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REVIEW ARTICLE

Parasitoids of Asian rice planthopper (Hemiptera: Delphacidae) pests and prospects for enhancing biological control by ecological engineering

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Abstract

The brown planthopper (BPH) *Nilaparvata lugens*, whitebacked planthopper (WBPH) *Sogatella furcifera* and smaller BPH *Laodelphax striatellus* increasingly exhibit resistance to insecticides and adaptation to resistant varieties, so they threaten food security. This review draws together, for the first time, information on the parasitoids of planthopper pests of rice from the non-English literature published in Asia. This is integrated with the English language literature to provide a comprehensive analysis. Planthopper pests of rice are attacked by a large range of parasitoids from Strepsiptera, Diptera and, especially, Hymenoptera. Levels of field parasitism vary widely between parasitoid species and locations. For many taxa, especially within Mymaridae, there is evidence that non-crop habitats are important as overwintering habitat in which alternative hosts are available. These source habitats may promote early season parasitism of pest Hemiptera in rice crops, and their movement into crops could be manipulated with applications of herbivore-induced plant volatiles. Non-crop plants can also provide nectar to improve parasitoid longevity and fecundity. Despite evidence for the importance of environmental factors affecting parasitoids of rice pests, the use of habitat manipulation to enhance biological control in the world's most important crop is surprisingly underrepresented in the literature. Current research in China, Vietnam and Thailand on ecological engineering, carefully selected vegetation diversity introduced without disrupting profitable farming, is briefly reported. Although the most important pest, BPH (*N. lugens*), is a migratory species, maintaining local communities of parasitoids and other natural enemies offers scope to prevent even *r*-selected pests from reaching damaging population densities.

Introduction

The human population is rapidly approaching seven billion and more than one half depend on rice as their food staple (International Rice Research Institute, 2010a). Continued population growth in developing countries and the inability of major rice importing countries, particularly in Africa and the Middle East and the Philippines, to significantly increase production is forecast to lead to increasing demand and greater international rice trade over the next decade (US Department of Agriculture, 2010). Although annual rice production has more than doubled from less than 200 million tonnes at the advent of the 'green revolution' in the 1960s, achieving future food security depends on development of better solutions for key rice pests.

Amongst the most important pests in Asian rice is the highly migratory brown planthopper (BPH) *Nilaparvata lugens* (Stål). This and related delphacids cause direct feeding damage, 'hopperburn', and transmit the viruses responsible for rice grassy stunt virus (RGSV), rice ragged stunt virus (RRSV), rice striped virus (RSV), rice black streaked dwarf virus (RBSDV) and south rice black streaked dwarf virus (SRBSDV). These Hemiptera are secondary, largely insecticide-induced, pests (Heinrichs & Mochida, 1984) and often cause more yield loss than by Lepidoptera pests such as stem borers or leaffolders (Dale, 1994).

Management of rice planthoppers employs host plant resistance (HPR), but field resistance levels are limited by the rapidity with which the delphacids, especially *N. lugens*, are able to overcome resistance genes (Horgan, 2009). As a result there continues to be heavy dependence on synthetic pesticides and this, in turn, has led to resistance to widely used neonicotinoid and phenylpyrazole compounds being reported from many Asian countries (Matsumura *et al*., 2009). The whitebacked planthopper (WBPH) *Sogatella furcifera* (Horvath) has also exhibited resistance to compounds such as fipronil in Japan, China and Vietnam (Matsumura *et al*., 2009).

A significant research effort has led to genetically modified rice expressing several traits. Amongst these, snowdrop lectin and *Allium sativum* leaf agglutinin have been shown experimentally to confer resistance to delphacids in modified rice (Nagadhara *et al*., 2004 and Yarasi *et al*., 2008, respectively). More widely used traits are *Bacillus thuringiensis* (*Bt*) and cowpea trypsin inhibitor, but these have no effect on sucking pests (Xia *et al*., 2010). In China, the world's largest rice producer and sixth largest exporter (US Department of Agriculture, 2010), *Bt* rice obtained its biosafety certificates in late 2009 and is now awaiting approval for commercialisation (Jia, 2010). Accordingly, whilst the possible use of this new technology offers scope to contribute to the management of key lepidopteran pests such as yellow stemborer, *Scirpophaga incertulas* (Walker), and the rice leaffolder, *Cnaphalocrocis medinalis* (Guenée) (Fam: Pyralidae) in the foreseeable future, it will have no direct effect on *N. lugens* and other sucking pests. There is, therefore, an urgent need to improve pest management of non-lepidopteran pests of rice so that rising levels of resistance to insecticides and breakdown of HPR do not lead to crop failure. Settele *et al*. (2008) go further and call for a 'switch' of research effort from GM to ecological engineering (*sensu* Gurr *et al*., 2004) in rice. Ecological engineering employs carefully selected vegetation diversity introduced without disrupting profitable farming to suppress pests either directly or via enhancement of natural enemy activity. Despite evidence for the importance of environmental factors affecting parasitoids of rice pests, the use of such approaches to enhance biological control in the world's most important crop is surprisingly underrepresented in the literature. This is illustrated by a keyword search of the Web of Science database for 'habitat manipulation' or 'conservation biological control' finds 348 articles but only three of these are on the world's most important crop species. Just two of these articles address insect pest management (Van Mele & Cuc, 2000; Drechsler & Settele, 2001); the other is about rats (Mill, 1993). Way & Javier (2001) also point out the neglect of biodiversity-related approaches to rice pest management.

That biological control offers scope to contribute to better rice pest management is indicated by a recently published food web for planthopper pests of Asian tropical rice (Dupo & Barrion, 2009). This consists of 244 natural enemy species, 89% of which are invertebrates, 7% vertebrates and 4% microbial or nematode pathogens. Such food webs are useful in indicating the complexity of trophic relationships in pest/natural enemy systems and the broad nature of the taxonomic groups in which antagonists are found. They are, however, limited in terms of directly supporting pest management. More detailed information is required to indicate which taxa are responsible for the highest levels of pest mortality and which offer scope to be manipulated to enhance their impact by habitat management (Landis *et al*., 2000). Whilst detailed information is available on many natural enemies of rice planthoppers, much of this exists only in non-English language (especially Chinese) publications or in the grey literature including institutional reports. These factors make much of the useful information inaccessible to the English-speaking scientific community and inhibit the flow of important information between differing non-English-speaking countries; for example from China to Vietnam and *vice versa*.

This review draws together for the first time, information on the natural enemies of planthopper pests of rice from the non-English literature published in Asia. This is integrated with the English language literature to provide a comprehensive analysis. The main digital tool for literature identification was Web of Science, and full text articles were then obtained either electronically or via interlibrary loan. In addition, the personal and institutional collections of books and reports of the authors were searched. Information from non-English sources was translated by the multilingual author team. The primary focus of the review is the three key delphacid pest species of Asian rice: rice smaller BPH, *Laodelphax striatellus* (Fallén); and the previously mentioned *N. lugens* and *S. furcifera*. In terms of natural enemy taxa, this review is concerned with parasitoids (Hymenoptera, Diptera, Strepsiptera) and considers scope for ecological engineering methods such as nectar plants and refuge vegetation (Gurr *et al*., 2004) to be used to combat the escalating pest problems. Relevant also is the availability of alternative hosts for the parasitoids. Accordingly, information is provided for some of the better researched species including the green rice leafhopper *Nephotettix virescens* (Distant) (Hemiptera: Cicadellidae). Our focus on parasitoids does not detract from the potential value of predators in biological control of rice planthoppers but reflects the fact that mortality of delphacid rice pests caused by parasitoids can be very high. For example, studies in Peninsular Malaysia found total egg mortality to be as high as 92% for *N. lugens* and 90% for *S. furcifera* with parasitoids responsible for 68% and 69%, respectively (Watanabe *et al*., 1992). The available literature suggests that spiders and predatory insects can also be important mortality factors (Heong *et al*., 1991; Settle *et al*., 1996). The ecological engineering strategies detailed herein to encourage parasitoids will potentially benefit predators by providing refuge habitat, moderated microclimate alternative prey and plant food (pollen).

Parasitoids of delphacid pests in Asian rice

Order: Hymenoptera

Family: Dryinidae

Approximately 20 dryinid species have been reported to parasitise *N. lugens*, *L. striatellus*, *S. furcifera* and *N. virescens* (Table 1). Female dryinids are solitary endoparasitoids that parasitise adult and all five nymphal stages of *N. lugens* (Sahragard *et al*., 1991). They are obligate host feeders with chelate fore tarsi adapted for holding prey which are typically first- to fourth-stage nymphs. Host feeding by the dryinid usually causes the host to die, and the cadaver is dropped from the plant whilst parasitised hosts are released from the forelegs and placed back on the food plant. Host feeding is important to dryinids because they are strongly synovigenic but feeding on host haemolymph is important for survival as well as egg maturation. An individual will, on average, feed on 3.2 nymphs and parasitise 4–9 nymphs per day (Chandra, 1980). Daily fecundity is reported to be 15–25 in *Echthrodelphax fairchildii* (Perkins) (Ito & Yamada, 2007). Laboratory work indicates that the combined effect could cause 54.9% host mortality although this is considered to be an overestimate of typical levels of field impact (Kitamura, 1982).

Dryinidae larvae develop within a sac that protrudes from the host's abdomen. When ready to pupate, they emerge from the host and pupate in a spun cocoon attached to the rice leaf or other substrate (Chiu, 1979). Host quality appears to affect parasitoid behaviour with third instar nymphs being preferred by female wasps and yielding the most strongly female-biased sex for parasitoid progeny (Kitamura & Iwami, 1998).

Dryinids migrate into rice crops principally within a parasitised host; indeed the female of many species is wingless. The food web of Dupo & Barrion (2009) suggests that dryinids are the most important natural enemies of nymphal/adult delphacids in terms of numbers of taxa (10 species). Field records, however, tend to suggest an inconsistent level of incidence and field parasitism. *Echthrodelphax fairchildii* and *Gonatopus yasumatsui* (Olmi) were reported to be uncommon in Peninsular Malaysia (van Vreden & Ahmadzabidi, 1986). Parasitism of *N. lugens* by dryinid wasps was generally under 2% in Japan, although parasitism of *L. striatellus* approached 10% in August/September (Kitamura, 1987). Parasitism of *S. furcifera* by dryinids tended to be higher, around 10% most of the season and peaking at 20% in June/July (Kitamura, 1987). In Japan, *Haplogonatopus atratus* (Esaki & Hashimoto) was the most dominant dryinid species. About five dryinid species have been recorded in rice fields in Vietnam but parasitism of *N. lugens* and *S. furcifera* by Dryinidae was reported to be less than 10% (Lam *et al*., 2002).

In the Philippines total parasitism rates for *E. fairchildii*, *Haplogonatopus* spp. and *Pseudogonatopus* spp. in *N. lugens* and *S. furcifera* were also relatively low: 9.7% and 6.4% in the wet and dry seasons, respectively (Peña & Shepard, 1986). In contrast, Chandra (1980) reported parasitism of *N. lugens* by dryinid wasps in the Philippines reached 35–40% in September–October in dryland rice fields. In Sri Lanka 40% parasitism was reached although this level of attack was not sufficient to control *N. lugens* and *S. furcifera* infestations (Ôtake *et al*., 1976). Dryinids appear to be still more important in China where parasitism of *L. striatellus* reached close to 50% as a result of the combined attack by: *Haplogonatopus japonicus* (Esaki & Hashimoto), *H. atratus* (Esaki & Hashimoto), *Pseudogonatopus flavifemur* (Esaki & Hashimoto), *Paragonatopus fulgori* (Nakagawa) and *Pseudogonatopus* sp.

Family: Mymaridae

Mymaridae are egg parasitoids of small to minute size reported attacking delphacid planthopper pests of rice widely throughout Asia from India east to China, northwards to Japan and south to Malaysia, Singapore and

Table 1 Dryinidae parasitoids reported from Hemiptera pests of Asian rice

Parasitoid	Host	Location	References
Anteon yasumatsui (Olmi)	*Nephotettix cincticeps* (Esaki & Hashimoto)	China	He & Xu (2002)
		India	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Thailand	He & Xu (2002)
Dicondylus indianus (Olmi) = *Pseudogonatopus flavifemur* (Esaki & Hashimoto)	*Nilaparvata lugens*	China (Sinan County, Guizhou)	Chen (1989)
		India	Sahragard *et al*. (1991) (citing Olmi, 1984)
		Japan	Chiu (1979) (citing Esaki, 1932; Sakai, 1932; Esaki & Hashimoto, 1933, 1936); Kitamura (1987)
		Philippines	Barrion *et al*. (1981); Chua *et al*. (1984); Dayanan & Esteban (1996); Sahragard *et al*. (1991) (citing Olmi, 1984)
		China (Taiwan)	Chu & Hirashima (1981); Sahragard *et al*. (1991) (citing Olmi, 1984)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	Asia	Dupo & Barrion (2009)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella vibix (Haupt)	Asia	Dupo & Barrion (2009)
	Tagosodes pusanus (Distant)	Asia	Dupo & Barrion (2009)
Echthrodelphax bicolor (Esaki & Hashimoto) NPPS & ZAU (1991) indicate *E. fairchildii* (Perkins) is synonymous with *E. bicolor* (Esaki & Hashimoto)	*Nilaparvata lugens*	China	Chu & Hirashima (1981); NPPS & ZAU (1991)
		Japan	Chiu (1979) (citing Esaki & Hashimoto, 1936)
		China (Taiwan)	Chu & Hirashima (1981)
	Sogatella furcifera	China	NPPS & ZAU (1991)
		Japan (Shimane)	Kitamura (1987)
	Laodelphax striatellus (Fallén)	China	NPPS & ZAU (1991)
Echthrodelphax fairchildii (Perkins)	*Laodelphax striatellus*	Japan	Ito & Yamada (2007)
	Nilaparvata lugens	India	Randhawa *et al*. (2006); Chiu (1979) (citing Rai, personal communication)
		India	Manjunath *et al*. (1978); Yadav & Pawar (1989)
		Japan	Ito & Yamada (2007); Yamada & Ikawa (2003)
		Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
		Philippines	Barrion *et al*. (1981); Peña & Shepard (1986)
	Perkinsiella saccharicida (Kirkaldy)	Asia	Dupo & Barrion (2009)
	Sogatella furcifera	India	Randhawa *et al*. (2006); Yadav & Pawar (1989)
		Japan	Ito & Yamada (2007); Yamada & Ikawa (2003)
		Philippines	Peña & Shepard (1986)
Echthrodelphax spp.	*Nephotettix cincticeps*	India	Greathead (1982)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)
	Nephotettix nigropictus (Stål) (Alternative spelling *N. nigropicta*)	India	Greathead (1982)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)
	Nephotettix virescens (Distant)	India	Greathead (1982)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)
	Nilaparvata lugens	India	Greathead (1982)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)

Table 1 Continued

Parasitoid	Host	Location	References
	Sogatella furcifera	India	Greathead (1982)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)
Epigonatopus sasakii (Esaki & Hashimoto)	*Nephotettix cincticeps*	China	NPPS & ZAU (1991)
Gonatopus camelinus (Kieffer)	*Laodelphax striatellus*	China (Guizhou)	He & Xu (2002)
Gonatopus cuscelidivorus (Xu & He)	*Nephotettix cincticeps*	China (Guangxi)	He & Xu (2002)
Gonatopus dromedarius (Costa)	*Laodelphax striatellus*	China	He & Xu (2002)
Gonatopus flavifemus	*Nilaparvata lugens*	China	Chen (1989); Chu & Hirashima (1981); NPPS & ZAU (1991)
		Japan	Chiu (1979) (citing Esaki, 1932; Esaki & Hashimoto, 1933, 1936; Sakai, 1932)
		Japan (Shimane)	Kitamura (1987)
		Philippines	Barrion *et al*. (1981); Chua *et al*. (1984); Dayanan & Esteban (1996)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Laodelphax striatellus	China	He & Xu (2002)
	Sogatella furcifera	Asia	Dupo & Barrion (2009)
		China	He & Xu (2002)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella vibix	Asia	Dupo & Barrion (2009)
	Tagosodes pusanus (Distant)	Asia	Dupo & Barrion (2009)
Gonatopus lucens (Olmi)	*Nephotettix cincticeps*	China (Guangxi, inner Mongolia)	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
	Nilaparvata lugens	China (Guangxi, inner Mongolia)	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
	Sogatella furcifera	China (Guangxi, inner Mongolia),	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
Gonatopus nigricans (Perkins)	*Laodelphax striatellus*	China	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
	Nilaparvata lugens	China	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
	Sogatella furcifera	China	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
Gonatopus nudus (Perkins)	*Nilaparvata lugens*	China	He & Xu (2002)
		India	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
		Sri Lanka	He & Xu (2002)
		Thailand	He & Xu (2002)

Table 1 Continued

Parasitoid	Host	Location	References
	Sogatella furcifera	China	He & Xu (2002)
		India	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
		Sri Lanka	He & Xu (2002)
		Thailand	He & Xu (2002)
	Recilia dorsalis	China	He & Xu (2002)
		India	He & Xu (2002)
		Indonesia	He & Xu (2002)
		Malaysia	He & Xu (2002)
		Philippines	He & Xu (2002)
		Sri Lanka	He & Xu (2002)
		Thailand	He & Xu (2002)
Gonatopus sakaii (Esaki & Hashmoto)	*Nephotettix cincticeps*	China	He & Xu (2002)
		Japan	He & Xu (2002)
Gonatopus schenklingi (Strand)	*Nilaparvata lugens*	China (Guangxi)	He & Xu (2002)
		India	He & Xu (2002)
		Japan	He & Xu (2002)
		China (Taiwan)	He & Xu (2002)
Gonatopus yasumatsui (Olmi)	*Nilaparvata lugens*	Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
Haplogonatopus sp. nr. *americanus* Perkins	*Nilaparvata lugens*	Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
Haplogonatopus apicalis (Perkins)	*Nilaparvata lugens*	China	NPPS & ZAU (1991)
Chen (1989) indicates *H. japonicas* is synonymous with *H. apicalis*		India	Randhawa *et al*. (2006)
		India (Madhya Pradesh)	Yadav & Pawar (1989)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	China	NPPS & ZAU (1991)
		India	Randhawa *et al*. (2006)
		India (Madhya Pradesh)	Yadav & Pawar (1989)
		Japan	Kitamura & Iwami (1998)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Laodelphax striatellus	China	NPPS & ZAU (1991)
Haplogonatopus atratus (Esaki & Hashimoto)	*Laodelphax striatellus*	China	NPPS & ZAU (1991)
		Japan	Kitamura (1982); Yamada & Kawamura (1999); Yamada & Miyamoto (1998)
		Japan (Shimane)	Kitamura (1987)
	Sogatella furcifera	China	NPPS & ZAU (1991)
		Japan	Kitamura (1982)
	Nilaparvata lugens	China	NPPS & ZAU (1991)
Haplogonatopus japonicus (Esaki & Hashimoto) Alternative spellings: *H. japonica*, *H. japonicas* Chen (1989) and Zhang & Jin (1992) indicate *H. japonicas* is synonymous with *H. apicalis*	*Nilaparvata lugens*	China	Li (1982); NPPS & ZAU (1991)
Haplogonatopus oratorius (Westwood)	*Nilaparvata lugens*	Asia	He & Xu (2002)
	Sogatella furcifera	Asia	He & Xu (2002)
	Laodelphax striatellus	Asia	Dupo & Barrion (2009)
Haplogonatopus orientalis (Rohwer)	*Nilaparvata lugens*	India	Randhawa *et al*. (2006); Shankar & Baskaran (1988,1992)
		Sri Lanka	Ôtake *et al*. (1976)
	Sogatella furcifera	India	Randhawa *et al*. (2006)
		Sri Lanka	Ôtake *et al*. (1976)
Haplogonatopus sp./spp.	*Nephotettix nigropictus*	India	Greathead (1982)
		Japan	Greathead (1982)

Table 1 Continued

Parasitoid	Host	Location	References
		Korea	Greathead (1982)
		Philippines	Greathead (1982)
	Nephotettix virescens	India	Greathead (1982)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Philippines	Greathead (1982); Chandra (1980)
	Nilaparvata lugens	India	Chiu (1979) (citing Rai, personal communication); Greathead (1982)
		India (Mandya, Karnataka)	Manjunath *et al*. (1978)
		Japan, Korea	Greathead (1982)
		Malaysia	Ooi (1982)
		Philippines	Barrion *et al*. (1981); Chandra (1980); Greathead (1982); Peña & Shepard (1986)
	Sogatella furcifera	India	Greathead (1982)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Ooi (1982)
		Philippines	Chandra (1980); Greathead (1982); Peña & Shepard (1986)
		Sri Lanka	Chiu (1979)
Monogonatopus orientalis (Rohwer)	*Nilaparvata lugens*	Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
Monogonatopus sp.	*Nilaparvata lugens*	China (Taiwan)	Chu & Hirashima (1981)
Neogonatopus sp.	*Nephotettix cincticeps*	China (Guangxi)	NPPS & ZAU (1991)
	Nephotettix virescens	China (Guangxi)	NPPS & ZAU (1991)
Paragonatopus fulgori (Nakagawa)	*Laodelphax striatellus*	China	NPPS & ZAU (1991)
		Japan	Kitamura (1989)
	Nilaparvata lugens	China	NPPS & ZAU (1991)
	Sogatella furcifera	China	NPPS & ZAU (1991)
		Japan	Kitamura (1989)
Pseudogonatopus hospes (Perkins)	*Nilaparvata lugens*	India	Yadav & Pawar (1989)
		Malaysia	Ooi (1982); van Vreden & Ahmadzabidi (1986)
		Thailand	Chiu (1979)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	India (Madhya Pradesh)	Yadav & Pawar (1989)
		Malaysia	Ooi (1982)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
Pseudogonatopus nudus (Perkins)	*Nilaparvata lugens*	China	Olmi (1991–92)
		India	Olmi (1991–92)
		Indonesia	Olmi (1991–92)
		Malaysia	Olmi (1991–92)
		Philippines	Chua *et al*. (1984); Dayanan & Esteban (1996); Olmi (1991–92)
		Sri Lanka	Olmi (1991–92)
		China (Taiwan)	Olmi (1991–92)
		Thailand	Olmi (1991)–92)
	Sogatella furcifera	Asia	Dupo & Barrion (2009)
Pseudogonatopus otaki (Olmi)	*Nilaparvata lugens*	Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
Pseudogonatopus ponomarenkoi Moczar	*Sogatella furcifera*		
Pseudogonatopus nr. *pusanus* (Olmi)	*Nilaparvata lugens*	India (Madhya Pradesh)	Yadav & Pawar (1989)
	Sogatella furcifera	India (Madhya Pradesh)	Yadav & Pawar (1989)
Pseudogonatopus sarawaki (Moczar)	*Nilaparvata lugens*	Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
Pseudogonatopus sp./ spp.	*Nephotettix cincticeps*	Japan	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)

Table 1 Continued

Parasitoid	Host	Location	References
	Nephotettix nigropictus	Japan	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)
	Nephotettix virescens	Japan	Greathead (1982)
		Philippines	Greathead (1982)
		China (Taiwan)	Greathead (1982)
	Nilaparvata lugens	Japan	Greathead (1982)
		Philippines	Chandra (1980); Greathead (1982); Peña & Shepard (1986)
		China (Taiwan)	Chu & Hirashima (1981); Greathead (1982)
	Sogatella furcifera	Japan	Chandra (1980); Greathead (1982)
		Philippines	Chandra (1980); Greathead (1982); Peña & Shepard (1986)
		China (Taiwan)	Greathead (1982
	Sogatella furcifera	Japan	Chandra (1980); Greathead (1982)
		Philippines	Chandra (1980); Greathead (1982); Peña & Shepard (1986
		China (Taiwan)	Greathead (1982

Vietnam (Table 2). Major hosts are *S. furcifera*, *N. lugens*, *Nephotettix cincticeps* (Uhler), *Nephotettix nigropictus* and *N. virescens* (Distant) (Greathead, 1982). Chandra (1980) describes the behaviour of the gravid *Anagrus* spp. females. On landing upon a plant the wasp walks rapidly over the substrate, drumming on the surface with the antennae. Drumming intensifies when a host egg mass is located. Oviposition occurs by the wasp first drilling through the leaf epidermis. The drumming appears to be involved in locating the eggs and locating a suitable position to drill. Failure rate is high; 95% attempts fail to penetrate and, of those that do, 89% do not successfully oviposit in an egg. When parasitoid density is high, one to three eggs are laid but only one will develop. Parasitism is readily detected through the transparent chorion of the host egg when the parasitoid larva is at least half grown.

Most species of egg parasitoids attacking delphacid planthopper pests of rice are mymarids (Dupo & Barrion, 2009). Mymarid egg parasitoids quickly migrate into crops from alternative hosts in other habitats, rapidly establish and cause pest mortality; consequently they are considered important biological control agents (Chandra, 1980).

The most important genus in this family is *Anagrus*. *Anagrus* sp. nr *flaveolus* Waterhouse has been reported to be the dominant parasitoid of *L. striatellus* in Japan (Ôtake, 1970a). This species did not show a preference between *N. lugens*, *S. furcifera* and *L. striatellus* (Ôtake, 1977). Parasitism rates of up to 95% have been reported for *A.* sp. nr *flaveolus* in *L. striatellus* (Hachiya, 1995). Published parasitism rates for mymarids and other egg parasitoids are more reliable and comparable across studies than those for parasitoids such as dryinids that attack other life stages. This is because a standard method based on bait plants has been developed, promoted by IRRI and widely used. Bait plants are prepared by introducing three to five gravid female planthoppers of the species of interest (most commonly *N. lugens*) to a 30-day-old rice plant for 24 h. Plants bearing host eggs are then placed in the field for 72 h before recovery to the laboratory. There, a piece of the leaf sheath containing an egg mass is placed in a closed Petri dish lined with paper towel moistened with antifungal solution. Numbers of host nymphs and adult parasitoids that emerge are counted and parasitism calculated by dividing numbers of the latter by the total number of insects (Reissig *et al*., 1986). Prior to the widespread use of this standard method, Chandra (1980) obtained adult egg parasitoids by dissecting field-collected rice leafsheaths containing host eggs and reared the parasitised eggs on a moist filter paper in Petri dish. The standard method is less labour intensive than direct observation and dissection of hosts but caution needs to be exercised when dealing with samples that contain polyembryonic parasitoids (e.g. Trichogramma) and facultative hyperparasitoids.

The parasitoid complex of Vietnamese rice includes the mymarid genera *Anagrus* and *Gonatocerus* and can give parasitism rates in range of 21.2–47.8% (Lam *et al*., 2002). Higher rates of parasitism, up to 72.5%, have been reported for *Anagrus* spp. in *S. furcifera* in Vietnam (Tao Ngoan, 1970). *Anagrus* is also considered the dominant parasitoid genus on *N. lugens* and *S. furcifera*

Table 2 Mymaridae parasitoids reported from Hemiptera pests of Asian rice

Parasitoid	Host	Location	References
Acmopolynema spp.	*Tagosodes pusanus*	Asia	Dupo & Barrion (2009)
	Toya propinqua (Distant)	Asia	Dupo & Barrion (2009)
Anagrus sp. nr *flaveolus* Waterhouse	*Laodelphax striatellus*	China (Fujian)	Lo & Zhuo (1980)
		Japan	Hachiya (1995); Ôtake (1970a); 1977
	Nephotettix cincticeps	China (Taiwan)	Chu & Hirashima (1981)
	Nilaparvata lugens	China	Yu (1996); Yu *et al*. (1998)
		China (Fujian)	Lo & Zhuo (1980)
		India	Singh *et al*. (1993)
		Japan	Chiu (1979) (citing Ôtake 1970*a*, *b*, 1976*a*, *b*; Yasumatsu & Watanabe, 1965); Ôtake (1977)
		Philippines	Barrion *et al*. (1981)
		Sri Lanka	Fowler *et al*. (1991)
		China (Taiwan)	Chu & Hirashima (1981)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	China	Yu (1996); Yu *et al*. (1998)
		China (Fujian)	Lo & Zhuo (1980)
		India	Nalini (2005); Randhawa *et al*. (2006)
		Japan	Ôtake (1977)
		Malaysia	Watanabe *et al*. (1992)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Tagosodes pusanus	China	Yu (1996); Yu *et al*. (1998)
	Toya spp.	China	Yu (1996)
Anagrus frequens (Perkins)	*Sogatella furcifera*	India	Randhawa *et al*. (2006)
Synonyms: *Anagrus armatus,*		Malaysia	Watanabe *et al*. (1992)
A. cicadulinae, A. toyae	*Perkinsella* sp.	China (Taiwan)	Triapitsyn & Beardsley (2000)
Anagrus incarnatus (Haliday)	*Harmalia albicolli* (Motschulsky)	Japan	Chantarasa-ard *et al*. (1984*a*)
	Laodelphax striatellus	Japan	Chantarasa-ard *et al*. (1984*a*)
	Macrosteles orientalis (Vilbaste)	Japan	Chantarasa-ard *et al*. (1984*a*)
	Nephotettix cincticeps	Japan	Chantarasa-ard *et al*. (1984*a*)
	Nilaparvata bakeri (Muir)	Japan	Chantarasa-ard *et al*. (1984*a*)
	Nilaparvata lugens	Bangladesh	Chen & Yu (1989)
		China	Chiappini & Lin (1998)
		Japan	Chantarasa-ard (1984); Chantarasa-ard *et al*. (1984a); Chen & Yu (1989)
		Korea	Chen & Yu (1989)
		China (Taiwan)	Chen & Yu (1989)
	Nilaparvata muiri (Caldwell)	Japan	Chantarasa-ard *et al*. (1984a)
	Sogatella furcifera	Japan	Chantarasa-ard (1984); Chantarasa-ard *et al*. (1984a;1984b)
	Sogatella longifurcifera (Esaki & Ishihara)	Japan	Chantarasa-ard *et al*. (1984a)
	Sogatella panicicola (Ishihara)	Japan	Chantarasa-ard *et al*. (1984a)
	Terthron albovittatum (Matsumura)	Japan	Chantarasa-ard *et al*. (1984a)
	Zuleica nipponica (Matsumura & Ishihara)	Japan	Chantarasa-ard *et al*. (1984a)
Anagrus longitubulosus (Pang & Wang)	*Laodelphax striatellus*	China	Luo & Zhuo (1980); NPPS & ZAU (1991)
	Nilaparvata lugens	China	Luo & Zhuo (1980); NPPS & ZAU (1991)
			Mao *et al*. (1999); Mao *et al*. (2002b); NPPS & ZAU (1991)
	Sogatella furcifera	China	Lo & Zhuo (1980); Luo & Zhuo (1980); NPPS & ZAU (1991)
Anagrus nilaparvatae (Pang & Wang)	*Laodelphax striatellus*	China	Chiappini & Lin (1998); Luo & Zhuo (1980); Mao *et al*. (2002a); NPPS & ZAU (1991)
	Nilaparvata bakeri	China	Chiappini & Lin (1998); Li & He (1991); NPPS & ZAU (1991)

Table 2 Continued

Parasitoid	Host	Location	References
	Nilaparvata lugens	China	Chiappini & Lin (1998); Li & He (1991); Luo & Zhuo (1980); Lou *et al*. (2005a); Mao *et al*. (1999); Mao *et al*. (2002a); NPPS & ZAU (1991); Xiang *et al*. (2008); Zheng *et al*. (2003b)
		India	Randhawa *et al*. (2006)
	Nilaparvata muiri	China	Chiappini & Lin (1998)
	Sogatella furcifera	China	Chiappini & Lin (1998); Li & He (1991); Luo & Zhuo (1980); (Mao *et al*. 2002a); NPPS & ZAU (1991); Zheng *et al*. (2003b)
		India	Randhawa *et al*. (2006)
	Sogatella panicicola (Synonymous with *S. vibix*)	China (Guangdong)	Li & He (1991)
	Toya propinqua	China (Guangdong)	Li & He (1991
	Toya tuberculosa (Distant)	China (Guangdong)	Li & He (1991)
Anagrus optabilis (Perkins) Mao *et al*. (2002a) indicate *A. paranilaparvatae* is a pseudonym of *A. optabilis* Triapitsyn, 2001 proposes the synonymy of *A. paranilaparvatae* under *A. optabilis* Synonyms: *Paranagrus optabilis* Perkins, *Paranagrus osborni* Fullway, *Anagrus panicicola* Sahad (Triapitsyn & Beardsley, 2000)	*Laodelphax striatellus*	Japan	Baquero & Jordana (1999) (citing Sahad & Hirashima (1984); Sahad (1984)
		China (Taiwan)	Miura *et al*. (1981)
	Nephotettix spp.	Thailand	Wongsiri *et al*. (1980)
	Nilaparvata lugens	China	Chiappini & Lin (1998); Yu *et al*. (1996); Zheng *et al*. (1999, 2003b)
		India	CAB International (2005); Shankar & Baskaran, (1988, 1992)
		Japan	Baquero & Jordana (1999) (citing Sahad & Hirashima 1984); Sahad (1984)
		Malaysia	Ooi (1982); van Vreden & Ahmadzabidi (1986); Watanabe *et al*. (1992)
		Sri Lanka	CAB International (2005); Fowler *et al*. (1991)
		China (Taiwan)	Miura *et al*. (1981)
		Thailand	Chiu (1979) (citing Yasumatsu *et al*., 1975; Nishida *et al*., 1976); Hirashima *et al*. (1979); Wongsiri *et al*. (1980)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	China	Miura *et al*. (1981); Yu *et al*. (1996)
		Japan	Sahad (1984)
		Malaysia	Ooi (1982)
		China (Taiwan)	Miura *et al*. (1979)
		Thailand	Hirashima *et al*. (1979); Miura *et al*. (1979)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Tagosodes pusanus	China	Yu (1996); Yu *et al*. (1998)
	Toya propinqua	China (Guangdong)	Li & He (1991)
	Toya spp.	China	Yu (1996); Yu *et al*. (1998)
Anagrus paranilaparvatae (Pang & Wang)	*Hirozuunka japonica* (Matsumura & Ishihara)	Japan	Triapitsyn & Beardsley (2000)
	Laodelphax striatellus	China	Lo & Zhuo (1980); Luo & Zhuo (1980); NPPS & ZAU (1991)
	Megamelus proserpina (Kirkaldy)	Philippines	Triapitsyn & Beardsley (2000)
	Nephotettix virescens	Philippines	Triapitsyn & Beardsley (2000)
	Nilaparvata lugens	China	Li & He (1991); Lo & Zhuo (1980); Luo & Zhuo (1980); Mao *et al*. (1999, 2002a); NPPS & ZAU (1991)
		India	Randhawa *et al*. (2006)
		India (Andhra Pradesh)	CAB International (2005)
		Malaysia (Peninsular)	Watanabe *et al*. (1992);
	Sogatella furcifera	China	Chiappini & Lin (1998); Lo & Zhuo (1980); Luo & Zhuo (1980); NPPS & ZAU (1991)

Table 2 Continued

Parasitoid	Host	Location	References
		India	Randhawa *et al*. (2006)
		Philippines	Triapitsyn & Beardsley (2000)
Anagrus shortitubulosus Pang & Wang	*Laodelphax striatellus*	China	Luo & Zhuo (1980); NPPS & ZAU (1991)
	Nilaparvata lugens	China	Luo & Zhuo (1980); NPPS & ZAU (1991)
	Sogatella furcifera	China	Luo & Zhuo (1980); NPPS & ZAU (1991)
Anagrus spp.	*Laodelphax striatellus*	China	Luo *et al*. (1981); Luo & Zhuo (1983)
	Nephotettix cincticeps	Japan	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982
		Philippines	Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Chu & Hirashima (1981); Greathead (1982)
		Thailand	Greathead (1982)
		Vietnam	Greathead (1982)
	Nephotettix nigropictus	Japan	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982)
		Philippines	Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982)
		Thailand	Greathead (1982)
		Vietnam	Greathead (1982)
	Nephotettix virescens	Japan	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982)
		Philippines	Chandra (1980); Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982)
		Thailand	Greathead (1982)
		Vietnam	Greathead (1982)
	Nilaparvata lugens	China	Luo *et al*. (1981); Luo & Zhuo (1983); Mao *et al*. (1999)
		India	Gupta & Pawar (1989)
		Indonesia	Claridge *et al*. (1999)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982); Ooi (1982)
		Philippines	Barrion *et al*. (1981); Chandra (1980); Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Chu & Hirashima (1981); Chui (1979); Greathead (1982)
		Thailand	Greathead (1982); Vungsilabutr (1981)
		Vietnam	Greathead (1982)
	Sogatella furcifera	China (Fujian)	Luo *et al*. (1981); Luo & Zhuo (1983); Luo & Zhuo (1986); Zhang (1991)
		Japan	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982); Ooi (1982)
		Philippines	Chandra (1980); Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982)
		Thailand	Greathead (1982); Vungsilabutr (1981)
		Vietnam	Greathead (1982); Tao & Ngoan (1970)
Anaphes spp	*Nephotettix cincticeps*	China (Taiwan)	Chu & Hirashima (1981)
	Nilaparvata lugens	China (Taiwan)	Chu & Hirashima (1981)
		Sri Lanka	Fowler *et al*. (1991)
		China (Taiwan)	Chu & Hirashima (1981)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)

Table 2 Continued

Parasitoid	Host	Location	References
	Sogatella furcifera	China	Yu (1996); Yu *et al*. (1998)
		China (Fujian)	Lo & Zhuo (1980)
		India	Nalini (2005); Randhawa *et al*. (2006)
		Japan	Ôtake (1977)
		Malaysia	Watanabe *et al*. (1992)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Tagosodes pusanus	China	Yu (1996); Yu *et al*. (1998)
	Toya spp.	China	Yu (1996)
Emoemas sp.	*Nilaparvata lugens*	China (Guangxi)	NPPS & ZAU (1991)
Gonatocerus longicrus (Kieffer)	*Laodelphax striatellus*	China	NPPS & ZAU (1991)
	Nephotettix cincticeps	China	NPPS & ZAU (1991)
Gonatocerus sp.	*Nephotettix cincticeps*	Korea, Philippines	Greathead (1982)
		China (Taiwan)	Chu & Hirashima (1981); Greathead (1982)
		Thailand	Greathead (1982)
	Nephotettix nigropictus	Korea, Philippines, Taiwan	Greathead (1982)
		Thailand	Greathead (1982); Vungsilabutr (1981)
	Nephotettix virescens	Korea	Greathead (1982)
		Philippines	Chandra (1980); Greathead (1982)
		China (Taiwan)	Greathead (1982)
		Thailand	Greathead (1982); Vungsilabutr (1981)
	Nilaparvata lugens	China (Guangxi)	NPPS & ZAU (1991)
		Korea	Ôtake (1977) (citing Yasumatsu, personal communication)
		Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
		China (Taiwan)	Chu & Hirashima (1981)
		Thailand	Wongsiri *et al*. (1980); Chiu (1979) (citing, Yasumatsu *et al*.,1975)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
Lymaenon sp.	Planthoppers	China (Fujian)	Lo & Zhou (1980)
Mymar indica (Mani)	*Nephotettix cincticeps*	China (Taiwan)	Chu & Hirashima (1981)
	Nilaparvata lugens	China (Taiwan)	Chiu (1979) (citing Lin 1974)
		Thailand	Chiu (1979) (citing, Yasumatsu *et al*.,1975)
Mymar taprobanicum (Ward)	*Nilaparvata lugens*	Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
		Philippines	Barrion *et al*. (1981); Chandra (1980)
		China (Taiwan)	NPPS & ZAU (1991)
		Thailand	Chiu (1979) (citing Yasumatsu *et al*., 1975); Wongsiri *et al*. (1980); NPPS & ZAU (1991)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	Thailand	Wongsiri *et al*.(1980)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Nephotettix cincticeps	China (Taiwan)	NPPS & ZAU, (1991)
Polynema sp.	*Nilaparvata lugens*	Philippines	Barrion *et al*. (1981)
Ooctonus sp.	*Nilaparvata lugens*	China (Guangxi)	NPPS & ZAU (1991)

in the central plain of Thailand (Vungsilabutr, 1981). In Malaysia a parasitism rate of 47% was reported in *S. furcifera* (Watanabe *et al*., 1992).

Mymarid parasitoids tend to be favoured by moderate temperatures. For example, *Anagrus nilaparvatae* (Pang & Wang) has an optimum temperature of 27°C and both fecundity and survival of immature stages is greatly reduced at high temperatures (Chiappini & Lin, 1998). Reflecting this general tendency, parasitism rates in Japan by *Anagrus* sp. nr *flaveolus* are greatest in May and June (11.3–29.6%) and September–November (3.3–38.1%) (Chiu, 1979). The low threshold temperature for development of female *Anagrus longitubulosus* (Pang & Wang) was found to be 11.7°C and 11.3°C for *A. nilaparvatae* (Li & He, 1991).

Anagrus nr. *flaveolus* has a strong tendency to disperse and this is important for its ability to overwintering in habitat other than paddy fields where it may use both delphacid and non-delphacid hosts (Ôtake, 1977). *Anagrus flaveolus*, the dominant parasitoid in

China, favours *Tagosodes pusanus* (Distant) when in grassy, non-rice habitat (Yu *et al*., 1998). Similarly, *Anagrus incarnatus* (Haliday) is capable of overwintering in eggs of *Nilaparvata muiri* (Caldwell) (Chantarasa-ard, 1984). Furthermore, *A. incarnatus* exhibits a wide host range including *Nilaparvata bakeri* (Muir), *Harmalia albicollis* (Motchulsky), *Sogatella longifurcifera* (Esaki & Ishihara), *Sogatella panicicola* (Ishihara), *Terthron albovittata* (Matsumura), *Zuleica nipponica* (Matsumura & Ishihara), *N. cincticeps* (Uhler) and *Macrosteles orientalis* (Vilbaste) (Chantarasa-ard *et al*., 1984a). Non-crop vegetation in which these host insects overwinter is, therefore, important habitat for Mymaridae that immigrate into rice crops early in the growing season. During the winter these potentially important biological control agents can use the alternative hosts in these habitats, either reproducing (in warmer tropical areas) or developing within the host (in areas with a cool winter).

Considerable information is available on the role of non-crop vegetation on mymarids in rice production systems of Asia, particularly from Chinese language journals. *A. nilaparvatae* is known to use several grassy plants during the winter in Guangdong Province, southern China (Li & He, 1991), particularly *Leersia hexandra* (Swartz), *Scirpus juncoides* (Roxb.), *Paspalum orbiculare* (G. Forst.). The final, 14th, generation of *Anagrus paranilaparvatae* (Pang & Wang) in Fujian Province of China, used grassy habitats as overwintering sites when rice crops were seasonally absent (Lo & Zhou, 1980).

Anagrus nr. *flaveolus* is known to develop in eggs of planthoppers living on weeds around the rice field during winter (Lo & Zhuo, 1980). Two of the 20 generations occurring in Fujian Province China take place in this non-crop habitat. Hosts used outside of rice crops are *Toya propinqua* (Muir) and *T. tuberculosa* (Distant) on *Panicum repens* (L.); *Kakuna sapporonis* (Matsumura) on *Paspalum distichum* (L.); *S. panicicola* on *Echinochloa crusgalli* (L.) P. Beauv.; *N. bakeri* on *L. hexandra*. In the case of *A. longitubulosus*, another species that overwinters in grassy areas, parasitoids were associated with the grasses *E. crusgalli*, *P. orbiculare*, *Adiantum capillus-veneris* (L.) (Li & He, 1991). Importantly, that work demonstrated that wasps emerging from eggs of a mixed community of planthopper species on weeds are smaller than those from the eggs of *S. furcifera* in rice. Taken in isolation, this finding suggests that the extent to which mymarids are readily able to 'switch' from non-crop habitats to parasitising major delphacid pests in rice crops is questionable. Indeed, later work by Yu *et al*. (1996) showed that the reproductive success of female parasitoids emerging from bait plants carrying *N. lugens* eggs is indeed significantly lower for wasps recovered from weedy areas than from rice or corn fields: 2.0, 9.6 and 12.6 offspring per female, respectively. Importantly, however, for the second generation of wasps the performance recovered; such that there were no significant differences between females, all producing between 8 and 11 progeny. This phenomenon was not an artefact of using bait plants using *N. lugens* eggs for a similar effect was apparent when using eggs of *T. pusanus*. Thus 'switching' from alternative hosts in non-rice habitats to attacking delphacid pests in rice seems to be accomplished with a partial reduction in performance that is short in the context of a species with approximately 20 generations per year.

The sex ratio, body size and parasitoid growth rate of *Anagrus optabilis* (Perkins) in Chinese rice fields and adjacent habitats were found to be influenced by host species, host plants and the surrounding habitat (Yu *et al*., 1996). Grass species that were found to be important for mymarids were *Digitaria ciliaris* (Retz.), *Brachiaria distachya* (L.) and *Cynodon dactylon* (L.) Pers. These habitats supported *A.* sp. nr *flaveolus*, *A. optabilis* as well as the trichogrammatids *Oligosita naias* (Girault) and *Oligosita aesopi* (Girault). In these grassy habitats, *A.* nr. *flaveolus* commonly parasitised *T. pusanus*. More recent Chinese work on the use of alternative hosts in non-crop habitats showed that *Anagrus* spp. used the hosts *Saccharosydne procerus* (Matsumura), *L. striatellus* (Fallén), *T. propinqua*, *T. tuberculosa*, *S. panicicola*, *N. bakeri*, *T. albovittatum*, *Delphacodes graminicola* (Matsumura), *S. furcifera* and *N. lugens* (Zheng *et al*., 2003a). The non-rice plants used included the grasses *E. crusgalli*, *L. hexandra*, *P. repens*, *C. dactylon*, *P. distichum*, *Digitaria* spp. and *L. chinensis.*

More concrete evidence for the importance of non-rice habitats as a source for parasitoids that can exert control of rice pests comes from studies of the vegetable crop *Zizania caduciflora* (Turcz.). This crop supports *S. procerus*, a delphacid that is unable to develop on rice so considered a non-pest species (Yu, 2001). However, this insect supports the parasitoid *A. optabilis* which is also an important parasitoid of *N. lugens* (Zheng *et al*., 1999). There is, however, evidence of an adaptation process. After rearing two generations on *N. lugens*, *A. optabilis* preferred to parasitise the eggs of *N. lugens* over the non-pest *S. procerus*. When these parasitoids are presented with *S. procerus*, numbers of progeny were lower than those that remained on *N. lugens* (Zheng *et al*., 2003a).

Other than providing alternative hosts, non-crop habitats may also offer nectar and this resource is utilised by *A. flaveolus* (Yu *et al*., 1996). Laboratory studies on *A. nilaparvatae* showed that longevity was extended by feeding with honey, corn pollen, soybean flowers and the honeydew of *N. lugens* and *Toya* spp. Of greater relevance to biological control, egg production by this parasitoid on

N. lugens was significantly increased when fed with those nutrient-rich diets except the honeydew excreted by *Toya* sp. (Zheng *et al.*, 2003b).

Family: Encyrtidae

The encyrtids *Chrysopophagus australiae* (Perkins) and *Echthrogonatopus exitiosus* (Perkins) have been reported from *N. lugens* in the Solomon Islands (Chiu, 1979) but appear to be relatively unimportant parasitoids of rice pests in Asia (Table 3). *Cheiloneurus exitiosus* (Perkins) has been recorded as a hyperparasitoid of *Gonatopus* sp., *Haplogonatopus* sp., *Pseudogonatopus hospes* (Perkins), *P. flavifemur* on *N. lugens* and *S. furcifera* (Guerrieri & Viggiani, 2005) whilst *Cheiloneurus* sp. has been recorded as a hyperparasitoid of dryinids on *N. lugens* in Vietnam (Lam, 1992, 1996, 2000, 2002).

Family: Eulophidae

Two genera of eulophids, *Ootetrastichus* and *Tetrastichus* have been reported from delphacid hosts in the Philippines, Vietnam, Malaysia and Thailand (Table 3). Overall, however, the limited published information suggests that this family is relatively unimportant in terms of biological control of delphacids in Asian rice systems.

Family: Pteromalidae

Only one pteromalid, *Panstenon* sp., has been reported from rice planthoppers from Sri Lanka (Fowler *et al.*, 1991) and Fujian Province, China (Lo & Zhou, 1980).

Family: Scelionidae

Scelionidae (Superfamily: Scelionoidea) is the only hymenopteran parasitoid family outside of the Superfamily Chalcidoidea to feature amongst the parasitoids reported attacking delphacid pests of rice in Asia. It appears to be a relatively unimportant family, represented by three genera from *N. lugens* in India (Table 3). These include a species of *Baeus*, a genus generally considered to be spider parasitoids but Manjunath *et al.* (1978) reports attack of *N. lugens*. The lack of verification by later workers may reflect a misidentification or simply a dearth of research in this region.

Family: Trichogrammatidae

This family of egg parasitoids has four genera that attack delphacid pests of rice: *Aphelinoidea*, *Oligosita*, *Paracentrobia* and *Trichogramma* (Table 3). Drumming the surface of the rice leaves and oviposition occurs in a similar manner to *Anagrus* spp. (Chandra, 1980). Unlike mymarids, however, Trichogrammatidae parasitoids cause the host egg to become dark grey in colour obscuring the view of the developing parasitoid. Dissecting the host eggs is not a good method of determining parasitisation because larvae and pupae of the wasp are very delicate and easily destroyed. Larvae within the eggs are difficult to observe as they are immobile. Adults emerge 11–12 days after oviposition; males tend to emerge first.

Parasitism rates reported for members of this family range from 5% and above for *Oligosita aesopi* (Girault) on *S. furcifera* to 68% in the case of *Oligosita naias* (Girault) in Malaysia (Watanabe *et al.*, 1992). *Oligosita aesopi* is a common parasitoid in Vietnam (Lam, 1992, 1996, 2000, 2002). *Oligosita naias* is considered an important egg parasitoid of delphacids in Chinese rice (Yu, 1996). In Sri Lanka, *Oligosita* spp. are more abundant than *Anagrus* spp. on *N. lugens*, with parasitism rates up to 32.7% (Fowler *et al.*, 1991). In India, Gupta and Pawar (1989) reported *Oligosita* sp./spp. along with *Anagrus* sp., to be the most common parasitoids of *N. lugens*. Greathead (1982) reported *Oligosita* sp./spp. from India, Korea, Malaysia, Philippines, Sri Lanka, Thailand and China on *N. lugens*, *S. furcifera*, *N. cincticeps*, *N. nigropictus* and *N. virescens*.

Like Mymaridae, trichogrammatids feed on sugars (Gurr & Nicol, 2000) and the nature of non-crop habitat close to rice where nectar may be available is considered important in population dynamics (Yu *et al.*, 1996). Non-crop habitat dominated by grasses close to paddy fields may also act as a reservoir of parasitoids of rice planthoppers (Yu, 1996). The limited number of studies available on Trichogrammatidae that attack delphacid pests of rice shows that this is a relatively poorly studied area.

Order: Strepsiptera

Although represented by few taxa (Table 4), parasitism rates (see below) suggest that this group of nymphal-adult parasitoids is important in control of delphacid pests in Asian rice production systems. They reproduce viviparously, individual females producing 1000–2000 triungulins. These are 0.15 mm long, light yellow, slightly curved, with well developed eyes, legs and caudal setae allowing them to crawl and jump. In the laboratory, most die within an hour. They enter hosts by piercing intersegmental membranes then shrink and transform into cylindrical legless larvae that develop over seven instars. Males pupate with their anterior end protruding from the host's abdomen whilst the female pupates within

Table 3 Encyrtidae, Eulophidae, Pteromalidae, Scelionidae and Trichogrammatidae parasitoids reported from Hemiptera pests of Asian rice

Parasitoid	Host	Location	References
Family: Encyrtidae			
Cheiloneurus sp.	*Nilaparvata lugens*	Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
Chrysopophagus australiae (Perkins)	*Nilaparvata lugens*	Solomon Islands	Chiu (1979)
Echthrogonatopus exitiosus (Perkins)	*Nilaparvata lugens*	Solomon Islands	Chiu (1979)
Family: Eulophidae			
Ootetrastichus nr. *formosanus* (Timberlake)	*Nilaparvata lugens*	Philippines	Barrion *et al*. (1981)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
Tetrastichus formosanus (Timberlake)	*Nilaparvata lugens*	Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
		Thailand	Wongsiri *et al*. (1980)
Family: Pteromalidae			
Panstenon sp	*Nilaparvata lugens*	Sri Lanka	Fowler *et al*. (1991)
	Planthoppers	China (Fujian)	Lo & Zhou (1980)
Family: Scelionidae			
Baeus sp.	*Nilaparvata lugens*	India	Manjunath *et al*. (1978)
Gryon sp.	*Nilaparvata lugens*	India	Manjunath *et al*. (1978)
Oxyscella sp.	*Nilaparvata lugens*	India	Manjunath *et al*. (1978)
Family: Trichogrammatidae			
Aphelinoidea sp.	*Nilaparvata lugens*	China (Taiwan)	Chiu (1979) (citing Fukuda 1934); Chu & Hirashima (1981)
Oligosita aesopi (Girault)	*Nilaparvata lugens*	China	Yu *et al*. (1996); Yu *et al*. (1998)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Sogatella furcifera	China	Yu *et al*. (1996)
		Malaysia	Watanabe *et al*. (1992)
		Vietnam	Lam (1992, 1996, 2000, 2001, 2002)
	Tagosodes pusanus	China	Yu (1996); Yu *et al*. (1998)
	Toya spp.,	China	Yu (1996); Yu *et al*. (1998)
Oligosita naias (Girault)	*Nilaparvata lugens*	China	Yu *et al*. (1996); Yu *et al*. (1998)
		India (Tamil Nadu)	CAB International (2005)
		Malaysia (Muda)	Watanabe *et al*. (1992)
	Sogatella furcifera	China	Yu *et al*. (1996)
		India	Randhawa *et al*. (2006)
	Tagosodes pusanus	China	Yu (1996); Yu *et al*. (1998)
	Toya spp.	China	Yu (1996); Yu *et al*. (1998)
Oligosita nephotetticum (Mani)	*Nephotettix cincticeps*	China	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nilaparvata lugens	China	Mao *et al*. (1999); NPPS & ZAU (1991)
		Indonesia	Claridge *et al*. (1999)
		China (Taiwan)	Chu & Hirashima (1981)
	Laodelphax striatellus	China	NPPS & ZAU (1991)
Oligosita shibuyae (Ishii)	*Nephotettix cincticeps*	China	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nilaparvata lugens	China (Guangdong)	Chu & Hirashima (1981); Mao *et al*. (1999)
		China (Taiwan)	Chu & Hirashima (1981); Mao *et al*. (1999)
	Sogatella furcifera	China	NPPS & ZAU (1991)
Oligosita tachikawai (Yashiro)	*Nilaparvata lugens*	India (Andhra Pradesh)	CAB International (2005)
Oligosita yasumatsui (Viggiani & Subba Rao)	*Nilaparvata lugens*	India (Andhra Pradesh)	CAB International (2005)
		Indonesia	Claridge *et al*. (1999)
		Malaysia (Peninsular)	van Vreden & Ahmadzabidi (1986)
		Thailand	Wongsiri *et al*. (1980)
	Sogatella furcifera	Thailand	Wongsiri *et al*. (1980)
Oligosita sp./spp.	*Nephotettix cincticeps*	India	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982)

Table 3 Continued

Parasitoid	Host	Location	References
		Philippines	Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Chu & Hirashima (1981); Greathead (1982)
		Thailand	Greathead (1982)
	Nephotettix nigropicta	India	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982)
		Philippines	Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982)
		Thailand	Greathead (1982)
	Nephotettix virescens	India	Greathead (1982)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982)
		Philippines	Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982)
		Thailand	Greathead (1982)
	Nilaparvata lugens	India	Greathead (1982); Gupta & Pawar (1989); Manjunath *et al*. (1978)
		Indonesia	Claridge *et al*. (1999)
		Korea	Greathead (1982)
		Malaysia	Greathead (1982); Ooi (1982); van Vreden & Ahmadzabidi (1986)
		Philippines	Barrion *et al*. (1981); Greathead (1982)
		Sri Lanka	Fowler *et al*. (1991); Greathead (1982)
		China (Taiwan)	Chiu (1979) citing Lin (1974); Chu & Hirashima (1981); Greathead (1982)
		Thailand	Chiu (1979) (citing Yasumatsu *et al*., 1975); Greathead (1982); Vungsilabutr (1981)
	Sogatella furcifera	India, Korea	Greathead (1982)
		Malaysia	Ooi (1982)
		Philippines	Greathead (1982)
		Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982)
		Thailand	Greathead (1982); Vungsilabutr (1981)
Paracentrobia andoi (Ishii)	*Nephotettix cincticeps*	China	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nephotettix nigropicta	China (Taiwan)	Chu & Hirashima (1981)
	Nephotettix virescens	China (Taiwan)	Chu & Hirashima (1981)
	Nilaparvata lugens	China (Guangdong)	Mao *et al*. (1999)
		Japan	Chiu (1979) (citing Suenaga 1963; Lin, 1974)
		China (Taiwan)	Chiu (1979) (citing Suenaga, 1963; Lin, 1974); Chu & Hirashima (1981); Miura *et al*. (1979)
	Planthoppers	China (Fujian)	Lo & Zhou (1980)
Paracentrobia garuda (Subba Rao)	*Nilaparvata lugens*	Malaysia (Peninsular	Van vreden & Ahmadzabidi (1986)
		Thailand	Chiu (1979) (citing Yasumatsu *et al*., 1975)
Paracentrobia yasumatsui (Subba Rao)	*Nilaparvata lugens*	Malaysia (Peninsular)	Van Vreden & Ahmadzabidi (1986)
		Thailand	Chiu (1979) (citing Yasumatsu *et al*. (1975); Wongsiri *et al*. (1980)
Stephanodes sp.	*Nilaparvata lugens*	Philippines	Barrion *et al*. (1981)
		China (Taiwan)	Barrion *et al*. (1981)

the host. Adult males emerge from the host and mate with adult females via the exposed cephalothorax.

Parasitised hosts have smaller genitalia and are identifiable by an extended abdomen and discoloured bodies as well as having the male parasitoid extruding from their abdomina or the female's cephalothorax visible. Host insects and female Strepsiptera adults die soon after triungulins have emerged whilst hosts vacated

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by males are vulnerable to disease via the exit hole (Chandra, 1980).

Moist conditions tend to favour strepsiptera with parasitism higher in rainy seasons (although mostly below 10%) and in wetland areas (Chandra, 1980). Strepsiptera parasitoids of hemipteran pests in rice are reported from Japan, India, Philippines, Thailand, Sarawak, Malaysia and Vietnam (Table 4). *Elenchus japonicus* (Esaki & Hashimoto) and *Elenchus yasumatsui* (Kifune & Hirashima) are reported attacking *N. lugens*, *L. striatellus* and *S. furcifera*. In Japan, *E. japonicus* parasitism rate of delphacids (predominantly *S. furcifera*) ranged up to 26.7% in August (Kitamura, 1987). A similar maximum parasitism rate, 25%, was reported from the Philippines (Peña & Shepard, 1986). In Sri Lanka parasitism by an unidentified species of *Elenchus* peaked at 40% (Ôtake *et al.*, 1976). In Thailand, *E. yasumatsui* is considered important in controlling *N. lugens* with parasitism rates up to 90% (Chiu, 1979). In contrast, only low rates of parasitism are reported from Vietnam (Lam & Thanh, 1989; Lam, 1992, 1996, 2000, 2002).

Order: Diptera

Represented by three genera in the family Pipunculidae (Table 5), these nymphal/adult parasitoids generally favour dryer conditions (Chandra, 1980) and this may partly explain why they are considered to be ineffective against *N. lugens* in Asian rice systems that are predominantly aquatic (Greathead, 1982). Low rates of parasitism are reported from Taiwan (Chiu, 1979) and from Vietnam (Lam 1992, 1996, 2000, 2002).

Table 4 Strepsiptera (Family: Elenchidae) parasitoids reported from Hemiptera pests of Asian rice

Parasitoid	Host	Location	References
Elenchus japonicus (Esaki & Hashimoto)	*Laodelphax striatellus*	China	NPPS & ZAU (1991)
		Japan (Shimane)	Kitamura (1987)
Alternative spelling: *E. japonica*	*Nilaparvata lugens*	China	Li (1982); NPPS & ZAU, (1991)
		India	Randhawa *et al.* (2006)
		Japan	CABI (2005); Chiu (1979) (citing Esaki 1932; Esaki & Hashimoto, 1932; Sakai, 1932; Okada, 1971; Kuno 1973)
		Japan (Shimane)	Kitamura (1987)
	Sogatella furcifera	China	NPPS & ZAU (1991)
		India	Randhawa *et al.* (2006)
		Japan (Shimane)	Kitamura (1987)
Elenchus yasumatsui (Kifune & Hirashima)	*Nilaparvata lugens*	Malaysia (Sarawak)	Hirashima & Kifune (1978)
		Philippines	Chandra (1980); Dayanan & Esteban (1996); Peña & Shepard (1986)
		Thailand	Chiu (1979) (citing FAO 1975; Kifune & Hirashima 1975; Ôtake, 1976; Yasumatsu *et al.*, 1975); Wongsiri *et al.* (1980)
	Sogatella furcifera	Malaysia (Sarawak)	Hirashima *et al.* (1979)
		Philippines	Chandra (1980); Peña & Shepard (1986)
		Thailand	Wongsiri *et al.* (1980)
Elenchus sp. spp.	*Nephotettix virescens*	India, Indonesia, Japan, Philippines, Sri Lanka, Thailand	Greathead (1982)
	Nilaparvata lugens	India	Greathead (1982); Shankar & Baskaran (1992)
		Indonesia, Japan	Greathead (1982)
		Malaysia	Ooi (1982)
		Philippines	Greathead (1982)
		Sri Lanka	Chiu (1979); Greathead (1982)
		Thailand	Greathead (1982)
		Vietnam	Lam (1992, 1996, 2000, 2002)
	Sogatella furcifera	India, Indonesia, Japan	Greathead (1982)
		Malaysia	Ooi (1982)
		Philippines	Greathead (1982)
		Sri Lanka	Greathead (1982); Ôtake *et al.* (1976)
		Thailand	Greathead (1982)
		Vietnam	Lam (1992, 1996, 2000, 2002)

Table 5 Diptera (Family: Pipunculidae) parasitoids reported from Hemiptera pests of Asian rice

Parasitoid	Host	Location	References
Dorylas sp.	*Nilaparvata lugens*	Sri Lanka	Chiu (1979)
Dorylomorpha lini Hardy	*Nephotettix cincticeps*		NPPS & ZAU (1991)
Pipunculus javanensis (de Meijere)	*Nephotettix cincticeps*	China (Guangxi)	Chu & Hirashima (1981); NPPS & ZAU (1991)
		China (Taiwan)	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nilaparvata lugens	China (Guangxi)	Chiu (1979); Chu & Hirashima (1981); NPPS & ZAU (1991)
		China (Taiwan)	Chiu (1979); Chu & Hirashima (1981); NPPS & ZAU (1991)
Pipunculus mutillatus (Loew)	*Nephotettix cincticeps*	China (Guangxi, Hunan, Sichun)	Chu & Hirashima (1981); NPPS & ZAU (1991)
		China (Taiwan)	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nephotettix nigropictus	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam (1992, 1996, 2000, 2002)
	Nephotettix virescens	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam 1992, 1996, 2000 (2002)
	Nilaparvata lugens	India	Randhawa *et al*. (2006)
Pipunculus orientalis (Koizumi)	*Nephotettix cincticeps*	China (Anhui)	NPPS & ZAU (1991)
		China (Taiwan)	NPPS & ZAU (1991)
Pipunculus roralis (Kerterz)	*Nephotettix cincticeps*	China (Guangxi)	NPPS & ZAU (1991)
		China (Taiwan)	NPPS & ZAU (1991)
Pipunculus javanensis (de Meijere)	*Nephotettix cincticeps*	China (Guangxi, Taiwan)	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nilaparvata lugens	China (Guangxi, Taiwan)	Chiu (1979); Chu & Hirashima (1981); NPPS & ZAU (1991)
Pipunculus mutillatus (Loew)	*Nephotettix cincticeps*	China (Guangxi, Hunan, Sichun, Taiwan)	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nephotettix nigropictus	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam (1992, 1996, 2000, 2002)
	Nephotettix virescens	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam (1992, 1996, 2000, 2002)
	Nilaparvata lugens	India	Randhawa *et al*. (2006)
Pipunculus orientalis (Koizumi)	*Nephotettix cincticeps*	China (Anhui, Taiwan)	NPPS & ZAU (1991)
Pipunculus roralis (Kerterz)	*Nephotettix cincticeps*	China (Guangxi, Taiwan)	NPPS & ZAU (1991)
Pipunculus sp.	*Nephotettix cincticeps*	Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982); Chu & Hirashima (1981)
	Nephotettix nigropictus	China (Taiwan)	Chu & Hirashima (1981)
	Nephotettix virescens	Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982); Chu & Hirashima, (1981)
	Nilaparvata lugens	Sri Lanka	Greathead (1982)
		China (Taiwan)	Greathead (1982)
Tomosvaryella epichalca (Perkins)	*Nephotettix cincticeps*		Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nilaparvata lugens		Chiu (1979); Chu & Hirashima (1981); NPPS & ZAU (1991)
Tomosvaryella inazumae (Koizumi)	*Recilia dorsalis* (Motschulsky)	China (Guangxi, Yunnan)	NPPS & ZAU (1991)
Tomosvaryella oryzaetora (Koizumi)	*Nephotettix cincticeps*	China	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nephotettix nigropictus	Thailand	Wongsiri *et al*. (1980)
	Nephotettix virescens	Thailand	Wongsiri *et al*. (1980)
	Nilaparvata lugens	India	Randhawa *et al*. (2006)
		China	Chiu (1979); Chu & Hirashima (1981)
Tomosvaryella subvirescens (Loew)	*Nephotettix cincticeps*	China (Fujian, Guangxi)	Chu & Hirashima (1981); NPPS & ZAU (1991)
		China (Taiwan)	Chu & Hirashima (1981); NPPS & ZAU (1991)
	Nephotettix nigropictus	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam (1992 1996, 2000, 2002)
	Nephotettix virescens	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam (1992, 1996, 2000, 2002)

Table 5 Continued

Parasitoid	Host	Location	References
	Nilaparvata lugens	China (Fujian, Guangxi)	Chu & Hirashima (1981); Chiu (1979); Yasumatsu *et al*. 1975); NPPS & ZAU (1991)
		China (Taiwan)	Chu & Hirashima (1981); Chiu (1979); Yasumatsu *et al*. 1975); NPPS & ZAU (1991)
		Thailand	Chu & Hirashima (1981); Chiu (1979); Yasumatsu *et al*. 1975)
		Vietnam	Lam (1992, 1996, 2000, 2002)
Tomosvaryella sylvatica (Meigen)	*Nilaparvata lugens*	China (Taiwan)	Chu & Hirashima (1981)
	Nephotettix cincticeps	China (Guangxi, Henan)	NPPS & ZAU (1991)
		China (Taiwan)	NPPS & ZAU (1991)
Tomosvaryella subvirescens (Loew)	*Nephotettix cincticeps*	China (Fujian, Guangxi, Taiwan)	Chu & Hirashima (1981) (NPPS & ZAU 1991)
	Nephotettix nigropictus	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam (1992 1996, 2000, 2002)
	Nephotettix virescens	Thailand	Wongsiri *et al*. (1980)
		Vietnam	Lam (1992, 1996, 2000, 2002)
	Nilaparvata lugens	China (Fujian, Guangxi, Taiwan)	Chu & Hirashima (1981); Chiu (1979); Yasumatsu *et al*. 1975); NPPS & ZAU (1991)
		Thailand	Chu & Hirashima (1981); Chiu (1979); Yasumatsu *et al*. 1975)
		Vietnam	Lam (1992, 1996, 2000, 2002)
Tomosvaryella sylvatica (Meigen)	*Nilaparvata lugens*	China (Taiwan)	Chu & Hirashima (1981)
	Nephotettix cincticeps	China (Guangxi, Henan, Taiwan)	NPPS & ZAU (1991)

Prospects for enhancing biological control by parasitoids

Ecological engineering to enhance natural enemy impact

The floral diversity of non-rice habitats around rice fields is considered to be important in biological control of rice pests (Lan *et al*., 2001), especially for planthopper parasitoids (Yu *et al*., 1998). Mechanistically, the availability of overwintering habitats is critical for egg parasitoids of planthopper species that do not overwinter locally. Unlike parasitoids of nymphs/adults, such as Dryinids, egg parasitoids are by definition not carried to new areas within the body of dispersing hosts. Accordingly in Japan, Korea and much of China where important delphacid pests such as *N. lugens* and *S. furcifera* do not overwinter, grassy refuge areas that support alternative host Hemiptera are critical in establishing biological control of rice pests in early season crops.

Non-crop vegetation can also favour biological control by providing plant foods, chiefly nectar, to natural enemies. Although there is a surprising lack of studies of the effects of nectar on parasitoids of rice pests there is a large literature on enhancement of Hymenoptera and Diptera natural enemies by food plants in other crop types (Landis *et al*., 2000; Gurr *et al*., 2004). Rice bunds have been largely overlooked as a means to provide plant foods to natural enemies. Whilst nectar could maximise longevity and fecundity of parasitoids, pollen could allow generalist predators to reside even during periods of prey scarcity (Wäckers, 2005).

Prospects for better biological control of planthoppers by ecological engineering approaches such as habitat manipulation appear particularly good in rice. An important reason for this is the heterogeneity, connectivity and generally small patch size of the habitat. Although rice crops may dominate landscapes in many rural Asian areas, several factors combine to make the sizes of individual crops small, with each bounded by a vegetated earthen bank ('bund'). First, rice is often grown in undulating, even steep, terrain and bunds are critical for controlling water and forming a series of flat, submerged terraces. Second, the area of land owned or controlled by individual families is small, often less than 1 ha. Bunds are important in delineating these and allowing foot traffic through otherwise inundated areas. Accordingly, rice landscapes are richly innervated by a network of bunds that offer scope to provide resources to natural enemies.

Although bund vegetation has been identified as a potentially important factor in rice pest management (Way & Heong, 1994), its potential is far from being fully realised (Gurr, 2009). A study of the effects of bund vegetation in the Philippines suggests that a reason for the relative lack of progress in this area is the possible risks (Marcos *et al*., 2001). Insect pests as well as natural enemies were more abundant and species richness was increased in rice paddies surrounded by bunds with vegetation than in paddies without this feature. This illustrates the importance of research to identify the types of vegetation that will preferentially favour natural enemies; essentially the same refinement as 'selective food plants' as found to be important in habitat manipulation to favour parasitoids over potato moth (*Phthorimaea operculella* (Zeller) in potato cropping (Baggen & Gurr, 1998; Baggen *et al.*, 1999) and over lightbrown apple moth (*Epiphyas postvittana* Walker) in vineyards (Begum *et al.*, 2004, 2006).

A broad indication that such selectivity might be possible for rice bunds comes from the results reported by Marcos *et al.* (2001). Natural enemies were most abundant in bunds with only broadleaf as opposed to grassy weeds. Furthermore, adding support to the need for careful selection of bund plant species, the grasses *Panicum repens*, *Cynodon dactylon*, *Dichanthium aristatum* and *Commelina diffusa* were found to be infected with sheath blight and the adjoining edges of rice paddies were sometimes also infected (Marcos *et al.*, 2001). That Philippine study also found that cowpea (*Vigna unguiculata* L.) crops were important reservoirs of natural enemies of rice pests. Parallel work in China found that soy bean (*Glycine max* L. Merr.) served the same function (Liu *et al.*, 2001). Ideally, growing rows of carefully selected plants on bunds could have the dual benefit of supporting natural enemies and excluding the grasses that potentially favour insect pests and plant diseases such as tungro (Bottenberg *et al.*, 1990) The need to allow human foot traffic on bunds does not seem to have been an impediment to the growth of other crop species including sesame (*Sesamum indicum* (L.)) and soybean on bunds in recent work (International Rice Research Institute, 2010b). Such crops can also be established in wider strips beside rice crops whenever they are bounded by larger banks such as beside river banks or roadways, an approach being used in Thai sites in the IRRI-led study.

Spatial manipulation of natural enemies with herbivore-induced plant volatiles

Recent advances in chemical ecology suggest scope for another way to enhance the impact of parasitoids and other natural enemy guilds in rice. It is well established that plants under attack by arthropod herbivores produce volatile chemicals that attract natural enemies (Bruce & Pickett, 2007). A range of such herbivore-induced plant volatiles (HIPVs) has been identified, synthesised and used in slow-release dispensers or as sprays. Under field conditions HIPVs such as methyl-salicylate, *cis*-3-hexen-1-ol, (Z)-3-hexenyl acetate and benzaldehyde have resulted in elevated catches of natural enemies (James, 2005). It also appears that the application to plants of a single HIPV not only acts directly in attracting natural enemies but can also induce the production of a natural blend of HIPVs (Lou *et al.*, 2005b). Such findings suggest that applying synthetic HIPVs to crops can – both directly and indirectly – attract the predators and parasitoids that could protect crops from pest damage. Recent field studies in sweetcorn, broccoli and grapevines have shown that this approach can elevate catches of a suite of hymenopteran parasitoid taxa in proximity to treated plants (Simpson *et al.*, 2010).

Prospects for such an approach to work in rice appear strong (Gurr, 2009). Work on the role of ethylene signalling in rice showed that this hormone is involved in induced defences against arthropod herbivores (Lu *et al.*, 2006). Rice attacked by *N. lugens* produced ethylene 2–24 h after infestation along with HIPVs. Thereafter, *A. nilaparvatae* was attracted to emitting plants. In other work, Lou *et al.* (2005b) showed that exogenous applications of jasmonic acid to rice plants dramatically elevated levels of several volatiles including aliphatic aldehydes, alcohols, monoterpenes, sesquiterpenes, methyl-salicylate and *n*-heptadecane. 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.

Although much remains to be resolved before HIPVs can be used commercially to enhance biological control (Gurr & Kvedaras, 2010) there is scope to develop an ecological engineering approach based on applying selected HIPV elicitors to rice to promote their sink status for natural enemy populations. This would be especially powerful if coupled with the provision of nearby vegetation that served as overwintering source vegetation for planthopper parasitoids. Indeed the whole viability of this method depends on the presence of sufficient source vegetation. Geospatial methods are increasingly being used to shed light on the types and placement of these habitat patches (Perović *et al.*, 2010) and these will be important in planning land use in response to climate change. HIPVs could be used to draw natural enemies into the crop when light trapping showed immigration of planthoppers and when egg laying by the pests was imminent. An additional layer in this strategy could be the presence of nectar sources on bunds in an 'attract and reward' strategy as proposed by Khan *et al.* (2008). The 'reward' component of this approach aims to maximise the fitness and performance of attracted natural enemies by providing appropriate sources of nectar, pollen and shelter.

Impacts of genetically modified rice on planthopper biological control

Higher rice yields are projected in China under a scenario where widespread use of genetically modified rice occurs (US Department of Agriculture, 2010). *Bt* rice is likely to reduce problems with lepidopteran pests, such as the leaffolder, and reduce the need for insecticide applications. This has direct bearing on prospects for improving biological control of planthopper pests. The current high levels of usage of insecticide applications targeting Lepidoptera are largely responsible for disrupting biological control as is the case in other crop systems such as apples (Valentine *et al.*, 1996). This disruption of 'top down' control of the pest population allows build-up of rice planthoppers (Heong & Schoenly, 1998; Catindig *et al.*, 2009). Reflecting this, a Chinese study found parasitoid communities were more stable in IPM areas compared to non-IPM areas where insecticide use was greater (Mao *et al.*, 2002a). But the extent to which the advent of genetically modified crop varieties might reduce insecticide inputs and allow natural enemy communities to maintain better biological control of pests depends on a range of ecological and operational issues (Gurr *et al.*, 2004).

At present there is very limited literature on the influence of genetically modified *Bt* rice on parasitoids. Chen *et al.* (2003) studied the effect of *Bt* transgenic rice on the dispersal of planthoppers, leafhoppers and their egg parasitoids. They reported that *Anagrus* spp. tended to disperse towards non-transgenic rice although reasons for this are unclear and little weight can be put on this finding for the study was not replicated. The consequences for pest management of any dilution of natural enemy activity would be particularly negative for planthopper problems because these will not be controlled by *Bt* toxins.

Accordingly, the limited literature on the *direct* effects of *Bt* rice on natural enemies and consequences for planthoppers is inconclusive but there is good reason to suspect that reductions in insecticide use will lead to beneficial *indirect* effects. Planthoppers were only a minor pest group before the 1960s (SBPH became major pest around mid-1960s in Japan and China, BPH became major pest in Asia in late-1960s) when broad-spectrum insecticides, combined with hybrid rice varieties, resulted in them becoming a major pest since 1980s (Sogawa *et al.*, 2003; Cheng *et al.*, 2008). Although it is likely that *Bt* rice will still require some insecticide applications, Wang *et al.* (2010) conducted a 2-year field study that compared *Bt* rice with non-*Bt* rice that was protected with insecticides when necessary as well as with unsprayed *Bt* and non-*Bt* rice. Larval densities of the Lepidoptera pests, *Chilo suppressalis* (Walker), *Tryporyza incertulas* (Walker) and *Cnaphalocrocis edinalis* (Guenee) were 87.5–100% lower in unsprayed *Bt* plots *than* in unsprayed non-*Bt* plots. Overall, insecticide use was reduced by 60 and 50% in protected *Bt* versus protected non-*Bt* plots in the 2 years of the study. But *Bt* plants still required some insecticide protection because its yield was 28–36% lower than that of protected *Bt* rice.

A reduction in insecticide inputs of around 50%, whether achieved by the introduction of *Bt* rice or other approaches such as tighter regulation of pesticide promotion and use, is likely to have significant benefits for natural enemy activity on planthoppers.

In the work by Chen *et al.* (2007), no consistent benefit of *Bt* rice was apparent on planthopper populations but the comparison was with non-*Bt* rice treatment plots that were not sprayed with insecticide without a comparison with normal crop management of rice involving multiple applications of insecticides as in the study by Wang *et al.* (2010). Products in widespread use for the control of rice stem borers and leaffolder in Asia are broad-spectrum chemicals known to be harmful to natural enemies (Tanaka *et al.*, 2000).

A further factor that may benefit planthopper biological control if *Bt* rice is widely grown in China (or should Lepidoptera specific insecticides become available and economically viable), is the need for a resistance management strategy (RMS). That for a *Bt* crop would involve refuge areas (High *et al.*, 2004) that maintain sufficient numbers of wild-type susceptible Lepidoptera adults in the population, individuals that have not been exposed to the selection pressure. This reduces the likelihood that the resistant mutants developing on the *Bt* rice will mate with each other and produce resistant progeny. Because refuges need to produce pest adults they will not be sprayed and this is likely to also make them sources for natural enemies that might contribute to better planthopper control.

Conclusion

Notwithstanding the consequences for biological control of planthoppers of the possible widespread growth of *Bt* rice in China, most countries will continue to grow conventional rice for the forseeable future. Prospects for better biological control of planthoppers in these areas appear good given the available information although reducing the currently high level of insecticide use is important. The perceived need on the part of farmers (often with low levels of education, training and literacy) to protect the yield rice is one of several factors that have led to high levels of synthetic insecticides being used. This effect extends beyond protection of grain yield to spraying in response to early season foliar damage that has no effect on grain yield but can make farmers lose ‘face’. This is driven by strong marketing and advertising to exploit farmers’ fears. Further, the high level of government subsidies, especially during pest outbreaks, reinforces the notion that spraying is beneficial and endorsed by the authorities. The present review of the available literature indicates that, despite the disruptive effects of insecticide use, parasitoids can cause high levels of parasitism in delphacid populations and that their impact can be manipulated ecologically. Mymarids in particular, are strongly influenced by non-rice vegetation. Adjacent habitat patches can support host insects and allow the persistence of planthopper parasitoids during the winter. This is an important factor because much rice production is in non-tropical parts of Asia. Here rice is absent during the cooler months and an absence of overwintering habitat would lead to local extinction of specialist natural enemies. Providing overwintering habitat would allow local persistence of a natural enemy community that facilitates a rapid response to immigrating pests. This is particularly important for *r*-selected pests such as *N. lugens* that otherwise are able to flee to enemy free space and rapidly multiply to damaging densities. With greater pressure on available land area for agricultural production and urbanisation there will be pressure to make the best possible use of those habitats that can be retained by applying optimal management and establishing the most appropriate plant species for natural enemy overwintering. Accordingly research effort is required to systematically investigate the relative merits for natural enemies of various non-rice crop species as well as the non-crop species used for grazing, erosion control or aesthetics. A ‘pull’ strategy based on synthetic HIPVs might be developed to attract natural enemies into rice crops from other habitats early in the season and prevent immigrating planthoppers from reproducing. Rice bunds have long been overlooked as a networked structure that could support carefully selected plant species that provide plant foods to natural enemies. Whilst nectar could maximise longevity and fecundity of parasitoids, pollen could allow generalist predators to reside even during periods of prey scarcity. If ecological engineering approaches could be expanded beyond delphacid pests, particularly for lepidopterans, a holistic, biologically based pest management strategy could emerge that would avoid the need for exogenous toxins (whether sprayed or the produce of transgenes) and the plea of Settele *et al*. (2008) be answered.

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