

The role of biodiversity in the dynamics and management of insect pests of tropical irrigated rice—a review

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Abstract

Biodiversity relevant to pest management of tropical irrigated rice pests is discussed in terms of variation within rice plants, rice fields, groups of rice fields and rice associated ecosystems. It is concluded that, in the unique cropping conditions and stable water supply of tropical irrigated rice, the manipulation of a relatively few manageable components of diversity can confer stability such that pests are mostly kept at levels which do not justify the use of insecticides. Durable rice plant resistance, including moderate resistance, together with ability to compensate for damage by certain key pests, are regarded as fundamental to successful biological control by the natural enemy complex. Reliable natural enemy action is also considered to depend on all-year-round continuity of prey or hosts made possible by the relatively short fallow periods between staggered two to three rice crops per year and by proximity of certain non-rice habitats, notably the vegetation-covered bunds (levées) surrounding each field. In contrast, synchronous cropping could upset stability by destroying the continuity needed for natural enemy success. Such conclusions are supported by the experience of farmers who use little or no insecticide. Much evidence on destruction of natural enemies by certain insecticides supports the contention that insecticide use, especially early in the crop season, upsets natural enemy control of insects such as *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) and also creates heavy selection pressure for strains of pests that can overcome previously resistant rice cultivars. Such circumstances create outbreaks of secondary pests and impair biological control of some key primary pests such as stem borers. It is concluded that pest management of much tropical irrigated rice must be based on natural controls rarely supplemented by insecticides. The success of this approach depends in particular on further research on dynamics of natural enemy and pest communities in rice ecosystems, especially where climatic conditions and water supply are marginally stable. Much more needs to be known about the nature and utilization of rice plant compensation for damage, particularly by defoliators and stem borers. The justification for, and supplementary use of, insecticides needs to be radically reassessed. There is no evidence that a natural control-based approach, as recommended in this review, is incompatible with farmer practicability or with future developments in rice production

technology, except perhaps the possible mechanization-driven increase in field size which would decrease bund area. In contrast, the insecticide-based approach is not only harmful to natural controls but is costly and mostly demands impracticable decision making by farmers on need-based use.

Introduction

Rice, as the single most important human energy source, feeds about half of the world's population (IRRI, 1989), so it was vital that predicted 1980's Asian famines (e.g. Ehrlich, 1968) were averted by the development of Green Revolution high yielding rices and technology between 1965 and 1975. Great advances were made in irrigated rice which provided over 72% of total yield and will remain outstandingly important (IRRI, 1989); with ecologically comparable rainfed lowland rice, it produces more than 92% of the world's crop, of which over 91% is grown in Asia.

Unfortunately, pest problems increased with the intensification of irrigated rice production, which included increased investments such as insecticides. In particular, insecticide use preceded outbreaks of secondary pests, notably the brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae), that was previously of minor significance (Kenmore, 1991; fig. 1). The intensification of insecticide use against increasingly large secondary pest outbreaks posed other problems, notably induced pest resistance, such that some large rice production schemes, as in the Solomon Islands, were abandoned (Rombach & Gallagher, 1994). Moreover, insecticide poisoning of farm workers became a serious issue (Teng & Heong, 1988) and chemicals used against rice pests induced insecticide resistance in human disease vectors that breed in flooded fields (Way, 1987).

In the first post-Green Revolution period lasting into the 1980s, rice cultivars resistant to some pests were quickly developed. Intense selection pressure on insecticide-created pest populations attacking particular rice cultivars planted over large areas (Kenmore, 1991) also invoked resistance-breaking virulent pest populations, particularly of the most

notorious secondary pest, *N. lugens*. New resistant rice cultivars were introduced to counter different *N. lugens* biotypes (Pathak & Saxena, 1980; Saxena & Khan, 1989) but they often failed after several pest generations (e.g. Pathak & Heinrichs, 1982). Such evidence therefore points to the need for a different pest management strategy from one dependent solely on insecticides and host plant resistance to counter insect pests of irrigated rice.

In the current second post-Green Revolution period it is recognized that the emphasis should be placed on sustainability and efficiency (IRRI, 1989; Bottrell *et al.*, in press) rather than on further intensification of expensive inputs, especially insecticides. In pest management the challenge is to make natural non-chemical controls collectively more effective, so largely dispensing with the need for costly insecticides that, besides exacerbating some pest problems, can also be environmentally damaging and may involve virtually unresolvable dilemmas for farmers' need-based use of insecticides (Goodell, 1984). Therefore this review critically analyses literature relevant to the roles and practical application of host-plant resistance, biological controls and cultural controls against insect pests of tropical irrigated rice. In conception, the use of such controls involves appropriate understanding of animal and plant species diversity at different levels of environmental complexity, as discussed in the next section. In practice, the objective of the review is to point to opportunities for the farmer to optimize the use of the diverse natural controls as an alternative to dependence on pesticides.

Biodiversity and pest incidence

The term biodiversity is used here to describe the richness and variety of living organisms. It covers variation within each species as well as the numbers and relative abundances of the different species in space and time in a defined system, such as a rice field. There is still uncritical acceptance that decreased biodiversity, as in monoculture crops such as rice, increases instability and therefore 'invites' pest attack (Ehrlich & Ehrlich, 1970), so increasing pest outbreaks (Elton, 1958; Pimentel, 1961). Yet this is countered by evidence that increased diversity in some agricultural systems may increase rather than decrease pest problems (Southwood & Way, 1970), that simple communities may not be inherently unstable (Pimm, 1984; Way, 1966) and in theory are more stable (May, 1971). Therefore environmental manipulation against pests should not, as often implied (e.g. Cohen *et al.*, in press), require the impossible prerequisite of quantitative, predictive understanding of complex links in a food web that, even in simple tropical irrigated rice fields, can comprise at least 680 animal and plant species (Schoenly *et al.*, in press). We therefore examine the evidence that relatively few manageable components of natural diversity are the key to insect pest management in irrigated rice in the tropics.

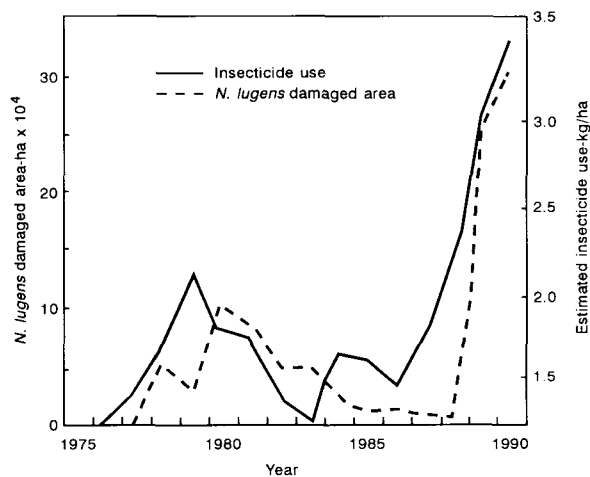


Fig. 1. Relationship between increase in insecticide use and area of *Nilaparvata lugens* infestation of irrigated rice in Thailand (adapted from Kenmore, 1991).

Relevant components of rice ecosystem biodiversity

Table 1 shows components of biodiversity relevant to rice pest management. Four levels are highlighted: first, within-species of plants and animals, in particular the diversity of the rice plant's resistance and tolerance to pests. Important aspects of within-species diversity of a pest include variation in ability to overcome host-plant resistance or to resist an insecticide. Within-species diversity in a natural enemy may similarly include variations in resistance to pesticides as well as other quality differences. The second level of diversity, that of the community, is defined as in a rice crop in a particular field; spatial diversity of rice plants within a particular field will depend on the nature of unplanned or planned purity of cultivars in the field; other animal and weed species in the community will also vary in diversity in space and time throughout the duration of the crop. The third level, defined here as compound community diversity, is that which occurs in groups of fields, where within-species and within-field diversity of rice is further complicated in space and time by field-to-field variation, especially of rice cultivars, their dates of planting, and different cultivation practices.

The determination of distribution and abundance of organisms important in the dynamics of the community of a rice crop, and hence in pest management, may depend for some, or all, of the time, on area-wide interactions involving associated non-rice crops and wild habitats, including the bunds (levées) that surround each rice field. In the rice pest management context the limits of this ecosystem may, however, be difficult to define. As an extreme example, *N. lugens* numbers in the tropics may be regulated within a relatively small ecosystem (Cook & Perfect, 1985, 1989b; Perfect & Cook, 1987, 1994). Yet, in temperate Japanese ecosystems, its dynamics depend on annual migrations of more than 700 km from sub-tropical ecosystems on the Asian mainland (Kisimoto, 1979).

Within-rice plant diversity and its pest management attributes

Natural selection, and human selection for over seven thousand years have created more than one hundred thousand *Oryza sativa* cultivars (Heinrichs, 1994; Vaughan & Sitch, 1991). Such intraspecific diversity is supplemented by that of about twenty other wild *Oryza* species, the value of which is evident from some insect resistant traits occurring about fifty times more frequently in wild germplasm than in cultivated rices (Chang, 1985). Indeed, the genus *Oryza* is unique in terms of its tremendous genetic resources for host-plant resistance and for other within-plant qualities of diversity relevant to pest management (Toenniessen & Herdt, 1989; Vaughan & Sitch, 1991).

Diversity in host-plant resistance

Here we confine the use of the term resistance to plant mechanisms which deter and/or inhibit development and survival of the pest on the plant. We distinguish this from plant mechanisms of tolerance/compensation which do not inhibit the pests' colonization or multiplication yet enable the tolerant cultivar to yield better than a similarly attacked non-tolerant cultivar.

The dramatic *N. lugens* outbreaks associated with the Green Revolution triggered much work on development of resistant rice cultivars. Seven genes were shown to confer moderate to high monogenic resistance to four specified *N. lugens* biotypes. Resistant cultivars planted over large areas created intense selection pressure for virulent resistance-breaking *N. lugens* biotypes in many regions, not only of *N. lugens* but also of the green leafhopper *Nephotettix virescens* (Distant) (Hemiptera: Cicadellidae) (up to eight genes for host-plant resistance) and of the gall midge *Orseolia oryzae* (Wood-Mason) (Diptera: Cecidomyiidae) (several genes) (Heinrichs & Pathak, 1981). Much genetical research has been undertaken aimed at understanding

Table 1. Components of diversity relevant to insect pest management in tropical irrigated rice.

Trophic levels	
1)	<i>Within species</i>
	1st-rice plant
	2nd-pest herbivore
	3rd-natural enemy
	duration of growth period, resistance to pests, tolerance to pest damage, attractiveness to natural enemies.
	life cycle, behaviour, resistance to insecticides, responses to rice host plant resistance.
	life cycle, behaviour, resistance to pesticides, response to host/prey, response to rice plant.
2)	<i>Within a rice field (community diversity)</i>
	1st-rice crop
	2nd-herbivore
	purity of cultivar.
	species composition, variation in time
3)	<i>Within groups of rice fields (compound community diversity)</i>
	rice crops
	as (2) above, plus between field cultivar diversity, dates of planting, following regimes, water supply, fertilization, soil conditions.
4)	<i>Within appropriate groupings of rice and non-rice habitats (ecosystem diversity)</i>
	As (2) and (3) above plus bunds
	size, species composition of vegetation, growth of vegetation.
	non-rice crop
	mostly as (3) above
	Wild habitats/waste areas
	size, species composition of vegetation

planthopper virulence. Present evidence does not support the original concept of a simple gene-for-gene relationship whereby each gene conferring resistance in rice is matched by a corresponding gene conferring virulence in *Nilaparvata lugens* (Claridge & den Hollander, 1983; Gallagher *et al.*, 1994). Indeed the genetic diversity in a single *N. lugens* biotype implies polygenic inheritance of virulence and a potential for seemingly unlimited ability of its populations to overcome resistant genes in rice cultivars (Claridge *et al.*, 1982; Claridge, 1991). It can only be concluded that, under intense selection pressure, field populations of *N. lugens* and other hoppers such as *Nephotettix virescens* possess the potential to adapt, as in the past, to new resistant cultivars. There are also problems of marked differences in a particular resistant gene's effectiveness in different cultivars (Gallagher *et al.*, 1994; Heong & Sogawa, in press).

Moderate, apparently polygenic, resistance to several stem borers has been established in a few high-yielding IRRIs (International Rice Research Institute) cultivars (Chaudhary *et al.*, 1984; Heinrichs, 1988, 1994) and there are some very resistant wild rice species (Chaudhary *et al.*, 1984). A large diameter lumen favours some stem borers (Chaudhary *et al.*, 1984) and this as well as much-favoured oviposition (IRRI, 1988) may explain replacement of *Chilo polychrysus* (Meyrick) by *Scirpophaga incertulas* (Walker) (both Lepidoptera: Pyralidae) when traditional rices were replaced by high yielding varieties in Malaysia (fig. 2). In summary, the present situation in available rice cultivars is one of unstable relatively high-level single gene resistance to *Nilaparvata lugens*, *Nephotettix virescens* and other hopper species, and to *O. oryzae* (Heinrichs, 1988, 1994; Hare, 1994). Some cultivars have moderate but seemingly polygenic resistance to stem borers, but there has been relatively little success against leaf feeders. So-called moderate, potentially stable, resistance to stem borers which has been characterized mainly by damage but not yield criteria (Heinrichs *et al.*, 1985; Rapusas & Heinrichs, 1987) seems to have been under-valued, as discussed later.

Embryo rescue techniques offer exciting opportunities for use of diverse alien genes for resistance, including those from other *Oryza* spp. (Jena & Khush, 1984) and even from

different phyla (Goodman *et al.*, 1987). In this context the Rockefeller Foundation's Rice Biotechnology Program lists resistance to insects or insect transmitted diseases (tungro virus, *S. incertulas*, *O. oryzae* and *Nilaparvata lugens*) in its top six priorities (Toenniessen & Herdt, 1989), but there are potential pitfalls. For example, under selection pressure in the field, alien single genes are as likely as native genes to be countered by virulent strains of pests such as *N. lugens* (Gould, 1988). Current efforts to incorporate genes for Bt endotoxin into the rice plant are similarly jeopardized by evidence that up to $\times 800$ resistance can be induced, even to mixtures of different Bt strains (Bennett, in press). In the absence of selection pressure, the main target stem borer pest, *S. incertulas*, already occurs in the Philippines as populations with at least $\times 50$ variation in susceptibility to a Bt strain (D.G. Bottrell, pers. comm.), nor can it be assumed that other potential transgenic resistance mechanisms involving trypsin inhibitors, chitinase genes and lectins will prove durable. Such deficiencies must not be glossed over by the glamour of a subject which faces similar limitations to those faced by over-dependence on the conventional resistance approach. However, unlike conventional techniques, genetic engineering could ultimately make it possible to pyramid a diversity of resistance genes of notably different characteristics into the same rice cultivar (Gould, 1988) which should confer more stable resistance. Another suggestion for lessening selection pressure for virulence of Bt is to develop methods for expressing it only in particular at-risk plant tissues or growth stages (Bottrell *et al.*, 1992).

There is a more fundamental question mark against the basis of much present day thinking on host-plant resistance which seems to be derived from outdated evidence of pest dynamics in general and *N. lugens* dynamics in particular. In the past, virulent populations of *N. lugens*, *N. virescens* and *O. oryzae* developed from insecticide-created outbreak populations (Kenmore, 1991; Gallagher *et al.*, 1994; Rombach & Gallagher, 1994). It is recognized that such conditions created intense selection pressure for virulence against each new widely established rice cultivar. Increased population size also increases the potential number of mutations for virulence whereas associated population interchanges favour virulence-increasing recombinations. Nowadays, although particular cultivars continue to predominate, the lessening of inappropriate insecticide use in many tropical areas has led to *N. lugens* reversion (e.g. fig. 6) (Gallagher *et al.*, 1994) towards its pre-insecticide-era status when it was a relatively insignificant pest on traditional rice cultivars despite their susceptibility to it (Dyck & Thomas, 1979). The exceptions are mainly in central Thailand and the Mekong delta in Vietnam where broad spectrum insecticides are still being intensively used against outbreaks on cultivars that were initially designated as resistant (Chau, 1990). Elsewhere, with much decreased insecticide use, the pest potential of *N. lugens* is not being realized. In such circumstances of insignificant selection pressure for virulence, low density endemic populations will have been selected for different fitness qualities. If so, then perhaps some originally selected resistance mechanisms will continue to suffice on occasions when there would otherwise be temporary escape from biological controls, as discussed later. This should be investigated because it could mean that current research on novel *N. lugens* resistance mechanisms is being over-emphasized.

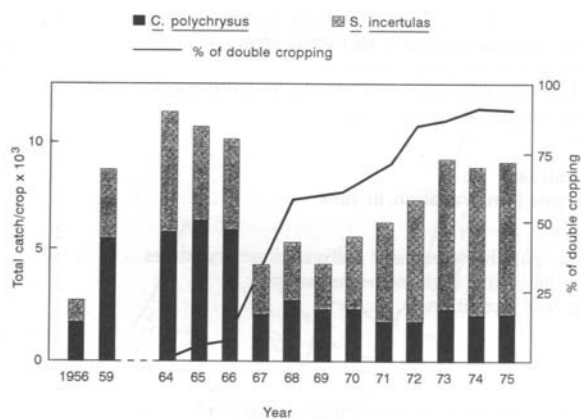


Fig. 2. Light trap catches of adult stem borers per crop in relation to the change from single to double rice cropping in North Krian, Malaysia (adapted from Lim & Heong, 1977).

Host-plant tolerance

As already defined, tolerance includes plant compensation for damage. Here we highlight compensation by first examining the history of insect damage in relation to crop loss of irrigated rice.

Rice yields in IRRI trials between 1964 and 1979 were about 40% less in insecticide unprotected crops (Pathak & Dhaliwal, 1981). This contrasts strikingly with the present day situation where there appears to be little or no crop loss in insecticide-untreated fields (Kenmore, 1991; Litsinger, 1991; den Braber & Meenankanit, 1992; Escalada *et al.*, 1992). Much of the present day situation was attributable to cultivars resistant to *N. lugens* in particular, but, recently at IRRI and elsewhere in the tropics, fields of susceptible cultivars have not been suffering greater crop loss if not insecticide treated (den Braber & Meenankanit, 1992; Kenmore, 1991). Unlike hoppers, defoliator species and stem borers were recorded as sometimes causing serious losses in the pre-Green Revolution era, and many advisors and farmers still perceive that foliar damage leads to yield losses that justify use of insecticides (Heong *et al.*, in press a, in press b). Stem borers provide the best example of changing and confused viewpoints on crop loss. Estimates implied that, from about the mid 1950s to the late 1960s, they were the most serious tropical rice insect pests, apparently causing crop losses of up to 70% in Bangladesh, 95% in India, 95% in Indonesia and 33% in Malaysia (Teng *et al.*, 1990). It was concluded from IRRI data (Israel & Abraham, 1967) that 1.6% and 2.2% yield losses were incurred from every 1% increase in deadhearts and whiteheads respectively, and recommended insecticidal action thresholds have ranged from 3% to 10% deadhearts (Smith *et al.*, 1989). However, such thresholds have not been adopted by farmers, who, according to surveys such as in the Philippines (Escalada *et al.*, 1992) and Vietnam (Vo Mai *et al.*, 1993), still apply insecticides on a calendar basis without reference to damage. A key question, however, is the validity of past and present day estimates of crop losses caused by stem borers in different circumstances. Moderate resistance, now incorporated in several high yielding varieties (Heinrichs, 1988, 1994) seems to be an important component of control against stem borers, notably against the most important species, *S. incertulas*. However, such resistance cannot explain the enormous discrepancy between the reported halving of yields at IRRI up to the 1960s (Pathak & Dyck, 1973), and some more recent estimates of no, or insignificant, yield losses (Teng, 1990), and also benefit-cost ratios in the Philippines which were best for insecticide untreated controls (Bandong & Litsinger, 1988), such data covering the insect pest complex, including stem borers. No doubt, earlier yield losses were exaggerated by assumptions based on damage rather than yield criteria (Rapusas & Heinrichs, 1987) as well as by worst-case reports, but the discrepancy seems also to be linked to two causes, fewer stem borers (fig. 3) associated with enhanced natural enemy action in the nowadays more insecticide-limited environment, and the ability of some modern cultivars to compensate for damage, particularly at the deadheart but also at the whitehead stage. Modern rices, unlike most traditional cultivars, produce many tillers of which some remain undeveloped. The ability of otherwise unproductive tillers to compensate for destroyed ones, and for surviving panicles to yield more was recognized in the 1950s (Rao *et al.*, 1987) and was

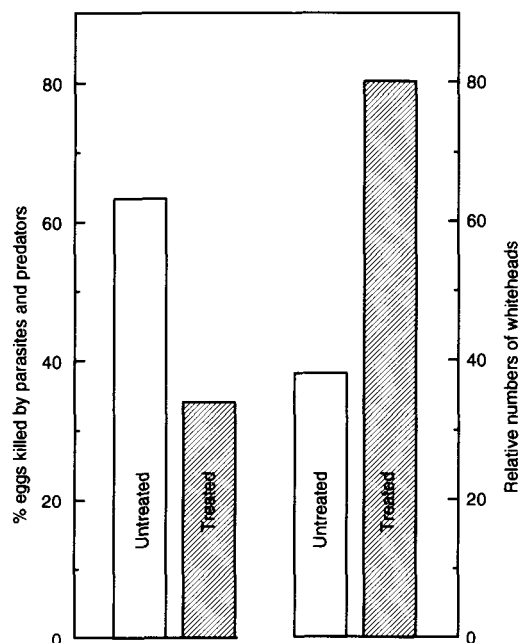


Fig. 3. Effect of recommended carbofuran treatment against *Scirpophaga innotata* on its egg mortality and on numbers of whiteheads caused by the larvae (adapted from Triwidodo *et al.*, 1994).

thought to be an important cause of lessened crop loss by the striped stem borer, *Chilo suppressalis* (Walker), in Japan (Kiritani, 1979). Rubia *et al.* (1989) concluded that up to about 30% loss of young tillers (deadhearts) caused by *S. incertulas* incurred no yield loss of one high yielding variety; furthermore, up to 10% of dead panicles (whiteheads) (about 1-2 per hill) was also compensated for, although such damage is still perceived by most rice farmers as far above that which they will tolerate. For example in Indonesia white stem borer, *S. innotata* (Walker), damage is visually greater on the cultivar IR64 than on Cisadane. However, loss per whitehead in IR64 was 1.3 times less than that of Cisadane because IR64 is more tolerant (IRRI, 1993a). Comparatively little plant tissue may be lost through deadheart or even whitehead damage, because most of the foliage of the damaged tiller remains alive and is a donor of photosynthates (Rubia, 1994). If rice is like wheat (Thorne & Wood, 1987), undamaged non-bearing tillers can also provide assimilates for panicle bearing tillers on the same plant.

It is becoming increasingly evident that the compensatory ability of some widely grown high yielding rice cultivars is also important against other rice pests. Some cultivars can compensate for >40% deadhearts caused by the stalk-eyed fly *Diopsis longicornis* Macquart (Diptera: Diopsidae) in Africa (Joshi *et al.*, 1992). There is similar compensation for destruction of tillers by gall midges, *Orseolia* spp., still regarded as very serious pests in some Asian and African countries (Katanyukul *et al.*, 1992; Rao, 1989). Besides compensation for pests that kill tillers, yield can be unaffected by much leaf folder damage (Bhudhasamai *et al.*, 1992; Graf *et al.*, 1992; Heong, 1990; Hu *et al.*, 1993), by leaf whorl maggot, *Hydrellia philippina* Ferino (Diptera: Ephydriidae), damage (Litsinger, 1991; Vijante & Heinrichs, 1986) and by a thrips which was shown to scarify foliage

on > 80% of young rice plants without affecting yield (Binh *et al.*, 1993). Such compensation for foliar damage to young plants is not unique to rice but is well known for some other arable crops in both temperate and tropical conditions (Jones *et al.*, 1955; Bardner & Fletcher, 1974; Russell *et al.*, 1993).

The above evidence opens up extraordinary opportunities for breeding to enhance compensatory ability against defoliation and tiller destruction by a very important group of stem boring and defoliating pests against which breeding for resistance has been relatively unsuccessful. It was fortunate that the dwarfing genes which created modern high yielding rices are linked to tillering qualities, but, present emphasis on an irrigated rice ideotype with few tillers and a few large panicles (IRRI, 1989) could be a regression to susceptibility characteristics of low tillering traditional varieties. Such developments, that seem likely to impair tolerance to stem borers, should be assessed at an early stage.

As discussed later, another important justification for choice of compensatory qualities is that the tolerance to greater numbers of pests must favour natural enemy retention and multiplication. Furthermore, in striking contrast to resistance, compensatory tolerance cannot be envisaged as creating selection pressure for pest virulence, so it is durable. This no doubt applies to the decision to forego easily-overcome host-plant resistance to a major South American planthopper pest, *Tagosodes orizicolus* (Muir) (Hemiptera: Delphacidae), in favour of breeding for tolerance (Weber & Parada, 1994).

Effects of cropping conditions on resistance and compensation

Weed competition and adverse abiotic factors, especially inadequate water, can decrease host-plant resistance (Litsinger, 1993) and also diminish ability to compensate. Conversely, growing conditions can be manipulated to enhance both resistance and compensatory ability, such as additional nitrogen fertilizer to boost growth following stem borer or defoliator damage (Peng, 1993), as had been independently recognized by some farmers (S. Masajo, pers. comm.). A recent major survey of farms in the main irrigated rice bowl of the Philippines has indicated that high yields are strongly correlated with good overall crop husbandry (weed control, fertilizers, planting conditions), but not with use of insecticides, whereas poor yields and insect pest damage, including insecticide usage, were associated with poor husbandry (Savary *et al.*, in press). These conclusions highlight the dependence of rice pest management on good overall crop management, and also the need to re-assess the role of plant compensation particularly where good crop management may be jeopardized by uncontrollable limitations in soil conditions and water supply (see below).

Manipulation of rice crop diversity

In this section we are concerned with cultural methods using within-species and compound community biodiversity to minimize pest build-up especially by helping delay or prevent selection of virulent pest populations. Such diversity is also examined later in relation to biological control. As already discussed, resistance to some pests has failed in conditions of heavy selection pressure. Simple Darwinian concepts dictate that the worst cropping strategy is one

where heavy selection pressure is created by continually planting large areas of rice all with the same single mechanism for resistance to a particular pest, as has been done in much of south-east Asia. So, an obvious method of decreasing selection pressure is through planned biodiversity based on appropriate deployment of the different genes for resistance within individual fields and between groups of fields.

Within-field (community) biodiversity

Here we are concerned with decreasing selection pressure for resistance by manipulating genetic diversity within a particular crop (Khush, 1984; Saxena & Barrion, 1985; Saxena & Khan, 1989). The field is planted with a mixture comprising seeds of different genes for resistance and susceptibility. This has proved helpful for disease management (Chin & Ajimilah, 1982) but is less applicable to insects which, unlike pathogens, can select preferred plants. Mathematical modelling suggests that, for insects, the composition and success of such mixtures may depend on the mode of action of virulent genes as well as on the insect's biology and host finding behaviour (Gould, 1986a; Kennedy *et al.*, 1987; Hare, 1994). Seemingly, much more needs to be known about relevant plant/insect interactions before the most appropriate mixtures can be designed. This should not inhibit use of empirically designed mixtures, though European experience with wheat has exposed practical problems in maintaining quality.

Between-field (compound community) biodiversity

There seem to be two main approaches, which could be used separately or collectively. First, using temporal diversity, a single widely used cultivar possessing a particular gene for resistance can be grown over a large area but, before pest virulence is likely to develop, can then be replaced sequentially in rotation with other cultivars each with different resistance genes (Gallun & Khush, 1980). This has been used successfully against Hessian fly *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae) (Foster *et al.*, 1991) but has not been tested experimentally with rice (Saxena & Barrion, 1985). Secondly, using spatial diversity, different fields are planted in a patchwork, each field with a single cultivar but with inter-field differences in genes for resistance or susceptibility, so greatly lessening large-area selection pressure for virulence. Most farmers plant fields with one predominant cultivar, though some farming communities are known to retain patchworks of different cultivars for reasons other than pest management but which appear to have avoided induction of virulent pests (J.A. Litsinger, pers. comm.).

Logically, a spatial patchwork of fields cropped with cultivars containing different resistance mechanisms and including fields of susceptible cultivars seems to be a simple and potentially effective strategy for minimizing selection for pest virulence. Although there is good evidence that insecticide-untreated fields of non-resistant cultivars planted among fields of resistant cultivars may nowadays be unharmed by hoppers (for example, Cook & Perfect (1985) and Kenmore (1991)), detailed medium to long term field work is needed in different regions on the potential risks and safe proportions of such fields planted with susceptible cultivars.

Theoretically it should be possible to define ideal strategies for deploying appropriate resistance patterns in both space and time across the compound community, and models have been developed for several crops (Gould, 1986a, 1986b) including rice (Mundt, in press; Winterer *et al.*, in press). Whilst they are no doubt useful research tools, insect models in particular start with a series of assumptions about the ecology of a pest, its virulence, the nature of host-plant resistance to it, and, as is well recognized (e.g. Pimm, 1984), are inevitably considerable simplifications of the highly complex real life situation. We are concerned with not one, but a complex of different pests, or potential pests, of differing ecology and behaviour, and differing genetic make-ups including different virulence potentials. In these circumstances elegant modelling seems of doubtful practical relevance to farmers' deployment of diversity. In particular, the farmers' choice of cultivars depends on market criteria that may be unrelated to theoretical pest control concepts (e.g. Goodell, 1984). So, while theoretical studies might provide strategic insights, their feasibility for farmer decision making seems question-

able, for which realistic empirical research and guidelines are needed, as discussed later.

Ecosystem biodiversity

Here we are mainly concerned with the pest management significance of diverse non-rice habitats in the rice ecosystem: whether they are a major source of pests, whether they are a source of natural enemies, and whether they should be preserved and manipulated in order to favour natural control of rice pests.

In the past, host-plants in non-rice habitats have sometimes been incriminated as sources of insect pests and of transmitted diseases such as tungro virus (Hibino & Cabunagan, 1986), but the situation is complicated by sub-speciation of potential vectors which might limit them to non-rice hosts (Claridge, 1991). Non-rice habitats are undoubtedly the source of occasional localized invasions of polyphagous pests such as armyworms and locusts. However, the great majority of important insect pests are specific or narrowly oligophagous for rice so their dynamics seem

Table 2. First arrivals of suction trap sampled pests and natural enemies at three low altitude irrigated rice fields in the Philippines (calculated from data of Schoenly *et al.*, unpublished).

Order Family Species	Days after transplanting	
	Mean	Overall range for each species at all sides
Pests		
Diptera		
Ephydriidae		
<i>Hydrellia philippina</i> Ferino	15	11–20
Homoptera		
Cicadellidae		
<i>Nephotettix nigropictus</i> (Stål)		
<i>Nephotettix virescens</i> (Distant)	17	6–27
<i>Recilia dorsalis</i> (Motschulsky)		
Delphacidae		
<i>Nilaparvata lugens</i> (Stål)	13	6–20
<i>Sogatella furcifera</i> (Horváth)		
Natural enemies		
Hemiptera		
Mesoveliidae + Veliidae		
<i>Mesovelia vittigera</i> (Horváth)	15	6–21
<i>Microvelia douglasi atrolineata</i> Bergroth		
Miridae		
<i>Cyrtorhinus lividipennis</i> Reuter	15	11–20
Araneae		
Lycosidae		
<i>Paradosa pseudoannulata</i> (Bösenberg) & Strand)	12	11–13
Tetragnathidae		
<i>Tetragnatha virescens</i> Okuma		
<i>Tetragnatha mixillosa</i> Thorello	10	6–13
<i>Dyschiriognatha</i> sp.		
Linyphiidae		
<i>Attypena formosana</i> (Oi)	17	11–21
Hymenoptera		
Mymaridae		
<i>Anagrus</i> sp.		
<i>Gonatocerus</i> sp.	31	20–56
Trichogrammatidae		
<i>Oligosita</i> sp.		

likely to be little affected, if at all, by such pests coming from non-rice habitats. In contrast, the non-rice habitats, particularly the narrow vegetation-covered bunds surrounding each field, seem especially important as a source of natural enemies, particularly early arriving species such as spiders (table 2). Parasitoids, taxonomically identical with those attacking rice hoppers, commonly parasitize non-rice hopper species on wild hosts during fallow periods and some have been shown to attack *N. lugens* eggs (K.L. Heong, pers. comm.). Another important very early arriving predator, *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae) (table 2), can also survive in the off-season as an egg predator of insects on wild plants (Bentur & Kalode, 1987). Non-rice habitats seem likely to be an important source of some other very early arriving predators, Gryllidae for example, that can seasonally concentrate on rice. A general simulation model that includes association of ecosystem diversity with dispersal and with mortality from predation might indicate how predator-prey interactions could be managed, but the necessary field data are conspicuously lacking (e.g. Dobël & Denno, 1994). In the meantime non-rice habitats must surely be recognized as potentially very important, particularly for off-season continuity of some natural enemies.

Natural biological control

The diversity of natural enemies

When little or no insecticide is used, tropical irrigated rice fields possess a rich arthropod community including many different kinds of natural enemies (FAO, 1979; Greathead, 1979), and in these circumstances, their species richness and abundance may sometimes be greater than those of pests (Heong *et al.*, 1991). In Thailand, food webs comprised over 50 families and many species of natural enemies associated with defoliator, stem borer, hopper and gall midge pests (Yasumatsu, 1967), and, most recently, Schoenly *et al.* (unpublished data) constructed a composite web of species of predators and parasitoids of major pests in the Philippines. Such lists include unrevised 'species' such as the parasitoid *Anagrus flaveolus* Waterhouse (Hymenoptera: Mymaridae) that comprise at least six separate species (Claridge, 1991). There are also many pathogens (Rombach *et al.*, 1987).

Predator and parasitoid guilds recorded in five different irrigated rice ecosystems in the Philippines included ten orders and 57 families of predators and three orders comprising 40 families of parasitoids (Heong *et al.*, 1991), of which 33 species are known natural enemies of pest Homoptera. This abundance and richness, and hence biological control potential, contrast with the relative paucity of natural enemies in temperate irrigated rice (Kuno, 1979; Cook & Perfect, 1989b; Heong *et al.*, 1991, 1992; Perfect & Cook, 1994).

Impact of natural enemies on rice pests

The potential role of naturally occurring biological control in tropical irrigated rice has been increasingly appreciated since the 1960s (Nickel, 1964; Yasumatsu & Torii, 1968; FAO, 1979). Evidence summarized in detail by Greathead (1979) shows, for example, that parasitoids may kill 0-70 of eggs and 0-20% of nymphal hoppers. Lim (1970) pointed to the severity of stem borer attack in

regions where insecticides were used but not where natural enemies remained unharmed. Parasitoids and predators caused >90% of the >98% mortality from egg to pupa in common stem borer species attacking traditionally grown irrigated rice in Sarawak (Rothschild, 1971), and the 'complete control' of *Chilo suppressalis* in Hawaii was attributed to introduced parasitoids (Kiritani, 1979). Against rice bugs, *Leptocorisa* spp. (Hemiptera: Coreidae), there are records of 11-75% egg parasitism and evidence that predators were responsible for about half of the 90% mortality from egg to the final nymphal instar (Rothschild, 1970). Apart from the classic work of Rothschild, who recorded sequential life-table mortalities by natural enemies, other pre-1980's records were mostly simple counts of mortality, especially by parasites, with comparatively little solid evidence of their contribution to pest suppression.

The impetus for better understanding of the role of natural enemies stemmed from widespread and devastating outbreaks of *N. lugens* associated with early Green Revolution technology in tropical Asia. At first the tillering and other growth characteristics of new rice cultivars and the use of nitrogenous fertilizers were largely blamed for the outbreaks (Dyck *et al.*, 1979). However, such outbreaks were also associated with widespread and intensive use of certain insecticides highly destructive to natural enemies (fig. 4), and there is little or no evidence that other components of the new technology were primarily responsible (Heinrichs *et al.*, 1982; Heinrichs & Mochida, 1984; Kenmore *et al.*, 1984). This has been confirmed in low latitude tropical countries throughout south-east Asia (Kenmore, 1991) culminating in Thailand where, despite intensive insecticide usage, outbreaks became increasingly serious up to 1989-90. Subsequent research (fig. 5) showed that *N. lugens* outbreaks in Thailand were associated with insecticide usage, not with fertilizer (den Braber & Meenankanit, 1992) which, in insecticide-free conditions, can seemingly benefit natural controls as well as yield (e.g. Arida & Heong, 1992).

The work of Kenmore *et al.* (1984) and Heong *et al.* (1990a, 1990b, 1992) indicated that relatively few of the large array of natural enemies, at least 188 species throughout its range (Khoo *et al.*, 1991), might be especially important in *N. lugens* control. Recently, in five different irrigated rice areas in the Philippines, Heteroptera comprised 59-89% and spiders 11-41% of all predators. In particular there were early strong numerical responses of the predators *Cyrtorhinus lividipennis* and *Microwelia douglasi atrolineata* Bergroth (Hemiptera: Veliidae) to patches of prey (Heong *et al.*, 1992). Such behaviour together with an immigration-related numerical response (Cook & Perfect, 1985) is a recognized attribute of population regulation by natural enemies. Significant features of the dynamics of the generalized predator complex associated with rice include their feeding on detritivores which arrive before the crop is sown or transplanted and are therefore the first to attract and retain predators (W. Settle, pers. comm.); also predator species-switching linked to prey species abundance (Heong *et al.*, 1991), and inter-predator predation including cannibalism, which no doubt aids survival of a predator community when pests are scarce. Although the predator complex is considered to be especially important (e.g. Dobël & Denno, 1994), parasitoids have been recorded as abundant in tropical Asia (Lim, 1970; Rothschild, 1971; Cook & Perfect, 1989b; Fowler *et al.*, 1991; Sawada *et al.*, 1992) so may also be important in some circumstances.

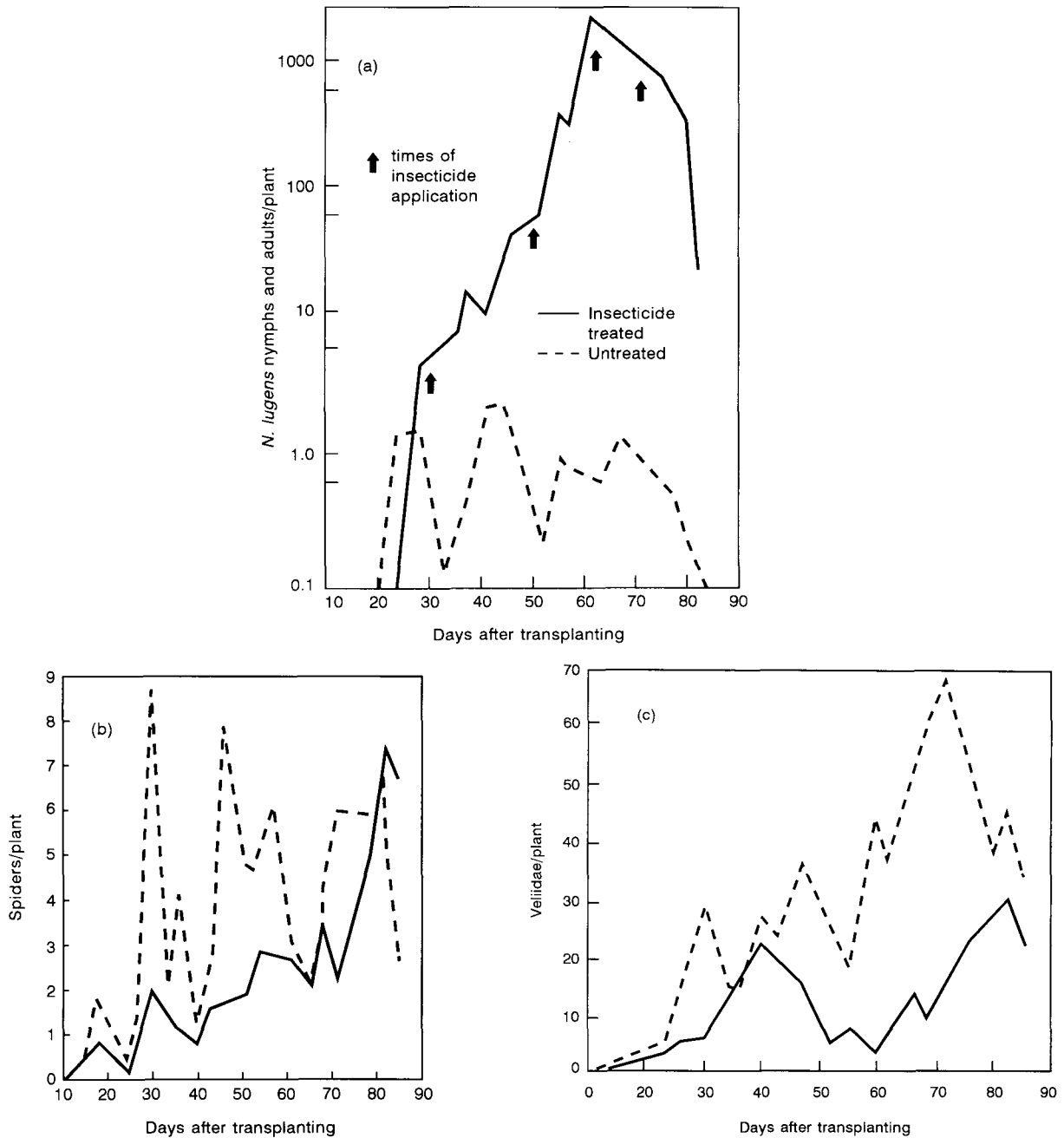


Fig. 4. Changes in number of *Nilaparvata lugens* and predators in insecticide treated and untreated irrigated rice fields in the Philippines (from Kenmore *et al.*, 1984). (a) nymphs and adults of *N. lugens*; (b) spiders; (c) Veliidae.

Irrigated rice is sown or transplanted into fields of bare soil, so a large proportion of the arthropod fauna must come from outside the cropped land. It therefore seems crucially important that key natural enemies should arrive as early in the crop as colonizing pests, the earliest in a recent study in the Philippines being two important spiders (table 2) and highly dispersive species such as *C. lividipennis* which was much the commonest of all insects, including pests, caught in aerial nets (Riley *et al.*, 1987). The more specific hymenopterous parasitoids arrived later in the conditions

studied by Schoenly *et al.* (unpublished data) but, as discussed later, not when there was notable asynchrony of planting dates (Sawada *et al.*, 1992). Moreover, in central Java, following a short fallow, water surface dwelling predators arrived even before the crop was transplanted, and at 5 days after transplanting (DAT) about 80% of all plants had two predators on or near them, rising to 95% and six predators by 11 DAT, some depending initially on detritivore prey (W. Settle, pers. comm.). Some, like the wolf spider *Pardosa pseudoannulata* (Bösenberg & Strand)

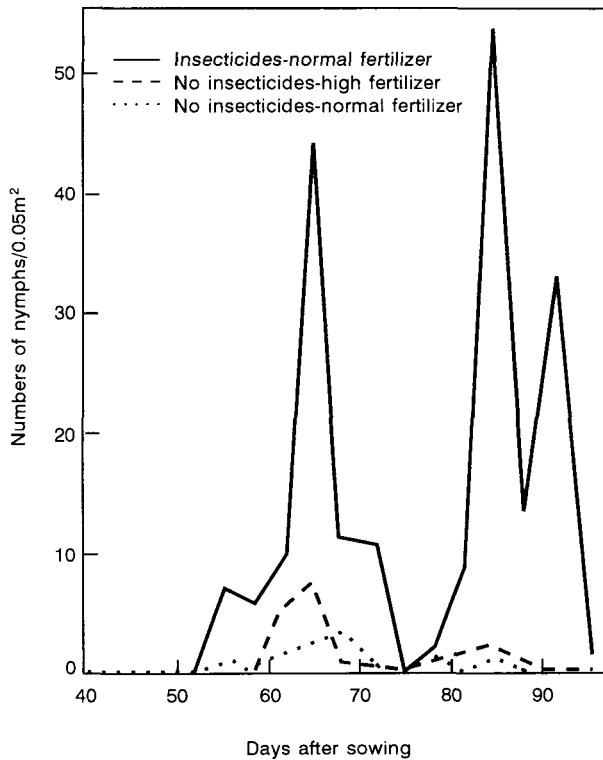


Fig. 5. Effects of insecticide treatment and fertilizer level on abundance of later instar hopper nymphs in crops of a rice cultivar susceptible to *N. lugens* in the field (from den Braber & Meenankanit, 1993).

(Araneae: Lycosidae), are commonly found in soil cracks in the fallow seasons (Arida & Heong, 1994).

In insecticide-free conditions, early arriving hopper pests mostly reached a peak about 30 DAT and then remained relatively unchanged or declined (Heong *et al.*, 1992). In these circumstances key predatory spiders and mirids continued to increase in numbers up to and sometimes beyond 40 DAT (fig. 6). Such evidence demonstrates that early arriving predators can quickly overtake and keep hopper populations at non-damaging levels. Accumulating evidence also confirms the importance of some predators and parasitoids against other primary pests, for example leafhoppers (K.L. Heong, pers. comm.). It should be emphasized that the potentially most damaging stem borer generation causing whiteheads begins ovipositing about 80 DAT when a rich natural enemy community will already have accumulated (fig. 6) including parasitoids which, according to Lim (1970), Rothschild (1971) and Triwidodo *et al.* (1992), can make a major contribution to stem borer control, unless insecticides are used, e.g. *S. innotata* egg predation and parasitism was halved and the numbers of whiteheads doubled by carbosulfan treatment recommended for controlling the pest (Triwidodo *et al.*, 1992) (fig. 3).

In conclusion, there is now abundant evidence of the vital role of certain natural enemies in control of most pests in two-or-more-crops-per-year tropical irrigated rice. We now discuss ways in which such natural enemy action might be enhanced against pests. First, we analyse the dilemma for natural biological control of two divergent

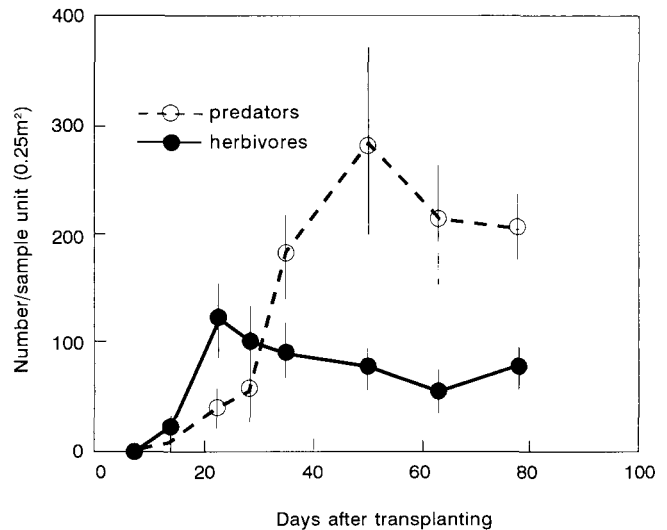


Fig. 6. Changes in abundance of herbivores and predators ($\pm 95\%$ confidence limits) on an insecticide-untreated rice crop in the Philippines (after Heong *et al.*, 1991).

temporal biodiversity approaches to rice pest integrated pest management (IPM).

Natural enemy action and crop synchrony

Early arrival of particular predators in newly planted rice fields (Cook & Perfect, 1985, 1989b; Heong *et al.*, 1991) depends on immigration from local sources, especially other rice crops. This would be benefited by asynchronous planting which would decrease the length of the area-wide fallow periods between crops. In contrast, the pest management goal of synchronous planting is to create the longest possible simultaneous area-wide fallow periods when pests, and consequently their natural enemies, are deprived of crop-dependent food. We are therefore faced with two divergent and incompatible IPM concepts, one based on dislocating the pests' life cycles and the other on continuity which favours natural biological controls. An appraisal of the pest management attributes of synchronously and asynchronously planted tropical irrigated rice is therefore needed.

Work in the early 1980s (Loevinsohn *et al.*, 1988) is still quoted (Loevinsohn, 1991, 1994) in support of his contention that double cropped relatively asynchronous planting has directly increased pests and that synchronous planting with long fallow periods should be the basis for insect pest management in tropical irrigated rice. Light trap catches of *N. lugens* at IRRI in the 1970s are still cited in support of the dogma, yet there have been dramatic decreases in the 1980s of both *N. lugens* and *S. incertulas* (fig. 7). This has happened in conditions of no change in asynchronous cropping practices with complete overlap of planting dates in the 182 ha IRRI farm and a continuation of notable asynchrony in the local Laguna rice growing area of about 50,000 ha. Resistant cultivars might be used to explain part of the decreases in *N. lugens* catches but not those of *S. incertulas*. The only major change has been decreased use of insecticides and hence increased abundance of natural enemies.

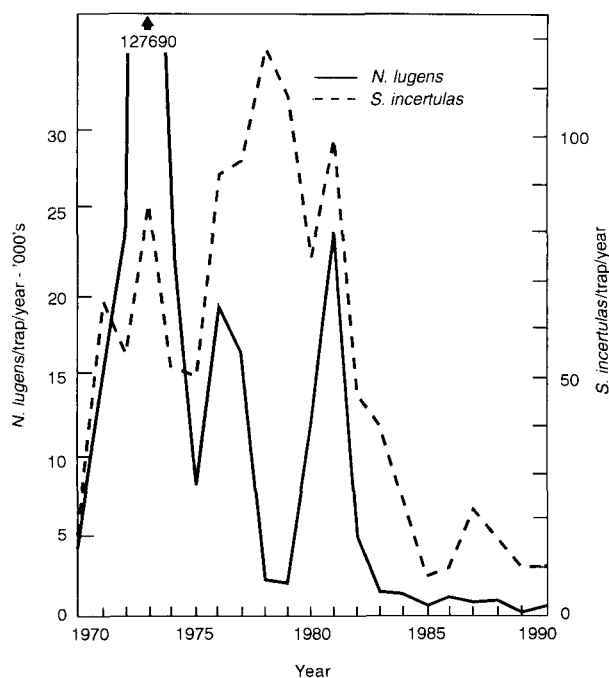


Fig. 7. Annual catches of adult *Nilaparvata lugens* and *Scirpophaga incertulas* by four crop-level light traps at IRRI.

The evidence that the annual trap catches of some insects increased as double cropping developed (Loevinsohn *et al.*, 1988) does not mean that the pests are worse—they come from two crops rather than one per year, with less from each crop (Lim & Heong, 1977) (fig. 2). Indeed, the decline in stem borer damage in Malaysia was attributed to improved control by natural enemies associated with increased double cropping and asynchrony (Lim & Heong, 1977), a conclusion which is supported by the much decreased light trap catches of adult *S. incertulas* in the Philippines (fig. 7). Furthermore, the argument against asynchrony had already been undermined in the 1970s by total annual yields of over 20 t/ha in an insecticide-untreated weekly planted rice garden with large natural enemy populations in the otherwise mostly insecticide treated IRRI farm (Pantua, 1979). Morooka *et al.* (1979) also reported the doubling of yield on four overlapping crops a year in rice gardens where insecticides were moderately or not used.

Although asynchronous cropping creates conditions that would be expected to favour build-up of an unconstrained pest population this, as already discussed, does not seem to happen except in insecticide-treated rice where, for example, in two adjoining fields, one untreated and one treated with a natural enemy-killing insecticide, $\times 300$ more *N. lugens* developed in the latter (Kenmore, 1979). Moreover, about $\times 7000$ more *N. lugens* immigrants than those that caused serious crop loss to long-fallow, natural enemy-sparse single crop Japanese temperate rice, did not harm overlapping crops of tropical rice in the Philippines, provided natural enemy-killing insecticides were not used (see also Cook & Perfect, 1985, 1989b).

We conclude that the contention of Loevinsohn (1991, 1994), also Manwan *et al.* (1987), Oka (1983, 1988) and

Widiarta *et al.* (1990), in favour of synchronous planting is therefore based on misinterpretation of evidence based on outdated conditions where natural enemy-killing insecticides were still being intensively used. In contrast, Sawada *et al.* (1992) reported relatively few *N. lugens* throughout the season in an asynchronously planted area where the population multiplied by $\times 5-10$ up to the third generation unlike an immediately adjoining synchronously planted area of the same cultivars where *N. lugens* populations increased by $\times 52-88$ culminating in outbreaks at the end of the season. This was attributed to natural enemy action, in particular to egg parasitoids in the asynchronous area where numbers of sampled adult parasitoids were 29 and 45 after 21 and 35 days respectively, compared with 1 and 3 in the synchronously planted area. In support of such evidence, Rombach & Gallagher (1994) refer to the failure to control pests in planned large scale synchronized plantings in China. The pest management value of asynchronous planting in benefiting tropical irrigated rice is also supported by other empirical evidence (Lim, 1970, 1974; Balasubramaniam & Ooi, 1977; Lim & Heong, 1977; FAO, 1979; Rombach & Gallagher, 1994), and by ecological theory (Southwood & Way, 1970; van Emden & Williams, 1974; Way, 1977; van Emden, 1990b; Altieri, 1991; Waage, 1991). However it needs further investigation in specific conditions, as when most crops in a region are asynchronised within usually practised limits but with some very late planted fields that may become the concentrated focus for later generation immigrants from the earlier sown crops. This has been observed for stem borers in circumstances where natural enemies were, however, being killed by insecticides (D.G. Bottrell, pers. comm.). Confirmation is needed that it does not happen in natural enemy protected conditions, but it remains a risk particularly from species like the rice bug *Leptocoris oratorius* (Fabricius) (Hemiptera: Coreidae) which is strikingly able to find and concentrate on small areas of out-of-season crops at times when there is no alternative food (Rothschild, 1970).

Crop asynchrony and the rice tungro virus disease (RTVD) problem

Insect transmitted virus diseases may pose special problems, for asynchronous planting. At times, epidemics have been catastrophic in a few localized tungro areas, though overall it represents relatively very little crop loss in south-east Asia (Thresh, 1986). Greater continuity of diseased plants through double and triple cropping, together with asynchrony, has been suggested as a major cause of epidemics, yet outside the definitive tungro areas, vastly greater areas of similarly asynchronously planted rice remain unaffected.

In present ignorance of the complicated two-virus epidemiology of RTVD, causes of outbreaks are speculative. However, the potential for such outbreaks has been linked to cultivar susceptibility, or breakdown of previous resistance to the key vector *Nephotettix virescens*. Infection is by viruliferous immigrants probably flying relatively short distances from disease sources (Cook & Perfect, 1989a), and a provisional model based on field evidence (Holt *et al.*, 1992) indicates that, as expected, infection of the at-risk crop is related to numbers of infected vectors emigrating from disease sources, and not to total numbers of hoppers. Infection, which can be immediately transmitted after uptake

by the vector, begins with plant-to-plant feeding by primary viruliferous migrants, and is perpetuated by secondary spread (Holt *et al.*, 1992). The question is whether double crop-asynchrony-benefited natural enemy action can play an important role in suppressing RTVD spread. There is much evidence that, as with *Nilaparvata lugens*, *Nephotettix virescens* populations greatly increase in fields treated with natural enemy-killing insecticides, but, for example, with natural enemies preserved, survivorship was only 0.3% from egg to adult (Cariño *et al.*, 1982). Even in fields at risk, natural enemies protected from insecticidal destruction would be expected to decrease within-field plant-to-plant spread; also, in view of evidence such as Cariño *et al.*'s (1982), they would be expected to decrease later secondary spread in the field. The impact of the natural enemy complex at sources of infection may, however, be much more important. Here, natural enemy-depleted *N. virescens* populations will produce fewer viruliferous migrants, perhaps negating their epidemic potential. Furthermore, as discussed later, natural enemies must be regarded as helping to delay or prevent loss of host-plant resistance. Because the practice of double/triple cropping will remain and probably intensify, such natural enemy-favouring cropping practices should be adopted as a means of preventing, rather than helping cause, tungro epidemics. In present circumstances the dogma that 'insect-vectored virus disease cannot be controlled by natural enemies' (Litsinger, 1989) must therefore be questioned for tungro and is entirely incorrect for *Nilaparvata lugens*-transmitted grassy and ragged stunt diseases. These are caused by persistent viruses and, after uptake, the vector must 'avoid' being killed by natural enemies for a 10 days' incubation period before the disease can be transmitted. That natural enemies can control diseases caused by such persistent viruses is evident from the association of epidemics with *N. lugens* outbreak populations caused by insecticidal destruction of natural enemies and not with natural enemy-associated low populations (Disthaporn, 1986).

At present the political status of RTVD in tungro areas has led to intensive government-supported insecticide applications at the first sign of infection, which, if natural enemies are as important as we suggest, can be responsible for perpetuating epidemics. Yet, an explanation is needed for the past sudden prevalence of the disease in tungro areas after years of little or no infection. We still postulate that a preserved natural enemy complex, in an appropriate pattern of fields planted with vector resistant cultivars, could prevent realization of the potential in these areas.

Stability as the ecological basis for rice pest management

Here, on evidence in this review, we highlight pest population and community stability as providing the ecological bases for rice pest management. We adopt the usual definition of stability, namely that which maintains an equilibrium value over time, about which there is varying fluctuation in numbers. We use the terms 'more' or 'less' stable to distinguish situations where the fluctuations about and below the equilibrium are respectively relatively small and relatively large. In pest management we aim for a permanently stable pest population in which high peaks as well as the equilibrium level are kept below those causing economic crop loss. A damaging population may reach

epidemic proportions when the peaks are prolonged or occur frequently as has happened with insecticide-induced *N. lugens* outbreaks. In these circumstances the population enters a less stable phase with a distinctly higher equilibrium value, the new high value being one created by loss of the regulatory contribution of natural enemies and the imposition in particular of other regulatory mechanisms such as intra-specific competition that do not operate, or operate much less, at the endemic equilibrium level. This contrast is demonstrated by *N. lugens* trap catches at IRRI, with wild fluctuations about an epidemic equilibrium (based on mean logs) of about 11,950 *N. lugens*/trap/year from 1970-1982 contrasting with small fluctuations about an equilibrium of about 850 from 1985-90 (fig. 7). We recognize a comparable situation with lower-density pests such as the lepidopterous and dipterous defoliators and stem borers. Such species are not epidemic, though we still envisage lower non-damaging equilibrium levels contrasting with higher less stable and more damaging levels in the absence of the regulatory role of natural enemies. Adult *S. incertulas* trap catches (fig. 7) exemplify such a change from a 1970-82 high (about 68/trap/year) to a lower 1985-90 equilibrium level of about 12/trap/year.

In rice pest management, therefore, we are seeking for appropriately low stable populations of the potentially damaging species and for predictable persistence of such stability. In attaining such persistence we require the functionally important part of the community to be resilient to possible disturbances that tend to increase the equilibrium values of pest populations and/or increase variation about the equilibrium. We envisage community resilience to disturbance as critically important, its maintenance depending basically on appropriately consistent crop production practices, including choice of cultivar, water, fertilizer, weed control, and times, methods and patterns of sowing. These provide a framework for appropriate host-plant diversity of resistance, tolerance and natural enemies to regulate pests at acceptably low levels. We have pointed in particular to the convincing evidence of how rice community resilience is undermined by inappropriately used insecticides which upset natural enemies and favour induced selection of virulent pest populations that can overcome host-plant resistance.

Evidence of the regulatory and pest controlling role of natural enemies, even in crops of rice cultivars recognized as susceptible might be used to question the indispensable role of some host-plant resistances. In our view, regardless of evidence of its less predominant role, host-plant resistance must still provide the fundamental element of stability and resilience needed for successful pest management. It is fundamentally important partly because even low levels of resistance must help to lower pest numbers to levels susceptible to natural enemy action. We also envisage host-plant resistance as underwriting natural enemy action should the latter temporarily lose its controlling role through pesticide misuse, or perhaps through other disturbance such as aberrant weather. In these circumstances host-plant resistance would be essential against pest species such as hoppers which can multiply rapidly if otherwise unconstrained. Such species include virus disease vectors, notably *Nephotettix virescens* against which, as implied earlier, host-plant resistance may fulfil much more than an underwriting role. The status of host-plant resistance is different from some non-epidemic key primary pests of rice against which resistance

breeding has been relatively unsuccessful. However, as already discussed, a well grown tropical irrigated rice plant has an enormous potential for damage compensation. In these circumstances we envisage compensation as providing a crucial complement to moderate host-plant resistance as well as a replacement for it in circumstances where resistance breeding has been unsuccessful. For example, resilience through compensation permits a higher pest equilibrium level and/or greater flexibility in numbers about the equilibrium than if the plant could not compensate. So, plant compensation is not only underwriting, but also acting mutually with, biological control, whereas host-plant resistance and biological control have been regarded as acting antagonistically in some circumstances (Kenmore *et al.*, 1984; Hare, 1994) although their action is compensatory. However, when compensatory ability is impaired, by insufficient water for example, a system based on compensation is probably less resilient to disturbance than is one based on host-plant resistance. These considerations relate to monophagous or oligophagous pest species, the dynamics of which depend primarily on interactions within the irrigated rice ecosystem. They do not apply to exogenous pests from non-rice host-plants which may sporadically attack rice, for example armyworms and locusts. Similarly, damage by polyphagous rice bugs may be caused by immigrants that have bred on other host species rather than on other rice crops where natural enemies can still cause large mortalities (Rothschild, 1970).

As already implied, stable population and stable community-dependent rice pest management depends in turn on maintenance of stabilized cropping conditions. The next section examines conditions that are likely to be destabilizing.

Constraints to stability-based rice pest management

Throughout, we have emphasized the unique stability of two or more crops per year rice production in relatively low latitude tropical regions where there is uniformly favourable temperature, water supply, good overall farming practice and appropriately sequential cropping. Destabilizing variables can be separated into those occurring in the otherwise favourable low latitude equatorial zone and those of higher latitude tropics, sub-tropics and warm temperate zones.

Low latitude tropics

Extreme weather fluctuations can be destabilizing in otherwise favourable conditions, as in Malaysia, where excessive rain once caused complete submergence of large areas of rice. This created a *Nilaparvata lugens* outbreak, probably because its eggs survived whereas most natural enemies were destroyed allowing temporarily uncontrolled multiplication to outbreak densities (G.S. Lim, pers. comm.). Climatic perturbations are recognized as advantageous to some pests of different crops (Wellington & Dixon, 1987; Dobél & Denno, 1994) and this needs to be taken into account for several rice pests, especially in marginal conditions.

Insufficient water and/or unsuitable terrain have limited rice production to one crop per year in rain-fed lowland and upland conditions. In this context, we emphasize the destabilizing effect of a long non-rice dry season on the natural enemy community in rainfed lowland and upland rice.

Though not the subject of this review, there are alternative strategies for pest control in upland rice based on direct dislocation of pest life cycles, as is characteristic of many different dry land crop situations, e.g. other cereals (Burn, 1987).

Higher latitude tropics and sub-tropics

In these conditions the more pronounced dry and wet seasons must be recognized as destabilizing, basically because this tends to impose greater crop synchrony often with a single seasonal rice crop and an increasingly pronounced non-rice season as the latitude increases. Such conditions can uncouple and therefore destabilize the natural enemy/pest relationship through limitations in crop continuity such that *N. lugens*, for example, may sometimes behave as in temperate situations (Cook & Perfect, 1989b; Perfect & Cook, 1994). Moreover the climatic conditions have induced dry season aestivation or diapause in some key pests, notably stem borers such as *S. incertulas*. Diapause may also occur in equatorial regions, as with *S. innotata* in single crop parts of Java¹ (Triwidodo *et al.*, 1992), and it inevitably tends to upset natural enemy regulation, particularly by species with a life cycle not closely coupled with that of their prey. The Asian gall midge *O. oryzae* provides a good example of what appear to be destabilizing effects of seasonal change. This is not a pest in non-diapausing equatorial conditions, for example in southern Thailand, but until recently has caused serious damage in north and north-east Thailand (Hidaka *et al.*, 1974). After emergence from diapause, its early generations, relatively little affected by natural enemies, have damaged a high proportion of tillers of first grown crops. Later build-up of natural enemies coincided with decrease in gall midge incidence and little or no damage on later sown rice crops (Hidaka *et al.*, 1974). This exemplifies the dislocating effect of a pronounced off-season, though it does not explain the present comparative scarcity of gall midge in Thailand, perhaps associated with short duration cultivars that can upset its life cycle (T. Hidaka, pers. comm.). Stability-based stem borer control is also jeopardized in higher latitudes where, for example, water supply may become less favourable for crop compensation. In these circumstances, crop loss from some stem borers might be potentially more serious than in equatorial latitudes.

Temperate zones

Although outside the subject of this review, destabilizing winter conditions are no doubt responsible for relative paucity and ineffectiveness of natural enemies in temperate irrigated rice. As already mentioned, this explains damaging build-up of *N. lugens* from relatively small immigrant populations and consequent dependence on insecticidal control (Cook & Perfect, 1989b; Perfect & Cook, 1994). In these circumstances of characteristic temperate climate instability, insecticides can sometimes be used more crudely, as against other temperate crop pests, because natural enemy conservation becomes relatively less important (Southwood & Way, 1970).

¹In these circumstances dislocating controls can, however, become very successful such as delayed planting to avoid emergence of diapausing white stemborer (van der Goot, 1948).

Integration of pest management techniques

In this section we examine how various methods can be used mutually to benefit rather than harm each other's actions—the basis of the integrated pest management concept.

Host-plant resistance/tolerance and natural biological control

We regard this combination as the fundamental requirement, based on widespread evidence that outbreaks, of *N. lugens* in particular, occur when host-plant resistance has broken down in circumstances where natural enemies were killed by insecticides.

The complementary roles of host-plant resistance and natural enemy action were first described mathematically by van Emden (1990a) and are supported by empirical evidence and by experiments on irrigated rice (Heinrichs, 1988; Kartohardjono & Heinrichs, 1984; Myint *et al.*, 1986). Hoppers such as *N. lugens* breed slowly on rice cultivars recognized as very resistant (Aquino & Heinrichs, 1979), and rice may suffer no yield loss although infested by up to 30/plant on less resistant cultivars (IRRI, 1990). Partial resistance, like host-plant tolerance, is potentially important for retention of, and efficient control by, different species of natural enemies, particularly the more specific parasitoids, so, in contrast, a very high level of resistance could be detrimental because it could impair the enemies' response to subsequent pest population increase (Kenmore *et al.*, 1984). The slowed growth of some pest species on resistant cultivars extends the generation time during which predators can find them. Some cultivars also have qualities which make them relatively more attractive than others to certain predators (Bottrell & Rapusas, in press), which can be envisaged as contributing indirectly to host-plant resistance!

Besides the joint regulatory and pest controlling roles of host-plant resistance and biological controls in any particular field, there is the longer-term significance of their interaction in delaying or preventing the development of pest populations capable of overcoming previously resistant host-plants. The dramatic losses of cultivar resistances to virulent populations of several hoppers and gall midge all occurred in circumstances of widespread and intense insecticide treatment (Kenmore, 1991; Perfect & Cook, 1994). It is significant that there is no evidence of resistance breaking where natural enemy action is being preserved, so currently used resistant cultivars seem to be retaining their resistance. This confirms Gould *et al.*'s (1991) theoretical population genetics model showing that the combination of partial plant resistance with a second strong mortality factor (insecticide in their example) can accelerate adaptation by the pest to the plant's resistance compared with a weaker second mortality factor (natural enemies). Whether their contention that, in some circumstances, adaptation to the partial plant resistance could be enhanced by biological control itself, is an interesting abstraction which is not as yet supported by evidence from the field where it should be critically assessed as should other possibly complicating interactions discussed in detail by Hare (1994).

Research on the use of mutually beneficial effects of host-plant resistance, plant compensation and natural biological control has been neglected particularly against stem borers where moderate resistance seems to have been undervalued, and where plant compensation and natural

enemy action are individually known to be important. In particular, priority should be given to the mutualistic roles of host-plant compensation and biological control.

Integration of use of insecticides

It is unrealistic to assume that the manipulation of biodiversity will ever solve all pest problems all of the time without need for insecticides. So, we now refer briefly to the ancillary role of insecticides, highlighting the need for a radical reappraisal based on the contention that they are **not** needed, rather than that they **are**, as a **fundamental** component of irrigated rice pest management. Consequently the unreliable and unacceptable action thresholds for insecticide use (e.g. Bandong & Litsinger, 1988; Hu *et al.*, 1993) can be discarded, so relieving the farmer of impracticable decision making procedures (Goodell, 1984).

How therefore can insecticides be used only when needed and without harming biological controls? In conditions where insecticides were being applied extensively to irrigated rice, Lim & Heong (1984) listed methods for using them more selectively, including spot treatments on patches of evident attack, pre-planting treatments and choice of the most selective chemicals. However, whilst past research has focused on potency of insecticides and their application, much less attention has been given to answering the fundamental question whether particular pest damage warrants treatment at all. In this context, a crucial discovery was made on leafhoppers, notably *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae) (Heong, 1993), which are the commonest and most spectacularly damaging pests in early crop stages. Earlier literature contains numerous reports of heavy infestations (e.g. Khan *et al.*, 1988) and much effort has been expended on searching for genes for resistance and on insecticide treatment. Yet, the extent and frequency of crop losses were not assessed. Average larval densities are less than one per hill in the Philippines (Guo, 1990), but negligible yield loss is to be expected with larval populations less than about three per hill (Graf *et al.*, 1992) so economic loss from early season infestations is highly unlikely especially if natural enemies remain unharmed. Furthermore, research on the development of the arthropod community (Heong *et al.*, 1991; Heong *et al.*, 1992), on effects of insecticide perturbations (Cohen *et al.*, in press; Schoenly *et al.*, in press) and on modelling (Wareing *et al.*, 1990) showed that early season applications greatly favoured herbivore species. This led to the conclusion that prevention of outbreaks, particularly of hoppers, depended on protection of early-acting natural enemies by avoiding insecticide spraying during the first 30-40 days after transplanting or sowing the rice crop (ref. fig. 6). However, many rice farmers still perceive very visible defoliator pests as causing crop loss, so they use insecticides (Escalada & Heong, 1993). Avoidance of insecticides in the first 40 days is now being actively promoted through farmer experimentation (IRRI, 1993b; Escalada & Heong, 1993) in several tropical south-east Asian countries.

If insecticides are avoided for the first 30-40 days, key questions that arise subsequently include whether particular pests may still need chemical control, what chemicals are best and when to apply them. For example, against hoppers, insecticides that cause secondary outbreaks and pest resurgences, such as pyrethroids and some organophosphates, should be avoided in favour of appropriate carbamates and

the selective buprofezin. Insecticides should normally be regarded as unnecessary against deadheart damage by stem borers, but control of whitehead damage can present dilemmas. Chemical control is useless once whiteheads appear, and an appropriately timed application of a systemic prophylactic such as carbofuran is normally recommended. Yet, this can sometimes increase whitehead damage by selectively harming natural enemies (Triwidodo *et al.*, 1992) (fig. 3) and can also have a catastrophic effect on spiders (Pantua, 1979). In this context, evidence already discussed indicates that the combination of natural biological control, host-plant resistance and tolerance can prevent economic damage by stem borers, except perhaps in very out-of-phase, late planted fields. We conclude that only in these limited circumstances is prophylactic treatment justified, either with a chemical or, potentially, by using cultivars containing transgenic Bt. Similarly, pests such as rice bugs, which are widely dispersive, can be regarded as doing insignificant harm, except when forced to concentrate on a small proportion of out-of-phase, late planted fields. Here the use of appropriate carbamates applied at the milky plant growth stage may be justified. Insecticide sprays at this late crop stage would not be expected to impair natural enemy action against other pests. Such guidelines would not require impracticable action thresholds but they emphasize qualitative decision making based on individual farmers' attitudes to risk and their appreciation of unusual conditions known to favour pest attacks.

Conclusions

Basic considerations

Throughout we have emphasized the unique natural stability as well as the potential of man-manipulated stability in two or more-crops per year tropical irrigated rice. No other widely grown crops, perennial or annual, approach this continuity of year round growth stages and favourable climate. In such circumstances we have highlighted the value of a relatively few natural and man-manipulated components of diversity which can maintain stable insect populations at levels below pest densities. We envisage such a system as possessing features which are normally incompatible, namely resilience characteristics of early stages of plant succession together with the biological control-favouring stability of later perennial stages of succession.

Many rice areas comprise successional planted crops with relatively short fallow periods which may continue to carry living rice stubble. The key question is how the pests and associated natural enemy populations are linked within this patchwork of more or less continuously available rice. Each field can be recognized ecologically as a patch, with most of its insects moving to, and concentrating on, patches as they reach suitable growth stages (Way & Heong, unpublished data). The coincident very early arrival of some species of herbivores and natural enemies in each newly planted rice field (table 2) has perhaps developed during their long shared evolutionary history on irrigated rice but, anyway, there seems to be remarkable determinism involving definitive pathways towards a stable rice community (Way & Heong, unpublished data). In particular, the early appearance of some key species of generalized predators seems crucially important in view of evidence of their role in regulation and pest control, though the mechanisms are

little understood. Such ignorance contrasts strikingly with abundant experimental and theoretical knowledge of specialized species/species interrelationships. Analysis of interactions between complexes of predators and their prey seems far beyond the capacity of existing mathematical understanding (e.g. Carter, 1985), though there are some insights. For example, even in dislocated temperate conditions a few mostly non-specific denizens of fields and field boundaries seem to be important regulators of some cereal and brassica pests (Wratten, 1987; Ekbohm *et al.*, 1992; Jones *et al.*, 1993). Within the climatically stable tropical irrigated rice system we envisage a within-crop community of parasites and non-specific predators comprising key species complementing each other's action on different stages of pest herbivores at different times (Murdoch, 1990), so creating below-pest-density equilibria with their prey (Way & Heong, unpublished data). Switching of predation to detritivores, casual species, and other predators including their own species (Heong *et al.*, 1990b, 1990c; Heong & Rubia, 1990) is envisaged as a vital attribute of regulation by non-specific predators which retains a predator community when pests are scarce.

We have discussed the importance of an appropriate diverse framework of rice crops within which natural enemies operate, particularly diversity in time and space. Besides highlighting the significance of overlapping rice crop conditions we have also pointed to the likely importance of the bunds (levées) surrounding each field as well as non-rice crops and wild areas that form part of the tropical irrigated rice ecosystem. Bunds must be a vital source of some relatively immobile yet very early arriving predators such as spiders. Spiders represent one extreme of a spectrum of dispersiveness, the other comprising highly dispersive species such as *C. lividipennis* that were more commonly caught in aerial nets than any other insect species, pests included (Riley *et al.*, 1987). The combined impact of these very differently behaving natural enemies is no doubt linked to ecosystem diversity, but we remain ignorant of how diversity can be manipulated to improve timing of arrival and abundance of key natural enemies. For example, almost nothing is known about the bunds except that they can harbour important predatory spiders. Yet, bunds are abundantly colonized by the aggressive predatory ant *Solenopsis geminata* (Fabricius) (Hymenoptera: Formicidae) (Way *et al.*, unpublished data). Are they also beneficial predators or do they harm other natural enemies? Can simple bund manipulations improve their role as a source of natural enemies?

We envisage host-plant resistance as providing the crucial framework for rice IPM though we have queried the high priority placed on resistance breeding for secondary pests. We also question the value of breeding for high levels of resistance because this could encourage selection for virulent pests and may also be detrimental to natural enemy action. We also conclude that plant compensation, especially against defoliator and stem borer damage, has been greatly under-rated and hence neglected by plant breeders. The ability to compensate for defoliator damage is crucially important as the only alternative to insecticides during natural enemy establishment in the first 30-40 days of crop growth. We also recognize the vital role of compensatory ability integrated with resistance and biological controls, particularly against stem borers. Furthermore, plants possessing compensatory ability attract and maintain natural enemy communities and cannot invoke virulent pests.

Practical validity

In our view, the most important practical conclusion from this review is that crop production technologies needed for future increased rice yields (IRRI, 1989) should be compatible with natural control-based IPM. Besides appropriate developments in host-plant resistance/compensatory abilities, such technologies include further intensification of double and triple cropping with increased asynchrony of planting, which also benefit biological control as well as helping the farmer to spread his labour and make best use of the available water supply. Herbicide-based weed control and use of fertilizers, which are fundamental to attainment of yield potential, also favour host-plant resistance and compensatory ability as well as seemingly being harmless to natural enemy action. It is, for example, critically significant that the inherently pest-favouring effects of fertilizers can still be nullified by natural enemy action, providing insecticides are suitably avoided. Moreover, there is no evidence that natural controls are impaired by direct seeding and mechanization (Heong *et al.*, 1985) apart from reduction in amounts of bund from likely increases in field size to favour mechanization. Such potential loss of biodiversity may be critically important, and it further emphasizes the need for priority research on the role of bunds in rice pest dynamics and on ways in which they can be best used in practice as islands or corridors for natural enemies.

The validity of the natural control-based approach to high yielding tropical irrigated rice production is supported by present farmer experience (Kenmore, 1991; Bottrell *et al.*, in press; S. Masajo, pers. comm.) which fulfills Kenmore *et al.*'s (1985) practical definition of IPM as 'the best mix of control tactics for a given pest problem by comparison with the yield, profit and safety of alternative mixes'. In contrast, dependence on insecticides is costly, involves complications of choosing and applying different insecticides against different pests and often demands irrational decision-making on whether and when to use them. Hence, their misuse and catastrophic effects on biological control. We conclude that IPM in tropical irrigated rice should be based on the contention that insecticides are not needed rather than that they are, and that 'pests' should now be critically re-assessed and proven guilty before insecticide use is contemplated.

We have referred to situations where natural controls might be inadequate and where appropriate insecticides may be needed, particularly in higher but also in the low latitude tropics. We recommend as a priority the need to use year-to-year farmers' evidence for elucidating where and why natural controls may sometimes prove inadequate and how they can be enhanced in such circumstances. There is ignorance of the value of between-crop diversity in space, so empirical trials are also needed on crop patterning with cultivars of differing resistance qualities to assess their pest control qualities for farmer application. As already recognized (Kenmore, 1991; Escalada & Heong, 1993; Bottrell *et al.*, in press) much also depends on more widespread farmer understanding of, and confidence in, an appropriate diversity of natural controls as a replacement for dependence on insecticides.

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