31	22	9	0	0	0	0.29 ± 0.45 a
R/S	49	33	15	1	0	0	0.35 ± 0.51 a
S/R	35	8	14	8	4	1	1.31 ± 1.04 b
S/S	36	2	11	15	4	4	1.92 ± 1.04 b
Total	151	65	49	24	8	5	

[a]Phenotype: same as Table 3. Damage score: 0 = no damage; 1 = only lower leaves died; 2 = lower half of plant died; 3 = three-fourths of plant died; 4 = whole plant died. In each column, means followed by the same letter are not significantly different in the Kruskal-Wallis test.

plant damage were found on chromosomes 3 and 4. These loci were also involved in the QTLs associated with the sucking inhibitory trait. This QTL analysis showed that the major QTLs for nymphal density and damage intensity were all mapped at the identical locus where the putative sucking inhibitory gene is located. This indicates that the sucking inhibitory trait plays a major role in WBPH resistance in the CJ0-06/TN1 DH population.

Differential expressions of WBPH resistance in the field and SSST

Sucking inhibitory resistance to WBPH in CJ-06/TN1 DH lines was evaluated comparatively through a field experiment based on WBPH immigrant density and the SSST (Sogawa et al 2005b). All the susceptible lines in the field evaluation were susceptible in the SSST as well. However, 35 of the resistant 66 lines (53%) in the field were categorized in the susceptible groups in the SSST. Likewise, there were no significant differences in WBPH immigrant density between the DH lines that were highly resistant and susceptible in the SSST. These results revealed that the SSST could not properly evaluate WBPH resistance in the DH lines. Four QTLs for WBPH resistance phenotyped by immigrant density were detected on chromosomes 2, 3, 4, and 11. Of these, the QTL on chromosome 4 was the most effective as mentioned in the previous section. On the other hand, five QTLs associated with seedling mortality were mapped on chromosomes 2, 3, 4, 5, and 6. In addition to a major QTL on chromosome 4 (LOD 10.5, variance 68%), there was another major QTL located on chromosome 5 (LOD 12.1, variance 78%), which was an SSST-specific artifact, and entirely independent of the WBPH ecology and rice plant interactions in the field. Needless to say, the ovicidal resistance to WBPH in the DH lines cannot be evaluated by the SSST.

Molecular markers and QTL mapping offer more efficient approaches to analyze and use complex genetic traits for insect resistance in crop plants (Yencho et al 2000, Tao et al 2003). The QTL-based approach requires not only a well-saturated molecular marker map and appropriate recombinant inbred host-plant populations but also ecologically significant phenotyping procedures. The QTLs for each ecological trait would improve our understanding about the genetic basis and ecological mechanisms for insect resistance in crop plants. For this purpose, phenotyping is a prerequisite for meaningful QTL analysis for varietal resistance to insect pests in crop plants.

The SSST is a widely accepted procedure to evaluate genetic resistance to rice planthoppers in rice germplasm. However, in the SSST, the actual ecological and agricultural interactions between planthoppers and rice plants are virtually neglected. The SSST is based only on the immediate sucking damage to young rice seedlings infested artificially with newly hatched planthopper nymphs in the seedbox. Such a rice plant and planthopper interaction do not exist in paddy fields. Therefore, the QTLs detected by the SSST do not give any information about mechanisms for WBPH resistance and host-plant traits associated.

QTL-based analyses of host-plant traits for WBPH resistance should be performed based on the ecological interactions between planthopper populations and rice plants in a given agricultural context. In order to set up meaningful phenotyping tests, proper combinations among the morph and stage of WBPH, growth stage of rice plants, and trait or response to be measured are crucial. QTL mapping for critical planthopper and host-plant performance at each key stage in the insect and host-plant interactions in the field gave us very practical information about the mechanism of field resistance in rice plants. Successful gene-tagging for major resistance QTLs will promote MAS approaches to breed more IPM-compatible rice varieties with WBPH resistance (Yencho et al 2000).

Performance of WBPH resistance in CJ-06 in paddy ecosystems

The sucking inhibitory resistance in CJ-06 disrupts population establishment by WBPH in paddy fields at the first step of host-plant selection by macropterous WBPH immigrants (Tables 3 and 4). Low density of the initial immigrants is strongly attributed to the subsequent low density of the WBPH population and limited infestation to CJ-06. In addition, WBPH population growth is further suppressed in CJ-06 by ovicidal resistance, by which WBPH eggs suffer high mortality at the oviposition sites. These dual mechanisms of varietal resistance in CJ-06 could give this Chinese japonica rice a durable resistance to WBPH.

Japonica rice in East Asia has been exposed to massive migrations of rice planthoppers by Asian monsoon every year. Particularly, newly transplanted rice plants are directly infested with WBPH immigrants, whose density is much higher than that of BPH. The ovicidal resistance in japonica rice is not so distinct as sucking inhibitory resistance, but it is efficient enough to suppress the population densities of WBPH progeny within the ranges that the host plants have for coping with insect infestations by their compensatory vegetative growth. The ovicidal response in japonica rice is a necessary alternative defense mechanism against WBPH in newly transplanted

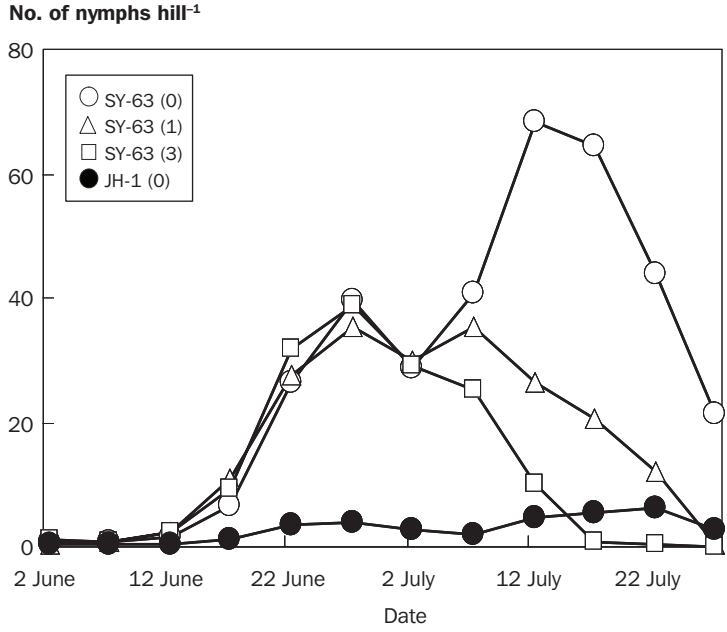

Fig. 11. Population trends of WBPH on JH-1 and SY-63 in Xiushan (2002). Values in parentheses indicate times of insecticide (imidacloprid) spray. Imidacloprid was sprayed on 2 July (single-spray plots), 11 July, and 2 August (3-spray plots). Imidacloprid is usually sprayed mixed with organophosphorus insecticides such as triazophos.

paddy fields, where the natural enemy fauna are not yet recruited enough to control WBPH immigrants. It is also known that the ovicidal trait in japonica rice affects BPH eggs, and possibly newly hatched stem borers as well. Such moderate and horizontal resistance due to the ovicidal trait in CJ-06 could be an efficient insurance to prevent the breakdown of species-specific monogenic sucking inhibitory resistance to WBPH by preventing the occurrence of WBPH biotypes. In exploring genetic considerations in the use of insect-resistant germplasm, we should focus on the problem of maximizing the durability of insect resistance by minimizing selection for virulent biotypes (Kennedy et al 1987). There has been no evidence of a breakdown in ovicidal resistance to WBPH in japonica rice so far. However, selection experiments indicated that WBPH has abilities to defeat possible sucking inhibitory resistance in indica rice, which is conferred by *Wbph 2* and *Wbph 5* genes (IRRI 1980, Shen et al 2003a,b). Also, it has been known that most of the rice varieties with *Wbph 1* genes for WBPH resistance are not resistant to the WBPH populations in India (IRRI 1978).

Our on-farm experiments demonstrated that the WBPH-resistant improved japonica rice Jinhua-1 (JH-1), which has the same genetic background for WBPH resistance as CJ-06, could stop the use of insecticides for controlling WBPH in a WBPH epidemic hybrid rice area (Fig. 11). In addition, the insecticide-free cultivation

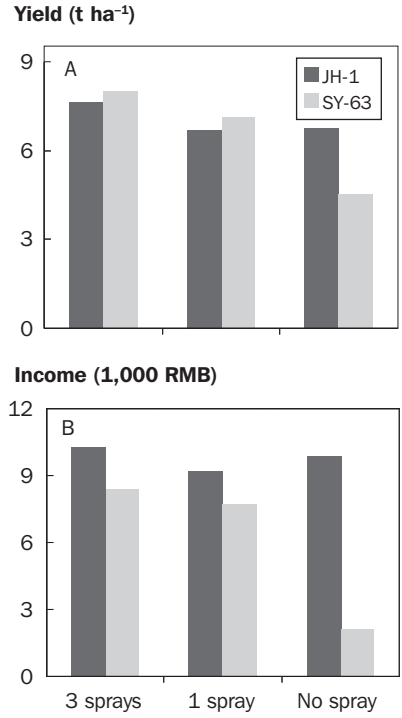

Fig. 12. Average rice yield (A) and income (B) from JH-1 and SY-63 planted under different numbers of insecticide (imidacloprid) sprays in Xiushan in 2003.

of the WBPH-resistant JH-1 was more profitable than the insecticide-dependent high-yielding cultivation of hybrid rice SY-63 (Liu et al 2003, 2006) (Fig. 12). Thus, WBPH-resistant japonica rice is an ecologically sound and economically profitable IPM component in WBPH epidemic japonica rice areas.

Conclusions

Because of rice monophagy, the pest status of WBPH is directly influenced by the quality of rice varieties and environmental conditions of paddy fields. Because of *r*-strategic biology, mismanagement of paddy ecosystems appears in the form of epidemics of WBPH. Highly susceptible and tolerant Chinese hybrid rice has offered WBPH more favorable nutrient resources and breeding habitats than inbred rice, which has led to an unusual upsurge of WBPH population density. Insecticide applications to protect insect-susceptible hybrid rice could further encourage WBPH epidemics by the destruction of bio-control agents in paddy ecosystems. We should not forget

the history of the BPH menace induced by insecticides, which were disseminated to rice farmers with high-yielding rice seeds as a packaged technology for the rice Green Revolution. A case study with a leading Chinese hybrid rice, Shanyou 63, shows that the improvement of hypersusceptibility to WBPH in the WA-CMS line is more necessary than the incorporation of a WBPH resistance gene to the restorer line.

Genetic resistance to WBPH in japonica rice germplasm was first discovered in a Chinese japonica rice, Chunjiang 06 (CJ-06). The WBPH resistance in CJ-06 is conferred by the dual modalities of resistance, namely, antixenosis due to sucking inhibition and antibiosis due to ovicidal response. Of these, ovicidal response, which is induced by WBPH oviposition, is restricted to japonica rice. The ovicidal trait cannot be evaluated by such a mechanistic evaluation method as the standardized seedbox screening test (SSST), which has exclusively been used to breed the rice planthopper-resistant HYVs. The occurrence of SSST-susceptible ovicidal resistance suggests the practical importance of evaluating insect resistance in rice based on the actual ecological interactions between the insect and rice plant in paddy ecosystems. QTL-based analyses based on ecological host-plant interactions will provide useful information about efficient genetic traits, which render ecologically appropriate resistance or defense mechanisms to host plants, and the recent development of molecular marker technology enables us to use such field resistance to insect pests through MAS approaches.

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Mechanisms of resistance: a major gap in understanding planthopper-rice interactions

Finbarr Horgan

Host-plant resistance (HPR) has been a valuable tool in the management of planthoppers. However, experience with the brown planthopper, *Nilaparvata lugens* (Stål), indicates that field resistance is limited because planthoppers can quickly overcome resistance genes. As new approaches to improving the durability of resistant rice varieties are being developed, there is a need to better predict the outcomes of gene deployment in terms of planthopper virulence responses. However, as this paper points out, major gaps still exist in our understanding of resistance mechanisms and of how these mechanisms relate to identified resistance genes. These knowledge gaps will hinder the future success of resistance breeding strategies and varietal deployment. Using the brown planthopper as an example, this paper reviews planthopper-HPR research since the 1970s, links available information on brown planthopper–rice interactions, and calls for increased attention to hypothesis-based research that will improve our capacity to manage field resistance and planthopper virulence.

Knowledge is essential for the efficient management of natural and derived ecosystems. To best predict the outcome of agricultural interventions, this knowledge should be based on an understanding of the processes underlying ecological patterns (Romesburg 1981). In the absence of manipulative experimentation, management predictions are based only on sets of observations that are directly related, but never tested, or perceived to be related, but the relations are indirect or there is no relation at all (Romesburg 1981). As knowledge is accumulated, information usually shifts from observations of patterns (descriptive studies) to an understanding of processes (manipulative studies with hypothetical-deductive (HD)-hypothesis testing) (Romesburg 1981). This paper suggests that our current understanding of interactions between planthoppers and the rice plant is largely based on descriptive studies. However, to improve planthopper management through host-plant resistance, increased attention should focus on the processes underlying resistance and on planthopper adaptations to resistant varieties.

Nearly 50 years of research has produced a considerable body of information on planthopper-rice interactions, including extensive information on levels of host-plant

resistance in rice (Kaneda et al 1981, Jung-Tsung et al 1986, Khush and Virk 2005), planthopper population and behavioral responses to resistant varieties (Padgham 1983, Velusamy and Heinrichs 1986, Padgham and Woodhead 1988, Kimmins 1989, Bing et al 2007), and, particularly in recent years, the genes associated with observed resistance (Yamasaki et al 2000, Huang et al 2001, Kawaguchi et al 2001, Murata et al 2001, Yang et al 2002, Jairin et al 2007). This research has had a major impact on rice production with the deployment of planthopper-resistant rice varieties throughout South and Southeast Asia (Khush and Virk 2005). However, despite the continued interest in rice resistance, successful management of planthoppers has been limited and recent major outbreaks have occurred in parts of India, Bangladesh, Thailand, Vietnam, China, and the Philippines (personal communications between national agricultural research institutes and IRRI).

Using resistance to brown planthopper (BPH) (*Nilaparvata lugens* Stål) as an example, this paper highlights major gaps in our understanding of planthopper-rice interactions. It suggests that our understanding of the functioning of resistance genes has been hindered by a lack of manipulative experimentation during the elucidation of mechanisms, and therefore that the effective deployment of resistance genes, the management of planthoppers, and the management of the viruses they transmit are limited by knowledge constraints. This paper suggests that reductionist experimentation, particularly during the screening of breeding materials and lines, has restricted our understanding of resistance to planthopper feeding responses and has therefore led to an overemphasis on nutrient-based and anti-feeding resistance mechanisms. Finally, a change in research direction is proposed to increase the future efficiency of varietal development for resistance, and to improve gene deployment at regional and farm levels.

A brief history of planthopper-rice research

Research into planthoppers increased dramatically in the early 1970s when Asian farmers began to experience extensive and sustained BPH outbreaks caused, largely, by an overuse of insecticides (Heinrichs 1994, Gallagher et al 1994). The scale of the problem during the 1970s is indicated by the rapid increase in scientific output at that time (Fig. 1). By 1973, the first resistant rice variety, IR26, was released in Asia. IR26 contained the dominant *Bph1* gene for resistance that became associated with initial dramatic declines in BPH populations. However, within 2 years, *Bph1* had "broken down" and planthopper densities began to increase again. In 1976, scientists responded with the release of IR36 and other varieties that contained the recessive *bph2* resistance gene. However, in the late 1980s and early 1990s, *bph2* also began to break down. IR56 and other varieties containing the *Bph3* resistance gene have been deployed since 1982 but these have also broken down in many regions (Gallagher et al 1994).

Studies into host-plant resistance have continued as a major focus of research on planthoppers, albeit with a lull in research output during the 1990s. Many early studies examined insect behavioral responses using electrical penetration graph (EPG)

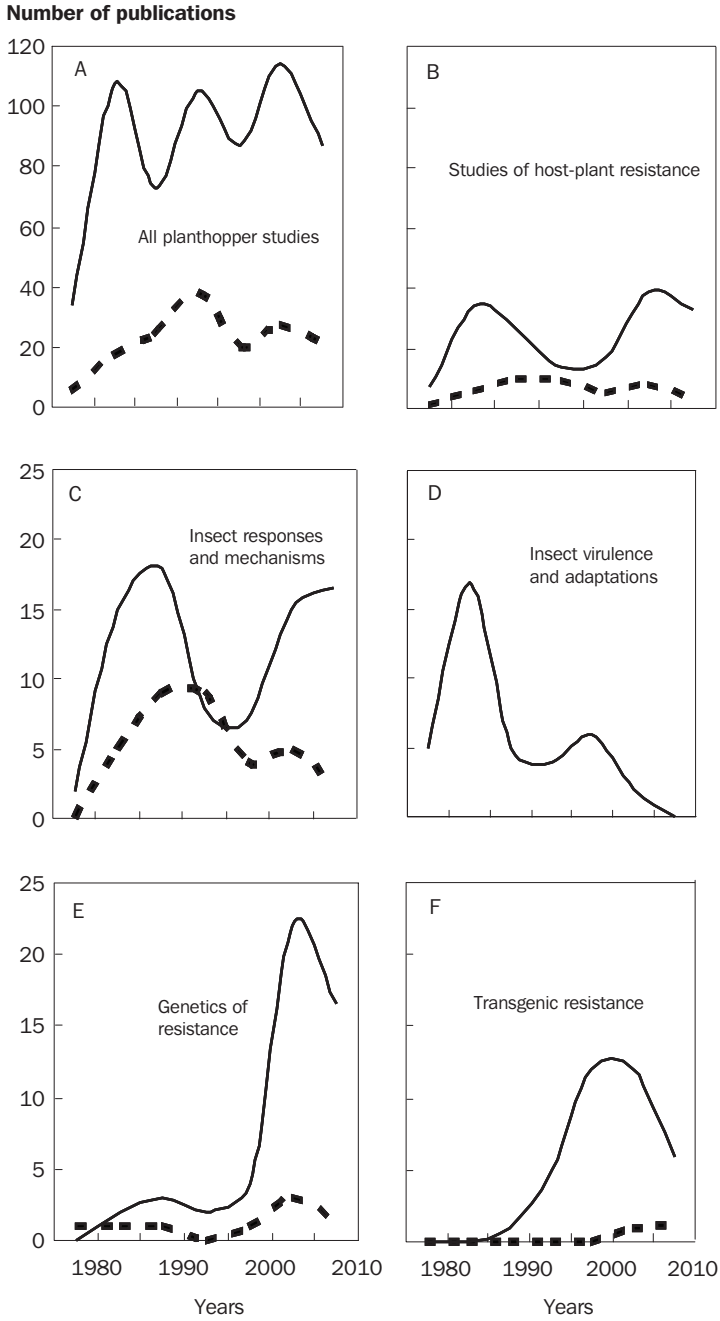

Fig. 1. Papers published on planthoppers (BPH [solid line] and WBPH [broken line]) between 1974 and 2008 as cited on ISI-Web of Knowledge (searches = *Nilaparvata lugens* or brown planthopper and *Sogatella furcifera* or white-backed planthopper). (A) All hopper papers, (B) papers concerning rice varietal resistance, (C) papers that quantified insect responses to resistant rice varieties and investigated resistance mechanisms (including induced mechanisms), (D) papers concerning "biotypes" or otherwise investigating insect selection on resistant rice varieties, (E) papers that employed genetic techniques or investigated the genetics behind constitutive resistance to hoppers, and (F) papers that investigated hopper responses to transgenic rice with genes for hopper damage reduction. Graphs on the same row have the same y-axes.

technology and measured fitness losses incurred on resistant varieties (Velusamy and Heinrichs 1986, Padgham and Woodhead 1988, Kimmins 1989). Furthermore, because of the increasing virulence of BPH populations against the *Bph1*, *bph2*, and *Bph3* genes, studies of "biotype" responses were a prevalent feature in the 1970s and 1980s; however, an inability to adequately define biotypes or to apply the biotype concept (Heinrichs 1994) may have led to an almost complete neglect of virulence issues in the past 10 to 15 years (Fig. 1). Advances in molecular techniques since the mid-1990s have led to an increase in our understanding of resistance and the identification of about 21 (some tentative) genes and various quantitative trait loci (QTLs) linked to resistance in established varieties and wild rice species (Yamasaki et al 2000, Huang et al 2001, Khush and Virk 2005, Myint et al 2009). Biotechnological advances have also led to an increased interest in engineered resistance (Tang et al 2001a,b, Saha et al 2006).

Overall, research since the 1970s has produced a number of resistant varieties, some with known resistance genes, and a clear indication of planthopper responses to some modern resistant and differential varieties (i.e., varieties [often landraces or traditional] generally possessing known resistance genes). However, there has been a relatively minor gain in the understanding of resistance mechanisms such that, to date, there is still no clear mechanistic link between major resistance genes and observed planthopper behavioral or fitness responses. Nevertheless, QTLs have been identified and linked to the ovicidal response (see Sogawa et al, this volume, and below) and a suite of genes has been linked to induced defenses (Wang et al 2004, Yang et al 2006, Hao et al 2008).

Planthopper responses to resistant varieties

Reductionist experimentation is essential in understanding plant-insect interactions. However, experiments and bioassays should be set in a holistic framework that incorporates plant and insect phenologies and adequately accounts for adaptation and genetic diversity in target organisms. Figure 2 is a schematic diagram of the planthopper life-behavior cycle broken down into key "behaviors" (or activities)—indicated by rectangles—(dispersal, feeding, probing, etc.) and major "behavior options"—indicated by diamonds. Behaviors are depicted as simple motor responses elicited through sensory evaluation of environmental cues. Options, which lead to specific behaviors, are influenced by plant volatiles, secondary chemicals, chemical taste, wax composition, and/or other plant characteristics, and are determined by the physiological state of the insect. In reductionist experimentation, observed behaviors can sometimes be determined by insect physiological drive alone. For example, in no-choice trials, Zaheruddeen and Prakasa Rao (1988) found BPH to oviposit on 72 host plants, including common weeds, wild rice species, and crops (wheat [*Triticum aestivum* L.], oats [*Avena sativa* L.], and barnyard millet [*Echinochloa frumentacea* (Roxb.) L.]); however, BPH, a monophagous insect, is unlikely to oviposit on most of these plants when not confined or when given a host-plant choice (i.e., Nagata and Hayakawa 1998, Hattori 2001).

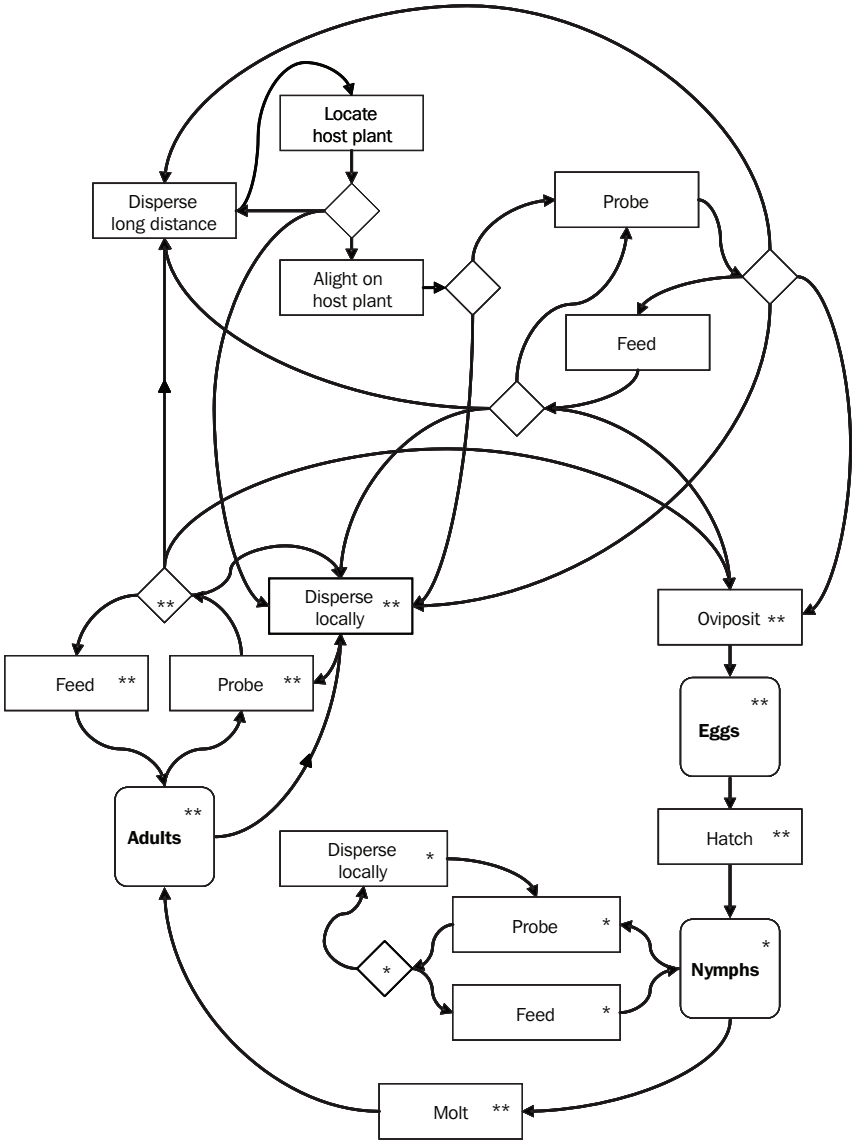

Fig. 2. Schematic depiction of the planthopper life-behavior cycle. The cycle indicates the three major life-history stages (bold squares) and their associated behavioral interactions with the rice plant (rectangles). Diamonds indicate key behavior options that are governed by internal (insect physiological) and external cues (plant kairomones, volatiles, etc.). A single asterisk indicates life-behavior entities incorporated into the SSST and MSST; a double asterisk indicates entities incorporated into the MSST alone. Field testing in hotspots can encompass the entire cycle.

Current knowledge of planthopper-rice interactions has been heavily influenced by the prevalence of a single reductionist screening method, the standard seedbox screening test (SSST), that continues to be widely used in the development of resistant varieties (personal communications between national agricultural research institutes and IRRI). In the SSST, seeds of each cultivar (usually >15 cultivars per test) are sown in a single row in a seedbox of about 60 × 40 × 10 cm. Suitable susceptible and resistant checks are sown in similar rows in the same box. Seven days after sowing, seedlings are thinned to about 20 plants per row and infested with about eight second-instar nymphs per seedling. 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). Different rice-breeding centers and laboratories sometimes vary minor details of the protocol (Kaneda et al 1981).

A second method, the modified seedbox screening test (MSST), was designed to overcome certain inconsistencies in the SSST and better detect "field resistance," that is, when resistance is maintained or increases as plants age. In the MSST, seeds are sown and thinned as in the SSST, but infested at 20 days after sowing with four second-instar nymphs per plant. Plants are evaluated at the time that susceptible checks are killed, using the same scale as in the SSST. With the MSST, usually mortality of the susceptible check is caused by F_1 BPH, that is, the original nymphs mature and reproduce in the seedbox, and their offspring kill the plants (Velusamy et al 1986). Although the MSST is an improvement on the SSST, because of its higher cost and longer turnover time, it is seldom used in bulk screening (personal communications between national agricultural research institutes and IRRI).

These two methods have been extremely useful for rapid, high-throughput, and inexpensive screening of the necessarily large amounts of material required to find and isolate resistance genes. Furthermore, they incorporate "choice," that is, the target insects can choose between a variety of options before initiating feeding (SSST and MSST) or oviposition (MSST) responses. However, as Figure 2 indicates, the SSST, the most widely used screening method, is only capable of evaluating nymphal feeding responses to the test plants. 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 (Fig. 2). When cultivars have different levels of resistance, nymphs will disperse between plants, the degree of movement (activity) being negatively correlated with feeding. Movement between plants is assumed to simulate field responses; however, it is largely governed by push-pull dynamics in the experimental arena, the strength of which is determined by the idiosyncrasies, combinations, and relative positions of the cultivars under testing, and is therefore unstable between successive tests. As Figure 2 indicates, four key behavior options that determine levels of field infestation are never considered when using the SSST or MSST. These are (1) the option to alight on a host plant after the host plant has been located, (2) the option to probe or disperse locally (within or between plants) on a host plant after alighting, (3) the option to disperse (long or short distances) or feed following probing (and possibly also to oviposit), and (4) the option to disperse

(long or short distances) or oviposit following feeding. Only field trials are capable of evaluating these responses.

Field screening of cultivars in BPH hotspots may include all aspects of the BPH life-behavior cycle; however, field studies are subject to varying planthopper densities at a series of nested scales. Published results from field screening studies are rare. Ōya and Fukamachi (1987) examined planthopper settlement on rice varieties (14 to 40 days after transplanting) in the field in Japan. They found that immigrant adult females alighted equally on plots of resistant and susceptible cultivars; however, the planthoppers did not stay on the resistant cultivars for more than 1 or 2 days; therefore, immigrants were stimulated to disperse from resistant cultivars, but the stimuli to settle on rice were similar among susceptible and resistant cultivars. Although the resistance mechanisms were likely related to anti-feeding, the prevalence of the SSST suggests that the resistant varieties used in these field trials were selected and developed precisely because of their anti-feeding effects. Therefore, prescreening and cultivar selection using the SSST may cause an overall bias toward feeding-related mechanisms even in field trials, further restricting our understanding of the available resistance mechanisms inherent to rice.

During the 1980s and early 1990s, a large number of studies were conducted to examine the responses of planthoppers to resistant rice varieties and to explain patterns emerging from SSSTs (Fig. 3). Differential varieties such as IR46 and Mudgo, which contain the *Bph1* gene, ASD7 with the *bph2* gene, IR62 and Rathu Heenati with the *Bph3* gene, and Babawee with the *bph4* gene were a prominent feature in these studies; however, aspects of planthopper response have been published for more than 100 resistant varieties or wild rice accessions (see references in Figs. 3 and 4). Perhaps unsurprisingly, because of the prevalence of the SSST in developing resistant varieties and because of converging experimental protocols (i.e., plants < 35 days old, planthoppers at a nymphal stage, and one variety, usually TN1, used both to rear planthoppers and as a susceptible check during experimentation), all planthopper responses can be related either directly or indirectly to nymphal feeding behavior (Fig. 3). Although the planthopper responses can be linked to specific genes by assessing behavior on differential varieties, they are for the most part general responses to resistance for which the underlying mechanisms are still largely unknown. Little attention has been given to any other types of host-plant-elicited behavioral responses that might determine susceptibility or resistance in the field. For example, there is no documented evidence to indicate that fit females (i.e., those unaffected by a poor diet) will avoid settling or reduce oviposition on resistant plants in the field. Such considerations are useful because viral transmission may occur during planthopper probing (Cabauatan et al, this volume), but is effectively avoided if planthoppers are deterred from settling on the plants. The logistics of determining field responses or developing resistant varieties with novel resistance mechanisms (i.e., not related to postprobing avoidance) are obviously considerable. What is important to note here is that, through our methodology, such mechanisms are rarely detected and have not been generally incorporated into resistant varieties.

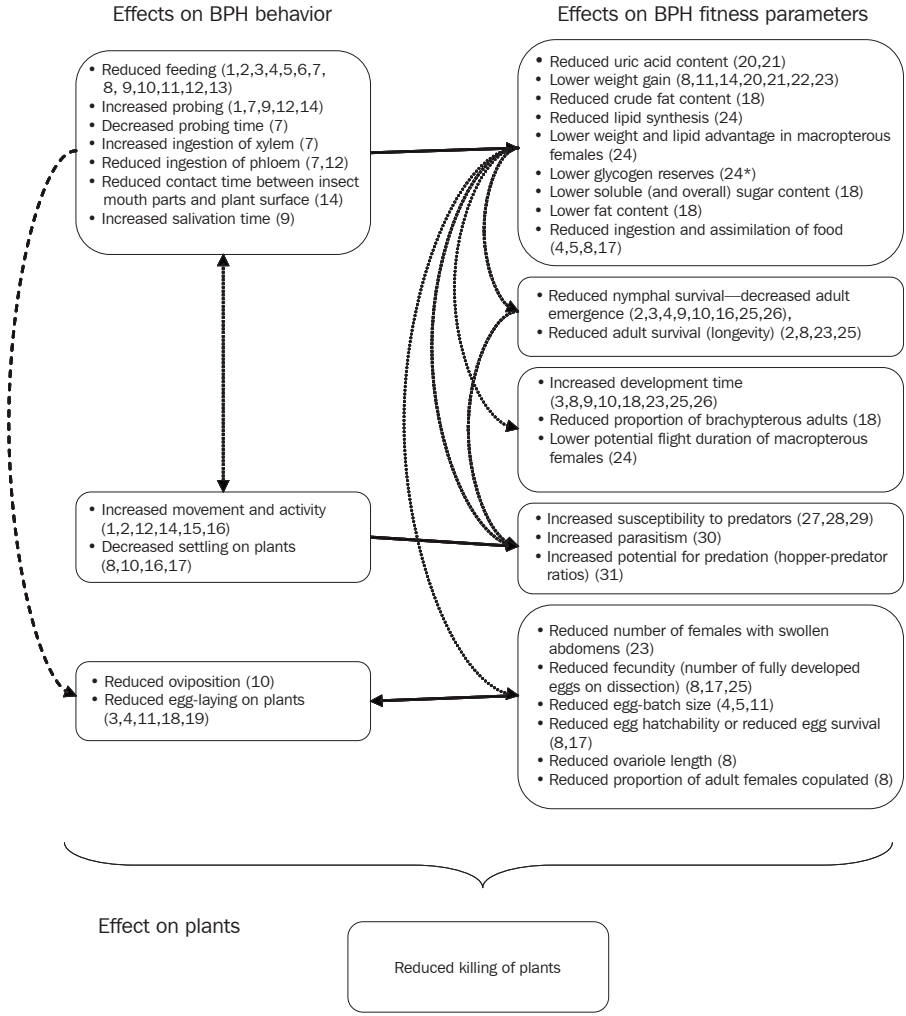

Fig. 3. Effects of resistant rice varieties on BPH behavior and fitness parameters. Note that feeding effects can be linked to all behavior and parameters (associated arrows). Numbers indicate examples as follows: 1—Padgham and Woodhead (1988); 2—Saxena and Okech (1985); 3—Cohen et al (1997); 4—Bing et al (2007); 5—Hattori (2001); 6—Shigematsu et al (1982); 7—Kimmins (1989); 8—Jung-Tsung et al (1986); 9—Velusamy and Heinrichs (1986); 10—Senguttuvan et al (1991); 11—Baqui and Kershaw (1993); 12—Hao et al (2008); 13—Velusamy et al (1986); 14—IRRI (1985); 15—Woodhead and Padgham (1988); 16—Velusamy et al (1990); 17—Velusamy (1988); 18—Yin et al (2008); 19—Zaheruddeen and Prakasa Rao (1988); 20—Hongoh and Ishikawa (1997); 21—Sasaki et al (1996); 22—Stevenson et al (1996); 23—Myint et al (2009); 24—Padgham (1983); 25—Cheng et al (2001); 26—Pathak and Kalode (1980a); 27—Kartohardjono and Heinrichs (1984); 28—Rapusas et al (1996); 29—Senguttuvan and Gopalan (1990); 30—Wang et al (2008 a); 31—Heinrichs et al (1986). Asterisk indicates that no difference was observed.

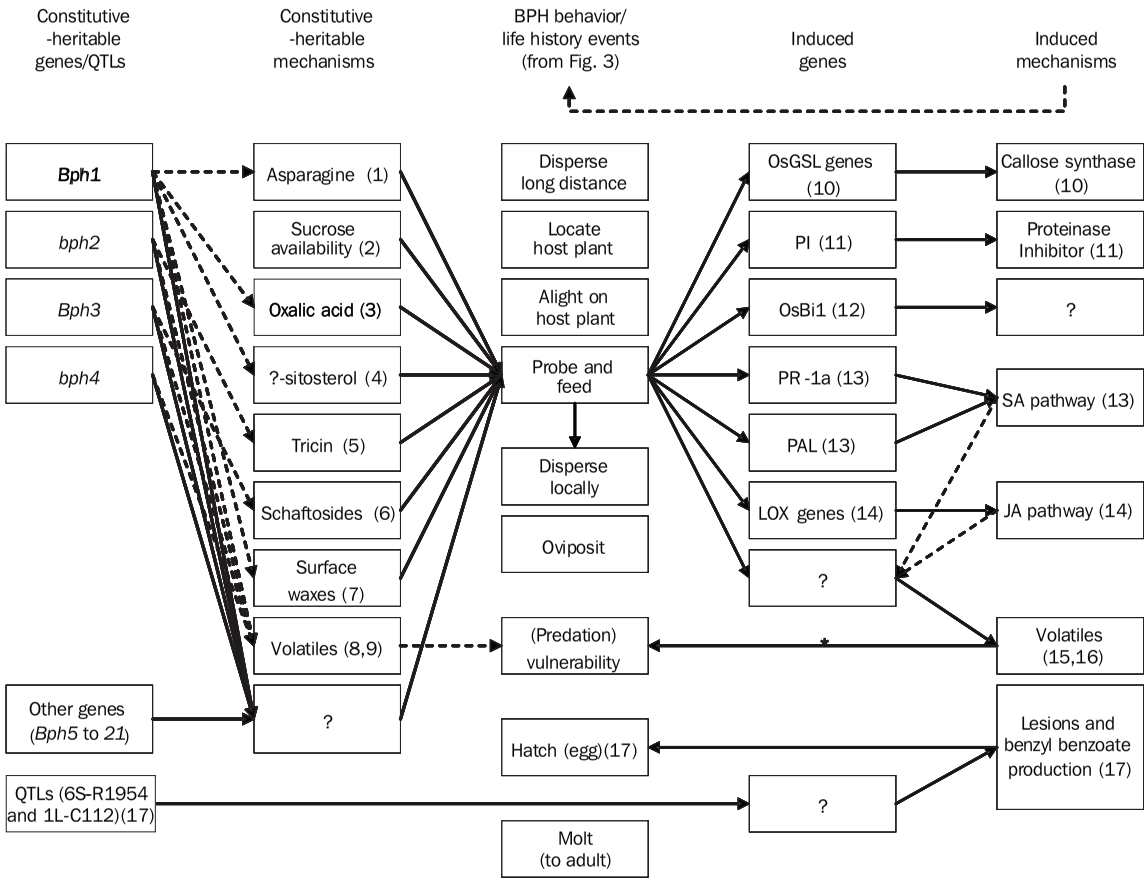

Fig. 4. Current information on mechanisms of resistance to BPH in rice, indicating relations between known genes, resistance mechanisms, insect responses, and induced responses. Solid arrows indicate reliable evidence for proposed links, broken arrows indicate links suggested through indirect evidence. Asterisk indicates a general effect occurring in susceptible and resistant rice. Numbers indicate sources as follows: 1—Sagawa and Pathak (1970); 2—Jung and Im (2007); 3—Yoshihara et al (1980); 4—Shigematsu et al (1982); 5—Bing et al (2007); 6—Stevenson et al (1996); 7—Woodhead and Padgham (1988); 8—Saxena and Okech (1985); 9—Velusamy et al (1990); 10—Hao et al (2008); 11—Weng et al (2003); 12—Wang et al (2004); 13—Xu et al (2003); 14—Wang et al (2008b); 15—Rapusas et al (1996); 16—Luo et al (2006); 17—Yamasaki et al (2000).

Manipulative experiments are required to test hypotheses concerning resistance mechanisms. This is because mechanisms are processes and therefore cannot be determined by simple descriptive studies (Romesburg 1981). However, in spite of this requirement, few studies have ever manipulated aspects of planthoppers or rice plants to gain an understanding of their interactions (but, see Saxena and Okech 1985, Shigematsu et al 1982, Woodhead and Padgham 1988, Stevenson et al 1996). Nevertheless, the small number of studies that have conducted manipulative experiments have given concrete evidence of some of the mechanisms behind heritable defenses (Fig. 4). These mechanisms can be grouped as (1) diet-related, (2) volatile or (secondary) chemical related, and (3) related to plant-surface characteristics.

Diet-related mechanisms

The ability to manipulate sugar concentrations and amino acid levels in artificial planthopper diets has helped determine possible diet effects on planthopper behavior and fitness. Feeding by planthoppers on susceptible rice varieties reduces stored sugar content (Loka Reddy et al 2004). Planthoppers require this sucrose for successful development and, on artificial diets, have maximum survival and moderate nymphal development times when fed 25% sucrose solution. Glucose, fructose, and maltose can also function as nutrients in the presence of sucrose (Koyama 1985). On examining the nutritional components of resistance in the Korean variety Cheongcheongbyeo, Jung and Im (2005) found that phloem of this resistant variety had sugar contents similar to those of the susceptible variety Taebaegbyeo; however, the amounts ingested and excreted were different between the varieties, with significantly less occurring in planthopper excretia from the resistant variety. This suggests that anti-feedants acted on insect taste sensilla, or that secondary chemicals disturbed the digestive or feeding processes of the insect, but that the resistant variety Cheongcheongbyeo was otherwise nutritionally adequate for planthopper feeding (Jung and Im 2005).

As early as the 1970s, the amino acid asparagine was noted to have a stimulatory effect on brown planthopper feeding (Sogawa and Pathak 1970). On artificial diets, the lack of single amino acids does not cause planthopper mortality; however, the loss of each of three sulfur-containing amino acids (cysteine, histidine, and methionine) increased nymphal development time and reduced survival; furthermore, the lack of all three sulfur-containing amino acids caused mortality of first instars (Koyama 1986). BPH survival and longevity increase when amino acids are combined with sucrose (5%) (Pathak and Kalode 1980a). In preference tests, asparagine, arginine, leucine, and valine strongly enhanced planthopper feeding on sucrose (5%). Vitamins also improved planthopper survival and enhanced settling (Pathak and Kalode 1980a).

Mechanisms involving volatiles and secondary chemicals

Saxena and Okech (1985) extracted rice plant volatiles as steam distillates from a range of susceptible (TN1) and resistant (Mudgo, ASD7, Rathu-Heenati, Babawee, Ptb33, and ARC6650) rice varieties. In a series of experiments in which distillates

were applied to the susceptible TN1, mixed with sugar solutions or topically applied to nymphs, they found steam distillate from resistant varieties to significantly decrease female settling and feeding activity, while it increased the mortality of adults and nymphs. Velusamy et al (1990) produced similar effects when they applied steam distillates (at 1,000 ppm and above) of *Oryza officinalis* in similar experiments. Using column chromatography, Bing et al (2007) isolated the flavonoid 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone (tricin) from IR36 (with the *bph2* gene). In experiments, successive levels of tricin reduced feeding by nymphs and reduced the numbers maturing to adults on an artificial diet; furthermore, tricin reduced feeding and egg-laying by adults on tricin-treated versus tricin-untreated rice seedlings. Unfortunately, in their experiments, neither Velusamy et al (1990) nor Bing et al (2007) presented results from controls, that is, volatiles (steam distillates) or solvent fractions (containing secondary compounds) from susceptible materials. Feeding inhibitors can occur in susceptible varieties: for example, silicic acid, which inhibits BPH sucking, is a "general inhibitor" that is found in the parenchyma of both susceptible and resistant rice plants (Yoshihara et al 1979).

Toxic secondary chemicals also play a role in resistance. For example, when BPH feeds on the resistant Chinese variety B5 (containing *Bph14* and *Bph15* genes), a gene (*Y342*) encoding for P450 is activated. In insects, P450s metabolize hormones and pheromones, but they are best known for their role in the metabolism of insecticides and host-plant chemicals (Yang et al 2006); however, it is unknown whether the specific toxic chemicals involved in B5 resistance are constitutive or induced. Oxalic acid in Mudgo (*Bph1*) inhibits BPH sucking in parafilm bioassays; however, there is still no evidence to indicate that oxalic acid content is higher in the phloem of Mudgo compared with susceptible varieties (TN1) (Yoshihara et al 1980). Stevenson et al (1996) found that the phloem of resistant rice varieties (Ratthu Heenati, BG300, and BG379/2) had higher individual concentrations of schaftoside, isoschaftoside, and total apigenin-C-glycosides (all are C-glycosidic flavonoids) than susceptible varieties (BG380, BG94/1). By altering the concentration of schaftoside in parafilm feeding sachet tests (with 20% sucrose solution), they found that BPH mortality increased as schaftoside concentrations increased from 250 to 500 μg mL^{-1}. The mechanism behind all three resistant varieties was derived from Ratthu Heenati (*Bph3* gene) and Stevenson et al (1996) suggest that this is anti-feeding rather than toxic. Using a pair of isogenic japonica rice lines, 80R (resistant) and 74S (susceptible), developed through repeated selection of F_{11} through F_{19} plants from an F_2 (Hoyoku × Mudgo) × Kochikaze cross (therefore containing the *Bph1* gene), Shigematsu et al (1982) determined that aerial plant parts of 80R contained beta-sitosterol, stigmasterol, and campesterol in larger quantities than 74S. Furthermore, honeydew collected from planthoppers feeding on 80R had cholesterol and beta-sitosterol, which caused a sucking inhibitory effect: in parafilm tests, 50 ppm of beta-sitosterol and 15% sucrose caused total inhibition of sucking. Other sterols showed similar effects: 80R also had about one-fifth of the asparagine content of 74S (this varied between plant parts and was measured in leaves, but not in the stem or sheath); asparagine also stimulates BPH feeding (Shigematsu et al 1982).

Mechanisms involving the plant surface

Evidence for plant-surface effects on planthopper behavior is limited to a single study (Woodhead and Padgham 1988). A lack of confirmed mechanisms involving the plant surface is perhaps largely due to limited research attention to rice surface features and their effects. Woodhead and Padgham (1988) extracted epicuticular waxes from IR22 (susceptible), IR46 (*Bph1* gene), and IR62 (*Bph3* gene) and manipulated plants by switching wax applications between varieties. They found wax composition to affect feeding; specifically, they suggest that a high ratio of long to short carbon-chain compounds in IR46 and the presence of shorter chain hydrocarbons in IR22 largely determined planthopper feeding responses. Plant-surface effects are also suggested from a study by Zhang et al (2004) comparing planthopper feeding on resistant variety B5 and susceptible variety MH63. They found more saliva sheaths on the upper part of stems of B5 plants, whereas those left in MH63 plants were mainly on the lower part of the stems. However, varying amounts of "general inhibitors" such as silicic acid can also determine the location of sucking sites (Yoshihari et al 1979).

Planthopper-induced defenses in rice

Planthopper attack causes a suite of responses in the rice plant, some of which ultimately lead to symptoms of hopper burn. Many of these responses, in both resistant and susceptible varieties, involve differential gene regulation related to such diverse functions as metabolism, energy, cell-cycle and DNA processing, transcription, protein synthesis, cellular transport, development, biogenesis of cellular components, subcellular localization (Wang et al 2008a), and starch breakdown (Loka Reddy et al 2004, Hao et al 2008). Plants infested by BPH also emit inducible volatiles (i.e., linalool, (3E)-4,8-dimethyl-1,3,7-nonatriene, indole) that are not detected in healthy or mechanically damaged plants (Xu et al 2002). Overall, feeding induces senescence in rice: genes involved in macromolecule degradation and plant defenses against stresses are generally up-regulated, whereas those involved in photosynthesis and cell growth are down-regulated (Yuan et al 2005). Using relatively new molecular techniques, particularly microarray analyses, considerable information has recently been gained concerning induced rice defenses to planthopper attack (i.e., Zhang et al 2004, Yuan et al 2005, Yang et al 2006, Hao et al 2008)

Attack-related elicitors, such as β-glucosidase, present in the saliva of BPH, have been linked to salicyclic acid (SA), hydrogen peroxide, and ethylene production (Wang et al 2008b). Ethylene in turn, can induce the expression of the *OsBi1* gene (*O. sativa* BPH-induced gene of unknown function), particularly in tissues around the bundle sheath, including vascular tissue, stomium, and tapetum of rice stems (Wang et al 2004). BPH damage also induces expression of the *PR-1a* gene (acidic pathogen-related protein 1), and chitinase (Pr-3) and *PAL* (phenylalanine ammonia-lyase), both of which are involved in the SA signaling pathway (Xu et al 2003). Whereas most evidence indicates that the plant response to BPH attack is similar to pathogen-induced responses, that is, through the SA pathway, there is some evidence that the jasmonic acid (JA) pathway is also activated (Zhang et al 2004, Wang et al 2008a). This is

mainly through expression of LOX genes, of which *OsLOX1* (*O. sativa* lipoxygenase 1) is likely to be the main LOX involved in the response to biotic and wounding stress. OsLOX1 protein, which builds up slowly during at least 48 h after BPH attack, is involved in JA and (Z)-3-hexenal synthesis (Wang et al 2008a). BPH infestation also induces expression of the Bowman-Birk *PI* gene (mainly in parenchyma of rice leaves and stems) to produce PI (proteinase inhibitor). This low-molecular-weight protein combines with proteinase to inhibit digestion in insects (Weng et al 2003).

Recently, Hao et al (2008) have demonstrated that callose is deposited on the sieve plates in BPH-infested rice. Where planthopper stylets had been inserted, callose deposition increased during the first 3 days of infestation in B5 (resistant) and TN1 (susceptible) rice. However, prolonged BPH feeding caused callose deposition to decrease in TN1 (Hao et al 2008). Callose deposition is coordinated through the activities of callose synthase and the callose-hydrolyzing enzyme β-1,3-glucanase; transcripts of four callose synthase encoding genes (*OsGSL1*, *OsGSL3*, *OsGSL5*, and *OsGSL7*) were detected following planthopper attack (Hao et al 2008). The expression patterns in six β-1,3-glucanase genes were also investigated. Three of these, *Osg1*, *Gns5*, and *Gns6,* were up-regulated following planthopper attack. A further gene, *Gns4*, appears to be constitutively expressed in B5, but induced in TN1 (Hao et al 2008).

As we gain information on the processes behind induced responses to planthopper attack, several features are emerging. First, rice responds to BPH attack predominantly, but perhaps not uniquely, through the SA pathway (Wang et al 2004, 2008b, Xu et al 2003). Second, the mechanisms involved in induced rice responses are secondary to constitutive defenses; therefore, continuous prolonged feeding on susceptible varieties induces defensive responses to a greater degree than in resistant varieties. For example, when comparing B5 (resistant) and MH63 (susceptible) rice varieties, PI is actually expressed at higher levels in the susceptible variety (Zhang et al 2004). In contrast, callose deposition was higher in B5 than in TN1 (Hao et al 2008); however, this could simply be a direct response to increased probing activity by planthoppers on resistant varieties (see Fig. 3), in the same way that β-1,3-glucanase breakdown of callose may be more apparent in TN1 because of increased salivation and extended feeding by planthoppers on this susceptible variety. A difficulty in controlling for planthopper activities on resistant and susceptible varieties (i.e., ensuring quantitatively equal amounts of probing, salivation, and feeding) prevents adequate comparisons of induced responses in resistant and susceptible varieties at micro-analytical scales. Furthermore, many induced responses are general responses to BPH that occur in both resistant and susceptible varieties; therefore, they appear to have little utility in defending rice against this planthopper, which, as part of its monophagous nature, may have overcome these specific defenses (i.e., by inducing β-1,3-glucanase [Hao et al 2008], or up-regulating the B-subunit of PP2A in response to plant PP2A production [Yang et al 2006]). Finally, except for the ovicidal response in japonica rice varieties (see below), induced defenses have not been linked to the known major resistance genes or resistance QTLs (Fig. 4), and there is no evidence to link planthopper-induced responses to any single resistant rice variety.

Although the influence of natural enemies is seldom considered when developing resistant varieties (the SSST and MSST are laboratory based and exclude natural enemies), interactions with natural enemies represent a further mechanism by which resistant rice varieties decrease BPH damage. Increased predator efficiency is often the result of poor herbivore fitness (as described below) and cannot be regarded as a true resistance mechanism. However, natural enemies are attracted to induced volatiles emitted during herbivore attack (Rapusas et al 1996, Xu et al 2002, Luo et al 2006). In a study by Rapusas et al (1996), resistant plants infested with BPH nymphs or eggs attracted significantly more *Cyrtorhinus lividipennis* Reuter (a mirid egg predator) and *Micraaspis hirashimai* (Sasaji) (a predatory coccinellid) than uninfested plants (however, the authors did not include a susceptible variety in their experiments). The authors indicate that some of the resistant rice plants emitted volatiles in response to BPH attack, which attracted these predators. In contrast, Luo et al (2006) indicate that the parasitoid *Anagrus nilaparvatae* Pand et Wang was attracted more to susceptible varieties than to resistant varieties.

Ovicidal response: linking induced and constitutive defenses

The japonica rice ovicidal response to planthopper oviposition (Sogawa 1991, Suzuki et al 1996, Seino et al 1996, Kiyonaga et al 1997, Yamasaki et al 2000) is different from other known rice resistance mechanisms for a number of reasons (Fig. 4). First, it was not selected through the SSST or MSST, but directly observed in the field: because it occurs in older plants (Suzuki et al 1996), it is overlooked by both screening methods. Second, because the response is quantifiable, it has been clearly linked to a series of QTLs (Yamasaki et al 2000, Sagawa et al, this volume). Third, it includes a heritable (Yamasaki et al 2000, Sagawa et al, this volume) induced component to defense that is linked to an established biochemical pathway (Seino et al 1996, Seino and Suzuki 1997).

The ovicidal response was first identified by Sogawa (1991) when he noted that dark brown discoloration of rice leaf sheaths in response to oviposition by whitebacked planthopper (WBPH), *Sogatella furcifera* (Horváth), was associated with early-stage egg mortality. Suzuki et al (1996) describe the reaction in detail: two distinct responses can occur. These they described as "watery" and "nonwatery" lesions. In nonwatery lesions, discoloration is restricted to the epidermal area around the region of egg insertion, whereas, in watery lesions, within 12 hours after oviposition, up to 11 rows of air spaces, including those containing the egg, become fully or partially filled with fluid. The formation of watery lesions causes necrosis of parenchymal cells in the lesion with the epidermis around the area of egg insertion gradually turning dark brown and often with eventual senescence of the entire leaf sheath (Suzuki et al 1996). BPH also suffers high egg mortality if a watery lesion is formed, but, unlike the plant response to WBPH, the response to BPH does not include discoloration of the leaf sheath (Suzuki et al 1996). The formation of a watery lesion is associated with up to 80% mortality of WBPH, whereas nonwatery lesions are associated with only about 12% mortality (Suzuki et al 1996). Benzyl benzoate, identified in extracts from watery lesions, has

been shown to cause ovicidal activity against WBPH at concentrations above 6.4 ppm (Seino et al 1996).

Using GC-MS (gas chromatography-mass spectrometry), Seino and Suzuki (1997) showed that C6-ring benzoic acid was used in biosynthesis of benzyl benzoate in watery-lesion tissues. They suggest that the benzyl benzoate biosynthesis pathway in watery lesions may include a series of intermediate reductions, including benzaldehyde and benzyl alcohol (Seino and Suzuki 1997). This pathway is apparently up-regulated in response to planthopper oviposition. Benzyl benzoate may cause direct egg mortality or may act indirectly by affecting planthopper symbionts (symbiont-free eggs cannot complete embryonic development, Schwemmler 1994 in Seino et al 1996). Ovicidal response to BPH is of a lower intensity than to WBPH; nevertheless, the grade of watery lesion can be associated with BPH egg mortality (Kiyonaga et al 1997, Yamasaki et al 2000). Using a set of 71 rice recombinant inbred lines (F_{11}) derived from a cross between Asominori (with ovicidal response) and IR24 (indica variety without ovicidal response), Yamasaki et al (2000) have linked the response to QTLs on chromosomes 1 and 6. Both these QTLs were located in the same chromosomal regions as two of the 10 known QTLs for ovicidal response to WBPH (Yamasaki et al 2000). The ovicidal response depends on plant age and is most intense at the maximum tillering stage, but negligible in small tillers (Suzuki et al 1996). Heritability and other aspects of ovicidal response are described in detail in Sogawa et al (this volume).

Resistance interactions with the rice ecosystem

Success in the deployment of resistant rice varieties depends on a series of factors inherent to the rice ecosystem. Whereas the genetic composition of resistant varieties is maintained through inbreeding or directed crosses (in hybrid varieties), herbivores, and their associated symbiotic gut flora (Sasaki et al 1996; Chen, this volume), respond through selection to the presence and availability of resistant material. For this reason, resistance breakdown has been a major feature in the history of BPH-resistant rice (Heinrichs 1994, Gallagher et al 1994). However, resistance is also influenced by farm management practices that affect soil nitrogen levels (Pathak and Kalode 1980b, Kajimura et al 1993, Visarto et al 2001), water availability (Baqui and Kershaw 1993b), and the density of natural enemies (Senguttuvan and Gopalan 1990, Heinrichs et al 1986, Gallagher et al 1994, Rapusas et al 1996, Cuong et al 1997, Luo et al 2006) or herbivore competitors (Cheng et al 2001).

Fertilizers

Excess fertilizer increases planthopper fitness on resistant rice varieties (IR72 and Mudgo), therefore compromising resistance (Pathak and Kalode 1980b, Visarto et al 2001). Excess nitrogen is known to increase the total free amino acids in Mudgo, but has no effect on soluble sugars (Pathak and Kalode 1980b). Kajimura et al (1993) found that BPH densities in organically farmed paddies were lower than in chemically fertilized and poultry-manured plots. This was not due to altered reproductive rates or differences in densities of natural enemies. However, the amino acid content in rice

differed between organic and chemically grown rice plants (Kajimura et al 1995): Kajimura et al (1995) found asparagine (1 of 20 amino acids analyzed) as the only amino acid that was significantly lower in organic rice than in chemically fertilized rice. Asparagine is a known BPH feeding stimulant and may have led to increased feeding and higher survival on the chemically fertilized plants (Kajimura et al 1995). It is still unknown how different rice varieties (including resistant and susceptible varieties) respond to the form and amount of nitrogen applied to fields.

Water

In a study by Baqui and Kershaw (1993), BPH honeydew excretion (linked to feeding), weight gain, and the number of eggs per egg-batch were reduced in TN1 (susceptible), but also in Mudgo (*Bph1*), ASD7 (*bph2*), Rathu-Heenati (*Bph3*), and Babawee (*bph4*) when these varieties were water stressed. In contrast, there was no effect of water stress on Ptb33 (with possibly two unknown resistance genes). However, overall, BPH did poorly on Ptb33 even under optimal water regimes.

Insecticides and natural enemies

The magnitude effect of natural enemies on BPH populations in the rice ecosystem has been determined through a number of field studies (see Way and Heong 1994 and references therein). The overuse and poor management of insecticides are often associated with planthopper outbreak (Cuong et al 1997, Heinrichs 1994). Insecticides may also decrease the durability of resistance in the field (Gallagher et al 1994) because BPH mortality is ultimately determined by interactions between varietal resistance and natural enemies (Karthhardjono and Heinrichs 1984, Senguttuvan and Gopalan 1990, Rapusas et al 1996, Cuong et al 1997, Luo et al 2006). Because of poor nutrition or intoxication, BPH developing on resistant varieties may be sluggish during evasive responses to their natural enemies; also, they move more frequently to find suitable feeding sites and have longer development times (Fig. 3). Although not specifically tested, these factors are suggested to increase BPH vulnerability to predators and parasitoids, causing observed higher predation on resistant compared with susceptible varieties (Karthhardjono and Heinrichs 1984, Senguttuvan and Gopalan 1990).

In a field study from Vietnam, BPH-predator ratios were also generally higher on resistant (IR64, IR62032-189) compared with susceptible (Jasmine) varieties in insecticide-free rice plots. However, insecticide-treated plots had higher BPH-predator ratios and the predator advantage of the resistant varieties was reduced (Cuong et al 1997). The success of early-maturing rice varieties in preventing BPH population buildup has also been linked to an increased efficiency of predators and observed lower BPH-predator ratios when compared with late-maturing varieties (Heinrichs et al 1986). The effects of insecticides on parasitoids have not been examined in the context of resistant rice varieties. Although parasitoids play a role in BPH population regulation, no evidence suggests that parasitoids more efficiently parasitize BPH on resistant varieties; rather, the opposite may occur. Luo et al (2006) found that the parasitoid *A. nilaparvatae* was less attracted to JA-treated resistant (IR26 and IR64)

than JA-treated susceptible varieties (TN1, B97-59, XS63) in paired (laboratory) and multichoice (field) tests.

Interestingly, Cheng et al (2001) have shown that rice resistance to BPH can break down after previous attack by planthoppers of a different species. In experiments with BPH and WBPH, the effects of feeding by one species increased fitness of the second species feeding on the same plant. This was not observed after feeding by a single planthopper species on the same plant. The mechanisms behind these observations have not yet been addressed.

Conclusions

The SSST and MSST have been extremely successful in identifying resistant phenotypes and leading to the large number of resistant rice varieties now available. However, in most modern varieties, BPH resistance is predominantly feeding-related. Novel resistance mechanisms may be required to improve durability, and this will require new screening methods. The pervasiveness of a single reductionist screening bioassay (the SSST) underlies many of the difficulties we now face concerning deployment for durable resistance in rice. New approaches to attaining durable resistance now confront these issues: strategies for pyramiding genes should depend on knowledge of gene function and, therefore, the related resistance mechanisms; however, apart from the ovicidal response, we have little understanding of how any of the major resistance genes or QTLs function. The management of BPH-transmitted viruses could also be improved by knowledge of varietal resistance mechanisms. Furthermore, predictions on the consequences of insecticide and nutrient management for gene deployment and durability would benefit from a greater understanding of these mechanisms.

Most of our current knowledge on resistance consists of identified resistance genes and planthopper responses to resistant varieties. The majority of these responses confirm that anti-feeding mechanisms underlie resistance in most modern varieties. This is probably not due to any lack of alternative mechanisms in the rice genome, but rather because of convergent protocols in most resistance studies and during varietal development. A small number of manipulative studies indicate that amino acids (some of which act as feeding stimulants) and secondary chemicals (many of which are anti-feedants) determine feeding responses. Certain volatiles and surface waxes can deter both feeding and settling. Only one mechanism unrelated to feeding behavior has been described: the ovicidal response. Unsurprisingly, this mechanism was first detected during field observations and is independent of the SSST. During the past 10 years, there has been increased attention to induced responses to planthopper attack on rice. Induced mechanisms are likely independent of the major resistance genes and act secondarily to constitutive defenses. Their value for rice breeding needs to be re-examined. Finally, resistant varieties are inserted into complex and diverse rice ecosystems that vary in soil nutrients, climatic regimes, landscape structure, and associated flora and fauna. Nutrient levels, determined by fertilizer regimes, and the density of natural enemies, determined by landscape features and insecticide usage,

interact with deployed varieties to determine the field success and durability of resistance.

In the face of this evidence, new screening techniques should be developed to identify genotypes with novel mechanisms that can be combined with known feeding-based mechanisms when pyramiding defenses. Further manipulative experimentation is required to clearly determine the mechanisms behind resistance. These and emerging mechanisms should be linked back to known, tagged resistance genes. Furthermore, attention should be given to issues of field resistance, that is, a stable resistance over the life-time of the plant. Finally, effective deployment of resistant varieties should be considered in the context of planthopper adaptations to genes and mechanisms, and the accelerating effects of fertilizers and pesticides on breakdown of the resistance genes that are currently available.

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Notes

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Resistance-breaking ability and feeding behavior of the brown planthopper, *Nilaparvata lugens*, recently collected in Korea

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Resistance-breaking ability of wild brown planthopper (BPH), *Nilaparvata lugens,* on resistant rice varieties has been reported in many Asian countries. To understand the development of this ability of wild BPH in Korea, we conducted a nymphal survivorship test and electrical penetration graph (EPG) study on susceptible and resistant rice varieties with four different BPH populations, which were collected in the early 1980s (S-BPH), 2005, 2006, and 2007. The S-BPH showed low survival rates on resistant rice varieties carrying *Bph1* and *bph2*. However, recent wild BPH populations seemed to have high resistance-breaking ability according to elevated survival rates on most other resistant rice varieties, except Gayabyeo (*Bph1* + *bph2*) and Rathu Heenati (*Bph3*). In addition, the two 2005-BPH populations selectively reared on ASD7 and Cheongcheongbyeo for three and seven generations, respectively, maintained their resistance-breaking ability against *Bph1* and *bph2* simultaneously. On the other hand, in stylet penetration behavior monitored with the EPG technique during a 15-h period, recent BPH could not easily feed on the phloem sap of three resistant rice varieties, Cheongcheongbyeo (*Bph1*), ASD7 (*bph2*), and Gayabyeo. The average time necessary for reaching the first phloem feeding pattern (Ph) by recent BPH on resistant rice varieties was about 6 hours, three times longer than on susceptible rice varieties (TN1, indica type, and Ilpumbyeo, japonica type). The total Ph duration of wild BPH also decreased significantly on the resistant rice varieties. From these results, we suggest that, though recent wild BPH collected in Korea simultaneously have high resistance-breaking ability on resistant rice varieties carrying *Bph1* and *bph2* through the increase in the survival rate, they still have to pay some price to feed on the phloem sap of resistant rice varieties.

Keywords: *Nilaparvata lugens*, resistant rice variety, resistance-breaking ability, survival rate, EPG, feeding behavior, phloem, cost

The brown planthopper (BPH), *Nilaparvata lugens* (Stål), is one of the major insect pests in Korea. It has been presumed that BPH migrate from the southeast part of China through the southwesterly airflow into Korea, mainly around mid-June to late July, the rice planting season, every year (Park 1973, Uhm et al 1988). BPH occasionally cause serious damage (hopperburn) to the rice plant in Korea by direct feeding during three or four generations. Because they cannot survive during the Korean winter season, the damage is caused by newly immigrant BPH every year (Park 1973).

Host-plant resistance has been emphasized as a major tactic in integrated pest management because of its economic and environment-friendly advantages (Heinrichs 1994). Nineteen major resistance genes have been identified in indica varieties (9 genes) and wild species (10 genes) since studies began on rice resistant to BPH (Chen et al 2006). However, the possibility that a high level of resistance-breaking ability of BPH on resistant rice varieties could be selected in laboratories has provided little opportunity for practical use of resistant rice varieties (Pathak and Heinrichs 1982, IRRI 1975, Nemoto and Yokoo 1994, Ketipearachchi et al 1998, Sogawa 1982). The development of resistance-breaking ability in wild BPH against resistant rice varieties carrying resistance gene *Bph1* or *bph2* has been reported in many Asian countries (Verma et al 1979, Ito et al 1994, Tanaka and Matsumura 2000, Matsumura 2001, Yu et al 2001). Sogawa (1992) documented that the BPH population capable of breaking down a resistant rice variety carrying the *Bph1* gene gradually increased between 1988 and 1990 in Japan. It has also been reported that the BPH population, which could survive on ASD7 carrying the *bph2* gene, increased in Japan in 1997 (Tanaka and Matsumura 2000) and in southern China in 1998 (Yu et al 2001). Since then, it has been necessary to carefully monitor the resistance-breaking ability of BPH against this resistant rice variety, because the migration scenario of BPH in East Asia has been closely related to that of immigrating BPH (Takahashi et al 1994, Tanaka and Matsumura 2000).

In Korea, breeding for rice resistant to BPH practically began in 1971, and Korean rice varieties that were resistant to BPH biotypes 1 and 2, 1 and 3, or three biotypes (1, 2, 3) have been released and cultivated since 1977 (Heu 1983, Kim et al 1985). BPH resistance genes were introduced into Korean rice varieties by crossing Korean breeding lines with IRRI lines in the 1970s-'80s. Three Korean BPH biotypes have been identified based on their differential varietal reactions. BPH biotype 1 indicates the BPH are able to infest only susceptible rice variety Chucheongbyeo. BPH biotypes 2 and 3 mean that BPH are able to infest not only Chucheongbyeo but also Cheongcheongbyeo (*Bph1*) and M63 (*bph2*), respectively (Lee et al 1982, 1985). BPH resistance lines from IRRI were screened with Korean BPH biotypes and their responses were similar to those of BPH biotypes in the Philippines (Kim et al 1983). In Korea, a BPH biotype 1 population was predominantly distributed in the 1980s and immigration of BPH biotypes 2 and 3 slowly increased until the late 1980s (Goh et al 1988, Park and Song 1988). In addition, the BPH population that simultaneously had the resistance-breaking ability of biotypes 2 and 3 was distributed in a low ratio in 1987 and 1988 surveys (Goh et al 1988). Unfortunately, data about distribution of resistance-breaking BPH have not been collected in Korea since the early 1990s. Thus,

this study was carried out to understand the resistance-breaking ability of recent wild BPH populations immigrating into Korea. Because the resistance-breaking ability of recent BPH occurring in Southeast Asia is much stronger and more complex together with insecticide resistance than that in the past, it is necessary to investigate thoroughly the BPH adaptation mechanism against resistant varieties and insecticides.

An electrical penetration graph (EPG) has been developed to monitor and record homopteran feeding behavior quantitatively (McLean and Kinsey 1967, Tjallingii 1978). The correlations between EPG and feeding activity of BPH have been investigated by recording EPG and simultaneously observing honeydew excretion (Velusamy and Heinrichs 1986, Kimmins 1989), the salivary sheath within the plant (Khan and Saxena 1988, Youn and Chang 1993), and the location of severed stylet tips remaining in rice tissue (Spiller 1990). The feeding behavior of BPH biotypes 1, 2, and 3 on differentially resistant rice varieties TN1 (no resistance gene), Mudgo (*Bph1* gene), and ASD7 (*bph2* gene) was monitored and analyzed with the EPG system (Khan and Saxena 1988). All three BPH biotypes ingested longer on their respective susceptible varieties than on other resistant varieties. Understanding of the feeding properties of wild BPH on resistant varieties will play an important role in revealing how wild BPH can obtain resistance-breaking ability. Using the EPG technique herein, we also tried to analyze the feeding behavior of recent BPH, relating to the survivorship of those insects.

Materials and methods

The experimental population of *N. lugens*

S-BPH was collected in the early 1980s and has been successively maintained on Chucheongbyeo (japonica type, susceptible) in the insectary of the National Institute of Agriculture and Technology, Rural Development Administration, for more than 20 years. We obtained a colony of the S-BPH population and have kept it in an insectary in the National Institute of Crop Science using TN1 (indica type, susceptible). Field populations were collected in Dang-jin, the west-seaside of Korea, for two years, 2005 and 2006, respectively, and have been reared on TN1 and Ilpumbyeo (japonica type, susceptible). Another BPH population was collected in Go-seong, the south-seaside of Korea, in 2007. According to the collecting year, we named each wild BPH populations as 2005-BPH, 2006-BPH, and 2007-BPH. On the other hand, to check whether the resistance-breaking ability of BPH for specific varieties can be maintained from generation to generation or not, 200 insects were collected from the 2005-BPH population and have been successively reared on resistant rice varieties Cheongcheongbyeo (seven generations) and ASD7 (three generations). The two subpopulations were named as Cheongcheongbyeo-BPH and ASD7-BPH depending on their rearing rice varieties. The rice seedlings for rearing insects were grown using only tap water. The brown planthoppers and rice seedlings were maintained at 25 ± 2 °C, 60 ± 5% RH, and 15L:9D photoperiod in the insectary.

Nymphal survivorship test

To understand the degree of resistance-breaking ability of BPH, survival rates of BPH nymphs on five resistant rice varieties—Cheongcheongbyeo (*Bph1*), M63 (*bph2*), ASD7 (*bph2*), Gayabyeo (*Bph1*+ *bph2*), and Rathu Heenati (*Bph3*)—were compared with those on susceptible varieties Taebaegbyeo, Ilpumbyeo, and TN1. The test plants were grown on soil in a greenhouse. After 15 days, one seedling of each rice variety was carefully pulled up from the soil and washed by tap water to remove the remaining soil from the roots. The root part of each rice seedling was curled around by cotton and put into a glass tube (3 cm in diameter, 20 cm in height). Ten third-instar nymphs from each BPH population were released into the glass tube, and the opening was covered with gauze. All experiments were replicated five to six times. The survival of BPH and the extent of damage to the plant were observed every day until the susceptible plant withered. Survival rate was calculated from the insect number on the second day in order to avoid counting artificially damaged insects. A survivorship test was conducted at 25 ± 2 °C, 60 ± 5% RH, and 15L:9D photoperiod in the insectary.

Electrical penetration graph

The feeding behavior of BPH was observed and recorded by a Giga-8 DC EPG amplifier with 10^9-Ω input resistance and an adjustable plant voltage (Wageningen Agricultural University, Wageningen, Netherlands). Females of S-, 2005-, and 2007-BPH were provided with only water on a filter paper for 2 hours before the experiments. A gold wire (20 μm in diameter and 3 cm in length) was attached on the dorsal thorax of BPH with a water-soluble silver conductive paint. Each susceptible and resistant rice plant in the third-leaf stage was planted in a plastic pot (8 cm in diameter) with soil. A copper wire (2 mm in diameter and 10 cm in length) for the plant electrode was inserted into the pot soil. A filter paper (Whatman No. 1) was set under the test plant to check honeydew excretion amount by spraying with 0.1% ninhydrin. Each female BPH was connected to the insect probe of the EPG system and was carefully attached on the stem of the rice plant. The gain was set at 50x and plant voltage was adjusted by ±5V during EPG recording. Recording was conducted simultaneously on eight plants (four susceptible and four resistant rice varieties) in a Faraday cage. The feeding behavior of BPH was recorded for 15 hours and analyzed using EPG analysis PROBE 3.0 software (Wageningen Agricultural University, Wageningen, Netherlands). If BPH left the rice plant during EPG recording, the data were removed from the analysis. All EPG tests were carried out at 25 ± 2°C, 60 ± 5% RH, and from 1800 to 0900 (dark condition) in the laboratory.

Feeding behavior analysis

Feeding behavior of BPH in the EPG waveform was grouped into seven different patterns: np, P, path, S, sPh, Ph, and X (Seo et al, unpublished data). Two parameters, the time from the first start of penetration to the first Ph pattern and the total duration of Ph pattern, were extracted from the patterns. Because we observed that BPH could not easily reach the phloem-feeding stage (Ph pattern) and its honeydew excretion amount was small on resistant rice varieties, we compared the two parameters closely

Table 1. Survival rate (%)[a] of three different BPH populations on resistant rice varieties in Korea.

Variety	Resistance gene	Tested populations		
		S-BPH	2005-BPH	2006-BPH
Taebaegbyeo	Susceptible	100.0	100.0	100.0
Cheongcheongbyeo	*Bph1*	0.0	88.0	112.6
ASD7	*bph2*	9.8	94.0	125.7
M63	*bph2*	16.3	95.7	117.1
Gayabyeo	*Bph1* + *bph2*	0.0	39.6	24.1
Rathu Heenati	*Bph3*	–[b]	–	18.8

[a]Survival rate was transformed into values relative to that of Taebaegbyeo. [b]Not tested.

related to phloem-feeding behavior between susceptible and resistant rice varieties. Comparisons on each parameter were conducted by Duncan's multiple range test ($P < 0.05$) (SAS Institute 2002).

Results and discussion

Resistance-breaking ability of BPH

Resistance-breaking ability of the three BPH populations was compared by their survival rates on resistant rice varieties (Table 1). We expected that most insects of the S-BPH population don't have resistance-breaking ability on the resistant rice varieties tested because its collection time was the early 1980s (Park and Choi 1991), and, at that time, biotype 1 was predominantly distributed (64.7–57.9% from 1985 to 1987) in the southern coastal regions of Korea (Park and Song 1988). As expected, S-BPH showed low survival rates on all tested resistant varieties, especially on Cheongcheongbyeo (*Bph1*) and Gayabyeo *(Bph1* + *bph2*). However, 2005-BPH and 2006-BPH showed very high survival rates, more than 88%, on resistant varieties carrying *Bph1* or *bph2*, except on Gayabyeo (39.6% and 24.1%, respectively). Although a small number of BPH developed into adults on Gayabyeo, those insects had small body size and didn't produce eggs (personal observation). The survival rate of 2006-BPH on Rathu Heenati (*Bph3*) was also low (18.8%). In 2007-BPH, nymphal survival rates were also similar to those of the 2005- and 2006-BPH (Fig. 1). But, the survival rate on Gayabyeo increased a little compared with that of two previous BPH populations. From the results of survival rate, it was concluded that BPH populations recently migrated into Korea could survive well on the resistant rice variety carrying an individual resistance gene, *Bph1* or *bph2*, unlike past BPH populations.

In order to check whether the resistance-breaking ability of BPH can be maintained from generation to generation or not, 2005-BPH populations were

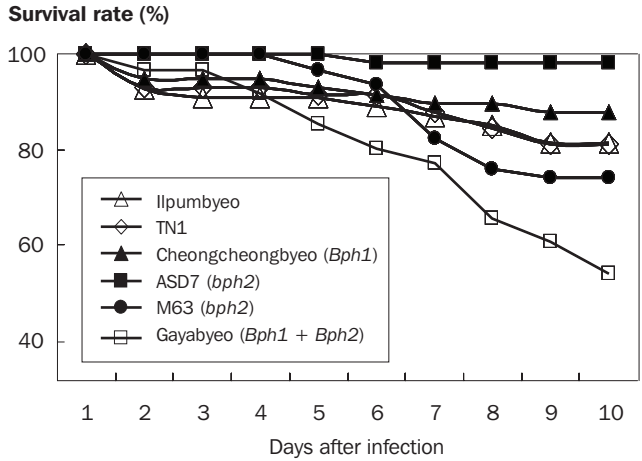

Fig. 1. Survival rate of 2007-BPH on susceptible and resistant rice varieties.

continuously reared on three different rice varieties, Ilpumbyeo (susceptible), Cheongcheongbyeo (*Bph1*), and ASD7 (*bph2*). For the results, the two subpopulations grew well on Cheongcheongbyeo and ASD7 during seven and three generations, respectively, and showed high survival rates on resistant rice varieties with each of the *Bph1* and *bph2* genes (Fig. 2), like the results for 2005-BPH (Table 1). This result suggests that the resistance-breaking property of 2005-BPH can be maintained on different resistant rice varieties for generations and that 2005-BPH simultaneously has high resistance-breaking ability against the two major BPH resistance genes, *Bph1* and *bph2*.

The resistance-breaking ability of recently collected BPH in Korea was similar to that of the South Asian BPH populations, which occurred in Bangladesh, Sri Lanka, and southern India, based on virulence to the resistance genes in Mudgo and ASD7 and nonvirulence to Rathu Heenati (*Bph3*) (Verma et al 1979, IRRI 1975, Smith 2005). This trend of resistance-breaking ability of wild BPH has also been reported in southern China and Japan (Yu et al 2001, Tanaka and Matsumura 2000).

It has been reported that Gayabyeo showed high resistance against three Korean BPH biotypes (biotypes 1, 2, and 3) as well as the rice green leafhopper, *Nephotettix cincticeps* Uhler (Kim et al 1983). In this study, all tested populations couldn't infest well Gayabyeo carrying *Bph1* and *bph2* together, although they could break down both resistant rice varieties containing a major resistance gene, *Bph1* or *bph2*, singly. The incorporation effect of both genes into a resistant variety or other unknown factors related to BPH resistance in Gayabyeo remain to be analyzed.

Feeding behavior of recent BPH on resistant rice varieties

Feeding behavior of BPH on resistant rice varieties has been investigated using the EPG technique (Khan and Saxena 1988, Kimmins 1989). Honeydew excretion

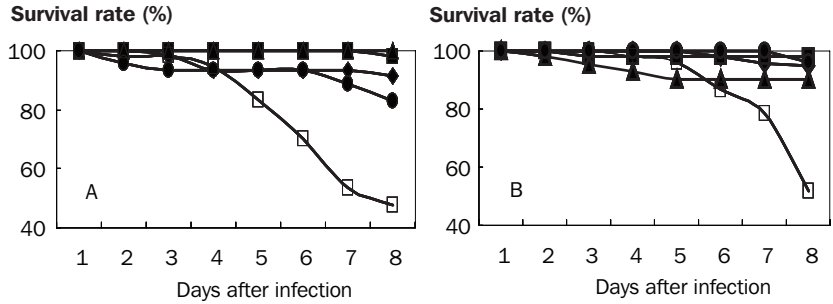

Fig. 2. Survival rate of Cheongcheongbyeo-BPH (A) and ASD7-BPH (B) on resistant rice varieties. ■ = ASD7, ♦ = Taebaegbyeo, ● = M63, ▲ = Cheongcheongbyeo, □ = Gayabyeo. Data represent means of five replicates.

has been used as a criterion for determining the amount of sap ingested by BPH on susceptible and resistant rice varieties (Sogawa and Pathak 1970). BPH is primarily a phloem feeder (Khan and Saxena 1984) and the quantity of honeydew excretion is much lower on resistant rice varieties than on susceptible ones (Paguia et al 1980, Park and Song 1988). Sap ingestion and honeydew excretion by BPH were assessed in the EPG by incorporating radioactive phosphorus into the rice plant (Hopkins 1991). When the amount of radioisotope within the insect and its excretion after 24 hours were monitored, the total radioactivity in both the BPH body and honeydew increased exponentially with the duration of the ingestion pattern. The total amount of label taken up by BPH on the resistant rice varieties was significantly less than that on the susceptible ones. Therefore, in the observation on feeding activities related to phloem ingestion using our EPG technique, we expected that recent BPH easily fed on the phloem sap of resistant rice varieties because they survived well even on resistant rice varieties. Table 2 shows the ratio of female BPH that could reach a phloem-feeding pattern (Ph) on rice varieties in EPG recording for a 15-hour period. In the result, a very low percentage of S-BPH females (0–4.2%) could reach Ph waveform on resistant varieties Cheongcheongbyeo and ASD7. More females in 2005- and 2007-BPH, however, showed Ph waveform on Cheongcheongbyeo and ASD7 (16.7–50%) within the 15-hour period. In 2005-BPH, none of the tested females could reach the phloem-feeding stage on Gayabyeo, but, in 2007-BPH, about 24% of the females reached the Ph waveform. This result coincided with the increased survivorship of 2007-BPH on Gayabyeo to some extent (Fig. 1). However, although the phloem-feeding potential of recent BPH on resistant varieties increased, the ratios were much smaller than that on the susceptible varieties in wild BPH. In addition, the honeydew excretion amount of recent BPH on the resistant varieties was smaller than that on the susceptible varieties. These results indicated that recent BPH could not easily feed on the phloem sap of three resistant rice varieties, Cheongcheongbyeo (*Bph1*), ASD7 (*bph2*), and Gayabyeo (*Bph1* + *bph2*).

To analyze this phenomenon, we compared two parameters in EPG recording: the time needed to reach the first Ph pattern from the initial penetration and the total

Table 2. Percentage of BPH capable of feeding on phloem of susceptible and resistant rice varieties within 15 hours.

Variety	S-BPH	2005-BPH	2007-BPH
Ilpumbyeo	60.0 (25)[a]	–	81.3 (16)
TN1	–[a]	100.0 (25)	–
Cheongcheongbyeo (*Bph1*)	0.0 (16)	31.6 (19)	37.5 (16)
ASD7 (*bph2*)	4.2 (24)	16.7 (24)	50.0 (16)
Gayabyeo (*Bph1* + *bph2*)	–	0.0 (10)	23.8 (21)

[a]( ) = number of female BPH. [b]Not tested.

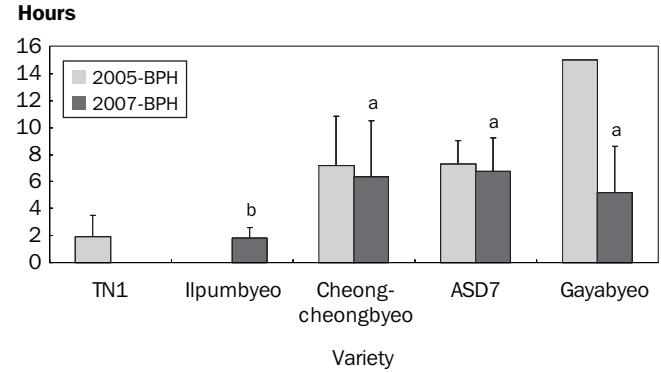

Fig. 3. The average time to reach the first Ph pattern on susceptible and resistant rice varieties within 15 hours. Electrical recording of 2005-BPH on Ilpumbyeo and 2007-BPH on TN1 was not conducted. The value of 2005-BPH on Gayabyeo was calculated as 15 hours due to the absence of BPH, which reached the Ph pattern during a 15-hour period. The same letter on the standard deviation means that there were no significant differences in Duncan's multiple range test ($P < 0.05$).

duration of Ph pattern. The average times needed to reach the first phloem-feeding pattern (Ph) by recent BPH on resistant rice varieties were significantly longer than those on susceptible rice varieties (Duncan's multiple range test, $P < 0.05$) (Fig. 3). The time to reach the phloem of Gayabyeo in 2005-BPH was calculated as 15 hours due to the absence of BPH that had Ph pattern. The S and sPh always precede Ph pattern, and both waveforms appeared more frequently on resistant varieties than on susceptible varieties. The change from sPh to Ph pattern hardly occurred on resistant varieties. In histological observation of plant tissue, the stylet tip position of BPH already arrived at the phloem sieve element in the S and sPh pattern. However, periodical honeydew excretion was observed only in the Ph pattern (Seo et al, unpublished data).

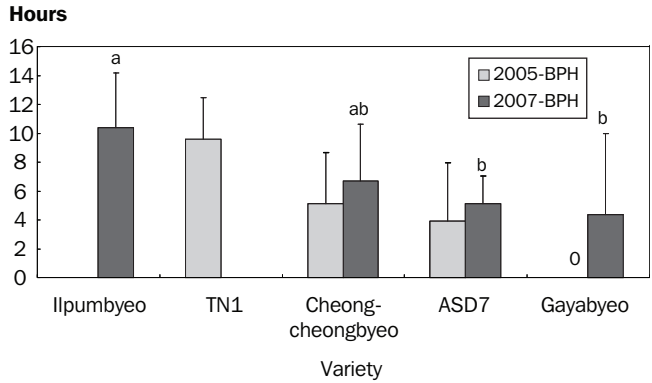

Fig. 4. The total duration of Ph pattern on susceptible and resistant rice varieties within 15 hours. Electrical recording of 2005-BPH on Ilpumbyeo and 2007-BPH on TN1 was not conducted. The same letter on the standard deviation means that there were no significant differences in Duncan's multiple range test ($P < 0.05$).

The total Ph pattern duration of wild BPH also decreased significantly on resistant rice varieties (Duncan's multiple range test, $P < 0.05$) (Fig. 4). This was mainly because of the delay in reaching the phloem-feeding stage and the reduction in the sustained duration of the phloem-feeding phase within the limited 15 hours. The results suggested that recent BPH can survive well on resistant rice varieties carrying *Bph1* or *bph2*, even though they cannot easily ingest phloem sap of resistant rice varieties. However, it has been reported that the high mortality of BPH on Cheongcheongbyeo was not caused by a lack of nutritional value in phloem sieve elements of the variety itself, but was caused by a lack of feeding amount from phloem sap (Jung and Im 2005). It has also been presumed that the interruption of phloem feeding on resistant rice varieties seems to be owing to either the presence of a feeding deterrent in the tissues adjacent to or within sieve elements of resistant rice varieties or sieve tube occlusion by sieve element proteins involved in the plugging of sieve pores (Velusamy and Heinrichs 1986). In our study, there is an inconsistency between the survivorship and feeding behavior of recent BPH on resistant rice varieties, and the limitation in phloem feeding cannot explain the high survivorship of recent BPH on resistant rice varieties. Therefore, a study on ecological and physiological costs of recent BPH to overcome the resistance of rice is necessary, which may play an important role in understanding the mechanism of BPH resistance-breaking ability and provide significant information for the strategy of resistance rice breeding as well as a pest management program.

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Variation in planthopper-rice interactions: possible interactions among three species?

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Throughout Asia, extensive programs exist to develop rice varieties with resistance to the brown planthopper, *Nilaparvata lugens*. Although more than 19 genes for *N. lugens* resistance have been identified in rice, *N. lugens* can rapidly adapt to new resistant varieties within several generations in the laboratory and several years in the field. A deeper understanding is needed to determine the factors that underlie variation in planthopper-rice interactions in order to support the widespread efforts to develop and deploy resistant rice varieties. I review host-plant acceptance for *N. lugens* and how it relates to phloem chemistry. I discuss the dependence of *N. lugens* upon yeast-like endosymbionts for the provisioning of essential amino acids. The final section covers *N. lugens* mating systems and evidence for population structure. I conclude by synthesizing the available evidence and developing several hypotheses on factors that could underlie the dramatic variation in planthopper-rice interactions across Asia.

The brown planthopper, *Nilaparvata lugens*, is an enormously successful secondary insect pest that arose from the Green Revolution. *N. lugens* has been able to rapidly adapt to all resistant rice varieties and an array of pesticide chemistries (Liu et al 2005, Yang et al 2005, Yin et al 2008). Rice entomologists and breeders have frequently observed that rice varieties may be resistant to *Nilaparvata lugens* in one geographic region but susceptible in another and rice varieties that were previously resistant may become susceptible over time. Planthopper adaptation to new rice varieties is demonstrated by increases in survival, body weight, honeydew production, and reproduction (Claridge and den Hollander 1980, Pathak and Heinrichs 1982, Denno et al 1989). Planthoppers can also adapt to resistant rice varieties within several generations through continuous rearing in the laboratory. Therefore, it is important to understand the factors underlying variability in planthopper-rice interactions to assist efforts to develop and deploy resistant germplasm.

In this review, I will discuss the factors associated with host selection and acceptance by *N. lugens*. I then review the biochemical basis of rice host-plant resistance and how current genomic tools have contributed to our understanding of rice resistance. The review then focuses on the yeast-like endosymbionts (YLS) within

planthoppers, and the role they may play in adaptation to plant resistance. Finally, I will cover *N. lugens* mating systems and how they may lead to rapid adaptation and structured populations. The purpose of this review is to synthesize currently available information on planthopper biology, genetics, and host-plant resistance to generate possible hypotheses explaining the variation in planthopper-rice interactions.

Host acceptance of *N. lugens*

The high host specificity of *N. lugens* is characteristic of delphacid planthoppers. Although most planthoppers are highly host-specific (Denno and Roderick 1990), planthopper host location appears to be quite passive (Cook and Denno 1994). In the field, *N. lugens* abundance may be initially similar among rice paddies, unplowed fields, and other crops, suggesting that they do not exhibit landing preferences (Cook and Perfect 1985). Laboratory studies have shown that *N. lugens* is attracted to the odor of host-plant extracts (Saxena and Pathak 1979). However, planthopper specialization does not appear to involve active host-plant location, but rather results from adults remaining on suitable plants (Cook and Denno 1994). The available evidence suggests that the major plant resistance to *N. lugens* is dependent upon phloem chemistry because rejection of a plant occurs only after ingesting phloem sap (Sogawa and Pathak 1970, Sogawa 1982).

Nilaparvata lugens host selection may be due to either plant nutritional content or chemical defense. Host selection by planthoppers is due to phloem chemistry, and likely involves the lack of particular feeding stimulants (Cook and Denno 1994). On resistant rice varieties, silicic and oxalic acid have been found to deter planthopper feeding (Yoshihara et al 1979a,b, 1980a). Phenolic acids in resistant varieties appear to be related to the inability of planthoppers to find and ingest phloem (Fisk 1980). On the other hand, planthoppers are more likely to reject rice varieties with low levels of essential amino acids in the phloem (Sogawa 1982). Shigematsu et al (1982) found that sterols acted as sucking inhibitors for *N. lugens* whereas asparagine stimulated sucking.

Rice resistance to *N. lugens*

Insect herbivore food preferences in grasses appear to be more governed by host nutritional factors than by plant defenses (Tscharntke and Greiler 1995). While grasses generally have fewer allelochemicals (Butler and Bailey 1973, Harbone and Williams 1976), allelochemicals in grasses can still play a role in structuring planthopper host range (Cook and Denno 1994). There is some evidence that the nutritional composition of the rice plant can influence *N. lugens* feeding behavior. The rice phloem sap consists mostly of sucrose (17–25%, w/v) and free amino acids (3–8%, w/v) (Fukumorita and Chino 1982). *N. lugens* feed less and excrete less honeydew when feeding on rice plants deficient in nitrogen (Sogawa 1982). Certain amino acids, sucrose, and organic acids were found to act as feeding stimulants (Sakai and Sogawa 1976). Low concentrations of asparagine may deter extended feeding (Sogawa and Pathak

1970). On the other hand, lower free amino acid concentrations have been found in resistant rice varieties (Das 1976, Mishra et al 1990). Therefore, amino acid content could vary between rice varieties, and could be related to differences in planthopper performance on different varieties.

Resistant rice varieties appear to have higher levels of phenolic compounds, lower levels of free amino acids, and lower concentrations of reducing sugars (Thayumanavan et al 1990). Resistant varieties contain higher concentrations of three types of flavenoid glycosides, which were shown to inhibit feeding (Grayer et al 1994). As a minor source of resistance, cuticular waxes have been identified as repellents to BPH (Cook et al 1987, Woodhead and Padgham 1988). Silicic acid (Yoshihara et al 1979c), oxalic acid Yoshihara et al (1980b), and β-sitosterol (Kaneda 1982, Shigematsu et al 1982) have been proposed to be feeding inhibitors. Because silicic acid is found outside of the phloem, Yoshihara et al (1979c) suggested that silicic acid may function to localize BPH feeding. However, silicic acid occurs in both resistant and susceptible rice varieties (Saxena 1986). The discovery of both nutritional and defensive compounds strongly suggests that resistant varieties may consist of lower concentrations of nutritional compounds and higher concentrations of defensive compounds.

New molecular techniques have provided insight into rice defensive responses to *N. lugens*. In general, phloem-feeding insects appear to be perceived by plants as pathogens and induce either salicylic acid or jasmonic acid/ethylene-signaling pathways, causing the plants to produce pathogenesis-related proteins (PR) (Walling 2000). Planthopper feeding on rice also induces PR proteins (Kanno et al 2005, Wang et al 2005) and the salicylic acid pathway (Xu et al 2003, Zhang et al 2004). *N. lugens* feeding also induces the expression of protease-inhibitor (PI) genes such as oryzacystatin (Zhang et al 2004, Wang et al 2005), which affects protein digestion in insect midguts (Broadway et al 1986, Jongsma and Bolter 1997). Rice resistance to sap-feeding insects is unlikely to be related to a single compound and is more likely a whole-plant response. The availability of molecular tools such as the rice genomic microarrays will certainly provide insight into the expression profiles and responses of resistant and susceptible plants.

The rice phloem largely consists of water and sugar. It contains some amino acids and phenolic compounds, and the balance between nutritional and defensive compounds appears to influence the feeding preference and nymphal performance of *N. lugens*. Further research should be encouraged that examines the relative importance of nutritional vs. defensive compounds on planthopper performance. For example, studies correlating the biochemical composition of phloem from resistant and susceptible rice varieties, planthopper honeydew biochemical composition, and planthopper feeding behavior could be analyzed using multivariate statistics to help discriminate the key biochemical factors linked with *N. lugens* host acceptance and performance.

Rapid adaptation to new varieties

The outbreaks of *N. lugens* in the early 1970s spurred intensive efforts to identify and develop germplasm resistant to *N. lugens*. Several genes, such as *bph1*, *bph2*, and *bph3*, were identified and bred into the germplasm by IRRI and other national research institutes in Asia (Khush 1979). While IR26 with the *Bph1* gene initially performed well in the field, planthopper outbreaks resumed within a few years of the release (Gallagher et al 1994). "Virulence," or the ability to exploit resistant varieties, evolves quickly when *N. lugens* are exposed and adapt to new varieties (Claridge and den Hollander 1980, den Hollander and Pathak 1981). The new populations of *N. lugens* that performed well on the resistant germplasm were labeled biotypes 1 and 2 (Pathak and Heinrichs 1982).

An intense debate surrounded these "biotypes" and whether they could be considered reproductively isolated populations (den Hollander and Pathak 1981, Claridge and den Hollander 1983, Saxena and Barrion 1985, Shufran and Whalon 1995). It has now been accepted that *N. lugens* are highly adaptable, and can quickly be selected to improve their performance on resistant varieties within several generations in the laboratory (Claridge and den Hollander 1982). The pattern has been repeated again on many other resistant varieties. Given the extreme variability within each "biotype" and the rapidity with which one biotype can adapt to another resistant variety, the concept of biotypes appears to be more of selected populations rather than host races on their way to speciation (Claridge and den Hollander 1983, Shufran and Whalon 1995). Many genes for resistance exist today, but it is unknown whether each of these genes is linked with a different biochemical product or pathway. The extremely rapid rate by which *N. lugens* can adapt to resistant rice varieties strongly indicates that a mechanistic understanding of planthopper adaptation is needed to guide host-plant resistance breeding activities. Given the variability in a current phenotyping assay such as the Standard Seedbox Screening Test, it will be much more reliable to select plants based upon phloem chemistry than by nymphal feeding preferences.

Endosymbionts support *N. lugens* amino acid metabolism

The nutritional imbalance and limited availability of amino acids in the phloem inhibit the growth and development of phloem-feeding insects. All phloem-feeding hemipteran insects support symbiotic microorganisms (Douglas 1989, 1998), and endosymbionts have recently emerged as a possibly major factor in determining host specialization in sap-feeding insects (Tsuchida et al 2004). Endosymbionts may also facilitate host specialization for *N. lugens* as well. In planthoppers, yeast-like endosymbionts (YLS) within the fungal family Clavicipitaceae (Suh et al 2001) reside intracellularly in the fat body cells of planthoppers (Buchner 1965, Noda 1974, Cheng and Hou 1996).

YLS are thought to provide rare nutrients to planthoppers to compensate for the unbalanced composition of amino acids in plant phloem (Noda and Saito 1977, 1979). Experimental removal of YLS in *N. lugens* nymphs results in weight loss and a reduced growth rate (Wilkinson and Ishikawa 2001). Aposymbiotic *N. lugens*

contain a lower percentage of total protein, higher concentrations of nonessential free amino acids such as glutamine and arginine, and significantly lower concentrations of the essential amino acid leucine (Wilkinson and Ishikawa 2001). YLS appears to play a role in providing protein through the recycling of uric acid (Sasaki et al 1996). Uric acid is stored in the fat bodies where the symbionts are located and quantities of uric acid within the planthopper decrease when nitrogen is unavailable (Sasaki et al 1996). In addition, YLS also synthesize ergosterol-5,7,24(28)-trienol, which is a precursor of cholesterol and the molting hormone ecdysone (Wetzel et al 1992). This suggests that the absence of YLS could impair successful development to adulthood. Therefore, YLS appear to play an essential role in supporting planthopper nutrition and development.

YLS could cause *N. lugens* reared on particular rice varieties to show higher nymphal survival or performance on that variety (Claridge and den Hollander 1980). Transplants onto "novel" rice varieties are usually coupled with a depression in nymphal performance for one to two generations. A recent study found that planthoppers reared on TN1 and then transplanted onto resistant host plants (ASD7 or Mudgo) showed a decrease in nymphal performance and increased mortality, but this was also accompanied by a decrease in the density of YLS and transaminase activity (Lu et al 2004). The increase in nymphal performance was also correlated with YLS abundance over subsequent planthopper generations. It is difficult to determine whether adaptation to different rice varieties is due to changes in abundance of different endosymbiont species or forms (Chen et al 2006a), environmental factors influencing endosymbiont activity (Chen et al 2006b), or changes in planthopper physiological machinery. Given that endosymbionts are maternally transmitted, variation in endosymbiont activity may give rise to planthopper populations that differ in feeding and metabolic performance. YLS appear to play an essential role in planthopper feeding performance, and may be linked to variation in rice resistance to *N. lugens*. Before any lasting progress can be made in breeding for rice resistance to planthoppers, it is important to understand the biochemical basis of rice resistance and the relationship between rice plants, planthoppers, and their endosymbionts.

Reproductive isolation and population genetic structure of *N. lugens*

Geographic variation in planthopper-rice interactions suggests that mating structures may also spatially structure *N. lugens* populations in the field, despite annual long-distance migration to temperate rice-growing regions. Differentiation in acoustic signaling could maintain reproductive isolation between *Nilaparvata lugens* populations. Prereproductive courtship behavior of *N. lugens* involves acoustic signaling, and the pulse repetition frequency (PRF) appears to play a large part in mate choice and reproduction (Claridge et al 1985a, 1988). Acoustic playback experiments for both sexes confirm the role of acoustic signaling in mate recognition (Claridge et al 1985a). In studies of acoustic signaling of *N. lugens* associated with rice and a grass, *Leersia hexandra*, females selectively mated with males from the same host-associated population (Claridge et al 1984). The particular acoustic signals of the populations are

retained even when calling occurred on alternate host plants, so the signals were not direct responses to acoustics of the host plant but rather innate population differences (Claridge et al 1985a).

Male planthopper acoustic signaling varies among geographic populations associated with rice (Claridge et al 1985a). *N. lugens* populations from the Solomon Islands, Philippines, and Australia show the greatest differences in PRF and are also the most difficult to hybridize (Claridge et al 1985b). Males that successfully mate with females from another geographic population show PRF values that are more similar to the PRF of the female population (Claridge et al 1984). Also, calls of female planthoppers from the Philippines seem quite different from those of India and Sri Lanka (Claridge et al 1988). Geographic populations of *N. lugens* appear to be more reproductively isolated than a closely related species, *N. bakeri*, because *N. bakeri* shows little variation in PRF between geographic locations, and females appear to be less discriminating (Claridge and Morgan 1993).

Additional biological evidence suggests that rice planthoppers show significant geographic structure. Variation in the ability to migrate may also contribute to population structure. There are geographic differences in the frequency of macroptery, which appears to be under genetic control (Iwanaga et al 1987). Macroptery for *N. lugens* is readily induced in temperate populations, but not in tropical regions (Nagata and Masuda 1980, Iwanaga et al 1987). Therefore, greater gene flow may occur among northern populations than among tropical populations; likewise, tropical planthopper populations may be more differentiated than temperate populations. Planthopper virulence also shows significant variability among geographic populations. *N. lugens* populations in India and Sri Lanka appear to be more virulent against resistant rice varieties than in the rest of Asia (Claridge et al 1982). On the other hand, Australian populations cannot survive on Taichung Native 1, a common rice variety in Asia that is widely considered to be susceptible to planthopper feeding damage (Claridge et al 1988).

Molecular evidence suggests that planthoppers show geographic structure, but the loci used in previous studies did not have the ability to resolve differences between close geographic populations. Frequency differences in several allozyme loci were found among Asian populations, with the largest differences found between Asian and Australian populations (den Hollander 1989). *N. lugens* showed significant genetic variation in mitochondrial DNA among planthopper populations between geographic regions, but populations in Southeast Asia shared the same haplotype (Mun et al 1999). Although these previous studies have suggested that planthoppers show some geographic structure, the use of more variable neutral markers such as microsatellites would enhance the ability to resolve differences between rapidly evolving populations. Microsatellites evolve at a much higher rate, and could be used to resolve recent planthopper history. At IRRI, nine microsatellite loci specific to *N. lugens* have been developed that will be useful for determining *N. lugens* population structure (Ferrater et al, submitted). Also, a newly developed 35K EST library for *N. lugens* should help identify how planthoppers adapt to different rice varieties (Noda et al 2008).

The application of multilocus genotyping to the study of agricultural insect populations offers new opportunities to examine the origin, migration, and amount of differentiation of planthopper populations. It also offers a common tool that can be shared by rice entomologists to determine the degree of relatedness between regional planthopper populations. These new techniques enable us to (1) identify the ancestral source of immigrants, (2) determine the number of migrants between geographic regions or host plants, (3) determine the amount of genetic diversity, and (4) determine the degree of differentiation between geographic populations. Coupled with the whole-genome microarrays available for *N. lugens* and rice, a wealth of genomic resources are now available for the study of *N. lugens* and rice interactions.

Conclusions

The presence of mutualistic endosymbionts appears to increase the complexity of the interactions between *N. lugens* and rice. Planthoppers appear to respond strongly to variation in amino acid content, suggesting that amino acid content is very important in host-plant selection. The dependence of *N. lugens* on YLS for essential amino acids suggests that variation in YLS activity could help to explain variation in planthopper performance on different rice varieties (Lu et al 2004). If environmental conditions favor YLS populations or species differently, this could also increase variability in planthopper-rice interactions. Therefore, variation in planthopper activity across Asia and on different resistant varieties could be due to variation in endosymbiont activity. Given the host-associated mating system of planthoppers, planthoppers need to accept and feed on a particular variety in order to mate on it. This feeding requirement could result in assortative mating of planthoppers within rice—and lead toward substructure in planthopper populations.

Understanding the factors underlying variability in planthopper-rice interactions will benefit both breeding and deployment strategies. One of the key pieces currently lacking is a solid understanding of how phloem chemistry influences planthopper host acceptance and performance. Research activities could study whether resistance is due to nutritional or defensive chemicals in the phloem. Given the increasingly important role of endosymbionts in structuring herbivore diet breadth and activity, research on the role of endosymbionts in planthopper performance should also be prioritized. Further research could use multivariate statistical tools to correlate how the relative abundance of nutritional and defensive compounds in the phloem influences planthopper and YLS activity. Finally, a wide array of new genetic, biochemical, and genomics tools is now available to study YLS, planthoppers, and rice. These insights will certainly support the widespread efforts to develop and deploy resistant rice varieties throughout Asia.

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Notes

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Whitebacked planthopper–induced disease resistance in rice

Masaru Satoh, Kenji Gomi, Masaya Matsumura, Junji Takabayashi, Katsutomo Sasaki, Yuko Ohashi, and Hiroo Kanno

Preinfestation with the whitebacked planthopper (WBPH), *Sogatella furcifera* Horváth, conferred resistance to rice blast (RB) caused by *Magnaporthe grisea* in rice under both laboratory and field conditions. Infestation with either male or female WBPH induced resistance, indicating that their feeding behavior was responsible for the resistance. WBPH infestation restricted to the leaf sheaths also induced resistance, suggesting that the resistance is a systemic phenomenon. Simple mechanical wounding of rice plants did not induce resistance. WBPH infestation induced the expression of pathogen-responsive genes (*PBZ1, POX22.3, OsPR1a, OsPrb1,* and *OsWRKY70*); expression of these genes is normally induced after inoculation with avirulent *M. grisea* and/or *Xanthomonas oryzae* pv. *oryzae* (the pathogen causing bacterial blight of rice). We speculate that these genes play a role in increasing the ability of WBPH-infested rice to respond rapidly and effectively to subsequent pathogen attack.

Keywords: *Sogatella furcifera*, *Magnaporthe grisea*, induced resistance, *PBZ1*, *POX22.3*, *OsPR1a*, *OsPrb1*, *OsWRKY67*, *OsWRKY70*

Attacks by herbivorous insects induce chemical and physical changes in many host plants (Karban and Baldwin 1997, Dicke 1994). In several systems, host changes caused by herbivore damage have had deleterious effects on herbivores making subsequent host attacks. Herbivores that feed on damaged plant tissues have lower survival rates, reduced individual growth rates, and reduced adult weight or fecundity, or all three (Karban and Myers 1989, Denno et al 1995). Matsumura and Suzuki (2003) reported that infestation of rice plants with the whitebacked planthopper (WBPH) *Sogatella furcifera* Horváth (Homoptera: Delphacidae) induced resistance against subsequent infestation with WBPH and the brown planthopper (BPH) *Nilaparvata lugens*; that is, there was a deterioration in the performance and promotion of flight-capable adults that could disperse. However, information about the interspecific relationship between insects and pathogens is limited (Stout et al 2006).

In rice, WBPH infestation and rice blast (RB) disease caused by *Magnaporthe grisea* are economically important throughout Southeast and Far-East Asia, including

Japan. In general, WBPH does not hibernate in Japan. The entire WBPH population emigrates from mainland China to Japan during the rainy season from early June to early July. There, the population of the next generation increases rapidly in rice fields, and its peak occurs in about late July or early August (Watanabe et al 1991). At the same time, RB caused by *M. grisea* also commonly develops in the rice fields of Japan. In addition, Kashiwagi and Nagai (1975) found a correlation between the occurrence of WBPH and RB. We therefore evaluated the interspecific relationships between WBPH and *M. grisea* through the host plants.

Materials and methods

Plant and insect materials

Rice plants (*Oryza sativa* L. cv. Hinohikari) were grown from seed under glasshouse conditions (25 ± 1 ºC, 60–80% relative humidity) and used in all experiments. Tests were conducted on plants grown to around the 5-leaf stage (about 4 weeks postseeding). WBPHs were obtained from a laboratory-reared culture originating from adults collected in 1990 from a rice field in Chikugo, Fukuoka Prefecture, Japan.

Fungal inoculation

Magnaporthe grisea race 007, which was compatible with Hinohikari, was grown on oatmeal medium for 2 weeks at 26 ºC in the dark, and spore formation was induced by placing the cultures under a 20-W BLB light for 2 to 3 days at 24 ºC. Approximately 2 mL per plant of a spore suspension (3×10^5 conidia mL^{-1}) containing 0.05% Tween-20 was sprayed onto the rice plants. The inoculated plants were incubated at 25 ºC with high humidity in the dark for 20 h, and then moved to a greenhouse (25 ºC). The number of typical blast lesions, called S-lesions (susceptible lesions), on the plants was counted 7 days after inoculation.

Effect of WBPH infestation on RB incidence

To verify that infestation with WBPH induces resistance to RB in rice plants, we conducted an inoculation trial (Kanno and Fujita 2003). A cage (50 × 50 × 50 cm; plastic-rod frame covered with a fitted cotton-mesh net) containing 10 rice plants with 100 pairs of newly emerged WBPH adults was used for WBPH infestation. As a control, 10 plants were placed in another cage with no added insects. Twenty-four hours later, the cages and WBPHs were removed from the plants, and all the plants were then inoculated with *M. grisea* as described above. Seven days after inoculation, the number of S-lesions on the plants was counted. The experiment was performed three times. The data were analyzed by Student's *t*-test.

Effect of infestation with sex-segregated WBPHs on RB incidence

To determine whether the decrease in the number of blast lesions induced by infestation with WBPH was dependent on the sex of the insects, we conducted a sex-segregated infestation test (Kanno and Fujita 2003). Sixty rice plants were encased in transparent plastic cylinders (15 cm in diameter and 70 cm in height) and divided into three equal

groups containing 20 plants each. One group of plants was infested with adult male WBPHs, the second was infested with adult female WBPHs, and the third group served as the uninfested control. In the case of the first two categories, 20 male adult WBPHs or 20 female adults were released into the cylinder and allowed to feed and lay eggs on the plants. Twenty-four hours later, the cylinders and WBPHs were removed from the plants, and all the plants were then inoculated with *M. grisea* as described above. Seven days after inoculation, the number of S-lesions on the plants was counted. The data were analyzed by the Tukey-Kramer test.

Effect of restricted infestation with WBPHs on RB incidence

We conducted this test to determine whether or not the observed resistance to RB induced by WBPH feeding was a systemic phenomenon (Kanno and Fujita 2003). In this experiment, to restrict WBPH infestation to the leaf sheaths, rice plants were encased in transparent plastic cylinders (5 cm in diameter and 15 cm in height) that covered only the leaf sheath region, and 5 pairs of adult WBPHs per plant were released into each cylinder. The leaf sheaths of control plants were covered by transparent plastic cylinders without planthoppers. Each group contained 20 plants. Twenty-four hours later, the cylinders and WBPHs were removed from plants, and all the plants were then inoculated with *M. grisea* as described above. Seven days after inoculation, the number of S-lesions on the leaves was counted. Data were analyzed by Student's *t*-test.

Effect of simple mechanical damage on RB incidence

This test was conducted to investigate the effect of the mechanical simulation of WBPH feeding on the incidence of blast lesions (Kanno et al 2005). The leaves of 10 plants were mechanically wounded by puncture with a needle. The plant was punctured 50 times every 12 h for 48 h, so that the total number of needle punctures was 250 per plant. Another 10 plants were used as untreated controls. All the plants were then inoculated with *M. grisea* as described above. Seven days after inoculation, the number of S-lesions on the leaves was counted. Data were analyzed by Student's *t*-test.

Effect of WBPH infestation on RB incidence in the field

To extend the laboratory characterization of WBPH-induced resistance to RB, we evaluated the resistance induced under field conditions (Satoh et al 2005). A field test was conducted in paddy fields at the National Agricultural Research Center for Kyushu Okinawa Region, at Koshi in Kumamoto Prefecture, during the summers of 2002 and 2003. Two adjoining paddy fields (each 10 × 50 m) were used in this test. Four-week-old rice seedlings, raised in nursery boxes, were transplanted (two or three seedlings per hill) in a field in late June.

In the first experiment, we conducted an inoculation trial in a field to which we had applied pesticide to suppress WBPH. In 2002, just before transplanting, the planthopper pesticide fipronil was applied (50 g per nursery box) to half of the seedlings, which were then transplanted in a paddy field (field A). Untreated seedlings were transplanted in another paddy field (field B). To verify the effect of fipronil, population surveys of planthoppers were conducted twice according to Nagata and

Masuda (1978). Subsequently, 6 rice hills per paddy field were inoculated twice with *M. grisea* with the inoculation method using clear cover materials (Kobayashi et al 2001). Seven days after inoculation, the number of S-lesions on the leaves was counted. Data were analyzed by two-way analysis of variance (ANOVA). In 2003, each field was divided into two divisions (5 × 50 m each) with wavy plastic boards to prevent water from traversing the divisions. Just before transplanting, the planthopper and leafhopper pesticide imidacloprid was applied (50 g per nursery box) to half of the seedlings, which were transplanted into two of the four divisions. Pesticide-treated and untreated seedlings were transplanted in the other divisions. Population surveys of planthoppers and leafhoppers were also conducted twice. Eight rice hills in each division were then inoculated with *M. grisea*, as described above. Seven days after inoculation, the number of S-lesions on the leaves was counted. Data were analyzed by two-way ANOVA.

In the second experiment conducted in 2002, six clusters of rice hills (each cluster consisting of 6 hills) that had not been treated with insecticide were randomly selected. Each rice hill was individually encased in a transparent plastic cylinder (60 cm high, 9.5 cm in diameter, top of cylinder covered with gauze). They were divided into two equal groups: plants on which WBPH had and had not been released. Ten pairs of WBPHs were released into each of the 10 cylinders for the WBPH treatment. Two days later, all cylinders were removed and all test plants, both with and without WBPH, were inoculated with *M. grisea* by cluster, as described above. Seven days after inoculation, the number of S-lesions on the leaves was counted. Data were analyzed by Student's *t*-test.

Defense-related rice gene expression analysis in response to WBPH feeding

We used quantitative RT-PCR to analyze the expression patterns of defense-related genes in rice plants in response to WBPH infestation. We selected six genes, including some that encode PR (pathogenesis-related) proteins: *PBZ1* (encoding an intracellular, probenazole-inducible protein, *PR-10*), *POX22.3* (encoding a Class III plant peroxidase), *OsPR1a* (encoding an acidic PR-1-type pathogenesis-related protein), *OsPrb1* (encoding a PR-1 type pathogenesis-related protein), *OsWRKY67*, and *OsWRKY70* (encoding transcription factors involved in the regulation of plant defense response pathways). Rice plants covered with transparent plastic cylinders (15 cm in diameter and 70 cm high) were infested with 20 adult male WBPHs. As mock-treated controls, other plants were put in transparent plastic cylinders but insects were not released on them. All the cylinders and WBPHs were removed from plants, and immediately the 4th and 5th leaves were frozen in liquid nitrogen at time points of 0, 6, 12, 24, and 48 h. Total RNA was extracted from the leaves after each treatment by using Trizol (Invitrogen, Carlsbad, CA, USA) according to the manufacturer's instructions. Quantitative RT-PCR was performed using iQ SYBR Green Supermix (BioRad, Hercules, CA) in an iCycler (BioRad) according to the manufacturer's instructions. Data were analyzed by the method of De Vos et al (2005), with minor modifications. Transcript levels of each gene were normalized by comparison with levels of *actin* transcript.

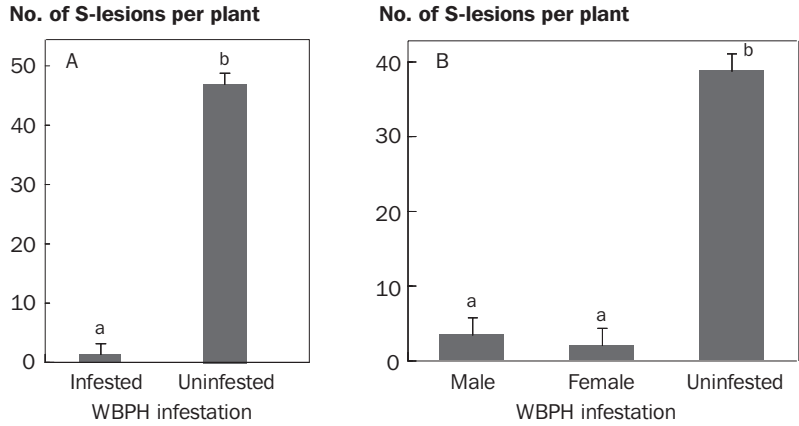

Fig. 1. Incidence of rice blast disease caused by *Magnaporthe grisea* on rice plants (cv. Hinohikari) infested previously with adults of whitebacked planthopper (WBPH), *Sogatella furcifera*. Standard bars indicate mean number of blast lesions per plant and vertical bars on the standard bars indicate SE. (A) Ten rice plants with 100 pairs of newly emerged WBPH adults were used for WBPH infestation. Means accompanied by different letters are significantly different ($P < 0.05$, Student's *t*-test). The experiment was replicated three times. (B) Rice plants were infested previously with male or female WBPH. Twenty male adults or 20 females per plant were released and infested rice plants. Means accompanied by different letters are significantly different ($P < 0.05$, Tukey–Kramer test) (Kanno and Fujita 2003).

Normalized transcript levels of the genes analyzed in each treatment were compared with those of the respective mock-treated controls, and the fold changes in expression level were calculated. The corresponding accession numbers used for quantitative RT-PCR were AK060893 for *actin*, AK071613 for *PBZ1*, AK073202 for *POX22.3*, AJ278436 for *OsPR1a*, AK060057 for *OsPrb1*, AK066252 for *OsWRKY67*, and AK119867 for *OsWRKY70*.

Results and discussion

RB resistance induced by WBPH feeding on rice plants

Rice plants that had previously been exposed to WBPHs were less likely than controls to develop blast lesions caused by *M. grisea*. The number of blast lesions on leaves that had been infested with WBPH was significantly lower at $P < 0.05$ than that on the uninfested plants (Fig. 1A). In the second experiment with sex-segregated WBPH populations, blast incidence on plants that had been infested with either male or female WBPHs was strongly suppressed compared with that on uninfested control plants. The difference in the number of blast lesions between male- and female-infested plants was very small and not statistically significant ($P > 0.05$) (Fig.1B).

These results show that WBPH infestation inhibits incidence of RB. In the first experiment, after removal of the insects, the plants were inoculated with *M. grisea*;

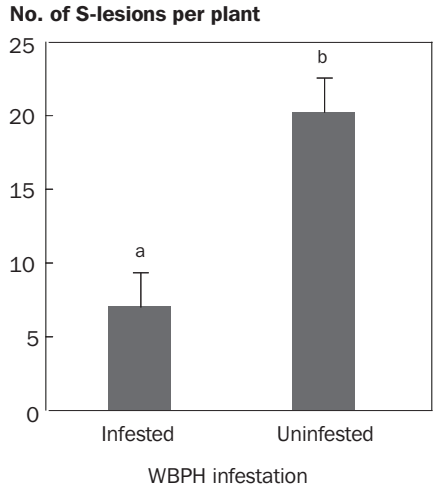

Fig. 2. Incidence of rice blast disease caused by *Magnaporthe grisea* on rice plants (cv. Hinohikari) infested previously on the leaf sheaths with adults of whitebacked planthopper (WBPH), *Sogatella furcifera*. Standard bars indicate mean number of blast lesions per plant and vertical bars on the standard bars indicate SE. Means accompanied by different letters are significantly different ($P < 0.05$, Student's *t*-test) (Kanno and Fujita 2003).

therefore, WBPH infestation induced physiological changes in the rice plant that reduced its susceptibility to later RB infection. It is known that japonica rice cultivars respond sensitively against oviposition of WBPH and produce an ovicidal substance, benzyl benzoate (Seino et al 1996). Moreover, the fact that the numbers of blast lesions did not differ significantly in the presence of all-male or all-female WBPHs indicates that disease inhibition was induced by the feeding behavior of either sex rather than by the oviposition behavior of females.

Systemic effect of WBPH-induced RB resistance

In the typical phenomenon of induced resistance in plants, systemic acquired resistance (SAR), plants respond to local attack by pathogens with a *de novo* production of compounds to resist pathogens. Responses occur not only in the plant organ originally attacked (local response) but also in yet unaffected distant parts (systemic response).

When WBPH infestation was restricted to the leaf sheaths, the number of blast lesions on the leaves that had been infested with WBPH was significantly lower at $P < 0.05$ than that on the uninfested control plants (Fig. 2). The number of blast lesions on plants of which the leaf sheaths had been previously infested with WBPH was about 40% lower than that on control plants. Therefore, WBPH-induced resistance to RB appears to be a systemic phenomenon such as SAR.

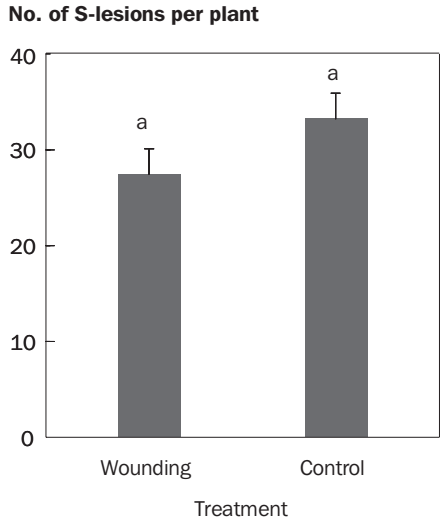

Fig. 3. Incidence of rice blast disease caused by *Magnaporthe grisea* on rice plants (cv. Hinohikari) wounded by puncture using a needle. Standard bars indicate mean number of blast lesions per plant and vertical bars on the standard bars indicate SE. Means accompanied by different letters are significantly different ($P < 0.05$, Student's *t*-test) (Kanno et al 2005).

Lack of effect of simple mechanical damage on RB incidence

The mean number of S-lesions on needle-punctured rice plants was only slightly lower than that on control plants. There was no significant difference ($P > 0.05$) in the incidence of RB between wounded plants treated by needling and untreated control plants (Fig. 3). This result suggests that the trigger for the induced resistance is not the simple mechanical effect of WBPH feeding behavior on the plants; instead, it must be some chemical substance or substances in the WBPH's saliva.

Efficacy of WBPH-induced RB resistance under field conditions

We used fipronil, a planthopper pesticide, to suppress WBPH in 2002. The population density of WBPH was lower on plants treated with fipronil than on untreated plants (Table 1). When the plants were inoculated with *M. grisea*, the number of blast lesions on plants treated with fipronil (Field A) was significantly higher than that on plants not treated with fipronil (Field B). In Field A rice plants inoculated with *M. grisea* on 16 July, the mean number of blast lesions per plant was 29.2; in Field B plants it was 11.2 (ANOVA, $F = 21.6$, $P < 0.001$). In Field A rice plants inoculated with *M. grisea* on 23 July, the mean number of blast lesions per plant was 13.2; in Field B it was 9.8 (ANOVA, $F = 14.3$, $P < 0.01$) (Table 2). In 2003, we used imidacloprid, a

Table 1. Field difference in population densities of Sogatella furcifera on fipronil-treated plants and untreated plants in 2002.

Date	No. of adults per hill (mean ± SE)		*P*-value[c]
	Field A[a]	Field B[b]	
27 June	0.01 ± 0.01	0.2 ± 0.05	< 0.001
8 July	0.02 ± 0.01	0.3 ± 0.05	< 0.001

[a]Containing plants to which fipronil had been applied as pretransplant seedlings. [b]Containing plants that had not received fipronil as pretransplant seedlings. [c]Number of adults was transformed to $(X + 0.5)^{1/2}$ before analysis. Significance was tested by Student's *t*-test.
Source: Satoh et al (2005).

Table 2. Incidence of rice blast disease caused by *Magnaporthe grisea* on rice plants in paddy fields where the occurrence of *Sogatella furcifera* was regulated by fipronil.

Date of inoculation of *M. grisea*	No. of blast lesions per hill (mean ± SE)	
	Field A[a]	Field B[b]
16 July	29.2 ± 2.8	11.2 ± 1.9
23 July	13.2 ± 2.0	9.8 ± 2.3

[a]Containing plants to which fipronil had been applied as pretransplant seedlings. [b]Containing plants that had not received fipronil as pretransplant seedlings.
Source: Satoh et al (2005).

pesticide of planthoppers and leafhoppers, to suppress WBPH because small numbers of the green rice leafhopper *Nephotettix cincticeps* (Uhler) (Homoptera: Cicadellidae) had been found in population surveys conducted the previous year. The population density of WBPH was lower on plants treated with imidacloprid than on untreated plants (Table 3). When the plants were inoculated with *M. grisea*, the number of blast lesions on plants that had been treated with imidacloprid was significantly higher than that on plants not treated with pesticide (ANOVA, $F = 13.7$, $P < 0.001$). There was no significant difference in the number of blast lesions between replications (ANOVA, $F = 3.4$, $P > 0.05$) (Table 4). These results indicate that the incidence of blast lesions in the field was significantly higher on plants to which fipronil or imidacloprid had been applied than on those to which pesticides had not been applied. The cause of this

Table 3. Effect of imidacloprid application to pretransplant seedlings on the population density of *Sogatella furcifera* in paddy fields in 2003.

Date	No. of adults per hill (mean ± SE)[a]		P-value
	Imidaclorid		
	Applied	Not applied	
3 July	0.4 ± 0.05	2.0 ± 0.2	<0.0001
10 July	0.06 ± 0.02	4.2 ± 0.2	<0.0001

[a]Number of adults was transformed to $(X + 0.5)^{1/2}$ before analysis. Significance was tested by Student's *t*-test.
Source: Satoh et al (2005).

Table 4. Incidence of rice blast disease caused by *Magnaporthe grisea* on rice plants in paddy fields where the occurrence of *Sogatella furcifera* was regulated by imidacloprid.

Replication	No. of rice blast lesions per hill (mean ± SE)	
	Imidacloprid	
	Applied	Not applied
Rep. 1	0.4 ± 0.05	2.0 ± 0.2
Rep. 2	0.06 ± 0.02	4.2 ± 0.2

Source: Satoh et al (2005).

difference is surely WBPH-induced RB resistance: we speculate that suppressing the occurrence of WBPH suppressed WBPH-induced RB resistance.

We also conducted WBPH-release experiments in the field. When WBPH was released and allowed to feed on rice plants, the blast lesions on plants on which WBPH had been released were significantly lower at $P < 0.005$ than those on plants not exposed to WBPH. WBPH-induced resistance to RB under field conditions with the release of WBPH reduced the number of blast lesions to 20% of that in the control (Fig. 4).

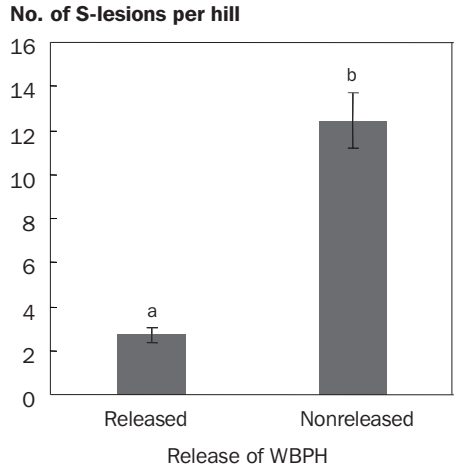

Fig. 4. Incidence of rice blast disease caused by *Magnaporthe grisea* on rice plants (cv. Hinohikari) in paddy fields to which adults of white-backed planthopper (WBPH), *Sogatella furcifera*, had previously been released. Standard bars indicate mean number of blast lesions per hill and vertical bars on the standard bars indicate SE. Means accompanied by different letters are significantly different ($P < 0.005$, Student's *t*-test) (Satoh et al 2005).

Defense-related gene expression analysis in rice plants

We had already investigated the up-regulation of two β-*1,3-glucanase* genes (*Gns4* and *Gns5*) in rice plants infested with WBPH and had confirmed that expression of both genes was up-regulated in WBPH-infested plants compared with that in uninfested controls. β-1,3-glucanase is a PR-2-type pathogenesis-related protein and is well known as a defense-related substance induced in plants against fungi (Kanno et al 2005).

We also analyzed the expression patterns of six defense-related genes, *PBZ1*, *POX22.3*, *OsPR1a*, *OsPrb1*, *OsWRKY67*, and *OsWRKY70*, in rice plants infested with WBPH. Expression of *PBZ1* was induced 12 h after WBPH infestation, peaking 24 h after infestation. *POX22.3*, *OsPR1a*, and *OsWRKY70* expression was induced and it peaked 24 h after WBPH infestation. *OsPrb1* expression was induced at 12 h and stayed at the same level until 48 h after WBPH infestation. Expression of *OsWRKY67* decreased quickly to half the basal level 6 h after infestation but increased slightly thereafter (Fig. 5). These genes are well established as defense-related genes involved in responses to inoculation of avirulent *M. oryzae* and/or *Xanthomonas oryzae* pv. *oryzae* (the pathogen causing bacterial blight of rice) (Midoh and Iwata 1996, Chittoor et al 1997, Kim et al 2001, Ryu et al 2006). Our results suggest a role for these induced genes in increasing the ability of WBPH-infested rice to respond rapidly and effectively to subsequent pathogen attacks.

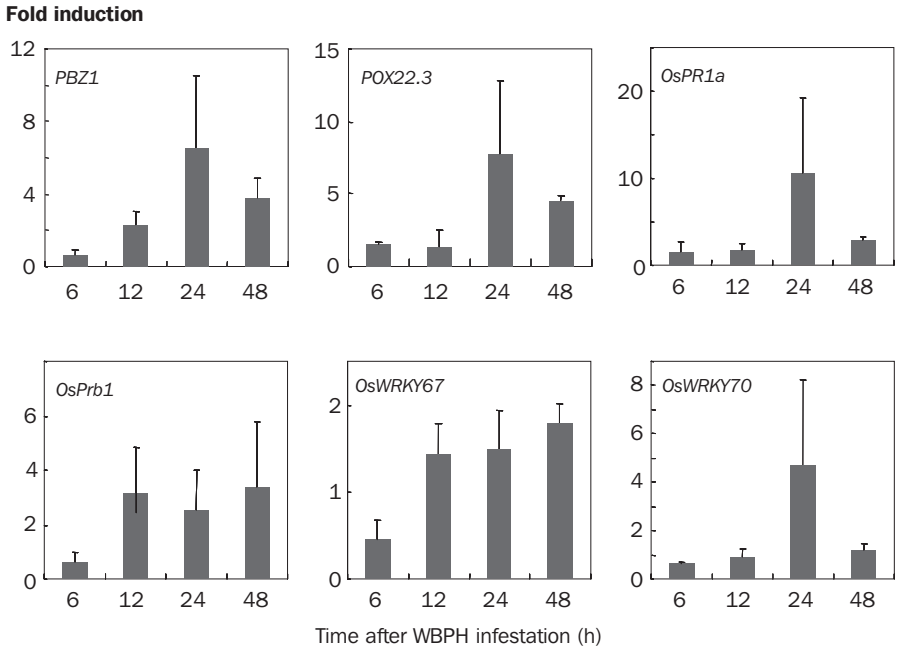

Fig. 5. Quantitative RT-PCR analysis of six genes in rice infested with whitebacked planthopper (WBPH), *Sogatella furcifera*. Expression of these genes is induced after inoculation with avirulent *Xanthomonas oryzae* pv. *oryzae* (Midoh and Iwata 1996, Chittoor et al 1997, Kim et al 2001, Ryu et al 2006) or avirulent *Magnaporthe oryzae* (Kim et al 2001) in rice. Fold induction of six genes at 6, 12, 24, and 48 hours after infestation of WBPH in rice is shown. Values are the means ± SD of four independent samples.

Conclusions and perspectives

As mentioned above, we revealed that infestation with WBPH induces resistance to subsequent attack by *M. grisea* and planthoppers. These facts suggest that the phenomenon of WBPH-induced resistance is effective against other pathogens. Consistent with this suggestion, we found that WBPH infestation also inhibits the development of bacterial blight of rice, which is among the most serious rice plant diseases of most rice-growing countries (Gomi et al, unpublished data). Moreover, we found that the induced resistance to the bacterial pathogen in rice was strong with WBPH but not with BPH infestation (Gomi et al, unpublished data). From these results, we speculated that various defense-related substances were produced in rice plants as a result of WBPH infestation but not of BPH infestation. Thus, we also performed large-scale screening with a rice DNA microarray to investigate the molecular mechanisms involved in WBPH-induced resistance. Up-regulation of vast amounts of genes, including many defense-related genes, was caused by the feeding of WBPHs but not by BPH on rice (Gomi et al, unpublished data). This suggests that rice plants undergo dramatic physiological changes in response to the feeding of WBPHs. Studies of the specificity of

the defense-related substances produced will be needed if we are to paint the whole picture of the rice plant response to WBPH feeding.

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Ecology and species interactions

Migration of rice planthoppers and simulation techniques

Akira Otuka

To analyze and predict long-distance migration of rice planthoppers, a variety of simulation models have been developed in the past. Initially, synoptic weather charts were used to find the relationship between immigrations and weather conditions. Subsequently, many two-dimensional computer simulation models have been proposed to predict migrations. Although these models were successful in migration prediction, there is room for improving prediction quality. A first three-dimensional simulation model was developed in the late 1990s, and it showed considerable advancement in prediction technologies. Recently, a migration prediction system was developed using a new Lagrandian type of three-dimensional model, and it presents real-time information on timing and areas of migration in eastern Asia. This chapter summarizes a history of state-of-the-art simulation models and presents recent migration analyses using these simulation techniques.

The brown planthopper *Nilaparvata lugens* (Stål) and the whitebacked planthopper *Sogatella furcifera* (Horváth) are major pests of rice in Asia. Many studies on the migration of these species, especially in East Asia, have been intensively conducted with a variety of methods, such as catches on ships and airplanes as well as in rice fields and on the tops of mountains (e.g., Kisimoto 1971, Ohkubo and Kisimoto 1971, Kisimoto 1976, Cheng et al 1979, Dung 1981, National Cooperative Research Group of Brown Planthopper 1981a,b). Meteorological analyses, radar observations, and mark and recapture field experiments have also been conducted (e.g., Kisimoto 1976, Nanjing Agricultural College et al 1981, Rosenberg and Magor 1983, Seino et al 1987, Watanabe and Seino 1991, Riley et al 1991, Sogawa 1995, Turner et al 1999). Based on these studies, it is now believed that the species migrate for long distances ranging from northern Vietnam to China, Korea, and Japan in a few generations.

The temporal change of the biotypes of various *N. lugens* populations indicated that the populations in Asia are grouped into three: the East Asian, Southeast Asian, and South Asian (Sogawa 1992). These populations have been shown to have different properties of insecticide susceptibility (Nagata 2002, Nagata et al 2002) and wing-form response (Nagata and Masuda 1980, Iwanaga et al 1987), as well as feeding

on resistant rice varieties (Sogawa 1992, Tanaka and Matsumura 2000). *N. lugens* occurring in the region ranging from northern Vietnam, China, and Korea to Japan belongs to the East Asian population (Sogawa 1992).

To analyze and predict the migration of the East Asian population, several two-dimensional methods have been proposed. For example, to find the migration source, backward trajectories in the wind fields obtained from upper-air data every 6 h have been calculated by using a streamline-isotach method (Rosenberg and Magor 1983). A similar two-dimensional model has been used for migration prediction in China (Zhou et al 1995). A prediction model that uses low-level jet development over the East China Sea was proposed (Seino et al 1987). Based on this model, a software application to predict migrations was developed (Watanabe et al 1990, 1991). To estimate migration sources for immigrants into western Japan, Sogawa (1995) used a backward trajectory analysis of migrations from 1987 to 1990 with 12-hourly data. However, since these methods used only weather data at a particular pressure level (mainly at 850 hPa) at long time intervals such as 6 or 12 hours, their analytical and prediction qualities were limited spatially and temporally. Moreover, a previous study by means of airplane collection indicated that the flight height of rice planthoppers flying over southern China in July over three years ranged from 300 to 2,500 m, with a peak of the aerial density at 1,500 to 2,000 m (Dung 1981). In late September and October, the flight height decreased to 500 to 1,000 m. The aerial density at lower levels dynamically changed to show an increase due to the drop in air temperature during weather changes (Dung 1981). Additionally, a radar observation in September in China revealed that the layers of these insects often had well-defined ceilings corresponding to an air temperature of 16 °C (Ohkubo 1973, Riley et al 1991). Since the insects dynamically fly at various altitudes depending on the air temperature, a migration simulation in three dimensions that can calculate aerial densities and trajectories at different levels has been needed.

Recently, three-dimensional migration models have been developed to improve analytical and prediction qualities. There are two types of migration models: one is a temporally forward model and the other is a backward one. The forward model calculates temporal evolution of the aerial density of rice planthoppers. The backward model tracks planthoppers' trajectories backward from an immigrated area to the source. This chapter reviews these recent models and their migration analyses.

Analyses by three-dimensional models

BLAYER model

Features of the model. A three-dimensional atmospheric numerical model for planthopper migration, BLAYER, was developed for the first time by an international team with researchers from New Zealand and South Korea (Turner et al 1999, Zhu et al 2000). This model simulates atmospheric flows in the boundary layer less than 2,200 m above the ground. It is a hydrostatic model. The relative aerial density of planthoppers in each grid cell of 0.5 degrees (about 50 km at mid-latitudes) is calculated by directly solving an advection-diffusion equation. This is a so-called an

Eulerian representation, in which the grid points are fixed, and parcels of flowing air with planthoppers are convected across the grid from one cell to another. Because of the lack of knowledge on the migration process, the following assumptions are made for the modeling of major immigrations into Korea in June and July: the source of rice planthoppers is assumed to be two regions depending on month—one a region south of 25°N and east of 105°E for analyses in June (mainly Guangdong and Guangxi in China and northern Vietnam), and the other a Chinese region north of 25°N, south of 30°N, and east of 105°E for analyses in July. The source moves with time because rice planthoppers invade northern regions in southern China in later seasons (Cheng et al 1979). Rice planthoppers are presumed to take off at 0900 local time, or 0100 UTC (Universal Time Coordinate), and to keep flying during the prediction duration of 48 h without landing along the way. It is also assumed that they fly at altitudes from 500 to 2,200 m (the model top).

Analytical results. The simulation results showed that the model could explain the large migrations captured by daily light traps in South Korea (Turner et al 1999). The model could reproduce the first migration of the season in early June and major migrations from late June to early July (Turner et al 1999).

The study importantly pointed out that the wind direction in the lower troposphere changes at different levels. When a geostrophic southwest wind blows parallel to isobars at a high level of 850 hPa, which is often the case in the *Bai-u* rainy season in East Asia, a southerly wind blows at the surface level. This is due to the surface friction of the rotating Earth, and this phenomenon is called the Ekman Spiral (Stull 1988, Ogura 1971). Therefore, the flight heights of migrants may affect their arriving areas. Inversely, immigrants arriving at different heights over the monitoring site may have come from different source regions.

BLAYER was successful for the planthopper migration simulation. However, there seems to be some room for improvement: (1) the top level of the model is limited (2,200 m), whereas the atmospheric dynamics above this layer are also important to simulate an accurate state of the whole atmosphere; (2) the takeoff time was mainly set to 0100 UTC, but observed takeoff events of rice planthoppers occur at dusk and dawn, or at about 1000 and 2100 UTC in summer (Ohkubo and Kisimoto 1971, Lai 1982, Riley et al 1991).

Backward trajectory analysis model (BTA model)

Features of the model. To estimate possible migration sources, models to calculate the backward trajectories of planthoppers from monitoring trap sites have been used. The first three-dimensional model is one developed by Otuka et al (2005a). The method employs both an advanced weather forecast model and a BTA model. The weather forecast model, MM5, calculates three-dimensional wind fields with temporally and spatially high resolutions and the BTA model calculates three-dimensional backward trajectories using simulated winds.

MM5 is a limited-area, nonhydrostatic, terrain-following sigma-coordinate model designed to simulate or predict mesoscale and regional-scale atmospheric circulation (Anthes and Warner 1978, Grell et al 1994, NCAR 2003). The model has

many sophisticated features such as choices of physical parameterization, multiple nesting capability, simulation output of high temporal and special resolutions, and global relocatability of calculation domains (NCAR 2003). This last feature enables researchers to simulate the atmosphere anywhere on Earth if global initial data are available. For analyses of past migration events, the initial data used in the simulation are NCEP/NCAR reanalysis data, which are 6-hourly global data with a 2.5-degree horizontal resolution (Kistler et al 2001). The horizontal resolution of the calculation domain is set at 33 km. The model's top level is usually 100 hPa (about 16 km in the standard atmosphere), and therefore the model simulates atmospheric flows in the troposphere as well as a lower part of the stratosphere. In the vertical direction, there were 24 levels from the surface to the top. The model outputs simulated data at 1-hour intervals.

In the BTA model, it is assumed that planthoppers travel at the same velocity as the wind during flight. Therefore, backward trajectories are calculated simply by the following equations:

$$\begin{aligned} x(t-1) &= x(t) - Udt \\ y(t-1) &= y(t) - Vdt \\ z(t-1) &= z(t) - Wdt \end{aligned} \tag{1}$$

where (x, y, z) denote insect position, (U, V, W) spatially and temporally interpolated values of wind velocity output by MM5, and t the calculation time step. One time step (dt) is set to 50 sec. The equations apparently do not consider air temperature in any way. Trajectories start over the trap site on a catch date and are terminated at dawn or dusk, when *N. lugens* and *S. furcifera* are known to take off (Ohkubo and Kisimoto 1971, Lai 1982). The distribution of terminal points over the land indicates possible migration sources.

Estimated sources. Kyushu, in the western part of Japan, is the front of immigration in the *Bai-u* rainy season (Fig. 1). Using catch data in both net traps in June from 1988 to 2001 in northern Kyushu and a suction trap in southern Kyushu, backward trajectories were calculated and possible sources were estimated (Otuka et al 2005d). The results indicated that the source was Fujian, eastern Guangdong, southern Jiangxi Province in China and Taiwan (Fig. 2). However, since harvesting of the first rice crop in Taiwan is usually completed by mid-June, only southern China is the possible source for migrations from late June to early July. The results also indicated that the possible source estimated by two-dimensional analysis tended to be the southwestern part of the source region estimated by the three-dimensional analysis. This was due to the difference in wind speed and direction at each level. The wind at 850 hPa, which is used in the two-dimensional analysis, shows higher speed and a more westerly component than the wind at lower levels.

*Cross-boundary migration***.** In the introduction, it was mentioned that the populations in Asia have been grouped into three (Sogawa 1992). The boundary between the East Asian and Southeast Asian populations lies between the Philippines and Taiwan. Migrations across this boundary have been investigated (Otuka et al 2005c). Three

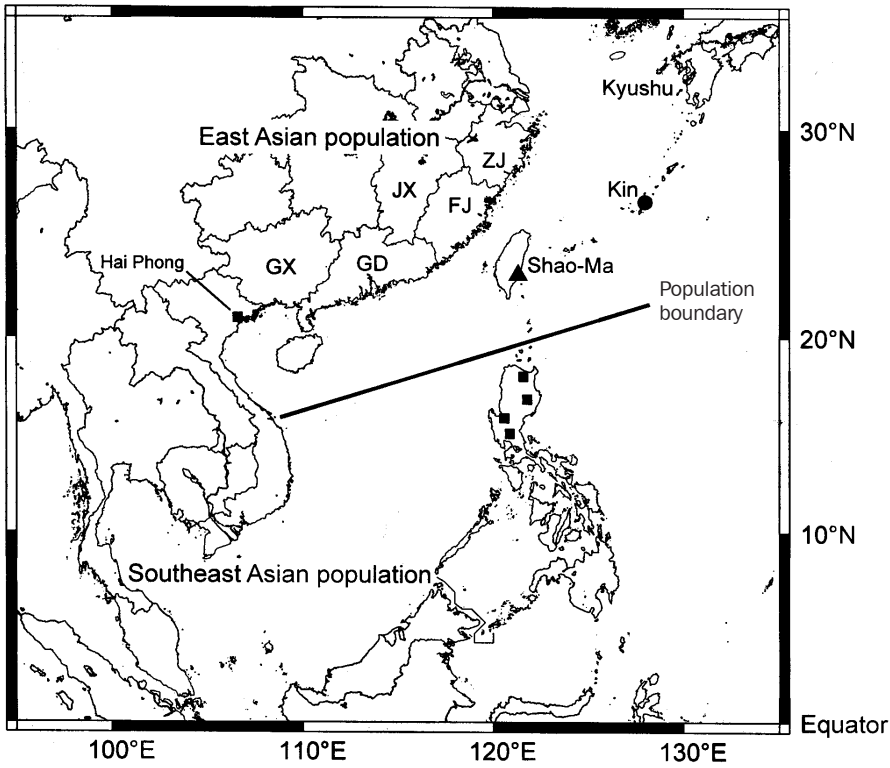

Fig. 1. Area of interest for this chapter. The boundary between the East Asian population and the Southeast Asian population lies between Taiwan and the Philippines. Solid squares in northern Vietnam and Luzon indicated takeoff areas for migration simulation by GEARN.

migration events have been found to be such a cross-boundary migration (CBM). Table 1 shows three peaks of *N. lugens* captured in eastern Taiwan and Okinawa Island of southwestern Japan. Figure 3 shows the distribution of terminal points of BTA for the three peaks. In all cases, the trajectories reached over the Philippines, where its population of *N. lugens* belongs to the Southeast Asian population, having different properties important for pest management such as insecticide susceptibility and wing-form response. It is still unknown how often CBM happens and how much impact on the East Asian population the gene mixing has. Continuous careful monitoring is necessary.

GEARN

Model description. A migration simulation model, GEARN, was developed under cooperation between atomic energy researchers and entomologists in Japan (Nature 2004, Furuno et al 2005). GEARN was originally a simulation model for predicting the dispersion of radioactive particles released in a future potential accident in an atomic

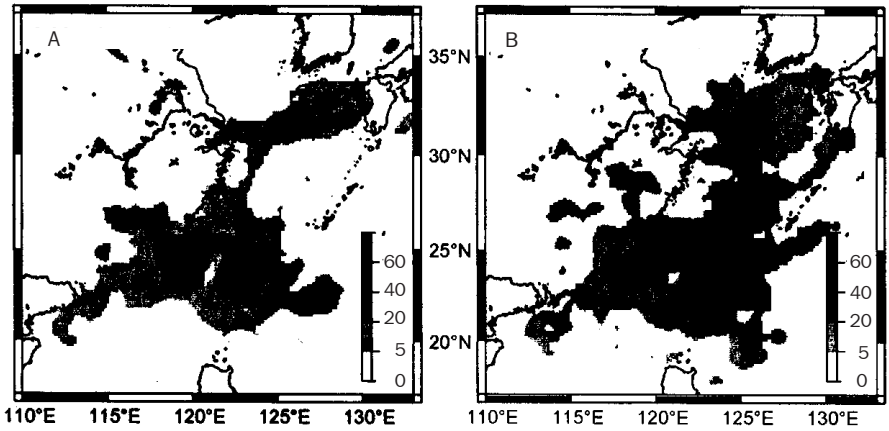

Fig. 2. Distribution of terminal points of backward trajectories that started over northern and southern Kyushu, western Japan. Terminal time was set at dusk or dawn in the source regions. (A) Trajectories started over northern Kyushu on dates with a catch peak in June from 1988 to 2001. (B) Trajectories started over southern Kyushu in June from 1988 to 2001. The number indicates the frequency of terminal points in the mesh of 0.5 degree in latitude and longitude. Gray areas of the land, such as Fujian, Guangdong, and Jiangxi provinces in China and Taiwan, indicate the possible migration source. (Modified from Otuka et al 2005c.)

Table 1. Catch number of *N. lugens* in western Japan and eastern Taiwan.[a]

Date	Site	Net/light trap	Number of *N. lugens*	Symbol in Figure 3
15 June 2000	Kin, Japan	Light	0	
16 June 2000	Kin, Japan	Light	3	
17 June 2000	Kin, Japan	Light	109	Circle
18 June 2000	Kin, Japan	Light	49	
17 June 1999	Kin, Japan	Light	0	
18 June 1999	Kin, Japan	Light	0	
19 June 1999	Kin, Japan	Light	23	Star
20 June 1999	Kin, Japan	Light	2	
26 August 1978	Shao-Ma, Taiwan	Net	36	Triangle

[a]Data from the Japan Plan Protection Network and Liu (1985). No catch of *S. furcifera* was recorded in the Japanese cases.

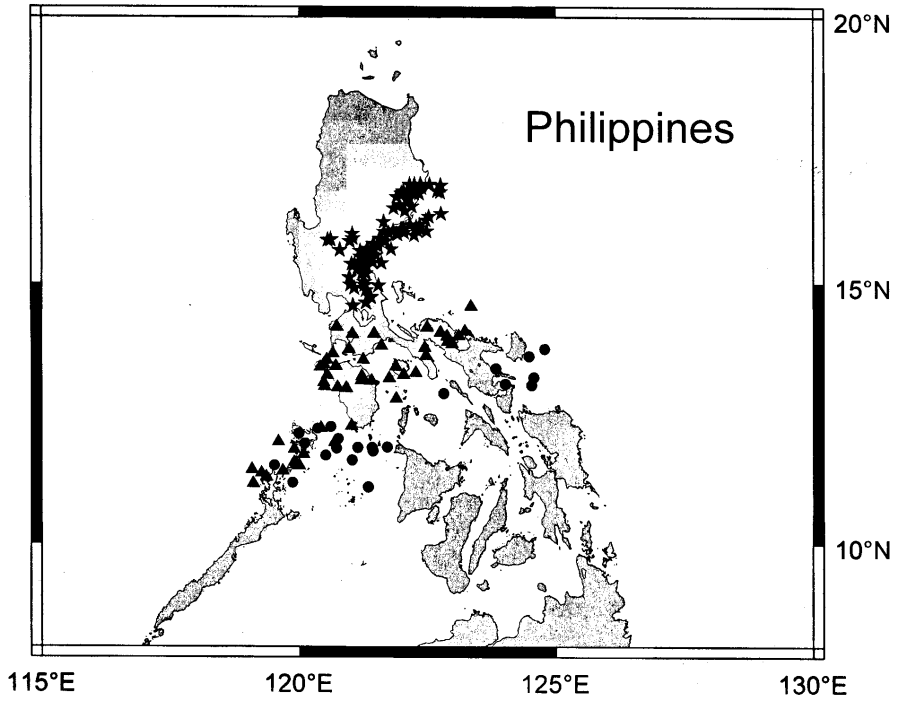

Fig. 3. Distributions of terminal points of backward trajectories that started over Kin and Shao-Ma on the dates of the catch peaks in Table 1. Solid circle indicates terminal point of the trajectories that started over Kin on 17 June 2000. Solid star and triangle indicate terminal points for Kin in 1999 and Shao-Ma in 1978. All the terminal points reached over Luzon. This result suggests cross-boundary migrations from the Philippines to the East Asian population. (Modified from Otuka et al 2005c.)

energy power plant. The model does not calculate the aerial density of planthoppers directly like BLAYER (an Eulerian representation), but traces step by step the three-dimensional positions of many planthoppers during migratory flight, and converts the number of planthoppers in a calculation cell into the aerial density. This is a so-called Lagrangian representation, in which each planthopper moves with flowing air, and the density is calculated as the number of planthoppers in each cell. For planthopper migration study, their various behaviors are mathematically modeled as in Figure 4. First, the model lets planthoppers take off at dawn or dusk in the source. This is based on the observations that *N. lugens* and *S. furcifera* take off during twilight periods of about 100 lx and have two peaks per day (Ohkubo and Kisimoto 1971, Lai 1982). As many as 34,000 insects take off at constant time intervals in 1 hour from random horizontal positions in a takeoff area of 50 km^2. Second, after the takeoff, the planthoppers actively climb upward for 1 hour at a vertical rate of 0.2 m s^{-1}. This rate has been estimated in a radar observation by Riley et al (1991). Third, air currents advect and diffuse the insects, but they won't go beyond the temperature ceiling of 16.5 °C,

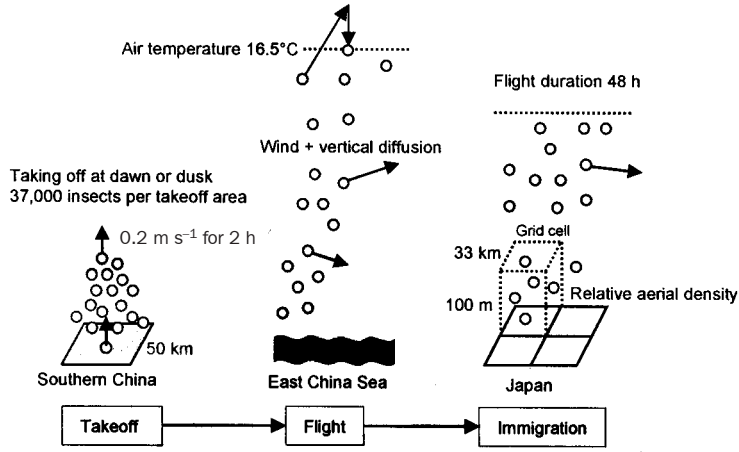

Fig. 4. Schematic diagram of the migration simulation model GEARN. Open circle indicates a planthopper. The insects fly upward for 1 hour after takeoff, and move at the same velocity as the wind, taking vertical diffusion into account. The dotted line indicates an air temperature of 16.5 °C. Planthoppers do not cross this level. Finally, the relative aerial density of the planthoppers over the destination is calculated based upon the number of insects in a grid cell in the lowest layer less than 100 m. (Modified from Otuka et al 2006.)

at which half of *N. lugens* have been found to stop wing-beating in a tethered flight experiment (Ohkubo 1973). Atmospheric data such as wind, temperature, and diffusion coefficients are outputs from the MM5 simulation. During flight, the insects keep flying and do not land on Earth's surface, which is the same as in the BLAYER model. This assumption is made because the landing rate of oversea migrants is unknown at present. The flight duration is set to 48 h. The relative aerial density is computed as insect number per a calculation grid cell at any time step of the simulation.

CBM analysis. By using GEARN, migrations in various regions, such as migrations from China to Japan (Otuka et al 2006), from the Philippines to China and Taiwan (Otuka et al 2005c), and from northern Vietnam to southern China (Otuka et al 2008), have been analyzed. The last two cases are introduced here. As described in the previous section, the backward trajectory analysis revealed that CBMs from the Philippines to East Asia were found to be feasible. If migrations from the Philippines to southern China occurred in the early season, April to June, the next generation of those immigrants in southern China could migrate to farther northern regions in East Asia about one or more months later. Since the insect's properties in the two populations are different from each other, this possible gene mixing could be important for pest management. For this reason, the forward simulation model GEARN estimated possible migrations from the Philippines from April to June under several weather patterns over the South China Sea favorable for such migrations (Otuka et al 2005c). The result showed that 21 migrations at dusk or dawn in 14 days over 10 years from

1995 to 2004 reached southern China. The typical weather patterns were low-pressure systems or typhoons located in the South China Sea, with winds blowing from the Philippines to China. The destination regions were mainly Guangdong, Fujian, and Hainan provinces, which are the source regions of migrations in the *Bai-u* rainy season. Although this result is circumstantial evidence for CBM, continuous careful attention must be paid to the possible change of the insect's properties due to future gene mixing.

Early migration. Simulation from northern Vietnam to southern China has been conducted with light trap data in northern Vietnam (Otuka at al 2008). Although the general pattern of northeastward migrations of *N. lugens* was proposed in previous studies (e.g., Cheng et al 1979), concrete survey data such as daily light trap data have not been reported. Recently, after an outbreak of *N. lugens* in China in 2005, China's provincial plant protection institutions began to release occurrence information with specific light trap data when large immigration peaks were recorded in their provinces. Migration simulations from northern Vietnam were evaluated with these Chinese light trap data. First, the light trap data at Hai Phong in northern Vietnam indicated that emigration peaks of *N. lugens* and *S. furcifera*, which multiplied on winter-spring rice, appeared in late April to early May (Otuka at al 2008) (Fig. 5A). Setting the dates of these peaks as starting dates, migration simulations were conducted. Figure 5B shows an example of a migration simulation that started over Hai Phong from 1100 to 1200 UTC on 28 April 2005. The destination regions of the area of nonzero aerial density at 24 h after takeoff were found to be distributed over southern Chinese provinces: Guangxi, southern Hunan, Jiangxi, northern Guangdong, and northwestern Fujian (Fig. 5C). The region formed a diagonal belt stretching northeast. In fact, according to the Chinese data, immigration catch peaks appeared in light traps along the diagonal belt region, which supported the simulation results.

Migration prediction

The migration simulation model GEARN is used for migration prediction when the weather model forecasts future atmospheric flows (Otuka et al 2005b). First, a 72-hour weather forecast over the East Asia region from Vietnam, the Philippines, China, and Korea to Japan was made with both mesh data output by a global model, the Global Spectral Model of the Japan Meteorological Agency (JMA), and a sea surface temperature data RTG SST of the U.S. National Oceanic and Atmospheric Administration. The temporal and horizontal resolution of the prediction data is 1 h and 33 km, respectively. Second, two sets of migration prediction of 48 h starting at dusk and dawn per 1 day were used. Hence, predictions for 2 days from today were obtained. The prediction results are available at http://agri.narc.affrc.go.jp/.

An example of the prediction performed on 1 July 2007 is shown in Figure 6, which provides information on the timing and area of migration. The hitting ratio of the migration prediction in 2004 to 2006 ranged from 74% to 85%. This value corresponded to the hitting ratio of the weather forecast by the JMA.

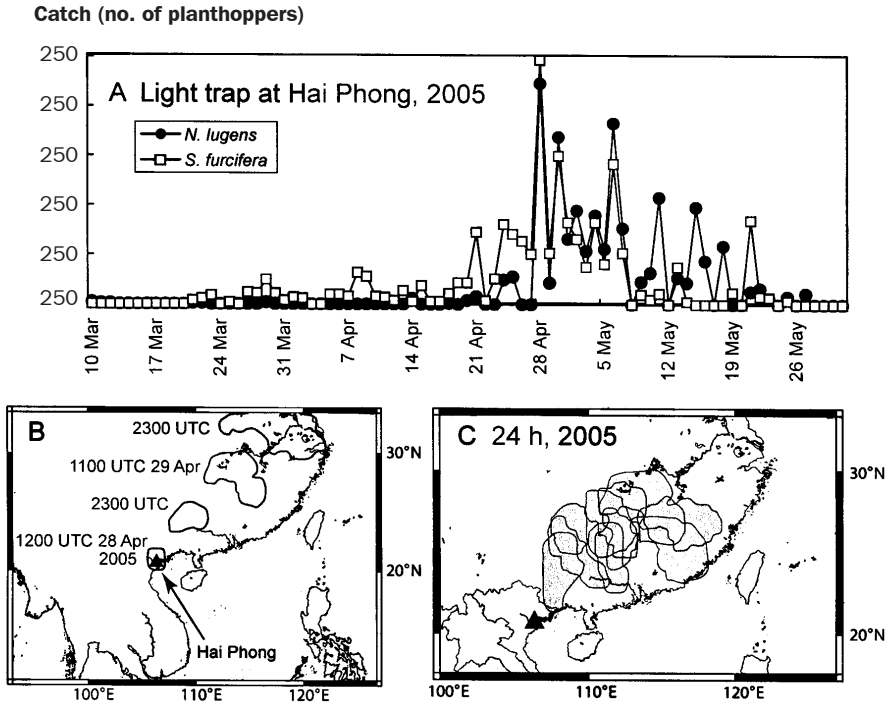

Fig. 5. The daily catch of rice planthoppers in the light trap at Hai Phong, northern Vietnam, in 2005 (A), and simulation results (B, C). (B) A migration cloud, nonzero density region, started over Hai Phong at 1100 UTC on 28 April 2005 and moved northeastward to southern China. (C) The migration simulations for clear catch peaks in Figure 5A were repeated and the migration clouds at 24 h after takeoff were superimposed on the map. This result shows major destination regions in the early migration. (Modified from Otuka et al 2008.)

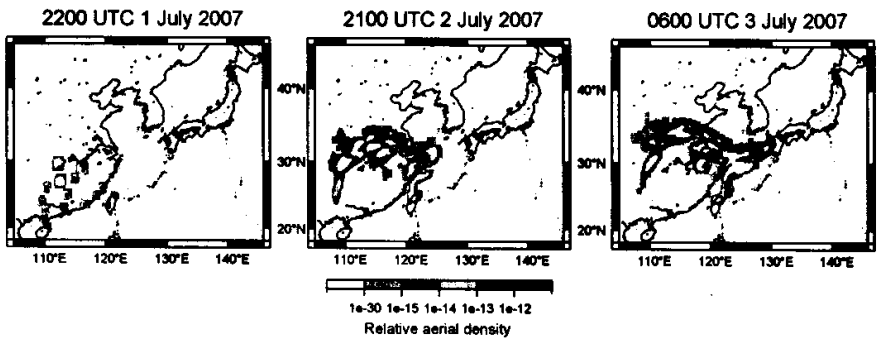

Fig. 6. An example of migration prediction from 1 to 3 July 2007. The migration clouds (regions in gray) from 16 takeoff areas started at 2100 UTC on 1 July 2007. At 0600 UTC on 3 July, the migration clouds reached over Kyushu (see Fig. 1). This prediction was successful, and in fact large catches were recorded mainly in southern Kyushu.

Summary

Since rice planthoppers fly at lower levels warmer than an air temperature of 16.5 °C during migratory flight, three-dimensional models are essential to simulating migrations at such levels. The models enable analyses and predictions with high temporal and spatial resolution. They have therefore become a standard method of migration analysis.

From the BTA and forward simulation results, it was suggested that CBMs are invading the East Asian population, which is a matter of concern and must be monitored. Sufficient information on migrations on the Indochina peninsula is not yet available. The occurrence of planthoppers on the peninsula seems quite different from that in the East Asian population. For example, outbreaks of serious virus diseases transmitted by *N. lugens*, rice grassy stunt and ragged stunt diseases, occurred in 2006 in the Mekong Delta in southern Vietnam, and these diseases remain serious threats. The dispersion of these viruses on the Indochina peninsula and possible CBMs into the neighboring populations should be carefully monitored. A future study on these migrations on the Indochina peninsula is being planned.

The small brown planthopper, *Laodelphax striatellus* (Fallén), is one of the rice planthoppers, and a vector of rice stripe virus (RSV) that causes rice stripe, a serious virus disease of rice. In western Japan, the proportion of viruliferous adults of *L. striatellus* has recently shown a gradual increase to 6–16% according to information released by local plant protection offices. At the same time, it has been reported that, in Jiangsu Province, China, which is located about 900 km west of Japan, an outbreak of *L. striatellus* on the two-crop system of wheat and rice occurred in 2004 and 2005 (Zhu 2006). Fifteen to 50% of the species carried RSV. Recent rice stripe virus epidemics in Zhejiang Province have also been reported (Wang et al 2008). The feasibility of overseas migration from China to Japan and its consequent impact on the local population are a subject of future investigation. Since wheat is harvested from mid-May to mid-June in Jiangsu Province and the dispersion of the insects could occur then, the first target of migration analysis would be possible migrations during that period of time.

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Rice viruses transmitted by the brown planthopper *Nilaparvata lugens* Stål

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The brown planthopper (BPH) *Nilaparvata lugens* transmits both rice grassy stunt (RGSV) and rice ragged stunt (RRSV) viruses in a persistent manner without transovarial passage. RGSV-infected rice plants show severe stunting and profuse tillering. The leaves are stiff and narrow and show occasional interveinal chlorosis and bronzing. RGSV is a member of the *Tenuivirus* group. RRSV-infected plants show stunting, abnormal leaves with serrated edges and/or twisted tips, and vein swelling or galls on the underside of the leaf blades and outer surface of the leaf sheaths. RRSV is a member of the *Oryzavirus* group of the family Reoviridae. In South Vietnam, the two viruses infect the rice plant together and cause the rice yellowing syndrome.

Virus diseases of rice spread by insect vectors have been considered to be of minor importance worldwide, being estimated to cause average actual crop losses of less than 1.5%. However, sporadic epidemics of rice virus diseases could cause devastating damage in a particular region or country (Ramasamy and Jatileksono 1996). For instance, the areas where rice tungro virus disease is epidemic are small in relation to the total rice production of the region or country, but affected fields may suffer a total yield loss. Such damages have a significant impact on the livelihood of farmers in Asia, who generally depend on the crops produced on relatively small farms (Azzam and Chancellor 2002).

The brown planthopper (BPH), *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae), is a serious insect pest of rice, especially in tropical Asia, where rice crops are continuously cultivated. Both nymphs and adults of BPH damage rice plants through extensive feeding on them. BPH also transmits viruses such as rice ragged stunt (RRSV) and rice grassy stunt (RGSV) (Hibino 1989, 1996). Thus, increased levels of BPH occasionally accompany substantial losses of rice crops by the virus diseases. From 2005 to 2006, more than 485,000 ha of rice production area in southern Vietnam were severely affected by viral diseases seemingly spread by BPH, resulting in the loss of 828,000 tons of rice valued at US$120 million (Du et al 2007). The rice virus disease widely observed in southern Vietnam has been called "yellowing syndrome" from the characteristic symptom of leaf yellowing. Rice yellowing syndrome was later found

highly associated with infection with RGSV or co-infection of RGSV with RRSV, both transmitted by BPH, although the symptoms vary depending on varieties and virus species, and the timing and sequence of infection (Du et al 2007).

Rice ragged stunt virus

Rice ragged stunt virus disease was first recognized in 1976 in Indonesia (Hibino et al 1977, Hibino 1979). Later, the disease was reported in Malaysia, the Philippines, Thailand, China, India, Sri Lanka, Taiwan (Hibino 1989, Chen et al 1979), and Japan (Shinkai et al 1980). High levels of RRSV were observed in Indonesia and the Philippines between 1977 and 1981, and in Thailand between 1980 and 1982, and again between 1989 and 1990 (Hibino 1996). Major outbreaks of RRSV incidences had not been reported in other countries until high levels of RRSV were observed in southern Vietnam in 2006 (Du et al 2007).

Rice plants infected with RRSV show stunting, dark-colored leaves with serrated edges or twisted tips, and vein swelling or galls on the underside of leaf blades and outer surface of the leaf sheaths (Fig. 1). The gall results from hyperplasia and hypertrophy of the phloem tissue. Plants infected with RRSV at the seedling stage develop new leaves with distinct symptoms such as twisting and serration 2 weeks after inoculation and thereafter develop leaves showing milder or no definite symptoms. At the flowering stage, the upper leaves and flag leaves may show twisting symptoms. Panicles of infected plants are fully exserted. Electron microscopic observation of diseased tissue revealed that RRSV is localized in the phloem and gall tissues. Inclusion bodies consisting of a viroplasmic matrix and numerous virus particles were observed in infected cells (Hibino 1989, 1996, Ling et al 1978).

RRSV is a member of the family *Reoviridae* and the type species of the genus *Oryzavirus* (Boccardo and Milne 1984, Holmes et al 1994, Nuss and Dall 1990). The virus particles are icosahedral of about 50 nm in diameter (Boccardo and Milne 1984). The virus genome is composed of 10 double-stranded RNA segments each having the genus-specific conserved terminal nucleotide sequences of 5′-GAUAAA---GUGC-3′ (Yan et al 1992). RRSV particles are composed of five major, highly immunoreactive structural proteins with estimated molecular weights of 33, 39, 43, 70, and 120 kDa and at least five minor structural proteins (49, 60, 76, 90, and 94 kDa). Three nonstructural proteins (31, 63, and 88 kDa) were also identified from in vitro translation of the RRSV genome (Lu et al 1988, 1990). The nucleotide sequences of RRSV genome segments S5, S8, and S9 have been determined. The genome segments S5, S8, and S9 apparently encode, respectively, a 90-kDa minor structural protein (Li et al 1996), a 67-kDa major structural protein, which appears to correspond to the 70-kDa protein reported by Lu et al (1988 and 1990) and Upadhyaya et al (1996), and a 38-kDa major structural protein, which appears to correspond to the 39-kDa protein reported by Lu et al (1988, 1990), Upadhyaya et al (1995), and Uyeda et al (1995). The 67-kDa protein is further proteolytically processed to 46-, 43-, and 26-kDa proteins (Upadhyaya et al 1996). Upadhyaya et al (1997) reported that the RRSV genome segments S7 and S10 encode nonstructural proteins of 68 and 32 kDa, respectively.

Fig. 1. Symptoms on rice plants caused by RRSV, RTSV, and RGSV. Variety Taichung Native 1 was inoculated with RGSV, RRSV, or RTSV through insect transmission. (A) Leaf yellowing and stunted growth caused by RGSV and RRSV. (B) Serrated leaf tissue caused by RRSV infection. (C) Twisted leaf tip caused by RRSV infection.

Rice grassy stunt virus

Rice grassy stunt virus disease was first reported in the Philippines in 1963 (Rivera et al 1966). It was also reported in China, Japan, Taiwan, and other countries in South and Southeast Asia (Hibino 1989). High levels of RGSV incidences were reported in Indonesia (1970 to 1977), the Philippines (1973 to 1977 and 1982 to 1983) (Hibino 1989, Hibino et al 1985), India (1972 to 1984) (Kulshreshtha et al 1974, Mariappan et al 1984), and Kyushu, Japan (1978) (Iwasaki and Shinkai 1979).

Rice plants infected with RGSV show pronounced stunting and proliferation of short, erect, and narrow leaves that are pale green or pale yellow in color and infected leaves may show mottling symptoms on young emerging leaves and rusty spots on older leaves (Fig. 1).

Severe strains of RGSV that cause yellow-orange leaf discoloration and premature death of plants were reported in Taiwan (Chen and Chiu 1982), the Philippines, Thailand (Hibino et al 1985), and India (Mariappan et al 1984). The severe strain in the Philippines was designated as RGSV 2 (Cabauatan et al 1985), while the severe strain in Taiwan was called rice wilted stunt virus (Chen and Chiu 1982). Rice cultivars with a gene with resistance to RGSV introduced from a wild rice species, *Oryza nivara* (Khush and Ling 1974), have been widely used. However, the severe strain of RGSV (RGSV 2) in the Philippines was highly pathogenic to the resistant cultivars (Cabauatan et al 1985, Hibino et al 1985).

RGSV-infected rice cells contain masses of fibrils in the nuclei and cytoplasm, and membrane-bound bodies with fibrils in the cytoplasm. Tubules associated with isometric particles of 18 to 25 nm in diameter can be observed in the sieve tubes (Hibino 1986a,b).

RGSV is a member of the genus *Tenuivirus*, which consists of six members with rice stripe virus (RSV) as the type species (Hibino 1986, Toriyama 1995, Falk and Tsai 1998, Mayo et al 2000). RGSV is serologically distantly related to RSV (Hibino et al 1985). Tenuiviruses other than RGSV have four single-stranded, ambisense RNA genome segments, while RGSV possesses six RNA segments (Miranda et al 2000, Toriyama et al 1997, 1998). RNA segments 1, 2, 5, and 6 of RGSV are equivalent to RNA segments 1, 2, 3, and 4 of RSV, respectively. RGSV RNA segments 3 and 4 are unique in this genus. RNA 1 of tenuiviruses except RGSV is negative sense and encodes RNA-dependent RNA polymerase (RdRp) on the complementary strand (cRNA 1), while RNA 1 of RGSV is ambisense and contains a small open reading frame on the viral strand (vRNA 1) (Miranda et al 2000, Toriyama et al 1998). Thus, the tenuivirus genome appeared to encode at least seven proteins, one on cRNA 1 and two each on three other ambisense RNA segments, although the expression and the function of most of them are yet to be investigated. Among the proteins encoded in the RGSV genome, only the functions of the 339-kDa RdRp encoded on cRNA 1 and the 35–36-kDa nucleocapsid protein (N) encoded on cRNA 3 (cRNA 5 in the case of RGSV) are known. The virions are thin filamentous ribonucleoprotein particles of 3–10 nm in diameter consisting of vRNA, cRNA, N proteins, and a few molecules per particle of RdRp (Mayo et al 2000). A 94-kDa protein encoded on cRNA 2 is hypothesized to be a membrane protein (Estabrook et al 1996). No enveloped virions have been observed in tenuivirus-infected plants or insects by electron microscopy (Falk and Tsai 1998). A 21-kDa p6 protein encoded on RGSV vRNA 6 and a 20-kDa protein encoded on vRNA 4 of maize stripe virus (MSpV) were shown to be expressed in infected plants and to form cytoplasmic inclusion bodies, but they have not been detected in the vector insects (Falk et al 1987, Miranda and Koganezawa 1995).

Relationships among BPH, BPH-transmitted viruses, and host plants

RRSV and RGSV are transmitted in a persistent manner by BPH and other species of *Nilaparvata* (Hibino 1986b, 1989, Milne and Ling 1982). The viruses multiply in the vectors. Once the vectors acquire the viruses, they retain the viruses throughout their lifespan even after molting but cannot transmit the viruses through the eggs. BPH carrying RGSV has a shorter lifespan and lower fecundity than virus-free BPH (Hirao et al 1987, Ling 1977). The ability of BPH to transmit the viruses appeared to be inheritable. Populations of BPH with low virus transmission ability can be selected by mating nonviruliferous BPH (Iwasaki et al 1982). RRSV particles were found aggregated in or around the viroplasmic inclusions or arranged in tubules in the cytoplasm of cells of BPH carrying RRSV. Isometric particles of RGSV were found in crystalline arrays in the fat body and tracheas of BPH carrying RGSV (Shikata et al 1980).

RRSV and RGSV can infect other graminaceous plants by artificial inoculation using BPH. However, natural infection of weeds and cereals other than rice is rare, as BPH survive and reproduce mainly in rice (Hibino 1979, 1989, Milne and Ling 1982). Infected rice plants, stubbles, and viruliferous BPH serve as the sources of the virus to spread. The outbreaks of RRSV and RGSV in some countries may have occurred

when the levels of the viruses present in fields reached epidemic proportions due to the increased population density of BPH (Ling et al 1978, Dyck and Thomas 1979). Another probable factor associated with outbreaks of RGSV and RRSV is the long-distance flight of BPH (Hirao et al 1984, Iwasaki et al 1985, Kishimoto 1976). BPH flies from fields affected with the viruses to newly planted rice fields in distant areas and disperses the viruses. BPH and BPH-transmitted viruses are often endemic in tropical Asia. In temperate countries, BPH can migrate annually during the monsoon season from the endemic areas (Cheng et al 1982, Kishimoto 1976, Lee and Park 1977).

Rice cultivars resistant to BPH have been used in many countries of Asia to control BPH and BPH-transmitted viruses. In many cases, the incidences of RGSV in the resistant cultivars initially appeared to be very low; however, biotypes of BPH that can overcome the resistance became prevalent a few or several years after the release of the cultivars (Hibino 1996, Claridge and Den Hollander 1980). Once populations of BPH that can colonize resistant cultivars develop, the cultivars may become a major source of virus spread in fields.

Resurgence of BPH-transmitted viruses in the Mekong Delta

Rice plants showing symptoms suspected to be of viral infection such as leaf yellowing had been reported as early as the 1960s in southern Vietnam and given names such as "yellow stunt," "chlorotic stunt," or "bushy stunt" (Toan 1969). Widespread occurrence of diseases in rice plants suspected to be caused by viruses was also observed in the northern part of Vietnam during 1964 to 1970, affecting virtually all varieties planted on about 50,000 ha (Du 1988). The viral nature of the diseases was not confirmed, but, because of the presence of high populations of green leafhoppers (GLH, *Nephotettix virescens* Distant) in the affected areas, the disease in northern Vietnam was suspected to be caused either by tungro viruses or by yellow dwarf mycoplasma. Rice tungro disease was reported in central Vietnam, but not in the Mekong Delta (Vien et al 1994, 1996). Another occasion of rice disease epidemic in the Mekong Delta supposedly caused by viruses was also recorded during 1978 to 1980 after the outbreak of BPH. The outbreak resulted in more than 90% losses of the rice crops. Rice plants in the affected areas showed typical symptoms of RRSV such as serrated leaves, twisted and malformed leaves, vein swelling on leaf sheaths and blades, leaf curling, and stunted growth (Trung 1985). Other studies also reported the occurrence of RRSV in Vietnam (Vu and Nguyen 1979, Luong and Nguyen 1995).

The rice disease called yellowing syndrome was observed in the Mekong Delta in 1989 but it became more evident after 1994 (Fig. 2). In 1997, the incidence of yellowing syndrome was estimated at 5–10% in many varieties grown in the region, and close to 50% in some fields that received high nitrogen fertilizer. Diseased tillers showed interveinal chlorosis to yellowish color, stunting, and no further growth. The disease was later called "benh vang lun," which means "stunting and yellowing syndrome" in Vietnamese. Based on the epidemiological characteristics, the symptoms, and abundance of BPH in the affected fields, it was suggested that the yellowing

Fig. 2. Rice plants affected by the yellowing syndrome in southern Vietnam, August 2006.

syndrome of rice was associated with "benh lua co dong 2" or "RGSV 2" (Du et al 2005).

The epidemiological characteristics of the yellowing syndrome in the Mekong Delta indicated the involvement of viruses and insect vectors; however, the exact causes of the disease had not been previously well understood. In order to elucidate viruses associated with the yellowing syndrome, samples were collected from rice plants showing symptoms of virus infection such as leaf yellowing and bronzing, and stunting (Fig. 3), in the Mekong Delta between 2005 and 2006, and the presence of viruses was examined. Virus infection in the plants was examined by enzyme-linked immunosorbent assay (ELISA) using antibodies to RRSV, RGSV, rice tungro spherical virus (RTSV), and rice tungro bacilliform virus (RTBV). Some of the results by ELISA were confirmed by reverse transcriptase-polymerase chain reaction (RT-PCR) for viral genome sequences.

The results indicated that in 2005 only a small proportion (19%) of plants showing the symptoms collected from one of the two sites were infected with RGSV, while no RRSV, RTSV, and RTBV infection was detected at either site (Table 1). In 2006, however, the levels of RGSV and RRSV infection were evidently higher than in 2005. RGSV was detected in at least 60% of plants showing symptoms collected from various sites. In addition, substantial portions of plants with the symptoms were found mix-infected with RGSV and RRSV. Only one plant among those examined during 2006 was found infected with RTSV, and RTBV was not detected in any of the plants. Thus, the yellowing syndrome was likely associated with the infection by RGSV or the mixed infection by RGSV and RRSV.

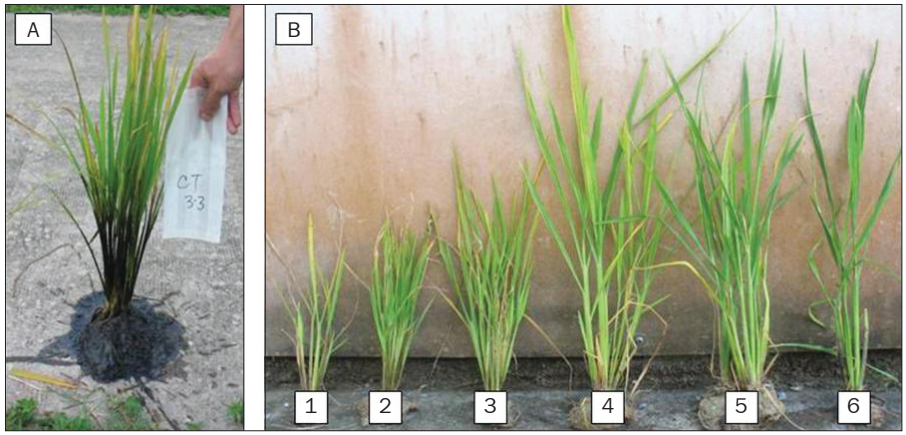

Fig. 3. Various symptoms in rice plants caused by mixed infection with RGSV and RRSV. (A) Characteristic symptoms of yellowing syndrome showing leaf yellowing and bronzing, and profuse tillering. (B) Various symptoms caused by RGSV and RRSV observed in a single field in southern Vietnam, October 2006. See text for the description of symptoms.

Types and severity of disease symptoms varied among plants mix-infected with RGSV and RRSV (Fig. 3). Some plants showed only yellowing, bronzing, and stunting but no profuse tillering (plant 1 of Fig. 3), while other plants showed profuse tillering typical of grassy stunt (plants 2 and 3 of Fig. 3). There were also plants exhibiting yellowing and serrated and twisted leaves without profuse tillering (plants 5 and 6 of Fig. 3). The variation in symptoms might be caused by the difference in the timing and sequence of infection with RGSV and RRSV in the field.

RGSV and RRSV were also detected from 49% and 74% of BPH collected at various sites of the Mekong Delta in 2006 (Table 1). The proportion of BPH from which both viruses were detected was 8%. The proportions of BPH carrying one of or both RGSV and RRSV varied depending on the time and the site of collection. During the surveys in 28 provinces of southern Vietnam in 2007, the proportion of RGSV-carrying BPH was higher than 50% in 8 provinces, and the proportion of BPH carrying both RGSV and RRSV was higher than 30% in 9 provinces.

The incidences similar to the yellowing syndrome observed in the Mekong Delta of Vietnam were also reported in central and northern regions of Vietnam and areas of Cambodia adjacent to Vietnam. In 2007, surveys for the distribution of rice viruses were conducted in those regions. Plants with leaf yellowing but not those with profuse tillering and leaf bronzing were also observed in central and northern regions of Vietnam. The plants showing yellowing were found infected with RRSV. No RGSV, RTSV, or RTBV was detected in the plants collected from the regions. Meanwhile, plants with leaf yellowing and bronzing were often observed in the areas of Cambodia adjacent to Vietnam. The plants collected in Cambodia were found infected with RGSV.

Table 1. Detection of RRSV and RGSV in rice leaf and BPH samples collected from areas in southern Vietnam from January 2005 to October 2006.

Time of sampling	Site of sampling	Type of sample	Number of samples	Percentage of viruses detected in samples		
				RRSV	RGSV	RRSV + RGSV
Jan 2005	Can Tho	Rice leaves	37	0	19	0
	An Giang	Rice leaves	15	0	0	0
Mar 2006	An Giang	Rice leaves	18	50	94	50
	Tien Giang	Rice leaves	12	83	83	66
Aug 2006	Ho Chi Minh	Rice leaves	119	39	63	35
	Long An	Rice leaves	82	42	64	32
	Tien Giang	Rice leaves	20	65	90	60
	Binh Phuoc	Rice leaves	204	59	84	54
	Tra Vinh	Rice leaves	5	20	100	20
	Dong Nai	Rice leaves	1	100	100	100
	Various sites	BPH	35	41	66	8
Oct 2006	Tien Giang	Rice leaves	90	18	94	18

Concluding remarks

Viruses transmitted by BPH have been an occasional but persistent problem for rice production in tropical Asia. Management of BPH populations should reduce the risk of damage by BPH-transmitted viruses in fields. However, the recent outbreaks of BPH-transmitted virus diseases also indicate the necessity for control of the viruses to minimize damage in case of BPH outbreaks. Eradication of virus sources in fields and the deployment of virus-resistant varieties are effective in preventing further spread of virus diseases. Regular monitoring of viruses in fields by economical diagnostic tools would facilitate the eradication and escape procedures for virus diseases. The effectual range of virus resistance in plants is often limited. Preliminary analysis of virus genomes indicated that the isolates of RGSV in the Mekong Delta appeared to be divergent from the isolates previously reported. Although it became evident that RGSV and RRSV transmitted by BPH are associated with the devastating disease in the Mekong Delta, the possible involvement of other viral agents in the disease cannot be eliminated. Thus, understanding of biological characteristics of host-vector-virus interrelationships is crucial for the development of durable resistance to viruses, and effective management of virus diseases spread by BPH.

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Approaches to management

Prospects for ecological engineering for planthoppers and other arthropod pests in rice

G.M. Gurr

Though traditional pest management methods such as companion planting, trap cropping, and other forms of polyculture have a long history, it is only in recent years that researchers have attempted to underpin such practices with ecologically driven research. "Ecological engineering" for pest management has emerged from conservation biological control and habitat manipulation and is characterized by being based more comprehensively on ecological theory and by being developed via rigorous experimentation. The process of development typically aims to identify and provide the most functional components of biodiversity, rather that simply increasing diversity in an untargeted fashion. This directed approach to understanding and using agricultural biodiversity is important because there are a number of pitfalls in the simplistic assumption that enhanced biodiversity will suppress pests in a risk-free fashion. Results from a range of studies are presented to show the benefits of the adoption of ecological engineering practices that suppress pests directly or indirectly (i.e., via enhanced natural enemy activity). Strategies are suggested that allow ecological engineering approaches to be integrated with mainstream agriculture. As an example, this chapter considers prospects for the management of tropical rice pests, especially brown planthopper (*Nilaparvata lugens*). Pest management in this system currently relies heavily on host-plant resistance and synthetic insecticide applications. There is potential for the management of rice pests, including brown planthopper, to be enhanced through the use of ecological engineering to reduce dependence on pesticides and slow the breakdown of host-plant resistance traits.

Agriculture is under pressure to reduce reliance on chemicals and focus on more sustainable methods of production (Brown and Glenn 1999, Tsakiris et al 2004). In recent decades, integrated pest management (IPM) has shown great potential for reducing the dependence of crop protection on chemical control methods (Pretty et al 1998, Atanassov et al 2002). IPM reflects the idea that pest management requires a coordinated approach, integrating diverse tactics, including cultural, biological, and chemical control (Dent 1991). The maintenance of pest damage below injurious (economically damaging) levels while minimizing hazards to humans and the

environment is another key component of IPM (Prokopy 1994). Even with the implementation of IPM in many crop systems, modern agroecosystems are often inhospitable to natural enemies because of decreasing landscape heterogeneity, frequent disturbance, agrochemical inputs, decreasing genetic diversity, and increasingly homogeneous vegetation (Letourneau 1998).

Despite the homogeneity of agroecosystems, there is wide acknowledgment that biodiversity in agricultural landscapes can potentially enhance a range of ecosystem services such as breakdown and cycling of nutrients, pollination of crop plants, buffering watercourses from runoff, protection from erosion, and biological control of crop pests. Indeed, Costanza et al (1997) estimate the total value of the ecosystem services provided by biodiversity worldwide to be on the order of US2.6×10^9. The value of biological control of crop pests alone was estimated at $100 billion worldwide per annum. Yet, despite the action of biological control, insect pests still destroy an estimated 15% of world food production and lead to annual applications of approximately 3 million tons of pesticides (Pimentel 2004).

Biological control is the activity of predators, parasites, and pathogens in maintaining a pest's population density at a lower average than would occur in the absence of such agents (De Bach 1964). Biological control may involve the inundative release of large numbers of agents in response to escalating pest densities or the inoculative release of exotic agents. Both of these approaches, however, have significant disadvantages. Arthropod agents are labor-intensive to produce and are often prohibitively expensive for all but the most high-value and intensively grown crops. The inundative releases of biological control agents can be economically viable in the case of microbial agents such as *Bacillus thuringiensis* bacterium or *Metarrhizium anisopliae* fungus that can be cultured in vitro. The inoculative release of exotic agents, otherwise known as classical biological control, carries a risk of introducing species that will have severe nontarget effects (Howarth 2000, Twyford 1991). Less well known is the fact that though classical biological control has enjoyed spectacular successes such as the vedalia beetle (*Rodolia cardinalis*) for cottony cushion scale (*Icerya purchasi*) control in California citrus groves (Caltagirone and Doutt 1989), around 90% of arthropod releases for arthropod pest control fail to bring the target species under effective control (Gurr et al 2000).

The aforementioned problems associated with inundative and inoculative biological control have led to growing interest over the last decade in conservation biological control. This approach aims to use cultural practices to enhance the impact of endemic and naturalized or introduced agents and avoid killing existing natural enemies through pesticide use. Pests can also be suppressed directly (i.e., not via natural enemy enhancement) via vegetation structure exerting "resource concentration" effects (Root 1973). Theoretical predictions and empirical data generally support the notion that herbivore abundance tends to be lower in diverse systems relative to simplified systems (Andow 1991, Murphy et al 1998). This fits neatly with the popular perception that diversity leads to stability and productivity (Tilman et al 2005) but, unfortunately, simply increasing the diversity of an agroecosystem is no guarantee of reduced pest damage. The effects of diversifying agricultural landscapes on both

insect pests and their natural enemies are highly variable (Ferro and McNeil 1998). The effect of any particular crop-crop or weed-crop assemblage on species richness, species composition, reproduction, survival, and efficacy of natural enemies is difficult to predict (Letourneau 1998, Barbosa and Wratten 1998). The outcomes can depend on the pest–natural enemy complexes being studied, including dispersal capabilities of the pest and enemies, habitat requirements, and resources necessary for survival and reproduction (Ferro and McNeil 1998). For example, manipulating the composition of ground cover within a crop and the vegetation adjacent to it might enhance biological control of a specific arthropod pest. It may, however, also result in effects that are counterproductive to the overall goal of integrated crop production (Prokopy 1994, Barbosa and Wratten 1998) by exacerbating other pest species, encouraging a crop disease, or introducing a weed species. The resources that diverse vegetation provides may also have a negative effect by enhancing predators or parasitoids of pests' natural enemies, an effect observed in a New Zealand orchard to which buckwheat was added (Stephens et al 1998). It is also possible that enhancing a community of natural enemies may result in intraguild interference, that is, natural enemies of pests interfering with each other. Such effects can result in reduced crop growth via a cascading effect down trophic levels (Snyder and Wise 2001). As a response to such problems and a pathway to better-targeted diversification of agricultural systems, this chapter explores "ecological engineering" for pest management (Gurr et al 2004) and, in particular, its potential in tropical rice pest management.

Ecological engineering

The term "ecological engineering" was first used by Odum (1962) to refer to the "environmental manipulation by man using small amounts of supplementary energy to control systems in which the main energy drives are still coming from natural sources." The concept of ecological engineering has continued to develop. The central theme of Mitsch and Jørgensen (2003) is the provision of "guidance and methodologies for systematic, intelligent design of ecological systems for the benefit of humans and nature." Characteristics of approaches that are consistent with ecological engineering as defined by its early proponents are (1) low dependence on external and synthetic inputs, (2) a reliance on natural processes, (3) based on ecological principles, and (4) scope for refinement by ecological experimentation.

The first explicit and systematic application of the broad ecological engineering concept to pest management (Gurr et al 2004) saw the cultural practices used to enhance biological control (i.e., habitat manipulation) as compatible with the ecological engineering philosophy. These methods include (1) trap crops to divert pests from crops, (2) various forms of polycultures to reduce pest immigration or residency, and (3) provision of resources to natural enemies.

The provision of nonhost or nonprey food is one of the most commonly exploited mechanisms of conservation biological control (Gurr et al 1998). For many parasitoids, the provision of sugars is important in maximizing longevity, searching ability, and fecundity (Jervis et al 2004, Shearer and Atanassov 2004). However, because of

the serious potential risks of diversity exacerbating pest damage as described above, there is a need to select carefully the ways in which resources are targeted at desired beneficial species.

Work on nectar quality and flower architecture offers scope to target benefits to specific natural enemy species (Patt et al 1997, Wackers 2004). "Selective" food plants have the potential to increase parasitoid activity without positively affecting pest species (Baggen et al 1999, Gurr et al 1998, Landis et al 2000). Mechanisms by which food plant selectivity works include temporal coincidence between nectar availability and insect foraging, differential attractiveness and morphometric compatibility between the inflorescence and the insect (Baggen et al 1999, Gurr et al 1998), as well as flower color (Begum et al 2004). Prospects for finding flower species that meet the needs of natural enemies, while denying benefit to pests, appear good because of the rapid recent advances in our understanding of selectivity mechanisms. Recent work on the landscape-scale response of pests and natural enemies even suggests that selectivity could be achieved by manipulating the composition of landscape elements (Bianchi et al 2006).

Cover crops of various types can attract natural enemy species by providing plant foods, moderating the microclimate, and supporting nonpest herbivores that serve as alternative host/prey. If not managed carefully, however, cover crops can also behave as weeds by competing with the crop for water and nutrients (Bugg and Waddington 1994, Meyer et al 1992, Nyczepir et al 1998). They can also increase the cost of production or decrease yields (Brown and Glenn 1999) as they require extra maintenance, water, and/or fertilizer beyond that required for the crop (Horn 2000). Noncrop plants can also favor at least some pest species, a risk that was identified in very early work on the potential for habitat manipulation in rice (Lim and Heong 1977).

In order to reduce the potential negative consequences of randomly increasing plant diversity, ecological engineering for pest suppression is characterized by a series of methodical steps aimed at identifying and providing appropriate forms of vegetational heterogeneity in the farm landscape. It would be rare, however, for all of the steps to be completed before some aspect of habitat manipulation is trialed in the field. These steps are

1. The identification of the principal pest species against which additional or augmented suppression is most urgent through field surveys, discussions with growers, and/or use of the literature.
2. A literature review and field surveys to distill available information on the ecology of the selected pest species, and secondary pest species. This includes the identification of endemic or naturalized natural enemies that exist in the region and whether an approach based on plant-herbivore interactions such as resource concentration effects of trap cropping is required. This work is likely to be done in combination with step one.

Table 1. Characteristics of plants to be considered during selection of species for ecological engineering (after Gurr et al 1998).

Hazards
Weed status of plant being considered
Act as an alternative host for a pathogen of the crop
Poison livestock
Potential for contamination of the crop
Economic factors
Dual crop status
Cost and availability of seed
Does not compete with the crop and reduce yields
Biological factors
Pollen production (total/temporal pattern)
Nectar production (total/temporal pattern)
Competitive ability (with weeds and the crop)
Agronomic compatibility with the crop
Flowering periods that do not coincide with the crop and divert pollinating insects
Information that they are able to provide important resources for natural enemies (e.g., food or shelter)
Agronomic tractability (e.g., ability to survive with little maintenance)

3. Preliminary modeling of the pest and natural enemy population dynamics to explore aspects such as the magnitude of pest suppression required for economic control in relation to the spatial and temporal dynamics of the pest and natural enemy populations.
4. Close consultation with growers and agronomists to determine the types of ecological engineering (e.g., field margin borders, within-crop strips, interplanting, ground covers, landscape heterogeneity) that could be accommodated without undue disruption to normal farm practices.
5. The identification of candidate plant species to be used in habitat manipulation through literature reviews, and discussions with growers and agronomists.
6. Risk assessment of candidate plant species (e.g., possible weed, toxic to livestock, or likely to contaminate produce). Such risks can be analyzed in a quantitative fashion using the graded weighted checklist approach of Gurr et al (1998), which assists in determining the suitability of each plant species for vegetation diversification by considering the properties of candidate plants (Table 1). In this system, each criterion is assigned a weighting, based on its relative importance in the particular farming system being examined. Plants (or other habitat manipulation options) are then rated against each criterion, such that a score for each strategy is obtained and the likely suitability determined.
7. The identification of the most efficacious of the candidate treatments using laboratory or glasshouse experiments. Laboratory bioassays are most commonly used to measure the extent of benefit to a small number of natural

enemy species. The earlier modeling (step 3) may, like that of Kean et al (2003), have identified the life-history parameters of the natural enemy that, if enhanced, will have maximum impact on the pest population. These parameters may include search rate, prey conversion efficiency, and consumption rate although, most commonly, fecundity and longevity are used because of the relative ease with which these can be measured. Examples of this include longevity and fecundity of the parasitoids *Copidosoma koehleri* (Baggen and Gurr 1998) and *Trichogramma carverae* (Begum et al 2003). Importantly, equivalent bioassays with the pest should be used in order to prevent the selection of plant species that provide benefit to adults or larvae. The work by Baggen and Gurr (1998) identified borage (*Borago officinalis*) and phacelia (*Phacelia tanacetifolia*) as "selective" food plants that prevented access to nectar by the potato moth (*Phthorimaea operculella*) but benefited strongly its parasitoid, *C. koehleri*. This concept was extended in work with the lightbrown apple moth, *Epiphyas postvittana* (Begum et al 2006), where foliage of candidate plant species was checked for suitability to support larval development as well as the nectar being checked as a food source for adults.

8. Field experimentation is required to develop practical guidelines for farmers on habitat manipulation methods to improve integrated pest management programs. Field studies enable researchers to investigate the spatial and temporal extent of effects on natural enemies and pests in the natural environment, where factors such as neighboring crops, climate, and photoperiod may influence plant-pest-natural enemy interactions. This would include assessing the impacts of those species (e.g., secondary pests and pathogens) not included in earlier laboratory experiments. Parasitoids of predators and hyperparasitoids (the fourth trophic level) may also be enhanced by supplementary resources such as nectar. Therefore, adverse effects of these on the third trophic level (e.g., Stephens et al 1998) need to be ruled out—or at least shown to be minor in relation to the overall enhancement of the third trophic level.
9. Finally, guidelines need to be extended to growers. An example of an ecological engineering project that culminated in the successful extension to growers is the use of raised earth banks sown to the perennial grasses—usually cocksfoot (*Dactylis glomerata*). Such "beetle banks" are now widely established in European cereal fields (MacLeod et al 2004). Adoption of this technology was encouraged by color extension materials produced with support from a major pesticide company and by being featured on national television.

Prospects for ecological engineering of rice pests

Having introduced the potential risks associated with the incautious use of diversity to suppress pests, and the way in which ecological engineering can reduce these in a generic manner, the rest of this chapter explores the potential for this approach in tropical rice.

A number of authors have commented on the fact that because of reduced amounts of disturbance, perennial, semi-permanent systems such as orchards have great potential for habitat manipulation and biological control (Brown 1999, Landis et al 2000). Indeed, habitat manipulation methods have been used successfully to enhance biological control in a number of orchard/vineyard crops worldwide, including grapes (Murphy et al 1998), apples (Brown and Glenn 1999, Brown and Schmitt 2001), pecans (Tedders 1983), citrus (Liang and Huang 1994), and, to a lesser extent, cherry and peach (Bugg and Waddington 1994). Given this background, rice—an annual species with high disturbance between cropping phases—appears to be a crop in which there may be relatively poor scope for ecological engineering to be developed. As elucidated below, however, this is not necessarily the case.

Tropical rice and biological control

Way and Heong (1994) identify several factors and conditions that favor biological control of pests in tropical rice:

1. Stable water supply.
2. Moderate host-plant resistance and the capacity of rice plants for compensatory growth after pest attack.
3. A short fallow period giving relatively stable arthropod populations.
4. Proximity to noncrop vegetation on rice bunds (levees).
5. Withholding early-season insecticide applications.

Although some of these factors are relatively intrinsic to the system, others are conditions that are strongly dependent on farmers adopting appropriate management tactics. For example, there had been significant debate over the value of an earlier recommendation that farmers in a given region adopt synchronous planting after a fallow period (Loevinsohn 1994). This strategy is supported in general terms because most serious rice pests have a narrow diet range (Way and Heong 1994) so would be suppressed by a fallow period without available host plants. Despite the logic of this, asynchronous rice plantings are now more widely accepted not to lead to pest buildup provided that insecticide use is moderated, allowing natural enemies to build up (Way and Heong 1994, Ives and Settle 1997). The presence of rice crops for much of the year and over large areas makes this system quasi-perennial in nature, thus approaching in terms of stability the woody perennial systems referred to above in which conservation biological control efforts have enjoyed success. This effect has contributed to a broader trend whereby rice farmers have shifted from a field-by-field approach to rice pest management toward an area-wide management approach that may extend over large regions (Matteson 2000).

The fact that broad-spectrum insecticide can have very strong *adverse* consequences for pest management is clearly evident in data for *Nilaparvata lugens* (Kenmore et al 1984). Numbers of natural enemies were greater and numbers of *N. lugens* far lower in unsprayed rice. This clearly illustrates the significance of one of the most basic conservation biological control tactics: to avoid pesticide-induced natural enemy mortality. This is further supported by the fact that *N. lugens* is an induced pest, one that was insignificant before the Green Revolution and the accompanying intensification of insecticide use (Heong and Schoenly 1998). Though cases of effects of pesticides on arthropod natural enemies are common, fewer studies focus on impacts upon other taxa of biological control agents. Work by Choo et al (1998) in which imidacloprid was shown to be one of the least harmful of several pesticides on the entomopathogenic nematode, *Agamermis unka,* illustrates the need to consider nonarthropod taxa when selecting insecticide regimes that are most compatible with biological control.

The value of population modeling was stressed in general terms in the earlier introduction to ecological engineering and some valuable work has been done for rice arthropods. Drechsler and Settele (2001) suggest that simplistic generalizations about natural enemy activity being enhanced by asynchronous planting of rice need to be treated with caution. Following an ecological engineering approach whereby habitat manipulation is informed by a knowledge of key aspects of pest and natural enemy biology, the different responses of natural enemies to landscape structure need to be considered as well as the interactions between natural enemy guilds. In tropical rice, a predatory mirid, *Cyrtorhinus lividipennis*, attacks planthopper eggs so is able to persist only in rice crops. Accordingly, when crops are asynchronous, numbers within rice depend on immigration from outside the system. Although this suggests that asynchronous cropping would be the optimal management strategy, favoring biological control of planthoppers, it ignores other natural enemy guilds. Hymenopteran egg parasitoids are particularly important among these but the mirid is not known to differentiate between parasitized and unparasitized eggs. Under the model's assumptions of the parasitoids being superior natural enemies of planthoppers but outcompeted by the mirid, asynchronous cropping conditions that favor the mirid actually increase planthopper numbers because the impact of parasitoids declines. As a result of such complexities, and until future empirical work fills information gaps in pest/natural enemy interactions, the only general conclusion of the modeling by Drechsler and Settele (2001) is that a high proportion of vegetable fields in the landscape reduces pest abundance. These, as well as fruit and timber trees, may serve as sources and sinks for natural enemies. Proximity of such landscape elements is important because, although some natural enemies such as *C. lividipennis* are highly vagile (Riley et al 1987), many others, especially wolf and web-building spiders, colonize rice from adjacent habitats. Noncrop vegetation may also support nonpest insects that serve as alternative hosts to parasitoids that attack planthopper pests. Accordingly, the preservation of such habitats in rice-growing areas may be a useful heuristic message to communicate to farmers.

Cases of antagonistic interactions between natural enemy species such as that mentioned above have helped drive a significant research thrust in agroecology over the last decade, seeking to understand the circumstances under which biological control agents may have additive or even synergistic effects on pest suppression. One particularly relevant study was that of rice pests by Wilby et al (2005). This showed that a complex of three predator species led to an enhancement of predation of the leaf-folder, *Marasima patnalis*, compared with treatments with a single species of predator. No such enhancement was evident for *N. lugens,* suggesting that the greater differences in morphology and behavior of the endopteregote lepidopteran allowed resource-use differentiation between the predator species to a greater extent than was possible for the exopteregote planthopper. Another study of interactions between *N. lugens* predators considered spiders and again illustrated that multiple species of natural enemy may be better than single species provided direct competition for prey was minimal (Sigsgaard 2007). In that work, the small linyphiid, *Atypena formosana*, preyed upon early instars of the planthopper while the larger lycosid, *Pardosa pseudoannulata,* was able to use larger nymphs and adult planthoppers. The presence of both resulted in more even control of pest life stages. That study also suggested that *A. formosana* (as well as the mirid *C. lividipennis*) may serve as intraguild prey of the lycosid.

Collectively, such studies suggest value in not following the typical classical and inundative biological control approach of identifying one or a small number of agents and introducing or releasing only these. A somewhat broader enhancement of several biological control agent species, including generalist predators, may be optimal. Certainly such an approach is more consistent with the "insurance hypothesis" of Yachi and Loreau (1999). This proposes that fluctuations in ecosystem processes such as biological control of pests are buffered more effectively by the presence of multiple (rather than single of few) species. When multiple species are present, apparently redundant species may become important after a disturbance to formerly dominant species. Such "insurance" can be especially important in systems with temporal disturbance that may adversely affect predatory arthropods (Tscharntke et al 2007); at least some species will persist or colonize the crop early and suppress early-season pest outbreaks (Bianchi et al 2006).

The applicability of this to rice is evident from studies in which levels of organic matter were experimentally enhanced (Settle et al 1996). Composted cow manure was added to plots of rice and subsequent arthropod numbers compared with control plots without organic matter supplementation. Results indicated that early-season populations of generalist predators were supported by abundant detritus- and plankton-feeding arthropods, with these alternative prey giving predators a "head start" on later-developing pest populations. A similar study by Jiang and Cheng (2004) investigated the same approach for enhancing biological control of whitebacked planthopper (*Sogatella furcifera*) in China. Composted barnyard manure was added to plots of rice and synthetic fertilizer added to the control plots at rates equivalent to the nutrient present in the manure. Abundance of collembola was enhanced by the manure treatment but effects on pest numbers were less dramatic. Ecologically, this strategy exploits the "detrital shunt" of the food webs (Polis and Strong 1994)

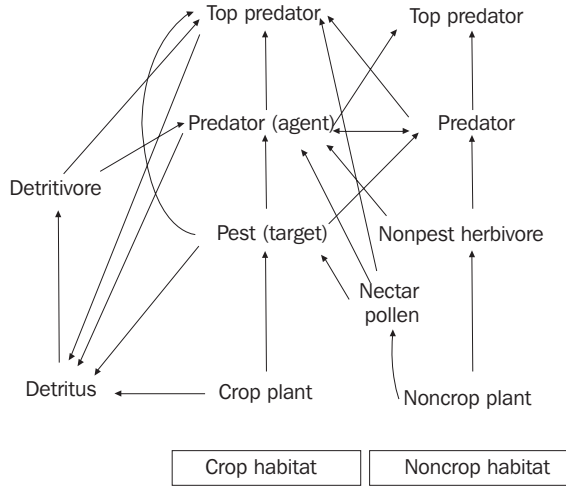

Fig. 1. Schematic representation of an agricultural system food web showing the potential importance of noncrop habitat and detritus. The latter can be augmented by application of organic matter to support predators, allowing populations to develop early in the season before pests arrive.

(Fig. 1) with the allochthonous organic matter constituting a resource subsidy that enhanced numbers of detritivore-feeding prey species. These in turn serve to decouple populations of natural enemies from reliance on pest herbivores. More generally, the role of freshwater aquatic habitats in supporting natural enemies of agricultural pests is not well understood and constitutes a potentially rich line of investigation for ecological engineering in systems such as rice. In tropical rice production, the paddies are connected to or in very close proximity to a network of human-made, natural, and seminatural aquatic habitats through which many invertebrates and prey of invertebrates (e.g., plankton) may readily move. There is significant research interest in the relevance to biological control of the connectivity and permeability of terrestrial vegetation features in farmlands (Tscharntke et al 2008). Extending the spatial analysis and metapopulation approaches from such work to understand and manipulate the aquatic component of agricultural landscapes is an exciting prospect.

Feeding studies on *A. formosana* by Sigsgaard et al (2001) suggest that alternative prey such as collembolan may still be more profoundly important. Spider survival on diets consisting solely of *N. lugens* or of the green leafhopper (*Nephotettix virescens*) led to very poor survival of spiders to the adult stage. In contrast, a mixed diet of either hemipteran with collembolan and drosophila gave faster development time and greater survival. This illustrated that availability of prey such as collembola is essential for the performance of this linyphiid, not simply an early-season, alternative food resource. Making progress in ecological engineering for tropical rice pest management will require an investment of research effort to establish some quite basic knowledge of natural enemy ecology. This is well illustrated by the observation by Way and Heong

(1994) that rice bunds were abundantly colonized by fire ants, *Solenopsis geminata,* but that their role as a natural enemy was unclear. It was not until the study of Way et al (2002) that this ant was shown to be a potentially important predator of *N. lugens,* and other rice pests, including corn rootworm (*Diabrotica adelpha*).

Studies of pest and natural enemy ecology also need to consider the response of each vegetation pattern at a range of spatial scales. Rice bunds are increasingly recognized as near-crop habitats that can support natural enemies. There is, however, a dearth of information on the optimal plant species to establish or encourage on these potentially critical features. An ecological engineering–based approach that experimentally tested the merits of various grass and broadleaf plant species could lead to a powerful strategy for enhancing biological control. Parasitoids, for example, could be enhanced by the presence of nectar-producing species as well as by moderated microclimate and possibly the presence of alternative hosts (Xiaoping et al 1996). Grasses allowed to flower may provide protein-rich pollen for predators as well as structural habitat analogous to that provided by "beetle banks" in temperate cereal production systems (Thomas et al 1991).

At a larger spatial scale, the significance of nonrice landscape elements such as vegetable crops identified through modeling by Drechsler and Settele (2001) provides valuable pointers for ecological engineering research. Crop species choice, timing of sowing and harvesting, spatial pattern, and proximity to rice all offer some scope for exploration. The use of mark-recapture and geographic information system–based studies can identify the temporal and spatial patterns of cropping that are most conducive to rice pest suppression via trap crop, decoy crop, push-pull, resource concentration, and natural enemy–mediated effects.

Woody perennial vegetation, whether cultivated for fruits and nuts or seminatural (possibly protected areas for biodiversity conservation), can provide a highly complex habitat, especially when understorey vegetation is present to provide multiple strata. Landscape elements of such types can support complexes of beneficial and pest arthropods, with diverse trophic relationships (Bugg and Waddington 1994, Altieri and Schmidt 1985).

Though food sprays have been shown to have utility in attracting natural enemies into target crops (Wade et al 2008), the costs are likely to be prohibitive for many tropical rice growers. An alternative approach for manipulating natural enemy movement based on chemical ecology may be viable in the future. It is now well established that plants under attack by arthropod herbivores produce volatile chemicals that attract natural enemies (Bruce and Pickett 2007). Some such herbivore-induced plant volatiles (HIPVs) have been identified, synthesized, and used in slow-release dispensers or as sprays. Under field conditions, methyl-salicylate, *cis*-3-hexen-1-ol, (Z)-3-hexenyl acetate, and benzaldehyde have resulted in elevated catches of biological control agents (James 2005). Remarkably, application to plants of a single HIPV, or of jasmonic acid, which is involved in related metabolic pathways, can also induce the production of a natural blend of HIPVs (Lou et al 2005). Such findings suggest that applying synthetic HIPVs to crops can, both directly and indirectly, attract the predators and parasites that could protect crops from pest damage.

Prospects for such an approach to work in rice appear strong. Work on the role of ethylene signaling in rice showed that this hormone is involved in induced defenses against arthropod herbivores (Lu et al 2006). Plants attacked by *N. lugens* produced ethylene 2 to 24 hours after infestation along with HIPVs, and *Anagrus nilaparvatae,* a parasitoid of *N. lugens,* was attracted to emitting plants. The same authors also considered it likely that *N. lugens* activates other—most notably the salicylate—signaling pathways. In other work, exogenous applications of jasmonic acid to rice plants have led to dramatically elevated levels of several volatiles, including aliphatic aldehydes, alcohols, monoterpenes, sesquiterpenes, methyl salicylate, and *n*-heptadecane (Lou et al 2005). The potential for such chemical ecology to be developed into a practical pest management strategy is evident from a doubling of parasitism of *N. lugens* eggs by *A. nilaparvatae* on rice plants that were surrounded by rice plants to which jasmonic acid had been applied compared with control plants. It is likely that other parasitoids, as well as rice pest predators, make use of such plant-provided chemical cues. The same cues may also affect pest behavior, making treated plants less attractive to planthoppers (Karban and Chen 2007).

An ecological engineering approach based on applying selected HIPV elicitors to rice to promote their sink status for natural enemy populations could be especially powerful if linked with manipulation of the nearby vegetation to make it a more effective source habitat for predators and parasitoids.

Conclusions

In conclusion, the ecological engineering approach to pest management is still young but it provides a strategic methodical framework for researchers wishing to apply ecological knowledge and experimentation to pest suppression in the field. Ecological engineering has the potential to complement IPM programs currently being used in many agricultural systems, including tropical rice, by improving the efficacy of natural enemies and reducing reliance on pesticides.

This review has covered the literature pertinent to the nine steps defined for an ecological engineering research program. In terms of the first three steps—that relate to amassing a solid foundation of knowledge on the major pests and their natural enemies and modeling the interactions between them—the economic significance of rice and the long history of research on rice pest management mean that there is a very significant body of work on the species involved but much more could be done to explore the interactions. Modeling as well as experimentation are required. In terms of step 4—liaison with growers and others involved in the industry to establish which types of habitat manipulation may be acceptable—there is a need to canvass the merits of those techniques that the available literature suggests could have utility.

These include

- Further rationalization of pesticide inputs such that timing, type, and spatial pattern of applications are based on rigorous, threshold-driven decision frameworks rather than overestimates of the seriousness of pest damage (Heong et al 1998), peer pressure (Heong and Escalada 1999), inappropriate marketing, and policy settings.
- Possible use of HIPV elicitors (and possibly food sprays) to encourage natural enemy movement into rice at appropriate times.
- Manipulating the detrital shunt of the rice pest food web by adding organic matter to rice paddies early in the season.
- Configuring rice paddies optimally with respect to the wider network of aquatic habitats such as ditches, streams, wetlands, etc., so as to maximize the availability of alternative prey items for natural enemies of rice pests, especially for the early stages of the rice crop.
- Managing the vegetation of bunds to encourage natural enemies such as parasitoids and ants.
- Managing the wider scale pattern of vegetation by preserving and re-establishing perennial woody vegetation.
- Manipulating the spatial and temporal pattern of rice plantings across entire regions.

Not all of these will be deemed acceptable by rice farmers in all production zones but it is encouraging that the available literature suggests potential for several methods that range from highly local strategies that individual growers could implement through to larger scale approaches that could be encouraged on a regional scale.

Those methods that are considered suitable in a given region could be pursued via steps 5–8 of the ecological engineering framework. These would involve experimentation to determine aspects such as which plant species should be preserved or sown into bunds to maximize their role as natural enemy sources and which HIPVs most effectively turn rice into sinks for natural enemy populations. Similarly, experimentation could indicate the efficacy of various forms of available organic matter as a means of providing early-season prey for the natural enemies of rice pests. Geographic information systems accompanied by field surveys could help authorities devise landscape configurations that best impeded rice pest colonization of rice crops while facilitating the early arrival and buildup of natural enemies. Careful studies at these varying spatial scales are required in order to avoid the possible adverse effects of diversity reviewed in the opening sections of this chapter.

Ultimately, step 9, experimentation in such areas, needs to be distilled into simple heuristics or "rules of thumb" that can be readily understood and implemented by farmers. The fact that pests such as *N. lugens* continue to cause severe losses in rice means that implementing an ecological engineering approach is important in order to lessen the dependence on insecticides and slow the breakdown of host-plant resistance traits.

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Notes

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The genetics of host-plant resistance to rice planthopper and leafhopper

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The incorporation of host-plant resistance to insect pests into elite rice cultivars and the sustainability of pest management using resistant cultivars are necessary for a stable food supply in most rice production areas. The brown planthopper (BPH), *Nilaparvata lugens* Stål., is one of the most serious and destructive rice pests that can be found throughout rice-growing areas in Asia. More than 19 major BPH resistance genes have been identified in several indica cultivars and wild relatives. The green rice leafhopper (GRH), *Nephotettix cincticeps* Uhler, is a major leafhopper species of cultivated rice and is found mostly in the temperate regions of East Asia. At least six loci of GRH resistance have been identified with the aid of DNA markers. Recent molecular mapping of genes that are resistant to the insect pests suggested that highly resistant cultivars/accessions often carried multiple genes for resistance. This suggests that gene pyramiding, which combines more than two resistance genes derived from different donors, will inhibit the occurrence of virulent biotypes. In our study, we describe the identification of BPH and GRH resistance genes and the development of near-isogenic lines for each resistance gene in order to improve rice cultivars through a molecular genetic approach. We also demonstrate the monitoring of the genetic constitution of the BPH populations. This probably involves several types virulent to the specific resistance gene(s), for sustainable pest management using cultivars resistant to BPH.

Keywords. Rice, brown planthopper (BPH), green rice leafhopper (GRH), resistance gene, near-isogenic line (NIL), pest management

Planthopper and leafhopper species damage the plant epidermis and parenchyma with their stylets and suck the plant sap from the phloem. Among the phloem-feeding insects, the brown planthopper (BPH), *Nilaparvata lugens* Stål, is the most serious insect pest of rice (*Oryza sativa* L.) throughout Asia. The populations migrate from China to Japan during the rainy season every year (Kisimoto 1976). Though the migrant populations are not large, the progenies sometimes break out. The insect sucks out the plant sap and causes damage to rice plants such as a reduction in crop vigor, plant height, productive tillers, perfect grains, and yield. In extreme cases, a heavy

infestation of BPH results in complete necrosis of the rice plants, a condition commonly known as "hopper burn." This influences yield loss and also causes poor grain quality. The BPH is also a vector of grassy stunt virus and ragged stunt virus, which seriously decrease rice production. Conversely, the green rice leafhopper (GRH), *Nephotettix cincticeps* Uhler, is a major species that subsists on rice and is distributed mostly in temperate regions of East Asia (Ghauri 1971). The GRH sucks sap from both the xylem and the phloem of susceptible rice varieties, leading to yield loss, particularly in northeast Japan. In addition to direct plant destruction, the insect also damages rice plants by transmitting other viral diseases, including the rice dwarf and waika viruses commonly seen in western Japan.

Several kinds of resistant cultivars and accessions of rice against planthoppers and leafhoppers have been reported (Heinrichs et al 1985). Host-plant resistance to insects has been classified into three mechanistic types: antibiosis, antixenosis, and tolerance (Painter 1951). However, distinguishing between these mechanisms against planthopper species and leafhopper species has been difficult with bulk seedling tests (Athwal et al 1971). Kishino and Ando (1978) established a simple method for evaluating antibiosis to GRH, and the survival ratio of GRH nymphs was examined on the tested cultivars. Using this evaluation method, genetic analyses of resistance to GRH have been carried out, and at least six loci for GRH resistance have been identified with the aid of DNA markers. Simple sequence repeat (SSR) marker loci are widely distributed throughout the genome and can be easily analyzed using a polymerase chain reaction (PCR). SSR markers have been used extensively to map agronomically important loci in rice, such as disease and insect resistance. This has opened the door to further revelations regarding the mechanisms of host-plant resistance to insect pests through molecular mapping and the cloning of genes that will confer resistance to GRH. The relationship between rice and GRH is a model case of plant-insect interaction. The knowledge obtained from a series of molecular cloning activities is expected to reveal the sucking resistance and system of host-plant resistance breakdown.

The objectives of our study are to understand the genetic basis for resistance to insect pests found in rice cultivars and accessions of wild rice, as well as facilitate the use of germplasm for future rice improvement. First, a quantitative trait loci (QTL) analysis for resistance to insect pests was conducted using an initial mapping population derived from a cross between a susceptible cultivar and a resistant accession. Subsequently, new loci for resistance to insect pests were mapped onto a molecular linkage map using a near-isogenic population, which was developed by continuous backcrossing and marker-assisted selection (MAS) of the targeted QTL region. Finally, we discuss the necessity of monitoring the genetic constitution of the insect populations. This probably involves several types virulent to the specific resistance gene(s), for sustainable pest management using cultivars resistant to insect pests.

Materials and methods

Plant materials

Eight rice cultivars with different levels of resistance to BPH—ADR52, Podiwi A8, Mudgo, ASD7, Rathu Heenati, Babawee, Balamawee, and Taichung 65 (T65) (no resistance gene)—were used. Near-isogenic lines derived from the GRH-resistant cultivar DV85 and IRGC105715, and BPH-resistant cultivar ADR52, were used.

Insect strains

In 2006, ten populations of BPH were collected in East Asia. Four populations were collected from the Red River Delta (RRD1, RRD2) in northern Vietnam and the Mekong River Delta (MRD1, MRD2) in southern Vietnam. Three populations were collected from the Philippines: Northern and Central Luzon islands (LZ1, LZ2) and Mindanao Island (MD). Single populations from Japan (JPN), China (CHI), and Taiwan (TW) were also collected. These populations were maintained by continuous rearing on susceptible cultivar Reiho at 25 ± 1 °C under 16 h light and 8 h dark conditions in the laboratory of the Pest Management System, National Agricultural Research Center for Kyushu-Okinawa Region, Kumamoto, Japan. A GRH population was collected in Fukuoka Prefecture in 1991 and was maintained by continuous rearing of insects on seedlings of japonica variety Nipponbare. Insects were kept at 25 ± 1 °C and 16 h light, 8 h dark.

Evaluation of resistance to BPH and GRH

The month-old plants were trimmed and covered with a transparent plastic cylindrical cage (5.5 cm d × 20 cm h). Five brachypterous (short-wing form) BPH females within 24 h after emergence were released to a cage and the open end was covered with gauze. A score was obtained starting from 3 days after infestation (DAI) to 5 DAI. The adult survival rates as well as the female abdomen were examined. We evaluated the females whose abdomens became heavily swollen or survived for 5 days as virulent. The classification of virulent and avirulent BPH females followed the method of Tanaka (2000). The experiment was carried out with 8 replications. The GRH antibiosis test was reported by Kishino and Ando (1978), and was modified for use in our study. Seedlings were infested with 7–10 first- or second-instar nymphs in test tubes approximately 2 weeks after sowing. Nymph mortality was then calculated at 4 days after infestation. Plants with nymph mortality in the range of 0–40% were categorized as susceptible, and those with 60–100% nymph mortality were categorized as resistant.

Statistical analysis

The data were analyzed using two-way ANOVA. Treatment means were pair-wise compared using the Turkey HSD test (SAS Institute Inc. 2002). The survival rate (%) was arcsine transformed prior to the analysis.

QTL analyses of cultivars highly resistant to BPH and developing the NILs

The advent of detailed molecular linkage maps in rice has made it possible to detect the quantitative trait loci (QTLs) that control agronomic characters such as biotic and abiotic stresses. In screening germplasm resistance to BPH under antibiosis tests, four indica cultivars (ADR 52, Podiwi A8, ASD7, and Balamawee) were selected as highly resistant. QTL analyses for antibiosis to BPH were conducted using F_2 populations derived from a cross between a susceptible japonica cultivar and resistant indica cultivar. The study has assured future mapping of the BPH-resistance gene using near-isogenic populations developed through marker-assisted selection (MAS). In the case of ADR52, a total of three QTLs controlling antibiosis to BPH were detected on chromosomes 5, 6, and 12. Near-isogenic lines (NILs) for the respective QTLs were developed through continuous backcrossing and MAS. The newly identified resistance genes on chromosomes 6 and 12 were tentatively designated as *bph20*(t) and *Bph21*(t), respectively.

Since highly resistant cultivars often carried multiple genes for resistance to BPH, a near-isogenic population was necessary to map the BPH resistance gene precisely. MAS for BPH resistance genes with advanced backcrossing with the recurrent parent can facilitate transferring the resistance to BPH from resistant cultivars and wild relatives. The NILs derived from resistant germplasm are useful not only for improving BPH resistance in rice breeding but also for monitoring BPH virulence to the specific resistance gene.

Molecular mapping and cloning of GRH resistance genes

Six genes (*Grh1, Grh2, Grh3, Grh4, Grh5,* and *Grh6*) resistant to GRH sucking inhibition have been identified through RFLP mapping. We developed NILs for *Grh2* and *Grh4* from a cross between susceptible japonica cultivar Kinmaze and resistant indica cultivar DV85 with the aid of molecular markers. A resistance evaluation of the NILs was carried out through antibiosis tests against two kinds of leafhopper species, *N. cinctieps* and *N. virescens*, which were serious vectors for several viral diseases in temperate and tropical areas. Nymph mortality of the NILs carrying one of the resistance genes showed only weak resistance and susceptibility. On the other hand, the NILs carrying both of the resistance genes, *Grh2* and *Grh4*, expressed strong resistance at the same level as resistant cultivar DV85. The results clarified that *Grh2* and *Grh4* interaction expresses strong resistance to the two leafhopper species in rice.

A large-scale segregating population of *Grh2* with a near-isogenic genetic background was analyzed for resistance to GRH through a map-based approach. The *Grh2* locus was finally delimited within 54.2 kb genomic sequences of resistant cultivars. Genomic complementation of the candidate genes revealed that two NBS-LRR genes provided a high level of resistance against GRH in the genetic background of *Grh4*, but that each single NBS-LRR gene had only partial resistance. We concluded that the classical *Grh2* locus consisted of two tightly linked NBS-LRR genes, designated

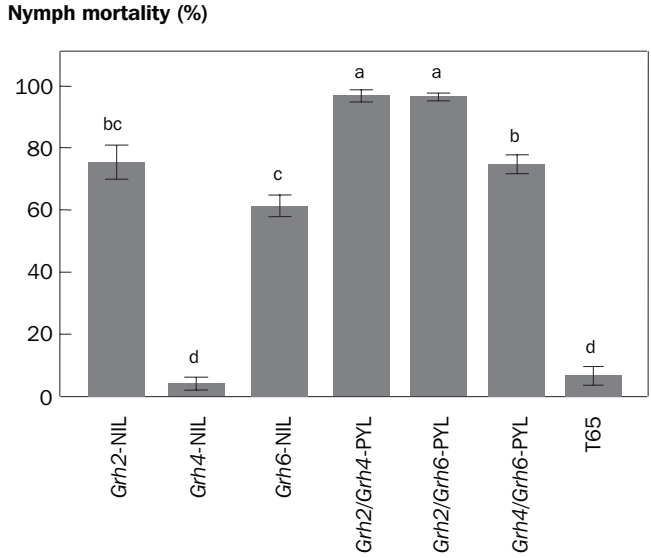

Fig. 1. The nymph mortality of NILs and corresponding PYLs at 3 days after infestation of *Nephotettix cincticeps* Uhler.

Grh2a and *Grh2b*, which mediated high resistance against two *Nephotettix* species, *N. virescens* and *N. cincticeps*, with a *Grh4* genetic background. It is crucial that the symphonic expression of host-plant resistance genes, two of them categorized in the R gene family, mediates durable resistance in plant cultivars.

Development of NILs and pyramided lines for GRH resistance genes

The six GRH resistance genes (*Grh1, Grh2, Grh3, Grh4, Grh5,* and *Grh6*) have been located on chromosomes 5, 11, 6, 3, 8, and 4, respectively. New SSR markers, which flanked *Grh1, Grh2, Grh4, Grh5,* and *Grh6-nivara*, were found to select NILs and pyramided lines (PYLs) for GRH resistance genes through MAS. The NILs carrying *Grh1, Grh2, Grh4, Grh5,* and *Grh6-nivara* with a background of japonica cultivar Taichung 65 (T65) have been developed derived from four GRH-resistant lines, IR24 (*Grh1*), DV85 (*Grh2* and *Grh4*), W1962 (*Grh5*), and IRGC105715 (*Grh6-nivara*), using MAS, respectively. The nymph mortality of the NILs carrying *Grh1, Grh2, Grh5,* and *Grh6* was lower than that of each donor parent, IR24, DV85, W1962, and IRGC105715. For example, we found that the highly resistant W1962, a development of *Oryza rufipogon*, was dependent on two loci conferring resistance to GRH, *Grh5* on chromosome 8 and the minor resistance gene on chromosome 4 (Fujita et al 2006). The PYLs carrying two GRH resistance genes with a background of T65 were developed using NILs carrying *Grh2, Grh4, Grh5,* and *Grh6-nivara*. The NILs and PYLs were used to compare the GRH resistance of NILs and PYLs using an antibiosis test. The nymph mortality of several PYLs, *Grh2/Grh4*-PYL, *Grh2/Grh6*-PYL, and *Grh4/Grh6*-PYL, was higher than that of NILs each carrying a single GRH resistance gene (Fig.1).

Understanding the mechanisms of a breakdown of the resistance gene

Virulent insect pests, the so-called new biotypes, often appear after the release of modern improved varieties of rice that carry a single major gene for resistance to the insect pests. These pests represent a serious threat to rice paddies because they have acquired virulence to the specific resistance gene, which will have subsequently lost its effectiveness in insect pest management. For example, the BPH populations migrating into Japan began to become virulent to *Bph1* (*Brown panthopper resistance 1*) in the late 1980s (Sogawa 1992) and have been highly virulent for rice cultivars carrying both *Bph1* and *bph2* since the late 1990s (Tanaka and Matsumura 2000). The virulent biotypes of BPH were experimentally identified by continuous rearing of BPH on resistant lines, each carrying a single major gene for BPH resistance (Ketipearachchi et al 1998). By a similar methodology, virulent biotypes against each of three resistance genes (*Grh1, Grh2,* and *Grh3*) were isolated (Hirae et al 2007). This suggests that natural strains of GRH are likely to feed on rice plants having a single major gene for the resistance. In contrast, virulent biotypes against PYLs carrying both *Grh2* and *Grh4* did not occur experimentally (Hirae et al 2007). We have demonstrated that, although the nymph mortality of *Grh4*-NIL showed susceptibility to GRH, the PYL carrying *Grh2* and *Grh4* showed higher nymph mortality than *Grh2*-NIL. Additionally, both *Grh2* and *Grh4* have been essential to express resistance to green leafhopper (GLH), which is closely related to GRH and is a major vector of tungro, a destructive viral disease found in tropical rice fields in Asia (Yasui and Yoshimura 1999). The PYLs carrying *Grh2* and *Grh4* may thus have an important role in expressing durable resistance to rice leafhoppers. This suggests that gene pyramiding that combines multiple resistance genes with different mechanistic types will suppress the dominance of virulent biotypes in the insect population. The PYLs carrying the resistance genes may suppress the dominance of virulent biotypes and show durable resistance to GRH. To study the durability of resistance to insect pests, the development of PYLs carrying multiple resistance genes is essential using MAS and advanced backcrossing with a recurrent parent.

Virulence of Asian BPH strains against differential rice cultivars

Tables 1 and 2 show the adult survival rate and ratio of virulent females of 10 Asian BPH strains on six differential cultivars and T65 (a susceptible check). Based on the resistance spectrum, the Asian BPH strains seem to be classified into three groups. The first group is virulent to Mudgo and ASD7 but avirulent to the other four differential cultivars. The second group involves quite a high percentage of BPH individuals virulent to Babawee and ADR52 in addition to Mudgo and ASD7. The third group is partially virulent to Babawee in addition to Mudgo and ASD7. The first group involved BPH strains collected from Japan, China, and Taiwan, and two strains from northern Vietnam. The second group consisted of two BPH strains collected from southern Vietnam. The third group consisted of three strains from the Philippines, one collected from Mindanao Island and involving about half of the BPH individuals virulent to Mudgo and ASD7. We concluded that cultivars Rathu Heenati and Balamawee still have a broad spectrum of resistance against the Asian BPH strains.

Table 1. Adult survival rate (%) of the Asian BPH rice strains collected in 2006 on differential cultivars in rice.

Cultivar	BPH strain									
	JPN	CH	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD
Mudgo	94.3 ± 3.7	74.3 ± 5.7	77.1 ± 6.8	100.0 ± 0.0	91.4 ± 4.0	91.4 ± 5.9	82.6 ± 5.2	80.0 ± 6.2	94.3 ± 5.7	51.4 ± 4.0
ASD7	94.3 ± 3.7	85.7 ± 3.7	80.0 ± 6.2	97.1 ± 2.9	97.1 ± 2.9	94.3 ± 3.7	85.7 ± 5.7	88.6 ± 4.0	91.4 ± 4.0	60.0 ± 0.0
Rathu Heenati	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2.9 ± 2.9	0.0 ± 0.0	11.4 ± 8.6	8.6 ± 5.9	8.6 ± 4.0	8.6 ± 4.0	0.0 ± 0.0
Babawee	11.4 ± 5.9	22.9 ± 10.2	8.6 ± 5.9	17.1 ± 9.2	11.4 ± 5.9	82.9 ± 5.2	77.1 ± 5.2	34.3 ± 3.7	37.1 ± 8.0	31.4 ± 4.0
ADR52	5.7 ± 5.7	5.7 ±5.7	0.0 ± 0.0	11.4 ± 5.9	0.0 ± 0.0	80.0 ± 7.6	71.4 ± 9.6	28.6 ± 7.3	25.7 ± 9.5	0.0 ± 0.0
Balamawee	0.0 ± 0.0	2.9 ± 2.9	0.0 ± 0.0	2.9 ± 2.9	2.9 ± 2.9	2.9 ± 2.9	8.6 ± 5.9	8.6 ± 4.0	5.7 ± 3.7	8.6 ± 5.9
T65 (check)	91.4 ± 5.9	80.0 ± 6.2	82.9 ± 6.8	94.3 ± 3.7	97.1 ± 2.9	88.6 ± 5.9	85.7 ± 5.7	85.7 ± 7.2	94.2 ± 3.7	77.1 ± 6.8

Table 2. The ratio of females with swollen abdomen of the Asian BPH strains collected in 2006 on differential cultivars in rice.

Cultivar	BPH strain									
	JPN	CHI	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD
Mudgo	94	74	77	100	91	91	83	80	86	40
ASD7	91	86	80	97	94	94	83	87	89	57
Rathu Heenati	0	0	0	0	0	0	0	0	0	0
Babawee	6	14	9	0	0	63	37	14	17	14
ADR52	0	0	0	0	0	51	23	0	0	0
Balamawee	0	0	0	0	0	0	0	0	0	0
T65 (check)	91	80	83	94	97	86	83	86	91	74

Monitoring BPH virulence using rice NILs

Tables 3 and 4 show that the adult survival rate and ratio of virulent females of 10 Asian BPH strains on the NILs and PYL carrying BPH resistance genes are derived from ADR52. Based on the resistance spectrum to NILs and the PYL for *bph20*(t) and *Bph21*(t), the Asian BPH strains seem to be classified into four groups. The first group is avirulent to all the tested lines. The second group is virulent to the *Bph21*(t)-NIL but avirulent to the *bph20*(t)-NIL and *bph20*(t) + *Bph21*(t)-PYL. The third group is virulent to both the *bph20*(t)-NIL and *Bph21*(t)-NIL but avirulent to *bph20*(t) + *Bph21*(t)-PYL. The fourth group is virulent to all tested lines. The first group is the Mindanao strain, which could not adapt to any lines. The second group consisted of BPH strains from China and Taiwan. The third group consisted of BPH strains from Japan and northern Vietnam and two Luzon strains from the Philippines. The discrimination between the second and third groups is still ambiguous because of differentiation among the BPH strains from China, Taiwan, and Japan as well as northern Vietnam, which have never been identified. The fourth group consisted of BPH strains from southern Vietnam; those were the most virulent and half of the adult females had swollen abdomens on the PYL within 5 days. The results indicate that both of the BPH resistance genes, *bph20*(t) and *Bph21*(t), are necessary to express broad-spectrum resistance against East Asian BPH strains. The PYL, however, had lost its resistance against the southern Vietnam strains of BPH. Monitoring the virulence of BPH strains using NILs and PYLs will open the door for the use of BPH-resistant cultivars and sustainable pest management in Asian rice fields.

Table 3. Adult survival rate (%) of Asian BPH strains collected in 2006 on NILs and the PL for the BPH resistance gene in rice.

NIL/PL	BPH strain									
	JPN	CHI	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD
bhp20(t)	85.7 ± 3.4	22.9 ± 4.8	31.4 ± 8.9	94.3 ± 5.3	60.0 ± 4.0	74.3 ± 5.3	88.6 ± 6.8	60.0 ± 5.7	85.7 ± 3.4	25.7 ± 5.3
Bhp21(t)	88.6 ± 5.5	80.0 ± 4.0	85.7 ± 3.4	91.4 ± 5.5	94.3 ± 3.4	94.3 ± 3.4	91.4 ± 3.7	91.4 ± 3.7	80.0 ± 5.7	37.1 ± 2.6
bhp20(t) + *Bhp21*(t)	17.1 ± 6.3	20.0 ± 4.0	28.6 ± 5.5	28.6 ± 3.7	25.7 ± 5.3	71.4 ± 6.8	65.7 ± 3.4	25.7 ± 6.7	17.1 ± 6.3	28.6 ± 7.9
T65 (check)	91.4 ± 3.7	94.3 ± 3.4	97.1 ± 2.6	97.1 ± 2.6	94.3 ± 3.4	91.4 ± 5.5	91.4 ± 3.7	94.3 ± 3.4	91.4 ± 5.5	91.4 ± 5.5

Table 4. The ratio of females with swollen abdomen of Asian BPH strains collected in 2006 on NILs and the PL for the BPH resistance gene in rice.

NIL/PL	BPH strain									
	JPN	CHI	TW	RRD1	RRD2	MRD1	MRD2	LZ1	LZ2	MD
bhp20(t)	63	0	0	83	51	69	71	34	37	0
Bhp21(t)	86	80	77	71	77	89	86	77	51	11
bhp20(t) + *Bhp21*(t)	0	0	0	0	0	49	51	0	0	0
T65 (check)	86	94	97	97	87	80	86	94	91	89

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Notes

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Breeding for resistance to planthoppers in rice

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Rice is an important cereal and a source of calories for one-third of the world population. Many diseases and insects attack the rice plant. Among the insect pests, planthoppers cause significant yield losses. Of the various strategies, host-plant resistance is the most practical and economical approach to control insect pests. Six kinds of planthoppers, brown planthopper (BPH), whitebacked planthopper (WBPH), green leafhopper (GLH), zigzag leafhopper (ZLH), small brown planthopper (SBPH), and green rice leafhopper (GRH), cause yield losses in rice to a variable extent. These hoppers are also vectors of major viral diseases, such as grassy stunt, ragged stunt, rice stripe virus, black streak, and tungro disease. A number of donors for resistance have been identified and used in breeding varieties resistant to hoppers. Genetics of resistance to planthoppers has been studied and several resistance genes have been identified from traditional landraces, including wild species. As many as 21 resistance genes have been identified for BPH, 8 for WBPH, 14 for GLH, 6 for GRH, and 3 for ZLH. Of the 21 BPH resistance genes, 15 have been mapped to different chromosomal locations. Some of the mapped BPH resistance genes have become available for use in marker-assisted selection (MAS). Similarly, a few genes resistant to other planthoppers are being mapped. In addition, QTLs have also been identified for BPH, WBPH, and GRH. Of the six hoppers, GRH is mostly found in temperate rice-growing regions. Six resistance genes for GRH have been mapped, on chromosomes 5, 11, 6, 3, 8, and 4. Near-isogenic lines have been developed in a japonica background using the MAS approach. ZLH occurs in the tropics and subtropics of Asia and has remained a minor pest of rice. One of the major challenges for plant breeders is to cope with the frequent changes in biotypes and populations of planthoppers, particularly in the context of climatic change. Future research should focus on establishing high-throughput screening protocols for field resistance, identifying new genes for resistance from diverse sources, and developing varieties with durable resistance to hoppers using MAS through pyramiding of major genes and QTLs. Furthermore, there is a need to develop gene-based markers, particularly single nucleotide polymorphism markers, to accelerate the transfer of genes into different genetic backgrounds and for breeding varieties resistant to hoppers. Characterization of insect populations/biotypes in different geographical regions is emphasized for the deployment of different genes for resistance to planthoppers.

Humans and insects have always competed for food and fiber, so they have been constantly at war with each other. Insects cause millions of dollars' worth of losses annually to food crops and other plants all over the world. Scientists have devised various control measures to minimize these losses. The most practical and economical control measure is varietal resistance to insects. Painter (1951) and others demonstrated that clear-cut cases of host resistance existed in crop species of importance to agriculture.

Rice is attacked by a large number of insects. Among these insect pests, planthoppers, stem borers, and gall midges are the most serious pests of rice. Six kinds of planthoppers, (1) brown planthopper—BPH (*Nilaparvata lugens* Stål), (2) small brown planthopper—SBPH (*Laodelphax striatellus* Fallen), (3) green leafhopper—GLH (*Nephotettix virescens* Distant), (4) green rice leafhopper—GRH (*Nephotettix cincticeps* Uhler), (5) whitebacked planthopper—WBPH (*Sogatella furcifera* Horvath), and (6) zigzag leafhopper—ZLH (*Recilia dorsalis* Motschulsky), attack rice plants. BPH causes direct damage by sucking plant sap, causes hopperburn, and transmits viral diseases such as grassy stunt and ragged stunt. SBPH transmits rice stripe virus and black streak dwarf virus diseases, GRH transmits rice dwarf virus, and GLH transmits the virus that causes tungro disease.

Lately, the BPH has caused devastating damage in China, Korea, Japan, and Vietnam. In 2005, China reported a loss of 2.7 millions tons of rice due to direct damage, while the loss reached 0.4 million tons in Vietnam, mainly from two virus diseases—grassy stunt and ragged stunt—carried by BPH in a persistent manner. Hybrid rice crops in China and northern Vietnam have favored another planthopper pest, the whitebacked planthopper. In central China, outbreaks of the smaller brown planthopper, which carries black streak dwarf virus disease, have recently been reported. Tungro virus disease, caused by two viruses vectored by the green leafhopper, also remained problematic in some areas. To develop sustainable management systems, it is important to find the right balance between breeding and management, so as to reduce pests' ecological fitness to keep them under economic threshold levels.

Screening techniques for evaluating germplasm for resistance to hoppers have been developed. Mass screening involving screening at the seedling stage has been the most commonly used technique at IRRI and by the national agricultural research and extension systems (NARES) for hoppers. A large number of germplasm accessions have been screened at IRRI for resistance to BPH (biotype 1, 2, 3), GLH, WBPH, and ZLH. As many as 44,335 accessions were screened for BPH biotype 1 (15.4% resistant); 10,553 for BPH biotype 2 (1.9% resistant); 13,021 for BPH biotype 3 (1.8% resistant); 50,137 for GLH (2.8% resistant); 52,042 for WBPH (1.7% resistant); 15,656 for yellow stem borer (3.8% resistant); and 6,881 for striped stem borer (<0.02% were resistant) (Jackson 1997). Several donors for resistance have been identified and used to develop hopper-resistant varieties (Table 1).

Table 1. Some genetic donors identified for resistance to planthoppers in rice.

Insect pest	Donors for resistance
Brown planthopper	Mudgo, ASD7, Ptb33, Rathu Heenati, Babawee, ARC10550, Swarnalata, *Oryza officinalis, O. australiensis, O. minuta*
Green leafhopper	Peta, Pankhari 203, Sigadis, Ptb8, ARC10313, ASD7, ASD8, DV85, Asmaita
Whitebacked planthopper	N22, ARC10239, ADR52, Podiwi-A8
Zigzag leafhopper	Rathu Heenati, Ptb21, Ptb33

Screening techniques for resistance to planthoppers

With the advent of insect-infestation devices and simple agronomic procedures for growing healthy plants, it is now possible to adopt techniques for mass screening large populations of segregating plant materials. This is an initial step in the screening technology needed to eliminate the majority of susceptible segregants and select the resistant ones. Such large-scale evaluation where insects are offered a free choice of plant materials can be accomplished in the greenhouse, screenhouse, or small field plots. The approach for screening and evaluating resistance will depend on the insect and the crop under study, the required insect numbers, as well as the availability of research facilities. If insect damage occurs at more than one stage of plant growth, it is important to evaluate resistance at each of those stages.

Breeding materials can be screened rapidly by infesting plants at the seedling stage, especially during an early mass-screening cycle, in the greenhouse. Greenhouse screening techniques are economical in space, time, and labor, and have been successfully employed in screening cultivars of several grains and forage crops, including rice (Heinrichs et al 1985), sorghum (Starks and Burton 1977), and alfalfa (Sorensen and Horber 1974).

The conventional seedbox screening test is a rapid method for screening large numbers of rice germplasm accessions for qualitative resistance to hoppers (Heinrichs et al 1985, Panda and Khush 1995). Seed sowing and infestation are timed according to the hopper-rearing schedule. Seeds are sown in rows in a standard seedbox (60 × 40 × 40 cm). The number of insects per seedling can be determined easily. Twenty-five seeds of each test entry are sown in a 12-cm row. Seven days after sowing (DAS), when the seedlings are at the two- to three-leaf stage, the seedboxes are placed in a water pan inside a screened room. The seedboxes are kept in the pan containing 5 cm of water. Planthopper nymphs (2nd instar) cultured on a susceptible variety are uniformly distributed on the test seedlings by holding the base of the feed plant and lightly tapping the plants and blowing on them. In this way, approximately 10 hop-

Table 2. Some examples of genes for planthoppers identified in rice.

Planthopper	Genes identified
Brown planthopper	*Bph1, bph2, Bph3, bph4, bph5, bph6, bph7, bph8, Bph9, Bph10, bph11, bph12, bph13, Bph14, bph15, Bph16, Bph17, Bph18*(t), *bph19*(t), *bph20, bph21*
Whitebacked planthopper	*Wbph1, Wbph2, Wbph3, wbph4, Wbph5, Wbph6, Wbph7*(t), *Wbhp8*(t)
Green leafhopper	*Glh1, Glh2, Glh3, glh4, Glh5, Glh6, Glh7, Glh8, Glh9, glh10*
Green rice leafhopper	*Grh1, Grh2, Grh3, Grh4, Grh5, Grh6*
Zigzag leafhopper	*Zlh1, Zlh2, Zlh3*

per nymphs are deposited on each seedling. Grading of the entries in each seedbox is done when about 90% of the susceptible check seedlings in that box are dead. The Standard Evaluation System (SES) scale (0–9) for rice (IRRI 1988) is used to score seedling damage: 0 = no damage; 1 = very slight damage; 3 = first and second leaves of most plants are partially yellow; 5 = pronounced yellowing and stunting or about half of the plants wilting or dead; 7 = more than half of the plants wilting or dead; 9 = all plants dead.

Genetics of resistance to hoppers

Information on the genetics of resistance is useful to breeders in deciding on a breeding methodology and breeding strategies to be adopted. Diverse genes for resistance are needed to cope with the development of new biotype populations and to attain regional deployment of genes. Entomologists and breeders have investigated the inheritance of resistance to identify diverse genes for resistance (Table 2). A number of genes for resistance to hoppers have been identified: 21 genes for BPH, 6 for WBPH, 10 for GLH, 6 for GRH, and 3 for ZLH.

Brown planthopper (*Nilaparvata lugens* Distant)

The BPH is the most serious of the rice pests. It causes considerable damage by direct feeding. It also transmits grassy stunt and ragged stunt virus diseases. Comprehensive information is available on the taxonomy of BPH outbreaks, migration, and varietal resistance, including chemical, biological, and cultural control (IRRI 1979). Sources of resistance to BPH were identified in 1967 (Pathak et al 1969). A program on breeding and genetics started in 1968. Two genes for resistance, *Bph1* and *bph2*, were identified in 1970 (Athwal et al 1971). The first resistant variety with *Bph1*, IR26, was released in 1973 (Khush 1971) and it was widely accepted in the Philippines, Indonesia, and

Vietnam but became susceptible in 1976-77 because of the development of biotype 2 of BPH. By that time, varieties IR36 and IR38 with the *bph2* gene had been developed and released (Khush 1977b). IR36 soon replaced IR26 and became the dominant rice variety. Its resistance to BPH lasted for 14 years, until 1991. Two biotypes of BPH existed before the large-scale introduction of BPH-resistant varieties. BPH-resistant variety IR26 with the *Bph1* gene for resistance was released in the Philippines in 1973 and in Indonesia and Vietnam in 1974. It was widely planted in those countries. A biotype appeared in 1977 that could damage IR26; it was designated as biotype 2. After the breakdown of resistance in IR26, IR36 and IR42 with the *bph2* gene were released (Khush 1977a). They were widely adopted in the Philippines, Indonesia, and Vietnam but were found to be susceptible to a South Asian biotype (biotype 4). IR42 became susceptible in North Sumatra Province of Indonesia in 1982. These varieties were resistant until 1989-90. IR56 with the *Bph3* gene was released in 1982 in the Philippines. Several other varieties (IR60, IR62, IR68, IR72, and IR74) were released and were resistant to biotype 3. Some varieties are resistant on the Indian subcontinent but in Southeast and East Asia have *bph5*, *Bph6*, or *bph7* genes for resistance. According to Jairin et al (2007), *Bph1*, *bph2*, *Bph3*, and *bph4* have been used extensively in Thai breeding programs. Improved rice cultivars carrying *Bph1*, *bph2*, *Bph3*, and *bph4*, however, lost their ability against BPH, although cultivars with *Bph3* have shown a higher degree and broader spectrum of resistance against BPH.

Sources of resistance to BPH were first identified in 1967 (Pathak et al 1969). Since then, many donors for resistance to BPH have been identified and used in breeding BPH-resistant varieties. Some of the donors are Mudgo, ASD7, Rathu Heenati, Babawee, ARC10550, Swarnalata, T12, Chin Saba, Balamawee, *O. officinalis, O. australiensis*, and *O. minuta* from cultivated and wild species of rice (Table 1).

In another study, 29 additional resistant varieties were analyzed genetically and two new genes, *Bph3* and *bph4*, were identified (Lakshminarayana and Khush 1977). These genes were incorporated into improved germplasm. In 1982, when a biotype capable of damaging IR36 appeared in small pockets in the Philippines and in Indonesia, IR56 and IR60 with the *Bph3* gene for resistance were released (IRRI 1983). IR66 with *bph4* for resistance was released in 1987 and IR68, IR70, and IR72, all with *Bph 3*, were released in 1988. These varieties were widely grown in tropical and subtropical rice-growing countries. If we had neglected gene identification work, the planned incorporation of diverse genes for resistance to BPH would have been impossible and we would not have been able to keep ahead of this shifting enemy of the rice crop. The value of genetic analysis of resistance cannot therefore be overemphasized.

More than 100 resistant cultivars have been analyzed genetically. Athwal et al (1971) showed that the resistance in Mudgo, CO22, and MTU15 was governed by the same dominant gene, which they designated *Bph1*. A single recessive gene, designated *bph2*, conveyed resistance in ASD7. *Bph1* and *bph2* are closely linked and no recombination between them has been observed. Chen and Chang (1971) also reported that a single dominant gene controls resistance in Mudgo. Athwal and Pathak (1972) reported that MGL2 possesses *Bph1* and Ptb18 possesses *bph2*. Martinez and

Khush (1974) investigated the inheritance of resistance in two breeding lines of rice that originated from crosses of susceptible parents. One of the lines, IR747B2-6, possessed *Bph1* for resistance. IR1154-243 is susceptible but a small number of F_2 progenies from its crosses with other susceptible varieties such as TN1, IR8, or IR24 are resistant. It was hypothesized that TKM6 is homozygous for *Bph1* as well as for the dominant inhibitory gene, *IBph1*, which inhibits *Bph1*.

In a genetic study of 28 varieties, Lakshinarayana and Khush (1977) found nine varieties with *Bph1*, 16 with *bph2*, and one variety with both genes. Two varieties were found to have new genes. A single dominant gene, which conveys resistance in Rathu Heenati, was designated *Bph3*. This gene segregates independently of *Bph1*. A single recessive gene, which controls resistance in Babawee, was designated *bph4*. This gene segregates independently of *bph2*. Genetic analysis of 20 resistant varieties by Sidhu and Khush (1978) revealed that seven varieties had *Bph3*, 10 had *bph4*, and resistance in the remaining three was governed by two genes. Sidhu et al (1979) also reported that *Bph3* and *bph4* were closely linked. Genes *bph4* and *Glh3* are also linked with a map distance of 34 units. The *bph4* gene appeared to be linked with *sd1* (recessive gene for semidwarf). However, *bph4* and *Xa4* (gene for bacterial blight resistance) are inherited independently. Kaneda et al (1981) reported on screening of 3,300 cultivars and breeding lines. About 60% of the Sri Lankan varieties possess *bph2* while only 10% of the Indian cultivars have this gene. Ikeda and Kaneda (1981) also found that both *bph2* and *Bph1* segregate independently of both *Bph3* and *bph4*, whereas *Bph3* and *bph4* as well as *Bph1* and *bph2* are closely linked. Ikeda and Kaneda (1982) reported that *Bph1* segregated independently of the gene for dwarf virus resistance in Kanto PL3 and also of the gene governing stripe disease resistance in Kanto PL2.

On the basis of trisomic analysis, Ikeda and Kaneda (1981) identified the loci of *Bph3* and *bph4* on chromosome 10. In another study, Ikeda and Kaneda (1983) located *Bph1* on chromosome 4. No linkage was detected between *Bph1* on the one hand and *lg* and *d11* markers of chromosome 4 on the other. However, *bph2* was found linked with *d-2* and had a 39.4% recombination value. Khush et al (1985) carried out genetic analysis of ARC10550. This cultivar is resistant to BPH populations in South Asia (biotype 4) but is susceptible to the population of biotypes 1, 2, and 3 in East and Southeast Asia. It was found to have a single recessive gene, *bph5*, for resistance, which segregates independently of *Bph1*, *bph2*, *Bph3*, and *bph4*.

Seventeen additional rice cultivars resistant to biotype 4 but susceptible to biotypes 1, 2, and 3 were analyzed by Kabir and Khush (1988). Seven were found to have a single dominant gene for resistance. The dominant gene(s) of these cultivars segregated independently of *bph5*. The dominant gene of cultivar Swarnalata was designated *Bph6*. In the remaining 10 cultivars, resistance was conferred by a single recessive gene. The recessive genes for resistance of eight cultivars were found to be allelic to *bph5*. However, the recessive genes of two cultivars are nonallelic to *bph5*. The recessive gene of T12 was designated *bph7*.

Thai varieties Col. 5 and Col. 11 and Chin Saba from Myanmar were reported to have single recessive genes for resistance that are allelic to each other but are nonallelic to *bph2* and *bph4*. Similarly, cultivars Kaharmana, Balamawee, and Pokkali

were found to have single dominant genes that are allelic to each other but different from *Bph1* and *bhp3* (Khush 1992). These cultivars are resistant to biotypes 1, 2, and 3, compared with cultivars with *bph5*, *Bph6*, and *bph7*, which are susceptible. Nemoto et al (1989) concluded that the recessive gene of Col. 5 and Col. 11 from Thailand, and Chin Saba, must also be different from *bph5* and *bph7*. They designated this gene as *bph8*. Similarly, the dominant gene of Kaharmana, Balamawee, and Pokkali was designated as *Bph9* (Murata et al 2001). A new locus for resistance to BPH was identified in the indica variety DV85 (Su et al 2005).

Ikeda and Kaneda (1981) located *Bph3* and *bph4* on chromosome 10 through trisomic analysis. Ikeda and Kaneda (1983) detected linkage of *bph2* with *d11* on chromosome 4. Multani et al (1994) identified BPH resistance on chromosome 12 through BPH bioassays of monosomic alien addition lines (MAAL). A gene for BPH resistance introgressed from *O. australiensis* mapped with RFLP on chromosome 12 (Ishii et al 1994). Of the 14 polymorphic probes on chromosome 12, RG457 detected introgression from *O. australiensis*, which co-segregated with BPH resistance, and RG457 was tagged with *Bph10* on chromosome 12 at a distance of 3.69 ± 1.29 cM.

Four BPH biotypes are known. Biotypes 1 and 2 are widely distributed in Southeast Asia, biotype 3 is a laboratory biotype produced in the Philippines, and biotype 4 occurs on the Indian subcontinent. The *Bph1* group confers resistance to biotypes 1 and 3 but is susceptible to biotype 2, the *bph2* group conveys resistance to biotypes 1 and 2 but is susceptible to biotype 3, and the *Bph3* group and *bph4*, *bph8*, and *Bph9* confer resistance to all four biotypes. Genes such as *bph5*, *Bph6*, and *bph7* convey resistance to biotype 4 only (Khush and Brar 1991). He (2007) mapped *bph7* and *bph8* on chromosome 4. Many workers have studied the relationship between BPH biotypes and genes for resistance (Table 3). IR varieties of rice carry *Bph1*, *bph2*, and *Bph3* genes and *Glh3*, *glh4*, *Glh9*, and *glh10* (Table 4). Wei et al (2009) used a proteomic approach and analyzed the interaction between rice and BPH. Proteins involved in multiple pathways showed significant changes in expression in response to BPH feeding, including jasmonic acid synthesis proteins and oxidative stress-response proteins. Wang et al (2008) used a cDNA microarray containing 1,920 suppression subtractive hybridization clones to detect transcript profile differences in resistant and susceptible cultivars under a control and BPH feeding. In total, 160 unique genes were detected as being significantly affected by BPH feeding. Shi et al (2003) constructed a genomic library from BPH-resistant B5. The library contained 36,864 clones with an average insert size of 60 kb. Eleven clones were identified covering the *Qbp1* locus (the locus between markers R1925 and G1318 on chromosome 3).

Molecular mapping of genes for BPH resistance

A total of 21 genes for BPH resistance have been identified from cultivated and wild species of *Oryza*. Of these 21 resistance genes, 15 are mapped to different chromosomal locations and 8 are tightly linked with molecular markers. A number of genes for resistance to BPH have been mapped using RFLP, RAPD, and SSR markers. Some QTLs have also been mapped (Table 5). Six of these genes, *Bph1*, *bph2*, *Bph9*,

Table 3. Interrelationships between biotypes of brown planthopper and genes for resistance in rice.

Variety	Gene	Reaction to biotypes[a]			
		1	2	3	4
Mudgo	*Bph1*	R	S	R	S
ASD7	*bph2*	R	R	S	S
Rathu Heenati	*Bph3*	R	R	R	R
Babawee	*bph4*	R	R	R	R
ARC 10550	*bph5*	S	S	S	R
Swarnalata	*Bph6*	S	S	S	R
T12	*bph7*	S	S	S	R
Chin Saba	*bph8*	R	R	R	–
Balamawee	*Bph9*	R	R	R	–
TN1	*none*	S	S	S	S
O. australiensis	*Bph18*	R	R	R	R
O. officinalis	*Bph6, Bph13*	R	R	R	R
O. minuta	*Bph20, Bph21*	R	–	–	
O. latifolia	*Bph12*	–	R	–	–

[a]R = resistant, S = susceptible.
Source: Modified from Zhang (2007).

Bph10, *Bph18,* and *Bph21,* are located on chromosome 12. *Bph12*, *Bph15*, *Bph17,* and *Bph20* are located on chromosome 4 (Rahman et al 2009). *Bph11*, *Bph13*, *Bph14*, and *Bph19* are located on chromosome 3, *Bph6* on chromosome 11, *Bph3* and *bph4* on chromosome 6, and *Bph13*(t) on chromosome 2. There is some inconsistency in assigning a gene number and mapping (Table 5). Huang et al (1997) used a doubled-haploid (DH) population (IR64 × Azucena) and located a BPH resistance gene from IR64 on chromosome 12. Three RFLP markers (RG493, RG901, and CD0344) and *sdh1* showed linkage with the BPH resistance gene. *Bph10* from IR65482-4-136-2-2 and *Bph1* from Mudgo for resistance to biotypes 1 and 3 were located near XNpb248. Although the pattern of resistance is different among these varieties, the genes are mapped in a similar position. The linkage between the RAPD marker $OPA16_{938}$ and the BPH resistance gene *Bph6* was 0.52 cM in the coupling phase. The 938-bp RAPD amplicon was cloned and used as a probe on 122 *Cla1*-digested DH plants from an IR64 × Azucena mapping population for RFLP inheritance analysis and was mapped onto rice chromosome 11. RAPD marker $OPA16_{938}$ could be used in a cost-effective way for marker-assisted selection (MAS) for BPH resistance (Jena et al 2002).

Renganayaki et al (2002) mapped the *Bph13*(t) gene derived from *O. officinalis* on chromosome 3 using a RAPD marker. The most closely linked marker was

Table 4. Genes for resistance to brown planthopper (BPH) and green leafhopper (GLH) in IR varieties.

Variety	BPH	GLH	Variety	BPH	GLH
IR5	0	*Glh3*	IR45	*Bph1*	*Glh3*
IR8	0	*Glh3*	IR46	*Bph1*	–
IR20	0	*Glh3*	IR48	*bph2*	–
IR22	0	0	IR50	*bph2*	*Glh9*
IR24	0	–	IR52	*bph2*	*Glh9*
IR26	*Bph1*	–	IR54	*bph2*	*Glh9*
IR28	*Bph1*	*Glh9*	IR56	*Bph3*	*Glh9*
IR29	*Bph1*	*Glh9*	IR58	*Bph3*	*Glh9*
IR30	*Bph1*	*Glh3*	IR60	*Bph3*	*Glh9*
IR32	*bph2*	–	IR62	*Bph3*	–
IR34	*Bph1*	*Glh9*	IR64	*Bph1*	–
IR36	*bph2*	*Glh10*	IR65	*bph2*	*Glh9*
IR38	*bph2*	–	IR66	*Bph3*	–
IR40	*bph2*	–	IR68	*Bph3*	–
IR42	*bph2*	*glh4*	IR70	*Bph3*	–
IR43	*0*	–	IR72	*Bph3*	–
IR44	*Bph1*	–	IR74	*Bph3*	–

Sources: Modified from Khush and Virk (2003) and Khush et al (2007).

converted into an STS marker and is mapped 1.3 cM from the resistance gene. An introgression line derived from *O. sativa* and *O. officinalis*, IR54741-3-21-22, was found to be resistant to an Indian biotype of BPH and resistance was controlled by a single dominant gene. Kim and Sohn (2005) used bulk segregant analysis with 520 RAPD markers for analysis of BPH resistance. One of these primers, OPE18, which amplified a 923-bp band, was tightly linked to BPH resistance. The *Bph1* gene was mapped at a distance of 3.8 cM from the STS marker BpE 18-3. Yang et al (2004) developed a high-resolution genetic map of *Bph15* by positioning 21 DNA markers in the target chromosomal region. An assay of the recombinants using subclones in combination with sequence analysis delimited the *Bph15* gene to a genomic segment of approximately 47 kb. Chen et al (2006) fine-mapped *bph19*(t) to a region of about 1 cM on the short arm of chromosome 3 flanked by RM6308 and RM3134. Sequence information of clones was used to construct a physical map of *bph19*(t) and the locus was physically defined to an interval of about 60 kb. Sun et al (2005) analyzed Sri Lankan indica rice cultivar Rathu Heenati and found it to be resistant to all four biotypes of BPH. Three loci detected by QTL analysis were assigned to chromosomes 3, 4, and

Table 5. Some examples of molecular mapping of genes for BPH resistance.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
Bph1	12	Mudgo	G148 (RFLP)	Biotype 1	Hirabayashi and Ogawa (1995), Sun et al (2006)
	12L	Mudgo	em5814N (AFLP)	Biotype 1	Sharma et al (2002)
	12	Samgangbyeo	BpE18-3 (STS)	Biotype 1	Kim and Sohn (2005)
	12L	IR28	XNpb248, XNpb336 (RFLP)	Biotype 1	Hirabayashi and Ogawa (1995)
	12L	Norin PL3	AFLP em5814N		
	12	Gayabyeo	OPD-7 RD7 (RAPD), RG869, RG457 (RFLP), RM247 (SSR)	Biotype 1 Biotype 1	Sharma et al (2004) Jeon et al (1999)
Qbp1	3L	B5 *(O. officinalis)*	R1925, R2443 (RFLP)	Biotypes 1 & 2	Huang et al (2001)
Qbp1 (*Bph14*t)	3	B5 *(O. officinalis)*	R1925, G1318 (RFLP)	–	Ren et al (2004)
bph2	12	Norin PL4 (*bph2* introgression line from IR1154-243)	G2140 (RFLP)	Biotypes 1 & 2	Murata et al (1998)
	2	ASD7 (Acc. no. 6303)	RM463, RM7102 (SSR)	Biotypes 1 & 2	Sun et al (2006)
	2	Norin PL4 (*bph2* introgression line from IR1154-243)	KAM4 (complete co-segregation with *bph2*), STS	–	Murai et al(2001), Sharma et al (2004)
	12	Norin PL4 (*bph2* introgression line from IR1154-243)	G2140 (SSR)	–	Sun et al (2006)
Qbph2	2L	Col.5 T	RM6843, RM3355 (SSR)	Mixture of biotypes 1 & 2	Sun et al (2007)
	4S	B5 *(O. officinalis)*	C820, R288 (RFLP)	Biotypes 1 & 2	Huang et al (2001)
	2L	*O. eichingeri* Acc. no. 105159	RFLP, SSR	–	Liu et al (2001)
	2	Yagyaw	5529-1358 (SSR)	–	Liu et al (2009)
Bph3	6S	Rathu Heenati (Acc. no. 6730)	RM589 (SSR)	Biotypes 1, 2, 3, 4	Jairin et al (2007a)
Qbph3	3	Rathu Heenati (Acc. no. 11730)	RM313, RM7 (SSR)	–	Sun et al (2005)

Continued on next page

Table 5 continued.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
bph4	6S	Babawee (Acc. no. 8978)	RM190 (SSR), C76A (RFLP)	–	Kawaguchi et al (2001)
	6S	Babawee	C891, C531 (RFLP)	–	Murata 1998, Nagato and Yoshimura 1998
Qbph4	4	Rathu Heenati (Acc. no. 11730)	RM8213, RM5953 (SSR)	–	Sun et al (2005)
	4S	Yagyaw	RM401, RM335 (SSR)	–	Liu et al (2009), Sun et al (2005), Yang et al (2004)
bph5		ARC 10550 (Acc. no. 12507)	–	Biotype of Bangladesh	Khush et al (1985), Kabir and Khush (1988)
Bph6		Swarnalata (Acc. no. 33964)	–	–	Kabir and Khush (1988)
Qbph6	6S	Col. 5 T	RM510 (SSR)	Mixture of biotypes 1 & 2	Sun et al (2007)
bph7		T12 (Acc. no. 59689)	–	Biotype of Bangladesh (biotype 4)	Kabir and Khush (1988)
Qbph7	7	Yagyaw	RM542, RM500 (SSR)	–	Liu et al (2009)
bph8(t)		Col. 5 T	–	Biotypes 1, 2, 3	Nemoto et al (1989)
bph8(t)		Chinsaba (Acc. no. 33016)	–	Biotypes 1, 2, 3	Nemoto et al (1989)
Bph9	12L	Karahamana	RM463, RM5341 (SSR)	Biotype 1	Su et al (2006)
	12L	Pokkali	OPR04 (RFLP), S2545 (RAPD)	–	Murata et al (2001)

Continued on next page

Table 5 continued.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
Qbph9		Yagyaw	RM3533, RM242 (SSR)	–	Liu et al (2009)
Bph10(t)	12L	IR65482-4-136-2-2 (*O. australiensis* Acc. no. 100882)	RG457 (RFLP)	Biotypes 1, 2, 3	Ishii et al (1994)
Qbph10	10	Rathu Heenati (Acc. no. 11730)	RM484, RM496 (SSR)	–	Sun et al (2005)
bph11(t)	3L	IR742-23-19-12-3-54 (*O. officinalis*)	G1318 (RFLP)	–	Hirabayashi et al (1998)
Bph12(t)	4S	B14 (*O. latifolia*)	RM261 (SSR)	Biotype of Japan	Yang et al (2002)
	4S	GSK185-2 (*O. officinalis*)	G271, R93 (RFLP)	–	Hirabayashi et al (1998)
	4	*O. latifolia*	RLPP	–	He (2007)
bph12(t)	4	*O. officinalis*	RFLP	–	Hirabayashi et al (1998)
Bph13(t)	2L	*O. eichingeri* Acc. no. 105159	RM250 (SSR), RFLP	–	Liu et al (2001)
	3S	IR54745-2-21-12-17-6 (*O. officinalis*)	AJ09b_{230} (RAPD), AJ09c (STS)	Biotype 4	Renganayaki et al (2002)
Bph14 (*Qbph1*)	3L	B5 (*O. officinalis*)	R1925, G1318 (RFLP)	–	Yang et al (2004)
Bph15 (*Qbph2*)	4S	B5 (*O. officinalis*)	C820, S11182 (RFLP)	Biotype from China	Yang et al (2004)
Qbp2 (*Bph15*(t)	4	B5 (*O. offcinalis*)	C820, R288 (RFLP)	–	Ren et al (2004)
Bph17(t)	4S	Rathu Heenati	RM8213, RM5953 (SSR)	–	Sun et al (2005)
Bph18(t)	12L	IR65482-7-216-1-2 (*O. australiensis* Acc. no. 100882)	RM1022 (SSR)	Biotype of Korea	Jena et al (2006)
bph 19(t)	3S	AS20-1	RM6308, RM3134 (SSR)	–	Chen et al (2006)

Continued on next page

Table 5 continued.

Gene	Chromosome	Donor	Markers	Resistance to biotypes	References
Bph20(t)	4	IR71033-121-15 (*O. minuta* Acc. no. 101141)	STS	Biotype of Korea	Rahman et al (2009)
Bph21(t)	12	IR71033-121-15(*O. minuta* Acc. no. 101141)	STS	Biotype of Korea	Rahman et al (2009)
BPH*	12	IR64	RG463, RG901, CDO 344 (RFLP) Sdh-1 (isozyme marker)	–	Huang et al (1997)
Bph6	11	IR54741-3-21-22	$OPA16_{938}$ (RAPD)	Biotype of India	Jena et al (2002)

*Gene not named.

10. The phenotypic variance of the three QTLs indicated that the QTL on chromosome 4 is a major BPH resistance gene in Rathu Heenati. Linkage analysis indicated that this BPH resistance gene was located between two SSR markers, RM8213 and RM5953, on the short arm of chromosome 4, with a map distance of 3.6 cM and 3.2 cM, respectively. This gene was tentatively designated as *Bph17*.

Li et al (2006) incorporated *Bph14* and *Bph15* through MAS into a number of parental lines used in hybrid rice breeding in China. Su et al (2005) located *qbph11*, which explained 68.4% of the phenotypic variation of BPH resistance (biotype 2) in the progenies derived from the cross between DV85 and Kaimaze. An introgression line derived from *O. sativa* and *O. officinalis*, IR54741-3-21-22, was found to be resistant to an Indian biotype of brown planthopper. Genetic analysis of 95 F_3 progeny rows of a cross between the resistant line IR54741-3-21-22 and a BPH-susceptible variety revealed that resistance was controlled by a single dominant gene. RAPD analysis showed that one primer, $OPA16_{938}$, amplified a resistant parental band in the resistant bulk and a susceptible parental band in the susceptible bulk by bulked segregant analysis. RAPD analysis of individual F_2 plants with primer $OPA16_{938}$ showed marker phenotype co-segregation for all, but only one recombinant was identified. The linkage between RAPD marker $OPA16_{938}$ and the BPH resistance gene was 0.52 cM in the coupling phase. The 938-bp RAPD amplicon was cloned and used as a probe on 122 *Cla1*-digested DH plants from an IR64 × Azucena mapping population for RFLP inheritance analysis and was mapped onto rice chromosome 11 (Jena et al 2002). RAPD marker $OPA16_{938}$ could be used in a cost-effective way for marker-assisted selection for BPH resistance.

Jairin et al (2007a,b) mapped *Bph3* on the short arm of chromosome 6 between two flanking markers, RM589 and RM586, within 0.9 cM and 1.4 cM, respectively. Molecular analysis of three mapping populations derived from Ptb33 × RD6, Rathu Heenati × KDML105, and IR71033-121-15 × KDML105 showed BPH resistance genes located in the same genomic region on the short arm of chromosome 6. A novel resistance gene, *Bph18*, has been identified in breeding line IR65482-7-216-1-2 that has inherited the gene from the EE genome wild species *O. australiensis* (Jena et al 2006). The *Bph18* gene has been located on the long arm of chromosome 12 in a 0.843-Mb genomic region flanked by markers RM6869 and R10289S. An STS marker, 7312.T4A, derived from the BAC clone OSJNBa0028L05 that encodes a resistance protein sequence present in the flanking region is tightly linked to the *Bph18* gene for BPH resistance. The marker 7312.T4A can be efficiently used for MAS breeding of BPH resistance in rice.

Alam and Cohen (1998) identified seven QTLs for BPH resistance on chromosomes 1, 2, 3, 4, 6, and 8 using 175 markers. Ramalingam et al (2003) reported four additional QTLs associated with BPH resistance in the same population using an additional 105 candidate gene markers. Huang et al (2001) reported QTLs in wild species for BPH resistance. Xu et al (2002) reported seven main-effect QTLs and many epistatic QTLs associated with quantitative resistance to BPH using a recombinant inbred line derived from Tequing × Lemont populations. Su et al (2002) detected QTLs on chromosomes 2, 10, and 12 using a Nipponbare × Kasalath backcross population.

Soundararajan et al (2004) used a DH population (IR64 × Azucena) and detected six QTLs on chromosomes 1, 2, 6, and 7 for BPH resistance. Of these, QTLs on chromosome 7 showed association with seedling resistance and QTLs on chromosome 2 with antibiosis, whereas QTLs on chromosomes 1, 6, and 7 were associated with tolerance (Xu et al 2002). There is a need to extend QTL analysis at different growth stages of the plant and over different environments, including the candidate gene approach. Sun et al (2007) analyzed 147 F_3 families derived from BPH-resistant cultivar Col. 5 from Thailand and susceptible cultivar 02428. The BPH population used for infestation was a mixture of biotypes 1 and 2. Two QTLs were identified on chromosome 2 (29.4% phenotypic variation) and chromosome 6 (46.2% phenotypic variation). Comparison of chromosomal locations and reactions to BPH biotypes indicated that the gene on chromosome 6 is different from the previously identified genes. Liu et al (2009) made crosses between BPH-resistant landrace Yagyaw and susceptible cultivar Cpslo17. Four QTLs (*Qbph-2*, *Qbph-4*, *Qbph 7*, and *Qbph-9*) accounting for 5.64% to 12.77% of the phenotypic variation for BPH resistance were located. Two QTLs showed a significant additive effect. One resistant allele was harbored by the susceptible parent.

Marker-assisted selection for BPH resistance

Sharma et al (2004) used MAS for pyramiding *Bph1* and *bph2* into a japonica line. The pyramided line showed higher resistance than *bph2* but was equivalent to *Bph1*. Li et al (2006) incorporated *Bph14* and *Bph15* through MAS into a number of parental lines used in hybrid rice breeding in China and observed that 92.3% of *Bph14* single introgression lines had moderate resistance to BPH and *Bph14*/*Bph15* pyramided lines had higher resistance than the single-gene introgression lines. Park et al (2008) used representational difference analysis (RDA) and found that OsBphi252 is tightly linked to BPH resistance and could be used in MAS.

Jena et al (2006) used MAS to transfer *Bph18* into the recurrent parent Junambyeo (susceptible to BPH) with the marker 7312.T4A. The cultivar Junambyeo is semidwarf, photo-insensitive, highly productive, and cultivated commercially in irrigated rice areas in South Korea. However, it is highly susceptible to the BPH biotype of Korea. We used a marker-assisted backcross breeding approach and developed backcross (BC) progenies from a cross between Junambyeo and IR65482-7-216-1-2, the source of the *Bph18* gene. BC_2F_2 progenies segregating for BPH resistance were bio-assayed for resistance and susceptibility in the greenhouse and individual plants were analyzed for foreground selection to detect the presence or absence of the resistance gene. The breeding lines with the resistance gene were advanced further for the selection of desirable agronomic characteristics (Table 6).

Some 265 BC_2F_2 progenies were bio-assayed for BPH resistance and 65 BC_2F_2 progeny rows were randomly selected based on strong resistance. Amplification of the 7312.T4A locus in BC_2F_2 resistant plants did not detect a homozygous-susceptible marker allele (1,033 bp) of Junambyeo but detected a resistance-specific marker allele (1,078 bp) in the resistant plants in either a homozygous or heterozygous state (Fig.

Table 6. Agronomic traits of some promising breeding lines carrying the *Bph18* gene with multiple resistance to brown planthopper (BPH), blast (Bl), bacterial leaf blight (BB), and rice black streak dwarf virus (RBSDV).[a]

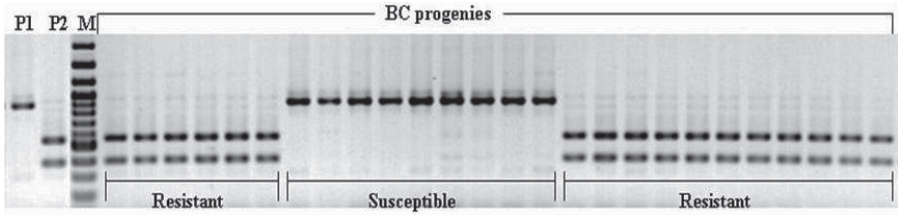
Breeding line	DTH (d)	CL (cm)	PL (cm)	PN	1,000-grain weight (g)	BPH	Bl	BB (K3a)	RBSDV (%)
IR83261-1-1-18-3-3-3-1	115	79	18.7	13	22.45	R	R	NT	31.6
IR83261-1-1-18-3-3-1-1	115	80	18.5	17	22.10	R	R	NT	22.2
IR83261-3-7-15-7-6-2	116	84	20.3	15	21.90	R	R	NT	26.3
IR83261-3-7-23-6-2-1-B	112	79	20.7	11	21.75	R	R	R	73.7
Junambyeo (RP)	116	75	17.7	11	22.55	S	MR	S	100.0

[a]DTH = days to heading, CL = culm length, P = panicle length, PN = panicle number, NT = not tested, RP = recurrent parent, R = resistant, S = susceptible, K3a = a new virulent BB race in Korea.
Source: Jena et al (unpublished).

1). Some 81 BC_2F_3 families comprising 5,235 plants were evaluated for desirable agronomic and grain quality characteristics and selected progenies were advanced to the BC_2F_5 generation using MAS for the *Bph18* gene. Some 77 BC_2F_5 BPH-resistant plants with agronomic traits similar or superior to those of the recurrent parent Junambyeo were again analyzed with the marker 7312.T4A. All the resistant plants had resistance-specific marker alleles of 7312.T4A in a homozygous state (Fig. 2) and confirmed the application of MAS for BPH resistance breeding. This MAS strategy for BPH resistance is useful for the development of breeding lines with superior agronomic traits and BPH resistance.

Green leafhopper (*Nephotettix virescens* Distant)

GLH is distributed throughout Asia but is a more serious pest in the tropics and subtropics. GLH causes yield losses by direct feeding as well as by acting as a vector for viruses causing tungro disease. A large number of varieties have been screened for GLH and many resistant donors (Pankhari 203, ASD7, Sigadis, Ptb8, DV85, Asmaita, ARC10313, ARC11554, *O. rufipogon*) have been identified. Genetic analysis has revealed 11 dominant and three recessive genes [*Glh1, Glh2, Glh3, glh4, Glh5, Glh6, Glh7, glh8, Glh9, glh10, Glh11, Glh12, Glh13, and Glh14* (Table 7)]. The inheritance of resistance to the GLH was first investigated by Athwal et al (1971) in varieties Pankhari 203, ASD7, and IR8. They found that resistance in each variety was controlled by one dominant gene. Three genes, *Glh1*, *Glh2*, and *Glh3*, were identified: Pankhari 203 had *Glh1*, ASD7 had *Glh2*, and IR8 had *Glh3*. The three genes segregated independently of each other. Siwi and Khush (1977) identified two more genes and analyzed 13 additional cultivars and identified one recessive gene, designated *glh4*, and a dominant gene, *Glh5*. Rezaul Karim and Pathak (1982) identified two dominant



P1 = (Junambyeo (recurrent parent), P2 = IR65482-7-216-1-2 (donor parent), M = molecular weight size market.

Fig. 1. MAS validation test of selected BC_2F_2 progenies by using gene-specific marker 7312. T4A followed by *Hinf*I digestion.

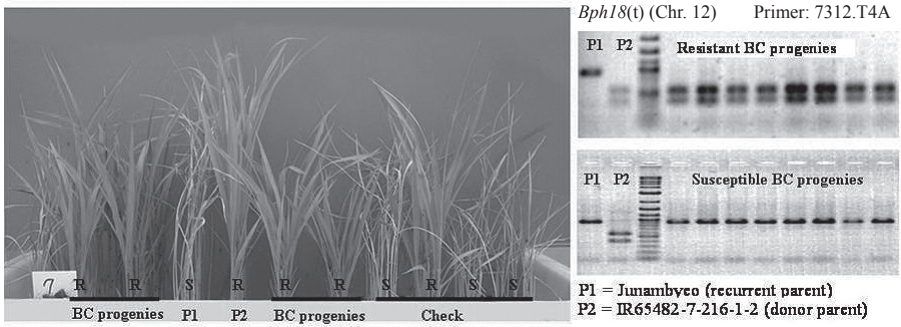


Fig. 2. Selected BC_2F_5 BPH-resistant progenies validated by marker 7312.T4A linked to the *Bph18* gene (right, upper panel). The susceptible progenies without the *Bph18* gene do not show a marker allele for resistance (right, lower panel). S = susceptible check, R = resistant check.

genes (*Glh6* and *Glh7*) and Ghani and Khush (1988) identified a recessive gene (*glh8*). Avesi and Khush (1984) studied the inheritance of resistance in 18 varieties. Two had *Glh1*, three had *Glh2*, two had *Glh3*, one had *glh4*, and three had two genes. Ruangsook and Khush (1987) analyzed 15 rice cultivars. The resistance was governed by two dominant genes in Katia Baudger 13-20, Laki 659, Lasane, Asmaita, and Choron Bawla, but by a single dominant gene in the remaining 10 cultivars. Allele tests with known genes revealed that one of the two dominant genes of Choron Bawla is allelic to *Glh2*. The single dominant gene in Chiknal and one of the two dominant genes in Laki 659 are allelic to *Glh3*. The second of the two dominant genes of Kaita Badger 13-20, Laki 659, and Lasane is allelic to *Glh5*. The two dominant genes of Asmaita and the single dominant gene of Hashikalmi, Ghaiya, ARC10313, and Garia are nonallelic to and independent of *Glh1*, *Glh2*, *Glh3*, *glh4*, and *Glh5*. Khush et al (2007) studied the genetics of resistance in 22 IRRI-bred rice varieties. These varieties were crossed with a susceptible Taichung Native 1 (TN1) and the reaction to green leafhopper was studied. Results showed that IR20, IR30, and IR45 are allelic to *Glh3*. On the other hand, IR34, IR50, IR52, IR54, IR56, IR58, IR60, and IR65 have *Glh9*. The dominant genes in IR24, IR26, IR29, IR43, and IR48 and the recessive genes in IR32, IR38, IR40, IR44, and IR46 segregate independently from *Glh1*, *Glh2*, and *Glh3*.

Table 7. Genes identified for resistance to green leafhopper.

Gene	Source	Chromosome
Glh1	Pankhari 203	5
Glh2	ASD7	11
Glh3	IR8	6
glh4	Ptb8	3
Glh5	ASD8, *O. rufipogon*	8
Glh6	TAPL796	5
Glh7	Maddani Karuppan	–
Glh8	DV85	–
Glh9	–	–
Glh10	–	–
Glh11	–	–
Glh12	–	–
Glh13	–	–
Glh14	ARC11554	4

Twenty-three landraces and wild species are included in the parentage of IR varieties. Of these, six landraces are resistant to GLH and, in all probability, are donors for resistance. IR8, IR5, IR20, IR30, and IR45 inherited *Glh3* from Peta. Gam Pai 30-12-15 is the donor of *Glh9* in IR28, IR34, IR50, IR52, IR54, IR56, IR58, IR60, and IR65. IR29 probably also has *Glh9* as it has Gam Pai 30-12-15 in its ancestry and because it was selected from the same cross as IR28.

Four varieties with recessive genes for resistance (IR32, IR38, IR40, and IR44) have CR49-13 in their ancestry and this variety is in all likelihood the donor of the resistance. CR94-13 is the donor of recessive gene *glh4* in IR42 (Avesi and Khush 1984) and also of *glh10* in IR36 (Angeles and Khush 2000). It appears that CR94-13 has two recessive genes, *glh4* and *glh10*. Thus, IR32, IR38, IR38, IR40, and IR44 may have inherited either of these recessive genes. Tetep is another source of resistance and it may have contributed its resistance gene to IR46. Further studies are needed to identify genes for resistance in other IR varieties.

Whitebacked planthopper (*Sogatella furcifera* Horvath)

WBPH occurs in all the rice-growing countries of Asia and does moderate damage to the crop. With the mass screening technique, germplasm collections have been evaluated and donors for resistance have been identified. More than 300 cultivars resistant to the WBPH have been identified and 80 of them have been analyzed genetically. Resistant donors (N22, ARC10239, ADR52, Podiwi-A8) have been identified (Table

Table 8. Genes identified for resistance to green rice leafhopper.

Gene	Source	Chromosome
Grh1	IR24, Pe-bi-hun	5
Grh2	DV85, Lepe dumai	11
Grh3	Rantaj emas 2	6
Grh4	DV85, Lepe Dumai, C203-1	3
Grh5	W1962 (O. rufipogon)	–
Grh6	Sml 17	4
Grh6	IRGC105715 (*O. rufipogon*)	4
Grh9	IRGC104038	9

8). Six genes for resistance (*Wbph1, Wbph2, Wbph3, wbph4, Wbph5, wbph6*) have been identified (Khush 1984). Tan et al (2004) identified another two genes (*Wbph7* (t) and *Wbph8*(t)). Kadrivel et al (1999) mapped QTLs for resistance to whitebacked planthopper. QTLs for ovicidal response have also been reported (Yamasaki et al 1999; Sogawata et al 2001).

A single dominant gene, designated *Wbph1*, was found to convey resistance to WBPH in variety N22 (Sidhu et al 1979). Resistance in ARC10239 is governed by a single dominant gene designated *Wbph2* (Angeles et al 1981). This gene segregates independently of *Wbph1*. Nair et al (1982) investigated 21 additional varieties; 19 had *Wbph1* and two had *Wbph2* and an additional recessive gene. The resistance of two of the 14 varieties analyzed by Hernandez and Khush (1981) was governed by *Wbph2*: 11 varieties each had a single dominant gene that segregated independently of *Wbph1* and *Wbph2*. The dominant gene of one such variety (ADR52) was designated *Wbph3*. Only one variety, Podiwi A8, had a recessive gene, which was designated *wbph4*. Saini et al (1982) analyzed 13 additional varieties. Resistance was governed by *Wbph1* in four varieties, by *Wbph2* in six, by *Wbph1* and *Wbph2* in two, and by a single dominant gene in Hornamawee segregated independently of *Wbph1* and *Wbph2*. Wu and Khush (1985) investigated the inheritance of resistance in 15 varieties. They found that resistance in nine was controlled by *Wbph1* and resistance in four was conferred by two genes. The remaining two varieties had single dominant genes for resistance, which segregated independently of *Wbph1, Wbph2*, and *Wbph3*. The dominant gene of N' Diang Marie was designated *Wbph5*. Jayaraj and Murty (1983) studied the inheritance of resistance in nine varieties. Resistance was controlled by a single dominant gene in three varieties and by a recessive gene in the other six varieties.

Inheritance of resistance in 10 cultivars was investigated by Singh et al (1990). Eight cultivars—ARC5838, ARC6579, ARC6624, ARC10464, ARC11321, ARC11320, Balamawee, and IR2425-90-4-3—were found to have a single recessive

Table 9. Genes identified for resistance to whitebacked planthopper.

Gene	Source	Chromosome
Wbph1	N22	7
Wbph2	ARC10239	6
Wbph3	ADR52	–
wbph4	Podiwi A8	–
Wbph5	N' Diang Marie	–
Wbph6	–	–
Wbph7	–	–

gene for resistance. The recessive genes of IR2425-90-4-3, ARC5838, and ARC11321 were found to be allelic to each other. Resistance in Pbt19 and IET6288 was found to be under dominant gene control. Sidhu et al (2005) studied the inheritance of resistance in five cultivars. A recessive gene conferred resistance to MR1523 and ARC11367, whereas resistance in NCS 2041 was conditioned by a dominant gene. The resistance in Mudgo and MO1 was governed by two independently inherited dominant genes. Padmarathi et al (2007) reported the recessive gene in ARC5984 and ARC6650 as allelic to Podiwi (*wbph4*). The dominant gene in ADR52 was different from that in cultivar Velluthecharra. He (2007) mapped *Wbph7* and *Wbph8* on chromosome 4.

Green rice leafhopper (*Nephotettix cincticeps* Uhler)

Green rice leafhopper (GRH) is mostly found in the temperate regions of East Asia. At least six genes (*Grh1*, *Grh2*, *Grh3*, *Grh4*, *Grh5*, and *Grh6*) have been identified and mapped on chromosomes 5, 11, 6, 3, 8, and 4, respectively (Table 9) (Yasui et al 2007). Near-isogenic lines (NILs) carrying *Grh1*, *Grh2*, *Grh4*, *Grh5*, and *Grh6* in the background of japonica cultivar Taichung 65 (T65) have been developed using MAS. W1962 (*O. rufipogon*) had *Grh5* and a minor gene on chromosome 4 (Fujita et al 2006). The nymph mortality of pyramided lines (*Grh2* + *Grh4*) and *Grh2* + *Grh6* and *Grh4* + *Grh6* was higher than that of the NILs each carrying a single resistance gene (Yasui et al 2007).

Zigzag leafhopper (*Recilia dorsalis* Motschulsky)

The zigzag leafhopper (ZLH) occurs in the tropics and subtropics of Asia. However, it is a minor pest of rice. Some donors (Rathu Heenati, Ptb21, Ptb33) for resistance have been identified (Heinrichs et al 1985). The genetics of resistance to the ZLH, WBHP, BPH, and GLH in cultivars Rathu Heenati, Ptb21, and Ptb33 was investigated by Angeles et al (1986). Single dominant genes that segregate independently of each other and that conveyed resistance to ZLH were designated *Zlh1* (Rathu Heenati), *Zlh2*

(Ptb21), and *Zlh3* (Ptb33). Tests for the independence of the various genes for resistance to leafhoppers and planthoppers revealed that *Zlh1*, *Zlh2*, and *Zlh3* are independent of *Wbph3*, *Zlh2*, and *Zlh3* and also segregated independently of *bph2* and *Bph3*.

Expression of snowdrop lectin in transgenic rice for resistance to BPH

Rao et al (1998) reported snowdrop lectin (*Galanthus nivalis agglutinin*; GNA) to be toxic toward BPH when administered in an artificial diet. Transgenic rice containing the *gna* gene in constructs in which its expression was driven by a phloem-specific promoter (from the rice sucrose synthase *RSs1* gene) and by a constitutive promoter (from the maize ubiquitin *ubi1* gene) conferred resistance to BPH. Rao et al (1998) used PCR and Southern analyses to confirm that the transgenes were transmitted to progeny. Western blot analyses revealed expression of GNA at up to 2.0% of total protein in some of the transgenic plants. GNA expression driven by the *RSs1* promoter was tissue-specific as shown by immunohistochemical localization of the protein in the nonlignified vascular tissue of transgenic plants. Insect bioassays and feeding studies showed that GNA expressed in transgenic rice plants decreased survival and overall fecundity (production of offspring) of the insects, retarded insect development, and had a deterrent effect on BPH feeding. *gna* is the first transgene to exhibit insecticidal activity toward sap-sucking insects in an important cereal crop plant.

Future research priorities

The following research priorities could be important for the future:

1. Establish high-throughput screening protocols for field resistance to planthoppers.
2. Identify new sources of resistance to hoppers.
3. Characterize insect populations/biotypes and genes with resistance against insect populations in the field for efficient deployment of such genes.
4. Evaluate existing varieties and elite inbreds/hybrids for field resistance to planthoppers in hot-spot areas in target countries and disseminate resistant varieties/hybrids.
5. Understand the genetic basis of field resistance to facilitate the development of the next generation of resistant cultivars.
6. Develop durable BPH-resistant varieties/hybrids through pyramiding of mapped genes and QTLs accelerated through marker-assisted selection.
7. Establish functional SNPs for selection for BPH resistance.

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Notes

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How can planthopper genomics be useful for planthopper management?

Hiroaki Noda

Recent developments in insect genomics, dealing with the entire genome of an insect, facilitate new approaches to study various aspects of fundamental and applied topics of the insect. To elucidate planthopper virulence against resistant rice varieties, pesticide resistance mechanisms, and virus transmission machinery, planthopper genomics will be powerful and useful. Expressed sequence tag (EST) analysis was performed on the brown planthopper *Nilaparvata lugens* (BPH), and a microarray was prepared as a functional study tool. Proteome studies also provide us with new information on molecules that take part in various biological phenomena of planthoppers. Molecular markers based on genetic information are becoming important as tools for monitoring and tracing planthopper migration routes. Planthopper genomics is expected to help in constructing a more powerful and sustainable planthopper management system, including developing novel insecticides.

Keywords: genomics, planthopper, EST, microarray, proteome, virulence, resistance, virus transmission, molecular markers

Planthoppers are a diverse group of phytophagous insects belonging to the superfamily Fulgoroidea, which is composed of approximately 20 described insect families (O'Brien and Wilson 1985). More than 9,200 species have been described (Woodward et al 1976, after O'Brien and Wilson 1985); some species attack important crops, such as maize, wheat, rice, and forage grasses. Among those, the most economically important species are doubtlessly three species of rice planthoppers: the brown planthopper *Nilaparvata lugens* (BPH), the whitebacked planthopper *Sogatella furcifera* (WBPH), and the small brown planthopper *Laodelphax striatellus* (SBPH). They belong to the family Delphacidae, which is a large group situated in a basal part of the phylogenetic tree of Fulgoroidea (Yeh et al 2005, Urban and Cryan 2007). BPH attacks only rice plants, WBPH mostly infests rice plants, and SBPH has a wider host range, including wheat and some grasses. BPH causes severe sucking damage and transmits virus diseases to rice plants, WBPH causes sucking damage on rice plants, and SBPH transmits a virus disease to rice plants.

BPH and WBPH are distributed in tropical Asia and have long-distance migration (Kisimoto 1976, 1979). In the temperate region, growing populations of these planthoppers start from the immigrants transported from the southern year-round planthopper area; they do not overwinter and die in cool and cold seasons. SBPH, on the other hand, has a wide range of distribution in the world. This species diapauses in cool regions. SBPH shows allozyme polymorphism among regional populations, suggesting that this species does not regularly show long-range dispersal (Hoshizaki 1997). The geographic variation of SBPH is also clearly supported by the trait of nymphal diapause; there is a geographic cline in the critical photoperiod for diapause (Noda 1992). Nevertheless, SBPH, as well as BPH and WBPH, shows wing dimorphism. Rice planthoppers show two wing patterns when they become adults: a long-wing (macropterous) form and a short-wing (brachypterous) form. Both males and females show wing dimorphism, but brachypterous males are rare in WBPH. The wing forms are closely related to population growth in the rice field and consequently to damage to rice. Macropterous planthoppers have wide distribution, and brachypterous ones deposit more eggs in rice plants, making their population density high. These traits or characteristics of planthoppers have been intensively studied from ecological and physiological viewpoints, and this has contributed to planthopper management.

Molecular studies in planthoppers, however, are still poor in spite of their economic importance. Recent developments in genomics in biology appear to enable us to form new approaches in studying, analyzing, and managing insect pests. Genomics is the field of study related to an organism's entire genome. Functional genomics studies, which deal with patterns of gene expression in various conditions, became popular in many organisms. Various fields, whose name has "-omics" or "-ome" in the suffix, have developed (http://omics.org/index.php/Main_Page). The suffix "-omics" usually means a field of study in biology, such as genomics, transcriptomics, proteomics, metabolomics, and so on. The suffix "-ome" indicates the objectives for study, such as transcriptome, proteome, metabolome, and so on. Molecular biology, which studies single genes and their functions, is also closely related to genomics. Genomics and related fields are surely changing biological studies, introducing computer science and bioinformatics into the life sciences.

In this chapter, various aspects of molecular studies and recent genomics studies of the brown planthopper are introduced, and what is required for planthopper management is discussed in terms of current biological and genomics trends. First, the present status of genomics studies in insects is reviewed. Second, a clear grasp of planthopper problems in rice production is attempted in order to know what we should study and how we could attack the problems using genomics and molecular approaches. Third, molecular information attributed to planthoppers is surveyed as statistical aspects of genome information. The information includes not only that on planthoppers themselves but also that on their associated microorganisms. Fourth, recent developments in genomics studies, especially EST studies and those using related tools, are presented. Finally, future studies on planthoppers in the next decade are discussed.

Genome sequencing in insects

Genomics in insects has been actively studied in the last decade. First, the entire genome was determined in the fruit fly *Drosophila melanogaster* (Adams et al 2000). The first whole-genome shotgun (WGS) sequencing method was applied to the higher eukaryotes in *D. melanogaster*, which definitely influenced the genome sequencing of higher eukaryotes thereafter. A whole-genome sequence of the mosquito *Anopheles gambiae* was reported in 2002 (Holt et al 2002); the genome of malaria *Plasmodium falciparum*, which is transmitted by *A. gambiae*, was also published simultaneously (Gardner et al 2002). The silkworm *Bombyx mori* genome was sequenced independently in Japan and China (Mita et al 2004, Xia et al 2004). The WGS sequence data from both countries were merged and reassembled; high-quality sequence data in the first lepidopteran species are released (The International Silkworm Genome Consortium 2008). Genome sequencing was followed by the honeybee, *Apis mellifera* (The Honeybee Genome Sequencing Consortium 2006); a virus-vector mosquito, *Aedes aegypti* (Nene et al 2007); and the red flour beetle, *Tribolium castaneum* (*Tribolium* Genome Sequencing Consortium 2008). Genome sequencing projects are carried out for many insects; Table 1 summarizes current genome sequencing projects in insects, ticks, and mites. Most of the genome sequences were determined by the whole-genome shotgun sequencing method, but clone-based sequencing was also performed in some species. Next-generation sequencing technologies have also been used recently.

Expressed sequence tag (EST) analyses were also performed in many insect species because EST analysis can be done at much lower cost than entire genome sequencing. EST analyses are also extensively done in the above-described insect species in which the genome sequence is mostly determined because the expressed gene sequences are useful information for genome annotation and analyses. Table 2 shows the insects or ticks in which a high number of ESTs are deposited in DNA databases.

What are the planthopper problems?

More than 30 years ago, in May 1977, a symposium was held at the International Rice Research Institute to discuss research results and to develop plans for brown planthopper control. The contents of talks of the symposium were published in the book *Brown planthopper: threat to rice production in Asia* (IRRI 1979). In this book, BPH was clearly regarded as the number-one insect pest in rice in Asia (Dyck and Thomas 1979) and some of the problems, which we still face, were already obvious. Breeding of various resistant rice varieties began in the late 1960s and the use of plant resistance for controlling pests was thought to be a simplistic solution. However, the first BPH-resistant rice variety, IR26, became susceptible in several years and a BPH biotype capable of destroying IR26 became abundant (Brady 1979). Resurgence of BPH also occurred where insecticides were used in the 1970s (Heinrichs 1979, 1994).

What are the problems or important topics in rice planthoppers now?

Table 1. Whole-genome sequencing projects in Insecta and Acari.[a]

Order/species	Genome size, Mb (no. of chromosomes)	Method	Sequence depth and status
Diptera			
Drosophila melanogaster	180 (4)	WGS, clone-based	–, complete
Anopheles gambiae	– (3)	WGS	10X, assembly
Culex pipiens			
quinquefasciatus	– (–)	WGS	–, assembly
Aedes aegypti	800 (3)	WGS	8X, assembly
Cochliomyia hominivorax	– (–)		–, in progress
Haematobia irritance	– (–)		–, in progress
Lepidoptera			
Bombyx mori	530 (28)	WGS	10X, assembly
Bicyclus anynana	490 (–)		–, in progress
Coleoptera			
Tribolium castaneum	200 (10)	WGS	7.3X, assembly
Hymenoptera			
Apis mellifera	200 (16)	WGS, clone-based	7-8X, assembly
Nasonia vitripennis	– (5)	WGS	6.2X, assembly
N. giraulti	– (5)	WGS	13X, in progress
N. longicornis	– (5)	WGS	13X, in progress
Hemiptera			
Acyrthosiphon pisum	525 (4)	WGS	6X, assembly
Rhodnius prolixus	670 (11)	WGS	8X, in progress
Diaphorina citri	– (–)		–, in progress
Isoptera			
Psammotermes	– (–)		–, in progress
Anoplura			
Pediculus humanus corporis	– (–)	WGS	8X, assembly
Acari			
Ixodes scapularis	– (–)	WGS, clone-based	6X, assembly
Tetranychus urticae	– (–)	WGS	–, in progress
Vorroa destructor	– (–)	WGS	8X, in progress

[a]Data are based on the Entrez Genome Project in the National Center for Biotechnology Information (NCBI) (www.ncbi.nlm.nih.gov/genomes/leuks.cgi, as of 4 November 2009). *Drosophila* species are not listed except *D. melanogaster*. WGS = whole-genome shotgun sequencing method.

Table 2. Species in which a high number of ESTs are deposited in DNA databases.

Species	Number of ESTs[a]
Drosophila melanogaster	821,005
Aedes aegypti	301,596
Bombyx mori	245,761
Culex quinquefasciatus	205,274
Ixodes scapularis	193,773
Acyrthosiphon pisum	169,928
Anopheles gambiae	153,273
Nasonia vitripennis	145,793
Drosophila simulans	118,742
Glossina morsitans morsitans	79,292
Apis mellifera	78,191
Tribolium castaneum	64,571
Locusta migratoria	45,708
Drosophila sechellia	38,257
Drosophila auraria	38,110
Nilaparvata lugens	37,312
Drosophila pseudoobscura	35,042
Spodoptera frugiperda	32,255
Nasonia giraulti	30,060
Myzus persicae	27,686
Drosophila willistoni	26,751

[a]NCBI (www.ncbi.nlm.nih.gov/dbEST/dbEST_summary.html), as of 4 November 2009.

The following seem to be those we have to pay attention to:

1. Insecticide resistance
2. Occurrence of biotypes (virulent strains) of BPH
3. Virus transmission by BPH and SBPH
4. Monitoring and occurrence forecasting of planthoppers
5. Wing dimorphism (macropterous and brachypterous forms)
6. Finding new targets for novel insecticides

Insecticide resistance

Various insecticides have been used for controlling planthoppers, especially for BPH. Organophosphorus insecticides were first used in the 1950s and carbamate compounds were first used in the 1960s (Heinrichs 1979). Pyrethroid compounds were then

introduced and neonicotinoid compounds are now popular for planthopper control. Insecticide resistance became obvious in BPH in the late 1960s. BPH insecticide resistance has been monitored in Japan since the late 1960s (Fukuda and Nagata 1969) and the recent trend of insecticide resistance status in BPH and WBPH is summarized by Matsumura et al (2007). The susceptibility of BPH to neonicotinoid insecticides and that of WBPH to fipronil decreased. The development of a neonicotinoid-resistant strain of BPH was observed in a laboratory colony, which showed mutation in genes of acetylcholine receptor subunits, the target molecules of neonicotinoid insecticides (Liu et al 2005). It is problematic that these lately introduced compounds have been showing lower effectiveness against planthopper populations.

Virulent strains of BPH

In these 30 years, the presence of many resistance genes against BPH was reported from rice plants; 21 resistance genes are so far known (Zhang 2007, Yasui et al 2007). New rice varieties that possess plural resistance genes have been developed and used successfully in some regions. However, it is generally admitted that virulent BPH strains capable of attacking resistant rice varieties appear when a BPH-resistant rice variety is cultivated in a wide area. Nevertheless, we do not know the mechanism of the resistance of rice against BPH and the virulence of BPH against resistant rice varieties. Molecular mapping of the genes with resistance to BPH is done for the rice plant; chromosomal positions of some genes are narrowed down by map-based approaches (Sharma et al 2004a, Chen et al 2006). These genes are expected to be isolated soon. Once the genes are isolated, functional analyses of them will be carried out. How virulent BPH make the work of the resistance genes ineffective is another problem to be solved by entomologists.

Virus transmission by BPH and SBPH

BPH transmits the rice ragged stunt virus (RRSV) and rice grassy stunt virus (RGSV) (Nault 1994, Hibino 1996). These virus diseases have occurred markedly since 2005 in the Mekong Delta in Vietnam, and are estimated to have caused a loss of 400,000 tons in two years (1.1% of Vietnam's total production) (Heong and Escalada 2008). SBPH transmits rice stripe virus, which belongs to the tenuivirus group. This persistently transmitted virus often prevails in some rice-growing areas; an outbreak in China was recently reported (Zhu 2006, Xiong et al 2008). Genomes of these viruses are determined and advanced detection methods for them are available. However, the interaction between the viruses and the host planthoppers is still poorly understood.

Monitoring and occurrence forecasting of planthoppers

Flight and migration of planthoppers are monitored by light or net traps. BPH and WBPH show long-distance flight; this is an important issue according to where the immigrants have flown from. The immigrants reflect the biological traits of planthoppers in the original region, for example, the level of insecticide resistance, the level of virulence against rice varieties, the infection rate of virus diseases, and wing dimorphic response under various conditions. Meteorological trajectory analysis is a

useful tool for estimating planthopper emigration area (Otuka et al 2005). However, we still do not have good molecular markers for distinguishing the local strains and for estimating the origin of immigrant planthoppers. We need to precisely evaluate molecular markers as classification tools of local populations because planthoppers fly a long distance and genetic variability seems to be small among geographical populations.

Wing dimorphism

Planthoppers show phase variation in wing form: some have a macropterous (long-wing) form for long-distance migration and others have a brachypterous (short-wing) form suitable for reproduction. This polymorphism is closely related to planthopper damage: macropterous planthoppers enlarge their territoty and brachypterous ones increase their offspring. Hormonal studies suggest that juvenile hormone stimulated the brachypterous form (Ayoade et al 1999, Bertuso et al 2002). The molecular mechanisms, however, including related genes, are not elucidated.

New targets for novel insecticides

The occurrence of insecticide-resistant populations reduces options in selecting insecticides for controlling planthoppers. Resistant planthoppers often show cross resistance to insecticides with a similar mode of action. Therefore, a group of insecticides might lose its effectiveness. Every year, some new insecticides are placed on the market. The insecticides that have a novel mode of action are rare among them. New insecticides against a novel target are very promising compounds for insect control. Mining new target molecules and finding major compounds against the target is important work in molecular and genomics studies.

Statistical aspects of genetic and genomics information in planthoppers

The genetic background is quite poor in planthoppers. Here, we survey studies related to planthopper genetics. Genetic and genomics information seems to be useful to create molecular markers to discriminate local populations or colonies showing specific biological traits.

Chromosomes of planthoppers

Chromosomes of homopterans are hollocentric and do not show a localized centromere during cell division. The chromosome number of BPH is 30: 14 autosomal bivalents and two sex chromosomes (Noda and Tatewaki 1990). Diploid chromosomes of males consist of 28 autosomes and each X and Y chromosome and those of females consist of 28 autosomes and two X chromosomes. In contrast, the chromosome number of WBPH and SBPH is 29 or 30: the male diploid number is 29 (28 + XO) and the female diploid number is 30 (28 + XX). In BPH, a Y chromosome-specific sequence can be used for sex discrimination since the Y chromosome is present only in males. PCR amplification using PCR primers corresponding to DNA sequences in the Y chromosome enables male detection in premature stages (Kobayashi and Noda 2007a).

Planthopper color mutants

Some mutants are observed when field populations are reared in the laboratory. Planthoppers with red eyes were often found in BPH, WBPH, and SBPH. One recessive gene is usually related to red-eyed phenotype: probably a gene that takes part in making black pigment in the eyes causes a mutation. A red-eyed mutant of BPH found by Mochida (1970) showed embryonic lethality in the eggs laid by homologous females. Red-eyed forms of SBPH, which were collected in Tokyo, led to the discovery of cytoplasmic incompatibility in SBPH through crossing experiments between a black-eyed western population and a red-eyed Tokyo colony (Noda 1984a, 1984b, 1987). Another example is body coloration in BPH. BPH usually shows brown body color; blackish planthoppers are sometimes found in the field and laboratory-reared colonies. Some genes might be involved in body color in BPH (Morooka et al 1988).

Ribosomal RNA

Ribosomal RNA is a central component of ribosome. A ribosomal RNA gene (rDNA) sequence is often used for the identification of species or strains as well as various phylogenetic studies. A single transcription unit of eukaryotes (45S) includes 18S, 5.8S, and 28S rRNAs and two internally transcribed spaces (ITS) between 18S and 5.8S and between 5.8S and 28S rDNA. The sequences of the 18S and 28S rDNA are very conservative and are good markers for species identification. In contrast, those of ITS regions are less conservative and provide useful information for discriminating strains or populations in the same species. In planthoppers, the ITS sequence is a good candidate gene for detecting local populations. WBPH has size variation in the ITS1 region. Now, we do not have a correlation between size variation and the locality of WBPH in Asian countries (unpublished). BPH had an R2 retrotransposon in the 28S rRNA gene. This R2 retrotransposon appears to be similar to those found in various other insect species (Burke et al 1993).

Mitochondrial genome sequence

Mitochondrial genomes of arthropods are usually circular: 14–20 kb long, with 2 ribosomal RNAs, 22 tRNAs, and 13 protein-coding regions; they contain a small noncoding region (Boore 1999). The genetic orders in the mitochondrial genomes are similar, allowing the proposal of an ancestral gene order. Mitochondrial genome sequences are available in many hemipteran insects (www.ncbi.nlm.nih.gov/genomes/OrganelleResource.cgi?opt=organelle&taxid=6656). Hemipteran insects have mitochondria whose gene order resembles the proposed ancestral one. However, whitefly species show mitochondrial gene rearrangements; several genes have changed their position from the ancestral gene order (Thao et al 2004). BPH had mitochondria of ancestral gene order; the genome size was about 17,250 (unpublished).

Sequence variation in the mitochondrial genome within species is useful information for elucidating geographic structure among rice planthopper populations in Southeast and East Asia. Mun et al (1999) reported sequence variation in the *cytochrome oxidase-I* gene (COI) in BPH and WBPH, showing the first geographic molecular variation, except allozyme analyses. Genetic variation of this gene, however,

is small among local populations in Asia; a much varied region or larger region in the mitochondrial genome might be more informative for this purpose.

Genes characterized from planthoppers

Sequences of some genes are determined and deposited in DNA databases. In BPH, nucleotide sequences of some enzyme genes involved in detoxifying insecticides, such as the genes of cytochrome P450, glutathione S-transferase (Yang et al 2005), and carboxylesterase (Small and Hemingway 2000), are available, as well as other enzyme genes, those of trypsine-like protease, cathepsin B-like protease (Foissac et al 2002), and NADH-quinone oxidoreductase (Yang et al 2005). Genes of nicotinic acetylcholine receptors (Liu et al 2005), a hexose transporter (Price et al 2007), diuretic hormone receptors (Price et al 2004), and ferritin (Du et al 2000) are determined in their nucleotide sequences. More than 37,000 ESTs were recently deposited in the database, which enable us to get partial sequences of various genes from BPH (Noda et al 2008).

Endosymbiotes of planthoppers

Planthoppers harbor various intracellular microorganisms. The habituation or infection of microorganisms in planthoppers might provide us with discriminative information from other strains or local populations. An indispensable microorganism for planthoppers is yeastlike symbiote (YLS). YLS resides in the fat body cells and is transmitted to the next generation through the female ovary (Noda 1974, 1977, Chen et al 1981, Suh et al 2001). *Wolbachia* are found from almost all WBPH and SBPH; *Wolbachia* in these two species were indistinguishable as far as the sequences of several *Wolbachia* genes are concerned (Noda et al 2001). Some BPH are infected with *Wolbachia* and other microorganisms, for example, rickettsia and spiroplasma (unpublished). Among eukaryotic and prokaryotic endosymbiotes of planthoppers, *Wolbachia* can be cultured in insect cell lines (Noda et al 2002). No other microorganisms in planthoppers were successful in cultivation in vitro.

BPH transmits two virus diseases as described above. Three other viruses are characterized from BPH. *Nilaparvata lugens* reovirus, NLRV, is infected with some populations of BPH (Noda et al 1991, Nakashima et al 1996). Himetobi P virus, HiPV, which was first found in SBPH, propagates often and highly in the midgut of BPH. *Nilaparvata lugens* commensal X virus, NLCXV, seems to be a satellite virus (Nakashima et al 2006).

Toward functional genomics in planthoppers

Expressed sequence tag (EST) analysis

In order to study gene and protein functions, to elucidate molecular mechanisms of biological phenomena in planthoppers, and to find effective control means of planthoppers, genomic information is a useful resource. EST analysis, which is the creation of many short sequences of a transcribed spliced nucleotide sequence, is a good introduction for functional genomics (Nagaraj et al 2006).

More than 37,000 ESTs were created from 18 libraries of various BPH tissues and stages (Noda et al 2008). Ribosomal RNA sequences, mitochondrial genome sequences, and planthopper-infected virus genome sequences were eliminated from the EST database (http://bphest.dna.affrc.go.jp/). Their average size is 627 bp; 10,200 clusters were made from whole EST sequences. The actin gene was the most abundantly expressed and the myosin gene was also highly expressed in BPH whole ESTs. Actin and myosin were largely expressed in the thorax, where the flight muscle is located. Some enzyme genes, such as trypsine-like protease and enolase, showed high expression. The ESTs of the mucin-like protein gene and vitellogenin gene were often found in the salivary glands. EST libraries created from various tissues are useful for selecting tissue specifically expressed genes. Gonad specifically expressed genes, for example, were extracted (unpublished). The function of many of them has not been analyzed yet; they are considered to play important roles in reproduction.

The EST database would facilitate the cloning of important genes. However, many of the nominated ESTs are housekeeping genes, and the EST database might not contain genes of low expression level. In order to enrich BPH ESTs, further ESTs should be collected from the libraries made from small tissues or from planthoppers reared in unusual conditons. Another effort is to determine the sequence of clones from full-length cDNA libararies. Collection of the sequences of 5′ and 3′ regions of genes from the full-length cDNA would ease our tedious work to get whole cDNA sequences or the full sequence of a protein-coding region.

Proteomic analysis

Proteome studies, which deal with the entire complement of proteins expressed in tissues or organisms, are also an important approach for functional genomics. Proteomics, the study of the proteome, usually uses two-dimensional polyacrylamide gel electrophoresis (2D-PAGE). Protein spots on the gel, which have moved to a specific location, are given further analysis using a peptide sequencer or mass spectrometer. Recently, shotgun proteomics after proteolytic enzyme digestion of samples has been used as an alternative techonology capable of identifying hundreds of proteins from single samples. When we use mass spectrometry for characterizing and identifying protein molecules, whole-genome sequences or well-accumulated genome information would be necessary. We do not have BPH genome sequences and have only some ESTs. Therefore, amino acid sequencing by a peptide sequencer is employed for BPH proteomics. The amino acid sequences obtained are then used in sequence similarity searches, FASTA or Basic Local Alignment Search Tool (BLAST), in public databases so as to annotate the protein molecules of interest. However, some proteins are difficult to annotate using public databases for the following two reasons. One is that many proteins in BPH are unique and we cannot find any similarity with the amino acid sequences in the databases. The other is the sequence length obtained from the peptide sequencer is not long enough to find similar proteins; usually, the obtained amino acid sequences are 20–30 residues. Moreover, N-terminal sequences often vary among homologous proteins among organisms. In these cases, the EST library is used to find the genes encoding the proteins. If we could find ESTs, the nucleotide

sequences and putative amino acid sequences of the peptide could be obtained, thus extending sequence information from small peptide fragments.

Proteomic analysis by insecticide application was performed in BPH. A carbamate insecticide, *o-sec*-butylphenyl methylcarbamate compound (BPMC), modulated 22 proteins at the expression level in 2D-PAGE compared with nontreated control BPH (Sharma et al 2004b). N-terminal and internal amino acid sequences were determined by a protein sequencer. The expression of putative serine/threonine protein kinase, paramyosin, heat shock protein (HSP) 90, beta-tubulin, calreticulin, ATP synthase, actin, and tropomyosin was elevated. That of beta-mitochondrial-processing peptidase, dihydrolipoamide dehydrogenase, enolase, and acyl-coA dehydrogenase was low. Cytoskeleton proteins were upregulated by BPMC treatment; an increased expression of cytoskeleton genes or proteins is often observed in response to toxic chemicals. Chaperone proteins HSP 90 and calreticulin increased after BPMC treatment, which might show insects' homeostasis maintenance under stress induced by insecticide exposure. Mitochondrial proteins showed different expression in response to BPMC, suggesting an overall change in mitochondrial response. A few enzymes, including enolase, one of the highly expressed genes in BPH (Noda et al 2008), decreased after treatment, suggesting a weakening of the usual metabolism.

Microarray

Microarray was developed as a high-throughput tool used for transcriptome analyses. A BPH microarray was fabricated based on the EST data accumulated from various tissues of BPH. Approximately 17,000 sequences were selected from all ESTs (about 37,000) based on a clustering analysis. Probes of 60-mer were designed for each sequence. Agilent's 22K oligonucleotide microarray (oligoarray) was first made and used for some studies, including preliminary test analyses. The oligoarray showed quite stable results and revealed that a twofold change in gene expression level could be reliably distinguished between two samples based on the color-swap data of Cy3 and Cy5. Now, a 4X 44K oligoarray is used for microarray analyses.

The following studies are now being done using microarray. First, expression profiles between BPH sucking resistant and susceptible rice plants were compared. Some genes were up-regulated or down-regulated in BPH sucking a resistant variety. Some of them were related to starvation in resistant rice plants. Second, genes related to wing dimorphism are sought using planthopper nymphs reared under different conditions; one is suitable for brachypterous expression and the other for macropterous expression in the adult stage (Kobayashi and Noda 2007b). Prior to the array experiment, sex-discriminating methods in nymphs were developed (Kobayashi and Noda 2007a) because males and females show a different response in wing formation to environmental stimuli (Kisimoto 1956, 1965, Kisimoto and Rosenberg 1994). Third, the effect of *Wolbachia*, alpha-proteobacteria that manipulate the sex and reproduction of host arthropods, on gene expression is studied in the testes of BPH. The *Wolbachia* taken from *Laodelphax striatellus* were cultivated in vitro (Noda et al 2002) and then introduced into BPH by micro-injection. These *Wolbachia* cause cytoplasmic incompatibility and embryonic death of eggs deposited by *Wolbachia*-

infected males and uninfected females. Microarray could be used for various molecular studies in BPH.

Genomics studies of planthoppers in the next ten years

Whole-genome sequencing

The results of first-round EST analyses are open to the public (http://bphest.dna.affrc.go.jp/), with sequence and annotated information on transcribed genes. Now, full-length cDNAs of BPH are analyzed and a combined database with ESTs and full-length cDNA will be created as a more efficient and useful resource. The next step in genomics studies in BPH is sequencing of the whole genome. Whole-genome sequencing needs the cooperation of many scientists and technical assistants, including those in entomology, genome-biology, bioinformatics, and general biology. The recent development of new DNA sequencers based on next-gereration sequencing technology would facilitate the determination of a large amount of sequence and decrease the cost of whole-genome sequencing.

Rice plant resistance and planthopper virulence

Many genes resistant to planthoppers, especially to BPH, have been reported (Zhang 2007) and some of these genes are mapped on the chromosomes of rice. Map-based cloning of resistance genes is performed based on rice genome sequence information (IRGSP 2005). Candidate genes involved in resistance are almost identified and await precise studies by plant physiologists and entomologists. In contrast, we do not have any clue to virulence against resistant rice varieties. Characterization of the resistance genes of rice might help to solve the virulence problem of planthoppers. Some approaches to elucidate the molecular basis of virulence have been developed (Hao et al 2008); this will be more actively studied using genome information and genomics tools.

Genome-based discovery of insecticide targets

Useful and excellent agricultural pesticides have been developed in the past 50 years. However, the efficiency in finding new major compounds through biological screening has decreased. Insecticidal target molecules are mostly related to the nerve or neuron and some to the respiratory machinery or cuticle formation. Chemicals acting on other targets are quite limited. Recent genome studies in insects appear to contribute to finding unexplored target molecules. To find the genes of target molecules, genome information-based and postgenome tools-based investigation, for example, microarrays or proteomic analyses, will be used as well as empirical investigation. When we find a novel target molecule, suitability and effectiveness of the candidate target molecule should be evaluated, namely, we should know whether insects are dead when we disturb the function of the molecule. RNA interference (RNAi) is convenient and is a simple method for target validation.

Once the target molecule is determined, an *in vitro* assay system will be constructed for high-throughput screening of chemical libraries. This kind of approach

has some more advantages. The mode of action of the newly developed pesticides is clear since the target molecules are already known. From the viewpoints of environmental problems and the insecticide resistance problem, it is highly desirable that the mode of action of the chemicals be fully clear. An insecticide resistance mechanism is also easy to study. Because of the recent trend of rising resistance in planthoppers against insecticides, novel compounds seem to be required in Asian rice production.

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Changes in rice farmers' pest management beliefs and practices in Vietnam: an analytical review of survey data from 1992 to 2007

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The changing trends in farmers' pest management beliefs and practices in the Mekong Delta of Vietnam from 1992 to 2007 were explored using 12 survey data sets collected during the period. Farmers' pest management practices, reflected in the number of insecticide sprays they apply in a season, decreased immediately after interventions, such as the mass media campaign, the radio soap opera, and farmer field school training. However after a few years, their insecticide sprays increased as the practices learned were discontinued. Farmers' reliance on pesticides as the main means of pest control had remained relatively unchanged. The discontinuance could be attributed to the lack of repetition and follow-ups after each of the interventions and the increase in frequency of pesticide advertising. Constant repetition, a strategy used in pesticide advertising, seemed to have eroded practices learned and supported availability biases of farmers. The farmers' average age over the period had also remained unchanged, implying that there had also been a turnover of farmers. To sustain pest management interventions, through campaigns, entertainment-education, or season-long training programs, it is important that follow-up programs and repetition strategies be implemented.

The agrochemical era of the 1960s and 1970s is said to have influenced chemical-oriented agricultural research and extension (Rossiter 1975) and this contributed to the rampant pesticide misuse in the Green Revolution. Rice intensification programs in Asia were dominated by campaigns, agricultural subsidies, and bank loans that promoted prophylactic insecticide applications (Kenmore et al 1987, Conway and Barbier 1990, Conway and Pretty 1991). Aggressive advertising and marketing campaigns launched by the pesticide industry also played a significant role. As a result, as much as 80% of the insecticide sprays farmers apply are deemed unnecessary (Heong et al 1995) and, with the poor sprayer equipment they use, more than 75% of the active ingredients do not reach the targets, ending up in the water. In most cases, rice farmers are better off not using them, and ecosystem services that naturally render protection from pest invasions can be better conserved. In the last 20 years, many programs have focused on changing rice farmers' pest management and rationalizing pesticide

use. Perhaps the most dominant program is the FAO-led farmer field schools (FFS) approach (Matteson et al 1994, Matteson 2000) to empower farmers through training to make better decisions. The FFS programs were well funded and conducted training for millions of farmers. These programs were costly, remained dependent on foreign funding, and were rarely sustainable and continued by national extension programs (Feder et al 2003, Bentley 2009).

The use of mass media to improve farmers' pest management decisions was explored in Vietnam (Escalada et al 1999, Huan et al 1999). Print materials, such as pamphlets and posters, billboards, and radio and TV programs were specifically designed to motivate farmers to avoid using insecticides in the first 40 days after sowing. Insecticide applications during this crop period have no economic return to farmers. Instead, the sprays destroy natural biological control linkages, making crops vulnerable to invading pests, such as leaffolders and planthoppers (Heong and Schoenly 1998). A complementary program using a radio soap opera series was also used (Heong et al 2008). These programs had positive effects on farmers' beliefs, attitudes, and practices, reducing insecticide sprays by more than 50%.

In each of the media projects, pretest and posttest surveys were conducted and, between 1992 and 2007, we carried out 12 such surveys in the Mekong Delta, interviewing a total of 9,067 farmers. Most of the variables in the surveys are similar and in this paper we report an analysis of these data sets, paying particular attention to changes over the 15-year period in rice farmers' pest management practices and attitudes toward pests, natural enemies, and pesticides.

Methods

Table 1 shows the details of the farmer survey data we analyzed. All the surveys were conducted in the same manner. Before each survey, a focus group discussion was conducted and its results were used to develop the questionnaires. The prototype questionnaires were first developed in English, then translated into Vietnamese to be pretested before they were finalized. Enumerators were trained and final-year students from the local agricultural technical colleges were supervised by one of us to ensure quality control. The data obtained were than coded using Microsoft Excel, cleaned up, and then uploaded into SPSS 11.5 (SPSS 2002) for analyses.

Results

Profiles of farmer respondents in the 12 surveys conducted

The average ages of farmers ranged from 43 to 49 years, which remained relatively stable in the last 15 years (Table 2). This implied that there had been a constant turnover in the farming communities. Farmers' education level of 6 to 7 years also remained relatively unchanged. Similarly, farm sizes remained small, which is attributed to the government's land tenure policy, while yields appeared to have increased slightly.

Table 1. Details of the farmer surveys conducted in the Mekong Delta.

No.	Location	Date	Purpose	No.	Reference
1	6 provinces	May 1992	Baseline	685	Heong et al (1993)
2	Long An Province	Aug 1994	Pretest	633	Escalada et al (1999)
3	Long An Province	Mar 1997	Posttest	628	Escalada et al (1999)
4	Can Tho Province	Aug 2002	Pretest	606	Huan et al (2008)
5	Tien Giang Province	Aug 2003	Pretest	600	Huan et al (2008)
6	Can Tho Province	Feb 2004	Posttest	611	Huan et al (2008)
7	Tien Giang Province	Sept 2004	Posttest	640	Huan et al (2008)
8	Vinh Long Province	May 2004	Pretest	600	Heong et al (2008)
9	Vinh Long Province	July 2005	Posttest	609	Heong et al (2008)
10	Can Tho Province	2006	Pretest	600	Unpublished
11	9 provinces	2006	Monitoring	1,800	Unpublished
12	Can Tho Province	2007	Posttest	602	Unpublished

Table 2. Respondents' profiles in the 12 surveys conducted in the Mekong Delta.

Survey	Age (years)	Education (years)[a]	Farm size (ha)	Yields reported (t ha^{-1})
6 provinces	45.2	n.a.	1.6	4.7
Long An Province	43.6	5.5	1.2	3.5
Long An Province	42.5	6.1	1.5	4.2
Can Tho Province	44.3	6.5	0.9	4.6
Tien Giang Province	45.6	6.8	0.8	4.5
Can Tho Province	43.9	6.6	1.1	5.6
Tien Giang Province	47.3	6.9	0.6	5.0
Vinh Long Province	49.4	6.1	0.8	4.8
Vinh Long Province	47.4	7.1	0.8	5.1
Can Tho Province	45.7	6.7	1.2	6.9
9 provinces	45.0	6.9	1.5	4.6
Can Tho Province	46.5	6.8	1.1	7.6

[a]n.a. = not applicable.

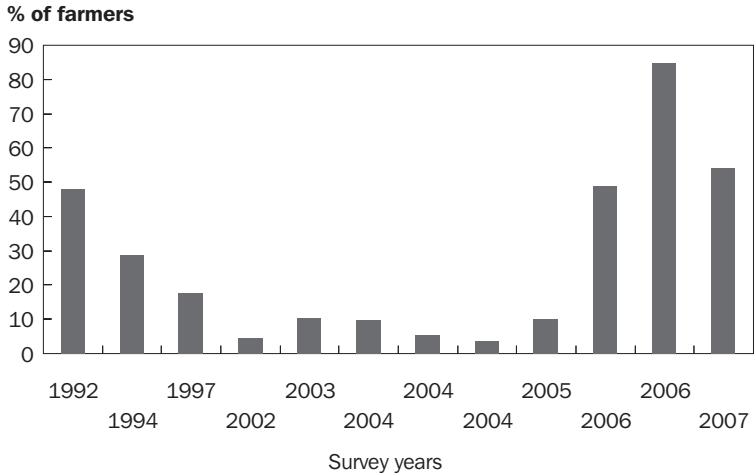

Fig. 1. Percentage of farmers reporting that planthoppers were their most serious pest problem in surveys between 1992 and 2007.

Trends in farmers' pest perceptions

Research has shown that leaf-feeding insects have little impact on rice yields (Graf et al 1992), yet farmers generally spray them because of the highly visible damage (Heong and Escalada 1977). We examined the pests farmers perceived to be most important and found that farmers named planthoppers as the most serious in the early 1990s. This subsequently declined to less than 10% of farmers naming planthoppers as serious but starting in 2006 planthoppers were again named as the most serious by more than 70% of the farmers (Fig. 1).

The media campaigns paid special attention to reducing early-season spraying of leaffolders, which is reflected in farmers perceiving leaf feeders as the most important pest. In each campaign, the proportion of farmers that listed leaf feeders as the most important declined by as much as 28% immediately after the launch of the campaign (Fig. 2). Generally, less than 10% of the farmers listed stem borers as the most important and this remained relatively stable over a span of 15 years.

Trends in farmers' pest management and insecticide usage

From 1992 to 2007, farmers continued to remain dependent on pesticides as more than 75% cited these as their primary means of insect control. Although the use of ducks had been cited occasionally, the use of resistant varieties was never mentioned once. Hand picking was cited, especially for snail and weed management. Some 30% to 84% of the farmers believed that insecticide spraying would result in higher yields. At the same time, 47% to 89% of the farmers also believed that insecticide would kill natural enemies.

Farmers' insecticide use in different provinces in Vietnam differed significantly. In Long An Province, where the first media campaign was carried out in 1994 (Escalada et al 1999), farmers' insecticide use declined by 53% immediately after the campaign

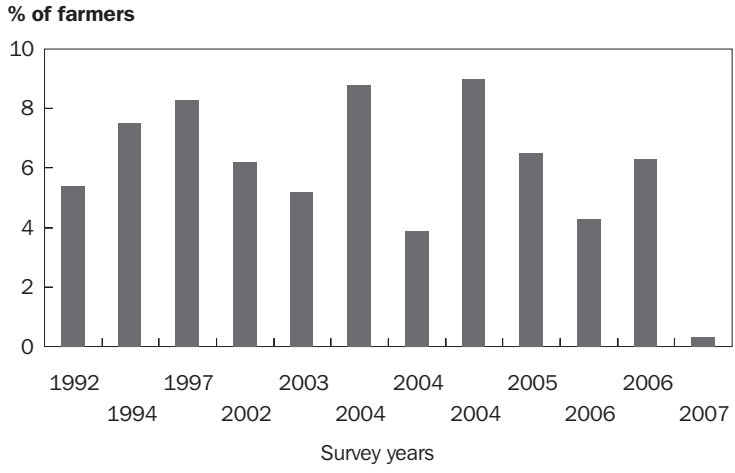

Fig. 2. Percentage of farmers reporting that stem borers were their most serious pest problem in surveys between 1992 and 2007.

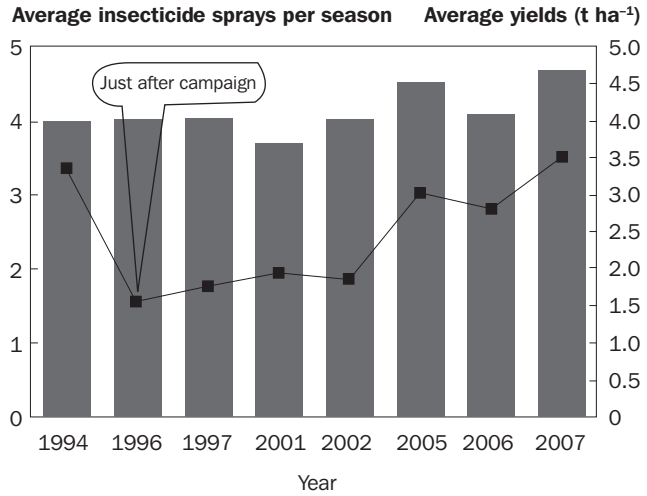

Fig. 3. Farmers' mean number of insecticide sprays and yields from surveys conducted between 1994 and 2007 in Long An Province.

and remained low for about 9 years (Fig. 3), whereas average yields increased moderately. The monitoring surveys in 2007 showed that insecticide sprays had returned to precampaign levels of about 3.5 sprays per season. Similarly, in Can Tho Province, farmers' insecticide use was about 1.2 sprays per season in 2002 and less than 1 per season in 2004, but rose to 1.8 and 2.5 sprays in 2006 and 2007, respectively (Fig. 4).

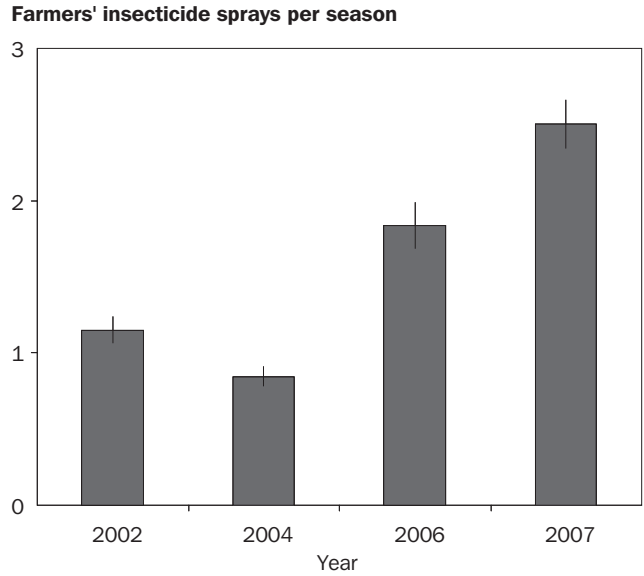

Fig. 4. Farmers' insecticide sprays in surveys conducted between 2002 and 2007 in Can Tho Province.

The types of insecticides used by farmers in the Mekong Delta changed over the 15 years. In the early 1990s, the main insecticides used were organophosphates (44.1%) and in 2007 only 22.5% of the sprays were organophosphates (Table 3). The main active ingredients used in 1992 were WHO Category I pesticides[1] monocrotophos, methyl parathion, and methamidophos. But these chemicals accounted for less than 0.5% of the sprays farmers used in 2007. The use of carbamates had been halved and BPMC remained the main active ingredient. Similarly, the use of pyrethroids declined from 12.4% to 7.9% and cypermethrin remained the main active ingredient used. There had been marked increases in the use of a nereistoxin, cartap, from 6.5% to 22.5%, and neonicotinoids, particularly fipronil and imidacloprid, from 0% to about 5%.

Discussion

From 1992 to 1997, marked reductions in farmers' insecticide use in the Mekong Delta from 3.1 to 1.0 sprays per season were reported (Huan et al 1999). There were also corresponding declines in farmers believing that planthoppers were serious problems. These trends continued until 2004, when opposite trends were observed. The general decline in farmers' insecticides was also reflected in the types of active ingredients used by farmers, which changed from broad-spectrum and highly hazardous compounds, such as monocrotophos and methyl parathion, to carbamates and cartap,

[1]Based on WHO classification by hazard: Category Ia is extremely hazardous to human health; Category Ib is highly hazardous; Category II is moderately hazardous; Category III, slightly hazardous; and Category IV, unlikely to present acute hazard in normal use.

Table 3. Main classes of insecticides used by farmers in the Mekong Delta in 1992 and 2007.

Chemical classes	Percent of sprays (multiple responses)	
	1992	2007
Organophosphates	48.1	22.5
Organochlorines	1.2	0.2
Carbamates	32.2	15.8
Pyrethroids	12.4	7.9
Nereistoxins	6.5	22.5
Neonicotinoids	0	4.7

which remained. Starting in 2004, there had been a general increase in farmers' use of neonicotinoids.

These changes could be attributed to a media campaign (Escalada et al 1999) and the implementation of farmer training in farmer field school (FFS) programs (Matteson 2000). The media campaign that started in Long An Province spread through provincial initiated programs and was estimated to have reached about 90% of the Mekong Delta's 2.3 million farmer households. The FFS started in 1992 had trained about 108,000 farmers in the Mekong Delta by 1997 and, assuming that about 30,000 farmers were trained per year, the total number of FFS-trained farmers would have been about 410,000 in 2007, or 18%. FFS-trained rice farmers generally reduced their insecticide use (Matteson 2000). Huan et al (1999) found that farmers in the Mekong Delta who were not exposed to either an FFS or media campaign applied insecticide sprays about 2.1 times, whereas those exposed to the media campaign alone sprayed 1.2 times and those exposed to both the media campaign and FFS training sprayed 0.5 time. Thus, the initial declining trends in farmers' insecticide use in both Long An and Can Tho provinces might be attributed to these two concurrent pesticide reduction activities in the Mekong Delta. Starting in 2005, there were increasing trends in farmers' insecticide use and, by 2007, farmers' insecticide use seemed to have surpassed the levels of precampaign and pre-FFS years.

Mass media channels are generally important at the knowledge stage in the innovation-decision process (Rogers 1995). Large audiences could be rapidly reached, spreading the new information, which could lead to changes in some attitudes. The rapid adoption of "no early spray" after the 1994 campaign, which reduced insecticide sprays by > 50% (Escalada et al 1999), illustrated this change in attitudes. However, discontinuance, a decision to reject an innovation after having previously adopted it (Rogers 1995), can often affect adopters. This is clearly evident in Long An and Can Tho provinces, where farmers' insecticide use trends declined after the campaigns, followed by an increase. Discontinuance is especially rapid when there is an abundance

of conflicting messages through mass media and marketing networks of pesticide companies.

In the Mekong Delta, 12 provincial TV stations in Long An, Tien Giang, Ben Tre, Dong Thap, Vinh Long, Tra Vinh, An Giang, Kien Giang, Hau Giang, Can Tho, Soc Trang, and Bac Lieu broadcast pesticide advertisements aimed at farmers. Each of these TV stations broadcast an average of three pesticide advertisements a day. Similarly, radio stations in the Mekong Delta reinforced TV ads by airing at least two pesticide ads per day. For both radio and TV, insecticides were more frequently an advertised product.

Modern-day advertising generally uses conditioning to create associations between products and consumer needs (Kincheloe and Horn 2006). Knowing that these kinds of connection are usually temporary, companies follow Pavlov's ideas of repetition and continually advertise to keep these associations in farmers' minds. Although the insecticide reduction campaigns had initially caused farmers to adopt "no early spray" practices and reduced their sprays, the lack of repetition and reinforcements had resulted in discontinuance. The need for continuous repetition, motivation, and reinforcement to sustain a learned behavior such as stopping unnecessary insecticide spraying and IPM practices is supported by Bandura's (1977) "Social Learning Theory," in which he emphasized the need to keep the learning going by various forms of reinforcements. The chemical industry, on the other hand, employs repetition in all its advertising campaigns and is thus able to establish higher credibility and brand familiarity.

Advertisements are repeated endlessly not only to attract new customers but also to reassure current customers. Sandman (2000) noted that repetition creates a direct relationship between the product and the fulfillment of customers' needs. Most advertising is targeted at customers who have already decided to buy the product and is intended to reinforce their decision and strengthen their behavioral commitment.

Another factor that could be contributing to the discontinuance of learned practices in the Mekong Delta is the turnover of farmers. The surveys showed practically no change in farmers' age, which could mean that the farmers trained in FFS or exposed to the "no early spray" campaigns might have moved on. This adds further to the need for repetition and continuous reinforcement programs to sustain gains obtained through training and campaign efforts.

Discontinuance could also be farmers' decisions being influenced by availability bias (Tversky and Kahneman 1974). Farmers tended to assess the frequency of pest losses as more common because of repetition and better recall. The repeated reminders through advertisements and pesticide salesmen and newspaper reports of pest outbreaks could play a significant role in farmers' erroneous judgments. Here, the lack of repetitions and follow-up after the "no early spray" campaign and the intensive IPM training would result in high discontinuance.

Planthoppers are secondary pests often induced by prophylactic insecticide usage that destroy the basic ecosystem services that control them (Heong and Schoenly 1998, Gallagher et al 1994). With the discontinuance of the "no early spray" and IPM practices, the increase in insecticide use motivated by continuous advertising by the

chemical industry seems likely to intensify the planthopper. The increasing trend in the use of neonicotinoids as prophylactic applications is another concern as planthoppers can develop resistance rapidly under such high selective pressures. Evidence of multiple-fold resistance developing in some rice-growing areas is reported by Matsumura et al (this volume).

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