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A food web approach to evaluating the effect of insecticide spraying on insect pest population dynamics in a Philippine irrigated rice ecosystem

J.E. COHEN[*], K. SCHOENLY[*†‡], K.L. HEONG[†], H. JUSTO[†§],
G. ARIDA[†], A.T. BARRION[†] and J.A. LITSINGER[†¶]
[*]Laboratory of Populations, Box 20, Rockefeller University, 1230 York Avenue, New York, New York 10021 USA; and [†]Entomology Division, International Rice Research Institute, Los Baños, Philippines

Summary

1. Data from a 645-taxa Philippines-wide food web and multiple regression models were used to predict population fluctuations of insect pests in a rice field. Independent variables of pest models included the biomass of rice plants in the field, the abundance of each pest, and the abundances of five highly correlated enemies of the pest, all as functions of time.

2. To test the ability of the models to reveal effects of insecticide spraying, a rice field at the International Rice Research Institute (IRRI) in the Philippines was divided into deltamethrin-sprayed and unsprayed plots. Data on the abundance of seven pest species (*Nephotettix virescens, Recilia dorsalis, Sogatella furcifera, Nilaparvata lugens, Hydrellia philippina, Ne. nigropictus* and *Cofana spectra*) and their natural enemies (predators and parasitoids) were collected during the dry season of 1990.

3. Spraying insecticide disorganized the population dynamics of insect species feeding in the IRRI field. Multiple regression models were less able in the sprayed plot than in the unsprayed plot to forecast the population fluctuations of pest species on the basis of various numbers and combinations of independent variables. For example, current pest abundance, by itself, was a significant predictor of future pest abundance for four of the seven pests (*Ne. virescens, R. dorsalis, S. furcifera, H. philippina*) in the unsprayed plot, but significant fits were found for only two pests (*R. dorsalis, H. philippina*) in the insecticide-sprayed plot.

4. In the unsprayed plot, independent variables were significant predictors of future pest abundance in four of seven initial models compared to one of seven models in the sprayed plot. Step-wise removal of independent variables in the models enhanced their forecasting power in both the sprayed and unsprayed plots, but significant models in the unsprayed plot nearly always outnumbered those in the sprayed plot.

5. In the unsprayed plot, *Ne. virescens* retained five of seven independent variables as significant predictors, compared to four for *S. furcifera*, three for *C. spectra*, and one for the remaining four pests. Classical models that contain one or two species as independent variables may not be sufficient to forecast future abundances of some Philippine rice pests in unsprayed and sprayed plots.

6. In general, models that included interaction terms and either the presence or absence of sprays among the independent variables did not improve the forecasting power of models in either the sprayed or unsprayed plot.

7. The methods developed here for studying the impact of spraying on the organization of arthropod communities in rice fields could be applied to other interventions

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[‡] Present address: Department of Biological Sciences, Louisiana Tech University, Ruston, LA, 71272, USA.
[§] Present address: Department of Entomology, Clemson University, Clemson, South Carolina 29634, USA.

[¶] Present address: 1365 Jacobs Place, Dixon, California 95620, USA.

besides spraying (such as the introduction of genetically engineered cultivars), other biotic communities besides arthropods, and other crops besides rice.

Key-words: tropical agro-ecosystems, food webs, rice pests, deltamethrin, multiple regression, population dynamics, natural enemies, biological control, community structure.

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Introduction

Many studies of pest management focus on specific pests and their principal natural enemies. However, farmers normally care about the net effect of all pests on their crops, not necessarily about individual species. Hence, there is value in approaches and methods that can evaluate the effects of interventions, such as spraying and biological control, on the entire community of pests and their natural enemies.

Ecological concepts can organize data on individual pest–enemy interactions into forms that are useful for understanding the effects of interventions on the community of pests and enemies (Cherrett 1989). For example, a food web pictures or tabulates which species eat which others (Pimm, Lawton & Cohen 1991). In a crop field, there are hundreds to thousands of different species of insects, arachnids, pathogens, nematodes, vertebrates and other organisms linked by their feeding relationships into an intricate food web. Food webs can help insect pest management because they clarify the functional interactions between populations. In some, but not many, cases, agricultural data on pests and their biological control species have been organized into food webs (Pierce *et al.* 1912; Yasumatsu & Torii 1968; Mayse & Price 1978; Gonzalez & Wilson 1982; Gutierrez, Baumgartner & Summers 1984; Hendrix *et al.* 1986; Neuenschwander, Hennessey & Herren 1987).

In tropical Asia, many rice insect pests are contained by the activity of not just a few arthropod natural enemies, but a whole array (Reissig *et al.* 1986; Barrion *et al.* 1991). Many pest outbreaks in tropical rice have been traced to overuse of insecticides (Kenmore *et al.* 1984). Food webs have been used to illustrate pest–enemy relationships in rice (Yasumatsu & Torii 1968), but these webs have been static (cumulative in the sense of Schoenly & Cohen 1991), not showing, for example, how pesticides affect various species in the food web at different times.

In this paper we show that the future abundances of Philippine rice pests are less predictable in an insecticide-sprayed plot than in an unsprayed plot. This result was obtained using data from a 645-taxa Philippines-wide food web and multiple regression models that incorporated the phenology (presence or absence over time), species abundances and food web position of major rice-field species. The models attempted to explain the population fluctuations observed in rice pests during a 1990 growing season at the International Rice Research Institute (IRRI) in the Philippines. Food web structure provided a qualitative framework in which to explore quantitative predictive models of pest population dynamics.

Materials and methods

FIELD SITE

Fieldwork was conducted in a lowland irrigated field at the IRRI farm, located in Laguna Province, Philippines, 62 km southeast of Manila, Luzon, 13°14′N, 121°15′E, 22 m above sea level. IRRI lies in the rain shadow of Mt. Makiling, a dormant volcano. The Mahaas clay soil of volcanic origin has pH 6·6 and is generally kept neutral by constant irrigation (Moormann & van Breemen 1978).

The climate at IRRI is dominated by cool dry (January–May) and hot wet (July–November) seasons. Annual precipitation at IRRI averages 2100 mm. Mean monthly maximum and minimum temperatures vary by 7–10 °C, May being the warmest (34·1 °C) and February the coolest (21·5 °C) months (IRRI 1992). Severe tropical typhoons with winds exceeding 120 kph occur each year, usually between September and November.

EXPERIMENTAL DESIGN AND DATA COLLECTION

The experiment was conducted on the IRRI farm during the dry season in 1990. One 24 × 90 m field (field 217) was divided into two 24 × 45 m plots. One plot was randomly assigned the insecticide treatment. The other received no insecticide. Before planting, the whole field was ploughed and then harrowed twice to puddle the soil, which was kept under standing water to lessen weed growth until transplanting of rice seedlings. On 20 March 1990, 20-day-old rice seedlings of cultivar IR1917–3–17 were transplanted by hand into the field. Transplanting was not synchronized with the surrounding fields. Standard agronomic practices were followed. These included planting two to four seedlings per hill in a 25 × 25 cm spacing pattern with fertilizer applied at three stages: basal, maximum tillering and panicle initiation, at the rate of 120 kg N (Planters Urea 46) per ha. Hand-weeding was conducted at fortnightly intervals. Hand-harvesting and threshing of the rice crop took place approximately 100 days after transplanting (DT).

Foliar spraying of insecticide in the treated plot followed morning sampling on 19 April (30 DT), 29 April (40 DT) and 9 May (50 DT). During the study, a 3-m wide no-spray zone was established along the perimeter of the sprayed plot to minimize insecticide carry-over into the unsprayed plot, because a previous study showed insecticide drift occurred within 3 m of a sprayed border (Litsinger *et al.* 1987). Standard field dosages of 12·5 g active ingredient (a.i.) ha^{-1} of deltamethrin, a high-toxicity pyrethroid (Croft 1990), were sprayed using a standard 161 hand-operated knapsack sprayer. Insecticide application was designed to mimic standard field practices of local farmers.

Using standard sampling methods for flooded rice communities (Heong, Aquino & Barrion 1991), arthropod samples were collected from 5 April (16 DT) to 21 May (62 DT), 1990. The sampling unit for this series was a cubed-shaped mylar enclosure (0·5 × 0·5 × 0·9 m high). This enclosure covers four hills after transplanting, but fewer hills after the plants reach maximum tillering. For each of 19 sampling dates, 10 randomly placed samples were taken from each of the two plots for a total of 380 samples; the average interval between consecutive dates was 2·6 days (SD 1·6 days). All organisms inside the enclosure were vacuumed using a portable FARMCOP suction device (Cariño, Kenmore & Dyck 1979). The device is a hand-carried vacuum cleaner (National, model HC-180) powered by two 12-volt rechargeable batteries with a capacity to move 0·8 m^3 air min^{-1}. Organisms and water were vacuumed through a rubber collection hose (1·5 cm internal diameter ×1·5 m long) into a plastic reservoir with a nylon mesh strainer. Collected material was flushed into a glass vial containing 70% ethanol. Time spent sampling varied from 2 to 5 min, depending on the age and size of the crop. The contents of each vial were sorted, counted and identified using a dissecting microscope, and recorded on standard data sheets. All taxa were identified to species or to genus whenever possible (Barrion & Litsinger, in press).

RICE PRODUCTION ESTIMATES

We estimated rice production over the growing season as grams dry weight of rice matter per hill using data in Kenmore (1980). Individual data points were extracted from Kenmore's eye-fitted curves of total dry matter of rice as a function of DT for insecticide-treated and insecticide-free plots at the IRRI farm during the dry season in 1979. In his insecticide-treated fields, diazinon, an organophosphate, was applied in standard field dosages of 750 g a.i. ha^{-1} on each of four dates: 34, 47, 58, and 69 DT. Decamethrin (now called deltamethrin) followed diazinon on the first three application dates and was sprayed at a rate of 8 g a.i. ha^{-1}. Since brown planthopper (*Ni. lugens*) outbreaks produced hopperburn on his insecticide-treated fields, Kenmore collected only green, non-hopperburned plants to estimate rice production in his insecticide-treated fields (Kenmore 1980).

THE PHILIPPINE RICE FOOD WEB

The cumulative food web of Philippine rice fields above the water line includes at least 645 taxa (viruses, fungal pathogens, nematodes, insects, spiders, mites, vertebrates) at 23 sites (IRRI 1980, 1983, 1984, 1985, 1986, 1987, 1988, 1989, 1990). Among these species are 25 putative major and minor pests of rice: *Sogatella furcifera* Horváth *Tagasodes pusanus* (Distant) (whitebacked planthoppers), *Recilia dorsalis* (Motschulsky) (rice zigzag leafhopper), *Cofana spectra* (Distant) (rice white leafhopper), *Chilo auricilius* (Dudgeon) (gold-fringed stemborer), *C. suppressalis* (Walker) (striped stemborer), *Marasmia exigua* (Butler), *M. patnalis* Bradley, *M. ruralis* (Walker), *Cnaphalocrocis medinalis* (Guenée) (rice leaffolders), *Nilaparvata lugens* (Stål) (rice brown planthopper), *Nephotettix virescens* (Distant), *N. malayanus* Ishihara and Kawase, *N. nigropictus* (Stål) (green leafhoppers), *Pelopidas mathias* Fabricius (rice skipper), *Melanitis leda ismene* (Cramer) (rice greenhorned caterpillar), *Atherigona oryzae* Malloch (seedling maggot), *A. orientalis* Stein (seedling maggot), *Hydrellia philippina* Ferino (rice whorl maggot), *Nymphula depunctalis* (Guenée) (rice caseworm), *Leptocorisa oratorius* (Fabricius), *Eysarcoris ventralis* (Westwood) (rice seed bugs), *Scotinophara latiscula* Breddin (rice black bug), *Scirpophaga incertulas* (Walker) (rice yellow stem borer) and *S. innotata* (Walker) (rice white stem borer). Mungbean is sometimes relay cropped with rice in the Philippines. Its pest and predator species are also included in the cumulative rice–mungbean food web (Litsinger *et al.* 1988).

The cumulative Philippines web has over 9000 trophic (consumer–resource) links, determined from field observations, exposing eggs of potential host species in the field to collect immature parasitoids and parasites, and predator preference and selectivity tests in the laboratory. At IRRI farm alone, researchers have logged approximately 2000 person-hours in the field elucidating consumer–resource links of the rice paddy system (A.T. Barrion, unpublished data).

Of the 645 taxa presently in the web, 121 taxa were reported in the 1990 IRRI experimental field. Webs representing sprayed and unsprayed plots were first constructed using the 645-taxa Philippines-wide web. We assumed that a feeding link from a prey to a predator was present in the IRRI farm if and only if such a link was present in the Philippine web (as in Schoenly & Cohen 1991). We then separated each known pest and the known enemies of each pest, and sorted the pests and enemies by total abundance, totalled over all sampling dates.

SELECTION OF PESTS, ENEMIES AND THE TIME-LAG

Mean abundances were nearly proportional to standard deviations of abundances for herbivore and enemies, over the 19 sampling dates, in sprayed and unsprayed plots (Fig. 1a and b). To stabilize the variances and create statistically normal distributions, these abundances were log-transformed before analysis, using $\log_{10}(x+1)$, where x is the counted abundance. Following log transformation, standard deviations were nearly uncorrelated with the means in the sprayed and unsprayed plots (Fig. 1c and d). We used herbivore and enemy taxa whose mean abundances, over the 19 dates, exceeded 0·355 on the log-transformed plots (or 1·26 individuals per sampling date or a total of 24 individuals on all 19 dates, Fig. 1a and b) as possible dependent and independent variables in the models (Fig. 1c and d).

To guide the choice of time-lag τ to use in the regression models, different values of τ were applied to the autocorrelation model $p(t+\tau) = a + bp(t)$, where $p(t)$ is the transformed pest abundance $\log_{10}(x+1)$ at time t. In both sprayed and unsprayed plots, current pest abundance predicted future pest abundance better when the time-lag between them was one sampling interval (average of 2·6 days) than after two sampling intervals, for five pests in the unsprayed plot (*Ne. virescens, R. dorsalis, N. lugens, H. philippina, Ne. nigropictus*) and two pests in the sprayed plot (*Ne. virescens, R. dorsalis, H. philippina*; Table 1). In the remaining six cases (two unsprayed and four sprayed pests), a time-lag of two sampling intervals (average of 5·2 days between samples) predicted pest abundance only slightly better than a time-lag of three sampling intervals, or 7·8 days. Given the overall better fit with the 2·6 day lag than with either the 5·2 or 7·8 day lags, all subsequent models used time-lag $\tau = 1$.

If population fluctuations of pests at the IRRI farm are strongly linked to the population fluctuations of their natural enemies, we assumed such linkages would be found by studying the commonest pests and their most highly correlated and abundant natural enemies. The pests included both major (*Ne. virescens, S. furcifera, Ni. lugens, H. philippina, Ne. nigropictus*) and minor pests (*R. dorsalis, C. spectra*) of Philippine irrigated rice fields (Reissig *et al.* 1986). To determine the enemy species of each pest, we first fitted the model $p(t+1) = a + b_i e_i(t)$, where p and e_i are the $\log_{10}(x+1)$ abundances of

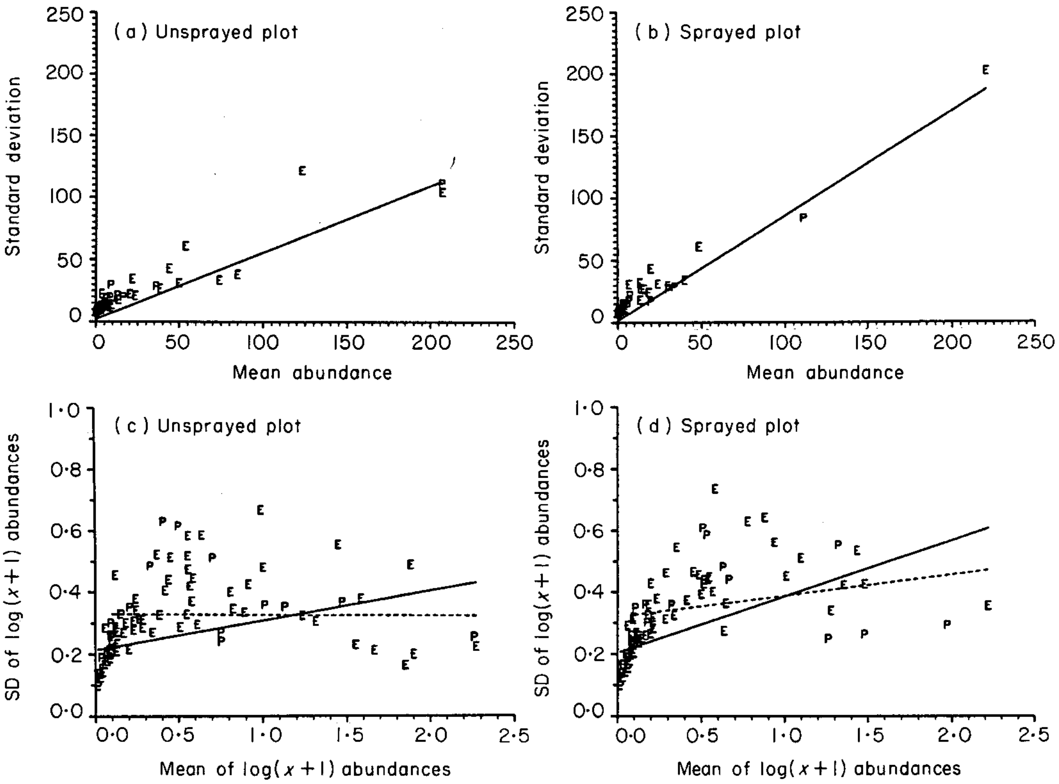

Fig. 1.(a–d) Standard deviation and mean of abundance, over 19 sampling dates, of each herbivore (P) and each enemy (E) sampled at IRRI farm from unsprayed and sprayed plots. Plots (a) and (b) are untransformed values for unsprayed and sprayed plots, respectively. Plots (c) and (d) are $\log_{10}(x+1)$ values for unsprayed and sprayed plots, respectively. Solid lines are least-squares fits encompassing all points in each graph; dashed lines represent best fits encompassing log-transformed means above 0·355 or 1·26 individuals per sampling date.

Table 1. Fits of a linear autocorrelation model $p(t+\tau)=a+bp(t)$, where $p(t)$ is $\log_{10}(x+1)$ abundance of the pest at time t, to the time-series of $\log_{10}(x+1)$ abundances of the seven most abundant pests, for time-lags $\tau=1, 2, 3$

	Unsprayed (U) plot			Sprayed (S) plot		
τ	1	2	3	1	2	3
df[†]	16	15	14	16	15	14
Ne. virescens						
b[‡]	0·87	0·76	0·73	0·39	−0·29	−0·32
SE[§]	0·14	0·21	0·25	0·25	0·22	0·21
r^2	0·71**	0·45**	0·37*	0·13	0·10	0·15
R. dorsalis						
b	0·45	0·31	0·47	0·40	0·35	0·52
SE	0·14	0·15	0·14	0·18	0·18	0·16
r^2	0·39**	0·21	0·45**	0·25*	0·20	0·43**
S. furcifera						
b	0·65	0·68	0·41	0·09	−0·15	−0·39
SE	0·23	0·23	0·29	0·25	0·26	0·25
r^2	0·33*	0·37**	0·13	0·008	0·02	0·15
Ni. lugens						
b	0·32	0·06	0·06	−0·09	−0·31	−0·09
SE	0·20	0·18	0·18	0·26	0·22	0·25
r^2	0·14	0·008	0·007	0·007	0·11	0·01
H. philippina						
b	0·74	0·63	0·55	0·72	0·53	0·49
SE	0·07	0·09	0·09	0·13	0·17	0·18
r^2	0·85**	0·77**	0·74**	0·65**	0·39**	0·34*
Ne. nigropictus						
b	0·22	0·10	0·14	−0·07	−0·08	−0·20
SE	0·21	0·22	0·23	0·27	0·27	0·27
r^2	0·06	0·01	0·03	0·004	0·006	0·04
C. spectra						
b	0·10	0·12	0·30	−0·13	−0·29	−0·27
SE	0·24	0·23	0·24	0·26	0·25	0·23
r^2	0·01	0·02	0·10	0·02	0·09	0·10

[†] Degrees of freedom.

[‡] Model fitted: $p(t+\tau)=a+bp(t)$. Thus, b is the increase in the average log abundance $p(t+\tau)$ per unit increase in the log abundance $p(t)$.

[§] SE, standard error of estimate of b.

* $P<0{\cdot}05$, ** $P<0{\cdot}01$.

the pest and enemy i, then used the coefficient of determination (r^2) to determine which current enemy abundance at time t best predicted future pest abundance at time $t+1$. To test the ability of the models to reveal differences between sprayed and unsprayed plots, the same enemies of each pest in the unsprayed plot were used in the sprayed plot. The final models included only enemy species whose average log-abundance exceeded 0·355. Because IRRI collections were limited to 19 samples per plot and bacause each new independent variable added to a regression model deducts one degree of freedom, we chose five as the limit of enemy taxa to use as independent variables in each initial pest model.

THE MODELS

We used multiple step-wise regression to describe the abundances of seven pest species observed in sprayed and unsprayed plots during a growing season. The independent variables of these models were the abundance of each pest, the biomass of rice, and the abundance of the five most highly correlated enemies of each pest. Suppose a pest species P eats rice R and is eaten or parasitized by enemy species E_1–E_5. E_1 refers to the most highly correlated enemy to P, E_2 to the second most highly correlated, and E_5 to the fifth most highly correlated enemy of P. Both the five enemies and their ordering may differ for different pests P. The sampled abundances of these species at time t are indicated by placing (t) after their name. Repeated sampling at the IRRI farm yielded a data table in which rice, pests and enemies corresponded to columns, and sampling dates correspond to rows. The food web guided the choice of independent variables. Before analysis began, rice, pest and enemy abundances were subjected to $\log_{10}(x+1)$ transformations; henceforth, $r(t)=\log_{10}[1+R(t)]$, $p(t)=\log_{10}[1+P(t)]$, and $e(t)=\log_{10}[1+E(t)]$ refer to log-transformed values of rice, pest, and enemy abundances at time t.

Three steps were employed to investigate differences in pest abundances between sprayed and unsprayed plots. For each pest at time $t + 1$, we first constructed multiple regression models containing the seven independent variables:

$$p(t + \tau) = a + bp(t) + cr(t) + d_1e_1(t) + \ldots + d_5e_5(t). \qquad \text{eqn (1)}$$

To find the best set of predictor variables in the models, we employed a backward elimination procedure (Sokal & Rohlf 1981) which involved stepwise removal of individual variables whose presence contributed the smallest partial correlation (r) to the relationship between the dependent and the remaining independent variables. Removals continued until the set of F-ratios and partial regression coefficients for all remaining variables were statistically significant. The remaining variables were considered as predictor variables. Backward elimination was performed on the unsprayed model to identify predictor variables, after which these variables were retained as the only 'predictor variables' in the sprayed plot following removal of the other variables.

The second step involved addition of interaction terms, if any were possible, to the model. Only those interactions which were statistically significant were retained. As before, backward elimination was performed first on variables of the model of the unsprayed plot. The same variables were then used in the model of the sprayed plot.

The third step added a dummy variable to assess the effect of insecticidal sprays on pest and enemy population dynamics. A column was added to the data matrix with value 1 to indicate the presence of spraying and value 0 to indicate the absence of spraying. These values were also transformed according to $\log_{10}(x + 1)$. In the unsprayed plot data matrix, all entries for the spray dummy variable were 0. Because deltamethrin applications followed morning sampling on 30, 40 and 50 DT, raw values of 1 were added to the 32, 42 and 52 DT rows of the data matrix. All statistical tests were judged at the nominal level of significance ($P = 0{\cdot}05$), and significant results in the text are indicated with one ($P < 0{\cdot}05$) or two ($P < 0{\cdot}01$) asterisks.

Results

TIME-LAG ANALYSIS

Table 1 shows the results of fitting the model $p(t + \tau) = a + bp(t)$ to the time-series of abundances of the seven most abundant pests. For the sprayed plot, there were 21 models: seven pests × three values of $\tau = 1,2,3$. Likewise, there were 21 models for the unsprayed plot. In the unsprayed plot, autocorrelations were significant ($P < 0{\cdot}05$) in 10 of 21 fitted models (48%) compared to only five (24%) in the sprayed plot. Nearly half of the significant models (7/15 or 47%) described the two most abundant pest species (*Ne. virescens, R. dorsalis*), whereas no significant autocorrelations were found among the two rarest pest species (*Ne. nigropictus* and *C. spectra*). Thus, current pest abundance was a better predictor of future pest abundance in the unsprayed plot than in the sprayed plot and this trend was more pronounced in models of the commoner pest species.

IRRI FOOD WEB AND PEST AND ENEMY ABUNDANCES

At the IRRI farm, each of the seven pest species shared the mirid bug, *Cyrtorhinus lividipennis* (Reuter), as one of its highly correlated enemies in the sprayed and unsprayed plots (Table 2). A tetragnathid spider, *Dyschiriognatha* sp., was an important enemy of six of the seven pests. The enemies of *S. furcifera* differed most from the enemies of the other six pests. Two pest species were more abundant in sprayed than unsprayed plots (Table 2).

The most highly correlated and abundant enemies of pests collected at IRRI in both sprayed and unsprayed plots were five predatory beetles [*Stilbus* sp., *Harmonia octomaculata, Ophionea nigrofasciata* (Schmidt-Goebel), *Scymnus* spp., *Opius* sp.], four spiders [*Dyschiriognatha* sp., *Atypena* (= *Callitrichia*) *formosana* Oi, *Tetragnatha* sp., *Araneus inustus* (L. Koch)], three hymenopterans (*Gonatocerus* spp., *Mymar taprobanicum*, *Pteromalus* sp.), two bugs [*Cyrtorhinus lividipennis* Reuter, *Mesovelia vittigera* (Horváth)], and one immature odonate (*Anisops kuroiwai*). With the exception of *C. lividipennis*, *Pteromalus* sp. and *A. kuroiwai*, the other 11 natural enemies were between 21% to 276% more abundant in the unsprayed plot than in the sprayed plot (Table 2).

Temporal variation in the abundance of each of the seven common pest species is shown in Fig. 2a–g. For the cicadellid homopterans (*Ne. virescens, R. dorsalis, Ne. nigropictus, C. spectra*), populations were nearly always lower after repeated application of deltamethrin (Fig. 2a, b, f, g). Shortly after each application, however, populations of cicadellids generally recovered to densities as high as in the untreated plot. In the case of the rice whorl maggot, *H. philippina* (Fig. 2e), populations in both sprayed and unsprayed plots declined steadily with crop age, although the unsprayed plot had slightly higher densities. For the two delphacid homopterans, *S. furcifera* and *Ni. lugens*, substantially higher densities were nearly always recorded in the sprayed plot than the unsprayed plot for the entire period following the first application of deltamethrin (Fig. 2c and d).

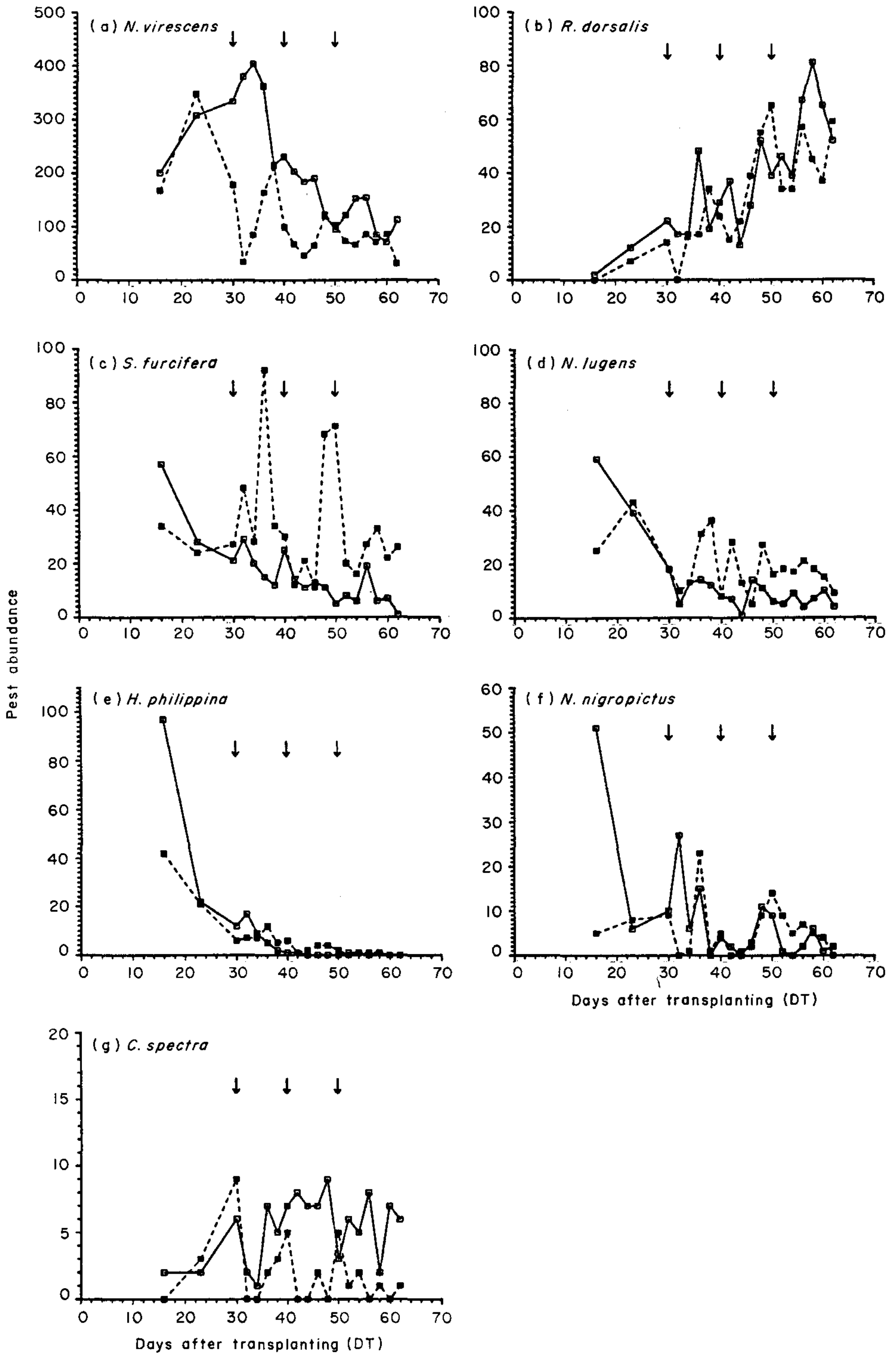

Fig. 2.(a–g) Raw counts of seven herbivore species sampled at the IRRI farm from deltamethrin-sprayed (■) and unsprayed (□) plots on each of 19 sampling dates during the dry season 1990. Counts are nymphs and adults collected per 2·5 m^2. Arrows indicate dates of insecticide application.

MULTIPLE REGRESSION ANALYSIS

Results of the regression analyses for each of the seven pests are summarized in Tables 3 and 4. For brevity, we will discuss results for only three of the seven pest species.

Nephotettix virescens

For this abundant pest, the initial model predicted future pest abundance significantly better in the unsprayed plot than in the sprayed plot (Table 3). In the unsprayed plot, the contributions of four independent variables were significant, whereas in the sprayed plot, no variables were significant.

Table 2. Seven rice pests of the IRRI farm and their five most highly correlated arthropod enemies. Pests are arranged in order of decreasing total abundance in the unsprayed (U) and sprayed (S) plots. The five arthropod enemies of each pest are arranged in order of decreasing r^2 values in the unsprayed plot. n refers to total counts in unsprayed and sprayed plots during dry season 1990. Squared correlation coefficients (r^2) are fits to the model: $p(t+1) = a + b_i e_i(t)$, where $p(t+1)$ = pest and $e_i(t)$ = enemy$_i$ $\log_{10}(x+1)$ abundances

		Arthropod enemies, $e_1(t)$–$e_5(t)$				
Pest species		$e_1(t)$	$e_2(t)$	$e_3(t)$	$e_4(t)$	$e_5(t)$
Ne. virescens		*C. lividipennis*	*O. nigrofasciata*	*A. formosana*	*H. octomaculata*	*Dyschiriognatha* sp.
(Cicadellidae: Homoptera; U = 3931, S = 2112)	U r^2	0·8252	0·5722	0·3701	0·2190	0·2144
	n	2340	88	1612	78	148
	S r^2	0·0566	0·1082	0·0013	0·1884	0·0856
	n	4192	73	761	47	67
R. dorsalis		*C. lividipennis*	*M. taprobanicum*	*O. nigrofasciata*	*Dyschiriognatha* sp.	*A. kuroiwai*
(Cicadellidae: Homoptera; U = 685, S = 574)	U r^2	0·5078	0·3848	0·3308	0·2516	0·2472
	n	2340	51	88	148	66
	S r^2	0·0003	0·3544	0·0986	0·2091	0·0128
	n	4192	26	73	67	81
S. furcifera		*C. lividipennis*	*Scymnus* spp.	*Stilbus* sp.	*M. taprobanicum*	*H. octomaculata*
(Delphacidae: Homoptera; U = 308, S = 644)	U r^2	0·6047	0·5433	0·5097	0·3517	0·2697
	n	2340	259	837	51	78
	S r^2	0·0496	0·0530	0·0000002	0·0012	0·0002
	n	4192	78	297	26	47
Ni. lugens		*Dyschiriognatha* sp.	*Scymnus* spp.	*Stilbus* sp.	*H. octomaculata*	*C. lividipennis*
(Delphacidae: Homoptera; U = 246, S = 371)	U r^2	0·4699	0·3840	0·3007	0·2591	0·1983
	n	148	259	837	78	2340
	S r^2	0·0844	0·0266	0·0587	0·1534	0·0297
	n	67	78	297	47	4192
H. philippina		*Tetragnatha* sp.	*Opius* sp.	*C. lividipennis*	*Dyschiriognatha* sp.	*M. vittigera*
(Ephydridae: Diptera; U = 169, S = 122)	U r^2	0·7627	0·6579	0·6157	0·3000	0·1480
	n	1024	417	2340	169	951
	S r^2	0·3599	0·4591	0·0063	0·1530	0·3902
	n	370	262	4192	67	253
N. nigropictus		*C. lividipennis*	*Dyschiriognatha* sp.	*Gonatocerus* spp.	*O. nigrofasciata*	*A. inustus*
(Cicadellidae: Homoptera; U = 156, S = 108)	U r^2	0·1487	0·0992	0·0547	0·0540	0·0339
	n	2340	148	737	88	140
	S r^2	0·0071	0·0004	0·0068	0·0021	0·0270
	n	4192	67	459	73	89
C. spectra		*Tetragnatha* sp.	*C. lividipennis*	*Dyschiriognatha* sp.	*Pteromalus* sp.	*Gonatocerus* spp.
(Cicadellidae: Homoptera; U = 100, S = 34)	U r^2	0·1604	0·1234	0·1114	0·1040	0·0722
	n	1024	2340	148	68	737
	S r^2	0·0766	0·1602	0·1175	0·0671	0·0614
	n	378	4192	67	70	459

Table 3. Multiple regression and analysis of variance for initial models that fitted the abundance $p(t+1)$ of the seven most abundant rice pests to seven independent variables. The independent variables are: $p(t)$, pest; $r(t)$, rice, $e_1(t), \ldots, e_5(t)$, five enemies of pest listed in Table 1. Original data taken at the IRRI farm on unsprayed and sprayed plots during dry season 1990

	Unsprayed plot			Sprayed plot		
Predictor variables	coef.†	SE‡	$t^{\S}$	coef.	SE	t
1. *Ne. virescens*	0·9439	0·6902	1·3676	2·3653	0·8460	2·7959**
p	0·4705	0·1590	2·9596**	−0·1750	0·5260	0·3326
r	−0·1792	0·1003	1·7876	−0·5439	0·3287	1·6547
e_1	0·2705	0·1305	2·0720*	0·3644	0·3192	1·1419
e_2	−0·1162	0·0591	1·9678*	0·2086	0·3446	0·6052
e_3	0·1629	0·1759	0·9265	−0·1880	0·2642	0·7116
e_4	−0·0222	0·0476	0·4661	−0·0398	0·2865	0·1388
e_5	−0·3506	0·0745	4·7068**	−0·0160	0·2111	1·0757
	F-ratio = 35·7280** with 7 df r^2 = 0·9616			F-ratio = 1·2229 with 7 df r^2 = 0·4401		
2. *R. dorsalis*	1·1974	0·7649	1·5656	0·1497	1·1173	0·1340
p	−0·2690	0·2938	0·9154	−0·1421	0·3712	0·3830
r	0·5651	0·3386	1·6689	0·9266	0·7041	1·3160
e_1	−0·1286	0·2282	0·4462	0·1383	0·3530	0·3918
e_2	−0·1859	0·2750	0·6762	0·3817	0·4642	0·8223
e_3	0·1825	0·2112	0·8635	−0·2437	0·3569	0·6828
e_4	0·1268	0·1932	0·6561	−0·0916	0·3805	0·2407
e_5	0·3306	0·1941	1·7029	−0·2227	0·3475	0·6410
	F-ratio = 3·2341* with 7 df r^2 = 0·6936			F-ratio = 1·9676 with 7 df r^2 = 0·5794		
3. *S. furcifera*	−0·2019	0·8128	0·2485	0·7322	0·9318	0·7858
p	−0·5219	0·2892	1·8045*	0·1347	0·4918	0·2739
r	0·7498	0·4260	1·7601	0·0889	0·3711	0·2395
e_1	1·0194	0·2608	3·9083**	0·2486	0·3988	0·6234
e_2	0·0536	0·3207	0·1671	−0·2734	0·2845	0·9611
e_3	−0·7799	0·2796	2·7887**	−0·0431	0·3060	0·1408
e_4	0·5560	0·2370	2·3460*	−0·0097	0·3895	0·0249
e_5	−0·1679	0·1471	1·1418	0·1619	0·3714	0·4358
	F-ratio = 7·8272** with 7 df r^2 = 0·8457			F-ratio = 0·5027 with 7 df r^2 = 0·2603		
4. *Ni. lugens*	1·9895	1·1214	1·7740	1·3180	0·8678	1·5188
p	−0·1927	0·2700	0·7138	−0·3750	0·3705	1·0121
r	−0·2358	0·6746	0·3496	0·0329	0·4040	0·0815
e_1	0·5093	0·2528	2·0147*	0·2242	0·2076	1·0802
e_2	−0·2557	0·4868	0·5253	−0·1082	0·2424	0·4464
e_3	−0·0183	0·3834	0·0477	0·0573	0·2648	0·2162
e_4	−0·0944	0·2214	0·4264	−0·2048	0·2846	0·7194
e_5	−0·3391	0·2730	1·2419	0·1573	0·2802	0·5615
	F-ratio = 2·2182 with 7 df r^2 = 0·6083			F-ratio = 0·6118 with 7 df r^2 = 0·2998		
5. *H. philippina*	0·0098	1·1209	0·0087	2·5325	0·6006	4·2164**
p	0·4168	0·2256	1·8474*	−0·0627	0·3324	1·1887
r	0·0785	0·5014	0·1566	−1·0332	0·5100	2·0261*
e_1	0·4352	0·3948	1·1309	0·1544	0·1846	0·8369
e_2	0·1010	0·2226	0·4539	0·6800	0·2528	2·6897*
e_3	0·1638	0·2500	0·6551	−0·3524	0·2707	1·3018
e_4	−0·2367	0·2086	1·1344	−0·2918	0·1513	0·9294*
e_5	−0·4947	0·3080	1·6065	−0·6500	0·2277	2·8549**
	F-ratio = 13·6790** with 7 df r^2 = 0·9054			F-ratio = 11·3083** with 7 df r^2 = 0·8878		

Table 3. (*continued*)

	Unsprayed plot			Sprayed plot		
Predictor variables	coef.[†]	SE[‡]	t[§]	coef.	SE	t
6. *Ne. nigropictus*	1·5160	2·0892	0·7257	0·9473	1·3264	0·7142
p	−0·0717	0·3581	0·2001	0·0620	0·5393	0·1150
r	−0·7942	0·7559	1·0507	−0·2911	0·6351	0·4584
e_1	−0·1297	0·7126	0·1820	−0·0087	0·8968	0·0097
e_2	0·0138	0·7249	0·0190	−0·1844	0·4659	0·3958
e_3	0·2936	0·9363	0·3135	−0·0505	0·7430	0·0680
e_4	0·2039	0·4464	0·4568	0·1552	0·6321	0·2455
e_5	−0·2858	1·4376	0·6532	0·1948	0·5061	0·3850
	F-ratio = 0·4889 with 7 df			F-ratio = 0·0764 with 7 df		
	r^2 = 0·2550			r^2 = 0·0508		
7. *C. spectra*	2·5757	1·2980	1·9844*	−0·3829	0·6234	0·6143
p	−0·6077	0·3405	1·7850	−0·3855	0·2463	1·5647
r	−0·2258	0·4423	0·5104	−0·8025	0·3945	2·0340*
e_1	−0·5575	0·4223	1·3202	−0·3989	0·3011	1·3249
e_2	−0·1003	0·2345	0·4278	1·1353	0·4128	2·7501**
e_3	−0·0327	0·2922	0·1119	0·2121	0·2247	0·9440
e_4	0·2805	0·1307	2·1468	0·2177	0·2371	0·9182
e_5	−0·0376	0·3817	0·0986	−0·4172	0·3623	1·1516
	F-ratio = 1·1816 with 7 df			F-ratio = 2·0804 with 7 df		
	r^2 = 0·4527			r^2 = 0·5929		

[†] y-intercept and regression coefficients estimated for equation 1.
[‡] standard error of regression coefficient.
[§] t value.
* $P < 0{\cdot}05$, ** $P < 0{\cdot}01$.

In the unsprayed plot, future abundance of *Ne. virescens* was significantly and positively correlated with current abundance (p) and the mirid bug *C. lividipennis* (e_1), and was significantly and negatively correlated with the carabid beetle *O. nigrofasciata* (e_2), and the spider *Dyschiriognatha* sp. (e_5). Rice was a marginally significant variable for both plots. For the full model, the total explained variance was 96% and 44% in the unsprayed and sprayed cases, respectively.

After step-wise removal of all non-significant variables in the unsprayed model of *Ne. virescens*, the F value jumped from 35·73 to 52·939, yielding a five variable model of future abundance of *Ne. virescens* that included itself, three of its enemies, and rice. The same five variables in the sprayed model, however, failed to produce a significant fit (Table 4). After the 10 pair-wise interaction terms were added to each model, neither model showed an improved fit, indicating an absence of significant interactions when the pest, three of its enemy species and rice were used in combination. The addition of sprays as a dummy variable in the five-variable sprayed version of the model reduced the fit in this case (Table 4).

Nilaparvata lugens

Although the combination of food web variables gave a higher fit in the unsprayed plot than in the sprayed plot, neither pest model was significant (Table 3). All but one of the correlations between the independent variables and future abundance of brown planthoppers were non-significant in the sprayed and unsprayed plots. The exceptional case was a positive correlation between *Ni. lugens* and one of its abundant natural enemies, *Dyschiriognatha* sp., in the unsprayed plot. The total percentage of variance explained by this single variable was twice as large in the unsprayed plot as in the sprayed plot (61% vs. 30%; Table 3).

Following step-wise removal of all non-significant variables in the unsprayed plot, the difference in F-values between the sprayed and unsprayed models of *Ni. lugens* abundance increased nearly eight-fold (Table 4). The result was a highly significant fit in the unsprayed plot between *Dyschiriognatha* sp. (e_1) and future pest abundance. The addition of sprays made the fit slightly worse in the sprayed plot.

Hydrellia philippina

Initial seven-variable models significantly predicted future pest abundance about equally well in the sprayed and unsprayed plots (Table 3). Significant predictors included the pest itself (p) in the unsprayed plot and rice, the braconid *Opius* sp. (e_2), *Dyschiriognatha* sp. (e_4) and the mesoveliid *M. vittigera* (e_5) in the sprayed plot. The percentage of variance explained by the seven-variable models of

Table 4. Multiple regression and analysis of variance for models with interaction and spray variables that fitted the abundance $p(t+1)$ of the seven most abundant pests, $b-e$ model = backward–elimination model

Pest and variable(s) in model	Unsprayed plot		Sprayed plot	
	coef.†	t	coef.†	t
1. *Ne. virescens*				
a. $b-e$ model				
y pest(t + 1)	1·5130	6·1623**	2·4134	3·0766**
p pest	0·4309	3·0307**	−0·2999	0·6443
r rice biomass	−0·2478	3·2404**	−0·5000	1·7194
e_1 *C. lividipennis*	0·1872	1·8804*	0·3293	1·1708
e_2 *O. nigrofasciata*	−0·1021	1·8266*	0·0570	0·2377
e_5 *Dyschiriognatha* sp.	−0·3113	4·9647**	−0·0102	0·0516
	F-ratio = 52·9297**		F-ratio = 1·6721	
b. Interactions				
(no significant x terms)	F-ratio = 9·2640		F-ratio = 1·5613	
c. Addition of sprays				
y pest (t + 1)	1·5130	6·1623**	2·8216	3·1705*
p pest	0·4309	3·0307**	−0·4163	0·8648
r rice biomass	−0·2478	3·2404**	−0·5524	1·8649*
e_1 *C. lividipennis*	0·1872	1·8804*	0·3001	1·0588
e_2 *O. nigrofasciata*	−0·1021	1·8266*	0·0592	0·2465
e_5 *Dyschiriognatha* sp.	−0·3113	4·9647**	−0·0440	0·2225
s *sprays*‡	0·0000	0·0000	−0·5954	0·9774
	F-ratio = 52·9297**		F-ratio = 1·5474	
2. *R. dorsalis*				
a. $b-e$ model				
y pest($t+1$)	0·9433	7·1657**	0·5166	2·0929*
r rice biomass	0·5054	4·6603**	0·7091	3·7420**
	F-ratio = 21·7183**		F-ratio = 14·0022**	
b. Interactions: none to add				
c. Addition of sprays				
y pest ($t+1$)	0·9433	7·1657**	0·5222	2·0387*
r rice biomass	0·5054	4·6603**	0·7102	3·6322**
s *sprays*‡	0·0000	0·0000	−0·1392	0·1991
	F-ratio = 21·7183**		F-ratio = 6·6006**	
3. *S. furcifera*				
a. $b-e$ model				
y pest (t + 1)	0·5067	0·7870	1·1188	2·3590*
p pest	−0·5288	1·7741*	−0·1517	0·3997
e_1 *C. lividipennis*	0·8182	3·9032**	0·2825	0·9142
e_3 *Stilbus* sp.	−0·4057	2·7746**	−0·0559	0·3524
e_4 *M. taprobanicum*	0·5207	2·3097*	−0·0043	0·0158
	F-ratio = 11·8797**		F-ratio = 0·2447	
b. Interactions				
(no significant x terms)	F-ratio = 3·5564		F-ratio = 0·6565	
c. Addition of sprays				
y pest ($t+1$)	0·5067	0·7870	1·2774	2·2996*
p pest	−0·5288	1·7741*	−0·1017	0·2554
e_1 *C. lividipennis*	0·8182	3·9032**	0·1833	0·5112
e_3 *Stilbus* sp.	−0·4057	2·7746**	−0·0251	0·1470
e_4 *M. taprobanicum*	0·5207	2·3097*	−0·0724	0·2303
s *sprays*‡	0·0000	0·0000	−0·4070	0·5917
	F-ratio = 11·8797**		F-ratio = 0·2560	
4. *Ni. lugens*				
a. $b-e$ model				
y pest ($t+1$)	0·4657	3·2559**	1·1821	15·0535**
e_1 *Dyschiriognatha* sp.	0·5909	3·7660**	0·1498	1·2142
	F-ratio = 14·1829**		F-ratio = 1·4743	

Table 4. (*continued*)

Pest and variable(s) in model	Unsprayed plot		Sprayed plot	
	coef.†	*t*	coef.†	*t*
4. *Ni. lugens* (*cont.*)				
b. Interactions: none to add				
c. Addition of sprays				
y pest ($t+1$)	0·4657	3·2559	1·1934	12·9878**
e_1 *Dyschiriognatha* sp.	0·5909	3·7660**	0·1398	1·0523
s sprays‡	0·0000	0·0000	−0·1292	0·2580
	F-ratio = 14·1829**		*F*-ratio = 0·7274	
5. *H. philippina*				
a. $b-e$ model				
y pest ($t+1$)	0·0242	0·4051	0·0948	0·9055
p pest	0·7441	9·6975**	0·7198	5·4161**
	F-ratio = 94·0415**		*F*-ratio = 29·3343**	
b. Interactions: none to add				
c. Addition of sprays				
y pest (t + 1)	0·0242	0·4051	0·0204	0·1814
p pest	0·7441	9·6975**	0·7746	5·8232**
s sprays‡	0·0000	0·0000	0·7613	1·5050
	F-ratio = 94·0415**		*F*-ratio = 16·9592**	
6. *Ne. nigropictus*				
a. $b-e$ model				
y pest ($t+1$)	1·2391	3·8899**	0·7236	2·1701*
r rice biomass	−0·5105	1·9454*	−0·0537	0·2097
	F-ratio = 3·7847		*F*-ratio = 0·0440	
b. Interactions: none to add				
c. Addition of sprays				
y pest (t + 1)	1·2391	3·8899**	0·7549	2·2302*
r rice biomass	−0·5105	1·9454*	−0·0474	0·1833
s sprays‡	0·0000	0·0000	−0·7804	0·8442
	F-ratio = 3·7847		*F*-ratio = 0·3780	
7. *C. spectra*				
a. $b-e$ model				
y pest (t + 1)	1·8439	4·3787**	0·3227	1·7755*
p pest	−0·5740	1·9878*	−0·2299	0·9169
e_1 *Tetragnatha* sp.	−0·4524	2·7791**	0·1835	1·2795
e_4 *Pteromalus* sp.	0·2639	2·4208*	−0·1806	0·9089
	F-ratio = 3·4363*		*F*-ratio = 1·0091	
b. Interactions				
(no significant x terms)	*F*-ratio = 1·6533		*F*-ratio = 0·4083	
c. Addition of sprays				
y pest (t + 1)	1·8439	4·3787**	0·3001	1·8364*
p pest	−0·5740	1·9878*	0·2420	0·7607
e_1 *Tetragnatha* sp.	−0·4524	2·7791**	0·1963	1·5243
e_4 *Pteromalus* sp.	0·2639	2·4208*	−0·2785	1·5113
s sprays‡	0·0000	0·0000	−1·9437	2·0977*
	F-ratio = 3·4363*		*F*-ratio = 2·0408	

† y-intercept and regression coefficients estimated for equation 1.
‡ Treated as a dummy variable.
* $P<0·05$, ** $P<0·01$.

H. philippina abundance was high in both sprayed and unsprayed plots (89% vs. 91%; Table 3).

One-variable models of future *H. philippina* abundance that included only current pest abundance were highly significant in both sprayed and unsprayed plots (Table 4). The addition of the spray term reduced the quantitative fit, but did not alter the nature of the relationship between future pest abundance and the independent variables in the sprayed plot.

SPRAYED VS. UNSPRAYED PLOTS

In the unsprayed plot, independent variables were significant predictors of future pest abundance in four out of seven of the initial models compared to one out of seven in the sprayed plot (Table 3). After the non-significant variables were removed from the initial models, the number of significant models increased by only one in the sprayed plot (*R. dorsalis*; Table 4), when the independent variables from the unsprayed models were used. The addition of interaction terms in three of the pest models (*Ne. virescens, S. furcifera, C. spectra*) did not significantly improve the overall fits of any of these models. Similarly, the addition of sprays as a dummy variable lessened the forecasting power of four of seven sprayed models and widened the differences found between them and the unsprayed models. In the exceptional cases, the larger *F* values following the addition of the spray term to the sprayed (*S. furcifera, Ne. nigropictus, C. spectra*) models did not alter the significance or non-significance of any of the models. Overall, when judged against 86% significant fits in the unsprayed plot, the addition of interaction terms and sprays variable to the models gave only 29% (2/7) significant fits in the sprayed plot.

NUMBER AND COMPOSITION OF SIGNIFICANT VARIABLES

The cicadellid, *Ne. virescens*, retained five of its original seven variables as significant predictors compared to four for *S. furcifera*, three for *C. spectra*, and one for the remaining pests (*R. dorsalis, Ni. lugens, H. philippina, Ne. nigropictus*; Table 3). As non-significant variables were dropped from the initial models, the number of significant fits in the unsprayed plot nearly always outnumbered that in the sprayed plot, for any number of independent variables retained in the models (Table 4).

In the unsprayed plot, rice was a non-significant predictor of future pest abundance for all seven pests in the initial seven-variable models, whereas, in the sprayed plot, rice was a significant predictor for two of the seven pests (*H. philippina, C. spectra*; Table 3). Following the step-down procedure, however, this trend reversed, as rice became a significant predictor for three pests in the unsprayed plot (*Ne. virescens, R. dorsalis, Ne. nigropictus*) and only two in the sprayed plot (*Ne. virescens, R. dorsalis*; Table 4).

In the unsprayed plot, current pest abundance by itself was a significant predictor of future pest abundance in initial models of three of the seven pest species: *Ne. virescens, S. furcifera, H. philippina* (Table 3). In the sprayed plot, current pest abundance was a non-significant predictor in all the initial models; however, after the step-down procedure, current pest abundance became a significant predictor of *H. philippina* future abundance (Table 4).

In the unsprayed plot, enemies were included as significant predictors for three out of seven pests of the initial seven-variable models (*Ne. virescens, S. furcifera, Ni. lugens*). Enemies were significant predictors for two pests in the sprayed plot (*H. philippina, C. spectra*; Table 3). Following the step-down process, the number of pests that included enemies as significant predictors increased to four in the unsprayed plot (*C. spectra*; Table 4). *Nephotettix virescens* and *S. furcifera* had the largest number of enemies as significant predictors (three each), followed by *C. spectra* (two) and *Ni. lugens* (one; Table 4).

Discussion

EFFECTS OF SPRAYING

Spraying disorganized the population dynamics of the IRRI paddy ecosystem. In every pair-wise comparison of models in the two plots, the percentage of models with significant fits was lower in the sprayed plot than in the unsprayed plot. Overall, the independent variables used in the model were significant predictors of future pest abundances in only one of seven initial models in the sprayed plot compared to four of seven initial models in the unsprayed plot. As non-significant variables were removed, and interaction and spray variables were added, the differences between sprayed and unsprayed plots became more striking. Thus, the power of models to forecast population fluctuations of pest species, derived from different numbers and combinations of independent variables, was diminished in the sprayed plot relative to the unsprayed plot.

The effect of spraying on abundance was different for different pest species and their natural enemies. Two pests, *S. furcifera* and *Ni. lugens*, had higher abundances in the sprayed plot than in the unsprayed plot (Table 2). For these pests, all of their common natural enemies, except *C. lividipennis* and *A. kuroiwai*, had conspicuously smaller populations in the sprayed plot than the unsprayed plot (Table 2). Moreover, in the sprayed plot, population sizes of these pest species increased following each insecticide application. Although factors other than spraying may be responsible for these (minor) pest outbreaks (e.g. changes in weather; Litsinger, Alviola & Canapi 1986; Mochida, Joshi & Litsinger 1987), other studies on tropical rice pests (e.g., Kenmore *et al.* 1984; Heinrichs & Mochida 1984) have experimentally demonstrated pesticide-induced pest outbreaks. Populations of the five other pest species (*Ne. virescens, R. dorsalis, H. philippina, Ne. nigropictus, C. spectra*) were lower in the sprayed plot than in the unsprayed plot. None of these five pests is known to resurge following insecticide application (Litsinger 1989). Perhaps the spray killed as intended, since the dosage was high. While it is possible that these pests simply left the sprayed plot following each insecticide application (DeBach 1974; van den Bosch 1978; Berryman 1987; Dent 1991), there is no direct evidence for this possibility (Litsinger *et al.* 1987).

From this study, it appears that the four cicadellids (Fig. 2a, b, f, g) were better controlled by deltamethrin than the other pest species, while for the two delphacids (Fig. 2c, d), sprays generally brought about population increases. Such responses in delphacids have been well documented for the brown planthopper, *Ni. lugens* (e.g., Kenmore *et al.* 1984; Heinrichs & Mochida 1984). In laboratory studies, reproductive rates of *Ni. lugens* feeding on plants sprayed with deltamethrin were higher than those feeding on unsprayed plants (Chelliah & Heinrichs 1980). However, this does not account for the rapid numerical recovery of hoppers after each spray. New cohorts of *Ni. lugens*, acquired through re-invasions of adults from surrounding fields and through egg hatching, may be more important. Thus, the differences in recovery between cicadellids and delphacids in the sprayed plot may be due mainly to re-invasions of delphacids and to reduced mortality from natural enemies.

Of the 11 enemies of rice pests featured in this study, only *C. lividipennis* was highly correlated with all seven pest species. This mirid bug had higher populations in the sprayed plot than the unsprayed plot (Table 2). In tropical Asia, *C. lividipennis* is an omnivorous herbivore and generalist predator in the rice paddy system. These omnivorous habits make *C. lividipennis* highly susceptible to pesticides (Ku & Wang 1981; Reissig, Heinrichs & Valencia 1982), even to narrow-spectrum pesticides broadcast over water or in root zones (Dyck & Orlido 1977). Despite this high pesticide susceptibility, *C. lividipennis* in this study recovered within 4–6 days following each deltamethrin application and in densities 47–878% higher in the sprayed plot than the unsprayed plot. Population increases of *C. lividipennis* can occur in response to high populations of *Ni. lugens* (Kiritani 1979). Thus, the re-establishment of *C. lividipennis* in large numbers after each insecticide application may have been stimulated, in part, by population increases of *Ni. lugens* and (some of) the other pests.

Although spider densities are known to fluctuate wildly even when collections are taken from single rice fields (Barrion & Litsinger 1984), their reductions in the sprayed plot, relative to the untreated plot, varied from 36% in *Araneus inustus* to 63% in *Tetragnatha* sp. (Table 2). Closer study of spider movements between fields, even if they involve insecticide-treated fields, may suggest how spiders can be better managed as biological control agents (Riechert & Lockley 1984), either through enhancing their habitat (Riechert & Lockley 1984; Riechert & Bishop 1990) or through reducing their enemies' habitat.

NUMBER OF INDEPENDENT VARIABLES AND FOOD WEB STRUCTURE

This study suggested that classical models that contain one or two species as independent variables may be sufficient to forecast future abundances of some but not all Philippine rice pests. For example, a rice-only model explained the largest fraction of total variance in the future abundances of *R. dorsalis* and *Ne. nigropictus* in the unsprayed plot (Table 4). Likewise, current pest abundance explained, in large part, the future abundance of *H. philippina* in the unsprayed plot. However, for *Ne. virescens* and *S. furcifera* populations, a rice + pest + enemies model was necessary to achieve the same level of statistical significance. To forecast the future abundances of *C. spectra*, a number of variables intermediate between one and five may be sufficient. Most independent variables that predicted pest abundance in the unsprayed plot did not predict well in the sprayed plot.

RESERVATIONS AND PROBLEMS

Several problems limited interpretation of the data. First, we did not measure rice production directly. Although our study and Kenmore's (1980) study were both conducted on the IRRI farm during the dry season, the two studies used different applications and types of insecticides and different rice cultivars. Nevertheless, because Kenmore's curves of the dry weight of the standing crops were similar for sprayed and unsprayed plots, we believe different rice production curves should be similar.

Secondly, the use of linear models glosses over the many non-linearities observed in pest (Fig. 2a–g) and enemy abundances. For example, the worst and best regressions of the initial seven-variable models we tested captured between 5% and 96%, respectively, of the total variation (Table 3). Only after step-wise removal of all non-significant variables in each pest model did the majority of the linear regressions show significant fits to the data. Our approach is intended as a first step towards using food web structure to guide analysis of the phenology and abundance of major crop species, as an aid to understanding pest population outbreaks.

Thirdly, the ecological setting and farm irrigation practices used at IRRI may differ from those at farmers' fields outside IRRI (Litsinger 1993). In contrast to farmers' fields, for example, possible residual effects of prior experiments at IRRI may have washed out observed spraying effects in this study. IRRI's soil (until recently planted year-round, with inadequate drying periods), irrigation practices, and asynchrony of planting probably differ from those of the surrounding farms in Laguna Province. Moreover, the chemical fertilizers, the teams of skilled field labourers, and fortnightly weeding used at the IRRI farm and farms in Laguna Province probably do not occur at other farmers' fields in the Philippines. Repeating these studies at more typical farmers' fields is clearly indicated. Analyses of population interactions and food web structure at four other sites in the Philippines (Banaue, Kiangan, Bayombong, Cabanatuan) are underway.

Fourth, all sampling methods have sampling biases. The commonly used D-VAC sampler collects organisms from the plant and soil surfaces (Dietrick 1961). The FARMCOP sampler used here (with its enclosure) was designed to collect organisms from the plant and water surfaces (Cariño *et al.* 1979). In a study to determine the most efficient extractor for deriving absolute population estimates of delphacids, cicadellids and their predators in flooded rice, Perfect, Cook & Ferrer (1983) compared D-VAC and FARMCOP catches. They found that both methods sampled relatively immobile taxa with equal efficiency (e.g. delphacid nymphs, *Ni. lugens* and *Nephotettix* spp. adults); that FARMCOP under-sampled some taxa that readily disperse when disturbed (e.g. *S. furcifera*, some cicadellid adults and nymphs); and that D-VAC under-sampled aquatic species such as the veliid bug, *Microvelia atrolineata*. In no case did a taxon captured by one method (FARMCOP or D-VAC) go uncaptured by the other. Both methods miss or under-sample the submerged rice–arthropod fauna, which includes culicids, ceratopogonids and chironomids. These results demonstrate that no single sampling method, even D-VAC, is sufficient to collect all members of the paddy system with equal precision and efficiency. (Since this study, FARMCOP's power supply has been replaced with a petrol-driven, blower-vac machine which provides greater portability at lower cost and more uniform and powerful suction than some earlier FARMCOP and D-VAC models; Arida & Heong 1992.)

Finally, this study had certain unintended design problems. First, planting dates of experimental and neighbouring fields were not synchronized. However, because the sprayed and unsprayed plots were planted on the same day, we believe asynchronous planting affected both plots in broadly similar ways. Secondly, despite a no-spray zone used around the sprayed plot, the proximity of the plots may have diminished the treatment effect due to insecticide carry-over into the unsprayed plot. This problem can under-estimate the effect of natural enemies (Sterling, Wilson & Gilstrap 1992), but the effect, if it exists, is expected to be small at IRRI (Litsinger *et al.* 1987). Thirdly, the interval between consecutive sampling dates was not constant (average of 2·6 days, SD 1·6 days). Fourthly, population sizes of samples following spraying may have been biased due to collection of live specimens mixed with insecticide-killed specimens. However, field experiments with six arthropod species showed that an average of 86% of individuals killed by insecticide submerged within 3 days, and an average of 95% of killed individuals submerged within 4 days (G. Arida, unpublished data); thus, in this study, only the first post-spray samples (taken 2 days after each application of deltamethrin) may have been biased. Fifth, the study is unreplicated; only a single sprayed plot and a single unsprayed plot have been compared. Replication was not possible due to the large number (>40 000) of arthropod specimens that required sorting and identification.

FUTURE RESEARCH

Several questions remain to be resolved by future field experiments and related empirical work. Do similar contrasts between sprayed and unsprayed plots hold at other sites and seasons in the Philippines, particularly in farmers' fields? In such fields, will residual effects of the prior use of insecticide blur comparisons of sprayed with unsprayed plots?

Our results pertain only to the spraying of deltamethrin on rice–arthropod populations. To our knowledge this work represents the first attempt to incorporate food web data, phenology, and relative abundance into multiple regression models to compare the effects of insecticide-sprayed and unsprayed cultivation on the population dynamics of tropical rice pests. It might prove rewarding to test these models on rice-community data already collected from sprayed and unsprayed fields that used different insecticides (Reissig *et al.* 1982; Fabellar & Heinrichs 1984; Heinrichs, Basilio & Valencia 1984; Salim & Heinrichs 1985). For example, fields sprayed with a broad-spectrum insecticide of medium persistence (e.g. a carbamate) and those sprayed with a target-specific insecticide of low persistence (e.g., an insect growth regulator; Croft 1990; Dent 1991) could be compared with unsprayed plots to assess the impacts of different sprays on pest and enemy population dynamics. Over single and multiple growing seasons, to what extent and for how long do residual effects of using different insecticides in rice fields disorganize pest and enemy population dynamics? Better understanding of these population fluctuations may hold the key to explaining pest outbreaks and the differences between sprayed and unsprayed fields.

The methods developed here have potential applications to other crops besides rice, to other ecological communities besides arthropods, and to other interventions besides insecticide spraying, such as intercropping, the release of genetically engineered rice varieties, and the introduction of putative biological enemies.

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References

Arida, G.S. & Heong, K.L. (1992) Blower-vac: a new suction apparatus for sampling rice arthropods. *International Rice Research Institute Newsletter*, **17**, 30–31.

Barrion, A.T. & Litsinger, J.A. (1984) The spider fauna of Philippine rice agroecosystems. II. Wetland. *Philippine Entomologist*, **6**, 11–37.

Barrion, A.T. & Litsinger, J.A. (*in press*) Taxonomy of rice insect pests and arthropod natural enemies. *Management of Rice Insect Pests* (ed. E.A. Heinrichs). John Wiley, New York.

Barrion, A.T., Litsinger, J.A., Medina, E.B., Aguda, R.M., Bandong, J.P., Pantua, Jr., P.C., Viajante, V.D., dela Cruz, C.G., Vega, C.R., Soriano, Jr., J.S., Camañg, E.E., Saxena, R.C., Tryon, E.H. & Shepard, B.M. (1991) The rice *Cnaphalocrocis* and *Marasmia* (Lepidoptera: Pyralidae) leaffolder complex in the Philippines: taxonomy, bionomics and control. *Philippines Entomologist*, **8**, 987–1074.

Berryman, A.A. (1987) The theory and classification of outbreaks. *Insect Outbreaks* (eds P. Barbosa & J.C. Schultz), pp. 3–30. Academic Press, New York.

Cariño, F.O., Kenmore, P.E. & Dyck, V.A. (1979) The FARMCOP suction sampler for hoppers and predators in flooded rice fields. *International Rice Research Institute Newsletter*, **4**, 21–22.

Chelliah, S. & Heinrichs, E.A. (1980) Factors affecting insecticide-induced resurgence of the brown planthopper, *Nilaparvata lugens*, on rice. *Environmental Entomology*, **9**, 773–777.

Cherrett, J.M. (1989) *Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World*. Blackwell Scientific, Oxford.

Croft, B.A. (1990) *Arthropod Biological Control Agents and Pesticides*. Wiley Interscience, New York.

DeBach, P. (1974) *Biological Control by Natural Enemies*. Cambridge University Press. Cambridge.

Dent, D. (1991) *Insect Pest Management*. C.A.B. International, Wallington, UK.

Dietrick, E.J. (1961) An improved back pack motor fan for suction sampling of insect populations. *Journal of Economic Entomology*, **54**, 394–395.

Dyck, V.A. & Orlido, G.C. (1977) Control of the brown planthopper (*Nilaparvata lugens*) by natural enemies and timely application of narrow-spectrum insecticides. *Annual Report for 1976*. International Rice Research Institute, Los Baños, Philippines.

Fabellar, L.T. & Heinrichs, E.A. (1984) Toxicity of insecticides to predators of rice brown planthoppers, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). *Environmental Entomology*, **13**, 832–837.

Gonzalez, D. & Wilson, L.T. (1982) A food-web approach to economic thresholds: a sequence of pests/predaceous arthropods on California cotton. *Entomophaga*, **27**, 31–43.

Gutierrez, A.P., Baumgartner, J.U. & Summers, C.G. (1984) Multitrophic models of predator-prey energetics. *Canadian Entomologist*, **116**, 923–963.

Heinrichs, E.A., Basilio, R.P. & Valencia, S.L. (1984) Buprofezin, a selective insecticide for the management of rice planthoppers (Homoptera: Delphacidae) and leafhoppers (Homoptera: Cicadellidae). *Environmental Entomology*, **13**, 515–521.

Heinrichs, E.A. & Mochida, O. (1984) From secondary to major pest status: the case of insecticide-induced rice brown planthopper, *Nilaparvata lugens*, resurgence. *Protection Ecology*, **1**, 201–218.

Hendrix, P.F., Parmalee, P.W., Crossley, D.A., Coleman, D.C., Odum, E.P. & Groffman, P.M. (1986) Detritus food webs and conventional and no-till agroecosystems. *BioScience*, **36**, 374–380.

Heong, K.L., Aquino, G.B. & Barrion, A.T. (1991) Arthropod community structures of rice ecosystems in the Philippines. *Bulletin of Entomological Research*, **81**, 407–416.

IRRI (1980) Food web of the brown planthopper. *Annual Report for 1979*, pp. 224–225. International Rice Research Institute, Los Baños, Philippines.

IRRI (1983) Food web of the white leafhopper. *Annual Report for 1982*, pp. 184–185. International Rice Research Institute, Los Baños, Philippines.

IRRI (1984) Food web of the yellow stem borer. *Annual Report for 1983*, pp. 182–183. International Rice Research Institute, Los Baños, Philippines.

IRRI (1985) Leaffolder food web. *Annual Report for 1984*, pp. 190–191. International Rice Research Institute, Los Baños, Philippines.

IRRI (1986) Green leafhopper food web. *Annual Report for 1985*, pp. 156–157. International Rice Research Institute, Los Baños, Philippines.

IRRI (1987) Rice whorl maggot food web. *Annual Report for 1986*, pp. 212–213. International Rice Research Institute, Los Baños, Philippines.

IRRI (1988) Whitebacked planthopper food web. *Annual Report for 1987*, pp. 239–240. International Rice Research Institute, Los Baños, Philippines.

IRRI (1989) Food web of *Chilo* stem borers. *Annual Report for 1988*, pp. 246–247. International Rice Research Institute, Los Baños, Philippines.

IRRI (1990) Rice caseworm food web and natural enemies. *Annual Report for 1989*, pp. 179–181. International Rice Research Institute, Los Baños, Philippines.

IRRI (1992) *Compilation of Weather Data*. International Rice Research Institute, Los Baños, Philippines.

Kenmore, P.E. (1980) *Ecology and outbreak of a tropical insect pest of the green revolution, the rice brown planthopper,* Nilaparvata lugens *(Stål)*. PhD Thesis., University of California, Berkeley.

Kenmore, P.E., Cariño, F.O., Perez, C.A., Dyck, V.A. & Gutierrez, A.P. (1984) Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stål) within rice fields in the Philippines. *Journal of Plant Protection in the Tropics*, **1**, 19–37.

Kiritani, K. (1979) Pest management in rice. *Annual Review of Entomology*, **24**, 279–312.

Ku, T.Y. & Wang, S.C. (1981) Insecticidal resistance of the major insect rice pests, and the effect of insecticides on natural enemies and non-target animals. *Phytopathology and Entomology*, **8**, 1–18.

Litsinger, J.A. (1989) Second generation insect pest problems on high yielding rices. *Tropical Pest Management*, **35**, 235–242.

Litsinger, J.A., Alviola, A.L. & Canapi, B.L. (1986) Effects of flooding on insect pests and spiders in a rainfed rice environment. *IRRI Newsletter*, **11**, 25–26.

Litsinger, J.A., Barrion, A.T., Bandong, J.P., dela Cruz, C.G., Canapi, B.L. & Apostol, R.F. (1988) Food web, yield loss and chemical control of insect pests of wetland rice-based mungbean in the Philippines. *Mungbean: Proceedings of the Second International Symposium*, pp. 355–365. Asian Vegetable Research and Development Center, Taipei, Taiwan.

Litsinger, J.A., Canapi, B.L., Bandong, J.P., dela Cruz, C.G., Apostol, R.F., Pantua, Jr., P.C., Lumaban, M.D., Alviola, A.L., Raymundo, F., Libetario, E.M., Loevinsohn, M.E. & Joshi, R.C. (1987) Rice crop loss from insect pests in wetland and dryland environments of Asia with emphasis on the Philippines. *Insect Science and Applications*, **8**, 677–692.

Litsinger, J.A. (1993) A farming systems approach to insect pest management for upland and lowland rice farmers in tropical Asia. *Crop Protection Strategies for Subsistence Farmers* (ed. M.A. Altieri) pp. 45–101. Westview Press, Boulder, Colorado.

Mayse, M.A. & Price, P.W. (1978) Seasonal development of soybean arthropod communities in East Central Illinois. *Agroecosystems*, **4**, 387–405.

Mochida, O.M., Joshi, R.C. & Litsinger, J.A. (1987) Climatic factors affecting the occurrence of insect pests. *Weather and Rice*, pp. 149–164. International Rice Research Institute, Los Baños, Philippines.

Moormann, F.R. & van Breemen, N. (1978) *Rice: Soil, Water, Land*. International Rice Research Institute, Los Baños, Philippines.

Neuenschwander, P., Hennessey, R.D. & Herren, H.R. (1987) Food web of insects associated with the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), and its introduced parasitoid, *Epidinocarsis lopezi* (DeSantis). *Bulletin of Entomological Research*, **77**, 177–189.

Perfect, T.J., Cook, A.G. & Ferrer, E.R. (1983) Population sampling for planthoppers, leafhoppers (Hemiptera: Delphacidae & Cicadellidae) and their predators in flooded rice. *Bulletin of Entomological Research*, **73**, 345–355.

Pierce, W.D., Cushman, R.A., Hood, C.E. & Hunter, W.D. (1912) The insect enemies of the cotton boll weevil. *U.S.D.A. Bureau Entomological Bulletin*, **100**, 9–99.

Pimm, S.L., Lawton, J.H. & Cohen, J.E. (1991) Food web patterns and their consequences. *Nature*, **350**, 669–674.

Reissig, W.H., Heinrichs, E.A., Litsinger, J.A., Moody, K., Fielder, L., Mew, T.W. & Barrion, A.T. (1986) *Illustrated Guide to Integrated Pest Management in Rice in Tropical Asia*. International Rice Research Institute, Los Baños, Philippines.

Reissig, W.H., Heinrichs, E.A. & Valencia, S.L. (1982) Effects of insecticides on *Nilaparvata lugens* and its predators: spiders, *Microvelia atrolineata*, and *Cyrtohinus lividipennis*. Environmental Entomology, **11**, 193–199.

Riechert, S.E. & Bishop, L. (1990) Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology*, **71**, 1441–1450.

Riechert, S.E. & Lockley, T. (1984) Spiders as biological control agents. *Annual Review of Entomology*, **29**, 299–320.

Salim, M. & Heinrichs, E.A. (1985) Relative toxicity of insecticides to the whitebacked planthopper *Sogatella furcifera* (Horvath) (Homoptera: Delphacidae) and its predators. *Journal of Plant Protection in the Tropics*, **2**, 45–47.

Schoenly, K. & Cohen, J.E. (1991) Temporal variation in food web structure: 16 empirical cases. *Ecological Monographs*, **61**, 267–298.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn W.H. Freeman, New York.

Sterling, W., Wilson, T. & Gilstrap, F. (1992) Contaminated experiments: a flaw that underestimates the effects of natural enemies. *American Entomologist*, **38**, 88.

van den Bosch, R. (1978) *The Pesticide Conspiracy*. University of California Press, Berkeley.

Yasumatsu, K. & Torii, T. (1968) Impact of parasites, predators, and diseases on rice pests. *Annual Review of Entomology*, **13**, 295–324.

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