

## Population Regulation of the Rice Brown Planthopper (*Nilaparvata lugens* Stål) within Rice Fields in the Philippines

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**Abstract:** Three sources of density-dependent population regulation of rice brown planthopper (BPH) in 6 insecticide-free rice crops were: (1) lower oviposition with increasing female density; (2) higher nymphal mortality with increased nymphal density; and (3) a higher proportion of adults emerging as long winged presumptive emigrants at very high adult densities causing severe hopperburn damage. Spider populations showed a significant numerical response to planthopper densities. Insecticide treatments reduced spider and velliid predator densities and caused over an 800-fold increase in BPH density. Increased survival of adult females and nymphs contributed more to this outbreak than physiologically enhanced oviposition. Physical exclusion of predators caused a 13 fold increase in BPH density. Field populations of BPH exhibited higher survival on the partially resistant rice variety IR26 than susceptible IR1917, partly due to higher predator densities in the susceptible crop. The disruptive impact of insecticides on BPH population regulation means that minimal, need-based use must replace calendar-based use of insecticides in proper management of tropical insect pests of rice.

**Keywords:** brown planthopper, rice, population regulation, Philippines

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### INTRODUCTION

The rice brown planthopper (BPH) (*Nilaparvata lugens* Stål) is the pre-eminent insect pest of the modern green revolution. Three international symposia (ASPAC, 1977; Sajad *et al.*, 1978 and IRRI, 1979) covered results through the mid 1970's, several recent review papers (Kisimoto, 1971; Heinrichs and Mochida, 1984 and Kiritani, 1979) covered studies through 1982, and two bibliographies are now available with over 1000 references each (Chu, 1982 and Flint and Magor, 1982). BPH has become a textbook example of an r-type pest (Conway, 1980) and evolution by natural selection (Futuyma, 1983). During every crop season, some farmers in every South and Southeast Asian country still experience near total loss of part or all their rice crops because this pest is mis-managed.

All authors agree that BPH became a threat to tropical rice production in the early 1970's (Dyck and Thomas, 1979). Four factors are commonly mentioned in connection with the rise of this threat. (1) Expansion of irrigation allowed double cropping of rice when (2) short duration photoperiod-insensitive rice varieties were released. (3) These varieties were often grown with more nitrogenous

fertilizer but even more frequently than they used more fertilizer, (4) farmers used more insecticide on the new varieties (for examples of rapid insecticide adoption see Battad, 1973; Canedo, 1980 and Ocampo-Garcia, 1979). Nearly all evidence for each of these factors as a cause of BPH outbreaks is anecdotal. A few studies on potted plants showed 2- to 10-fold increases in density at higher fertilizer levels (Mochida and Suryana, 1979 and Cheng, 1971) but not the 100- to over 1000-fold increases experienced in 'hopperburned' fields. Replicated field trials comparing either fertilizer levels or non-resistant modern vs older varieties (Dyck *et al.*, 1979) without using insecticides could show no significant increases in pest density per unit of plant mass.

While detailed population studies of BPH were conducted in Japan (Kuno, 1968; Kuno and Hokyo, 1970; Kisimoto, 1965) their dynamics did not match those observed at IRRI (Dyck *et al.*, 1979). Factors contributing

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to this contrast included the failure of the pest to survive Japanese winters, its re-invasion every spring in very small numbers, probably from China (Rosenberg, 1982 and Kisimoto, 1979), heavy use of insecticides in Japanese rice fields (Ito *et al.*, 1962), lower densities and diversity of predators, and possibly genetic differences between Northeast and Southeast Asian populations.

This study was conducted to describe in detail the dynamics of a tropical population of BPH in relation to its most numerous natural enemies. We shall discuss factors contributing to natural population regulation of this pest and how they are disrupted, especially by the influence of insecticides on natural enemies.

## MATERIALS AND METHODS

### Field Surveys

Field census surveys were conducted on the IRRI farm and a farmer's field 5 km away between August 1977 and July 1979. Field size was 25 × 50 meters, about the average size of a farmer's paddy. Three week old seedlings of IR20 or its sister line IR1917, both susceptible to Philippine BPH, were transplanted at 16 plants/m<sup>2</sup>. Stratified random samples were made of movable arthropods with the FARMCOP suction sampler (Cariño *et al.*, 1979) at least twice a week. The number of plants sampled was fixed for each field study and ranged from 20 to 128 per field per sample date. Total sample numbers thus ranged from 400 per crop to over 2000 per crop, depending on the numbers of field studies being conducted simultaneously and the number of sampling teams working.

Sampling of movable arthropods from irrigated rice has since been intensively investigated by Perfect *et al.* (1983); during our studies the standard errors of estimated mean densities ranged from 10% to over 100%, decreasing at higher densities. For example, a population density estimate of 10 BPH adults per plant (a common action threshold for BPH) carried a standard error close to 20% of the mean. The alcohol-preserved catch from each plant was sorted by species, and stage and wing morph

determined under a dissecting microscope in the laboratory and recorded separately.

The key produced by Perfect, Cook and associates (COPR, 1981) has made identification of hemipterans on rice easier and more accurate than was possible during the time of our study. In the generally high range of densities we found (over 1/plant), infestations tend to be nearly monospecific. This reduces the possible errors due to taxonomic inaccuracies.

Egg densities per plant were estimated by removing a fixed number of plants from the field, dissecting each tiller under a microscope and counting eggs of different species and developmental stages. Numbers of parasitized eggs were counted and recorded separately as were numbers of collapsed or torn egg shells left after attack by *Cyrtorhinus lividipennis*, an egg predator. Egg parasitization was then estimated using the method of Otake (1970) to correct for host age preference by *Anagrus nr. flaveolus*, the dominant egg parasite, and changing developmental rates following parasitization.

Instar to instar survivorship analyses were performed upon per plant densities using the method of Kiritani and Nakasuji (1967) as modified by Manly (1977). This method compares numbers of different instars found in successive samples and adjusts for irregular sampling intervals. In an intensive simulation test conducted by Manly (1974) it gave the best estimates of "true" survival (of stages in the simulated population) from samples of the population. In common with all methods for estimating survival from stage to stage, it makes the assumption that survival per day is constant and depends on distinguishing individual generations. Results were compared across crops using Spearman's Rank Correlation Analysis (Siegel, 1956).

### Field Experiments

Predator exclusion—one hundred cages made of bamboo, abaca twine, and nylon mesh cloth were set up on a field planted as described above. The cages were 50 cm × 50 cm by 1.5 m tall and the nylon mesh was long

enough to leave its lower margins buried in the mud below water level to close the cage. Every movable arthropod was removed by hand or suction machine from the four plants in each cage and the cages closed. After one week, any newly hatched or invading arthropods were removed. One hundred first instar BPH nymphs were placed in each cage; after 24 hours, during which time the nymphs settled to feed on the plants, the lower margin of every other cage was lifted and secured 10 cm above water level. This allowed free access to the plants in the cage by arthropods on or near the water surface. Four of these opened cages had sticky traps (plastic sheets 15 cm wide and coated with Tanglefoot®) surrounding the openings at the bottom to estimate the rates of BPH nymphs and adults leaving the cage.

#### Density and Oviposition

Twelve individually potted susceptible rice plants about 50 days old were covered by transparent plastic cylinders with nylon mesh windows. The plants were kept caged for one week while all hatching nymphs were removed. Each plant was trimmed to 8 roughly equal-sized tillers. The potted, plastic covered plants were placed together in a field under a single, shading but not surrounding canopy of dark netting on a bamboo framework. The plants were adjacent to each other in a completely randomized pattern.

Non-gravid macropterous females were collected from the field, caged with field-collected macropterous males for 24 hours, then placed on the potted plants at densities of 0.25, 1, and 4 females per tiller. The study continued for 17 days and all newly emerging nymphs were counted and removed. When the original females died, plants were dissected and remaining eggs counted.

#### Density and Adult Wing Morph Proportions

Six vegetative plants at the maximum tillering stage infested with varying densities of young nymphs were collected from infested fields and placed individually in field cages of the type used for the exclusion study. Adults were removed after emergence and numbers of each wing morph were counted. This gave a

relationship between density and wing morph proportions which allowed us to estimate the total indigenous adult density of a given generation from the density of brachypterous adults. Cook and Perfect (1982) have since shown that adult wing morph can be detected in fifth instar nymphs; this allows more precise estimation of indigenous adult population than we were able to achieve. This work has since revealed a wide range of proportions of brachypters at densities below those found in our studies. This could be a source of error in estimation of indigenous adult density.

#### Insecticide Check

A normal crop of IR20 was treated at 34 days after transplanting with a foliar spray 750 gm ai/ha of diazinon and at 47, 58, and 69 days with 8 gm ai/ha foliar spray of deltamethrin. Both of these compounds were known to induce population outbreaks of BPH (Heinrichs *et al.*, 1982, and Reissig *et al.*, 1982). Field sampling as described above was performed. A control field, 500 m away, was planted the same day with the same variety but was not treated.

#### Partial Vertical Resistance

In the wet season of 1978, a paddy of IR26 was planted next to one of IR1917 in a farmer's field. We sampled both fields as described earlier. Because IR26 is considered vertically resistant only to those BPH of phenotype named "Biotype 1" at IRRI, and the Laguna Province BPH population is a polymorphic one, it was expected that population dynamics on IR26 would differ from those on the adjacent susceptible variety.

## RESULTS

#### Density Effects on Oviposition

Per capita oviposition for eleven BPH generations in six untreated crops were estimated as the ratios of peak egg densities to peak female densities prior to the egg peak. These are plotted in Fig. 1a. There is an obvious decline in number of eggs per female with increasing female density per plant.

The densities of females were then adjusted to account for vegetative biomass, which

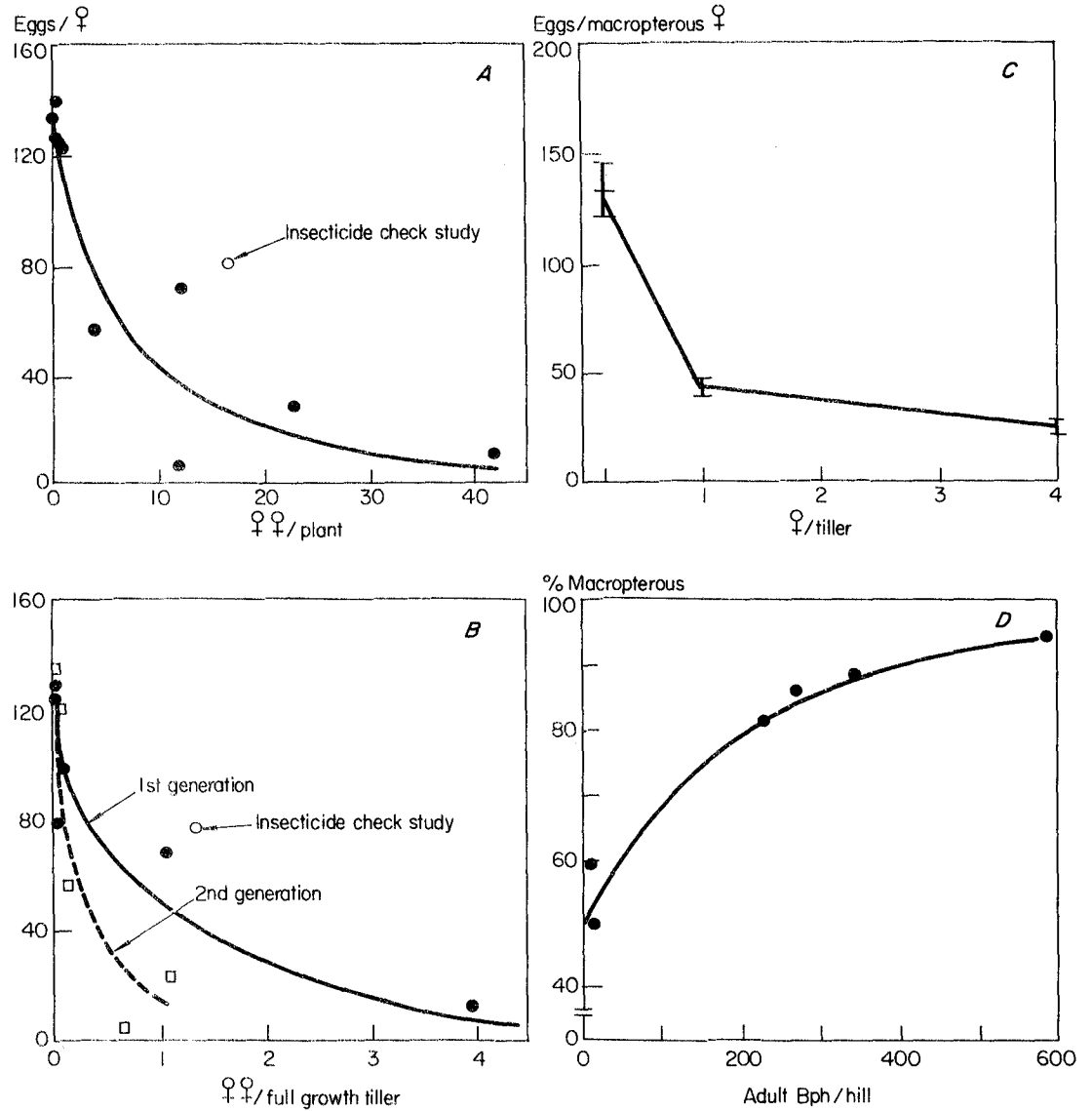


Fig. 1. Population regulating factors in Philippine *N. lugens* populations. (A) Reduction in egg laying with increasing female density per plant, data from field censuses. (B) Data from (A) replotted against female per tiller showing differences between earlier and later generations. (C) Data from potted caged plants trimmed to constant tiller number and kept in the field; all insects were field collected macropterous females. Bars give S.E. of the mean. (D) Increased percentage of macropterous adults with nymphal density; data from field collected nymphs placed in field cages at a range of densities.

increases with age of crop until flowering, by taking density as the number of females per fully emerged tiller. The plot in Fig. 1b shows that oviposition per female drops more quickly with female density for second generation than first generation females. This could be due to reduced plant nutritional quality from aging or previous feeding stress or to higher natural enemy densities later in the crop reducing the life span of ovipositing females.

The results of the study on caged plants at fixed densities confirms the field results (Fig. 1c). At higher densities, females produced significantly fewer eggs than at lower densities. Preliminary studies using colony-reared brachypterous females showed that the density effect was lost when plants were replaced every other day (Kenmore, 1980). This indicates that plant aging, lower nutritional quality (induced by heavier feeding) and/or limited space suitable for oviposition rather than purely physical interference were the mechanisms of reduced oviposition.

#### Density and Adult Wing Morph Proportions

As observed in Japanese populations (Kisimoto, 1965) the proportion of nymphs collected from the field which emerged macropterous increased with increasing density (Fig. 1d). At densities close to those found in the untreated fields surveyed, this proportion was about 50% to 67%. This allowed us to estimate indigenous adult populations, as distinct from immigrants, from the estimated densities of brachypterous adults which were assumed to be indigenous. We multiplied these densities by 2 (in the case of 9 generations) or 3 (in the case of 2 generations of higher density). The resulting estimates for adult densities were used to calculate survival of 5th instar nymphs.

#### Field Census Surveys

**Level of Damage:** While BPH can cause some yield loss without visible signs of damage (Kenmore, 1980), the characteristic yellowing followed by drying to a brown colour known as "hopperburn" is the threat

which concerns rice farmers (Cheng, 1978). The first major result of the six untreated survey crops is that *no* hopperburn symptoms were observed in *any* of them at *any* time.

The second major result is that no untreated BPH populations ever increased steadily through the crop season. As shown in Fig. 2, 3, and 5, populations either peaked in mid-season or fluctuated at a low level with no apparent peaks. Both of these results suggest that BPH populations were controlled without insecticides in all six crops and without varietal resistance in five crops. While the census sampling methods used precluded taking yield data, the absence of hopperburn suggests that economic control was adequate. In only one generation (Fig. 3b) did 5th instar and brachypterous adult densities exceed the significant sub-hopperburn damage threshold of 4/tiller in the dry season (Kenmore, 1980).

**Population Dynamics:** In wet season 1977 and dry season 1978 population densities were high enough to distinguish  $2\frac{1}{2}$  clear generations per crop (Fig. 2 and 3). In the remaining seasons, generation times were blurred because the sampling was not intensive enough to detect short changes (Fig. 5, 7).

Data from studies of survivorship of each instar each generation for six untreated crops are presented in Table 1. In one crop eggs were not sampled so only adult and nymphal population data are given. For the three low density crops, the entire season is shown here as a single generation because there was little difference between these estimates and those using 2 arbitrary generations/crop.

At no time did pre-adult survivorship exceed 4%; the populations in low density fields survived better than those in high density fields. Most mortality occurred before the first nymphal instar (65–91%). Factors contributing to this mortality included parasitization (Table 1), predation on eggs (only observed in high BPH density fields and when egg density exceeded 20/plant), failure to hatch (10–30.3% in 3 crops where this was

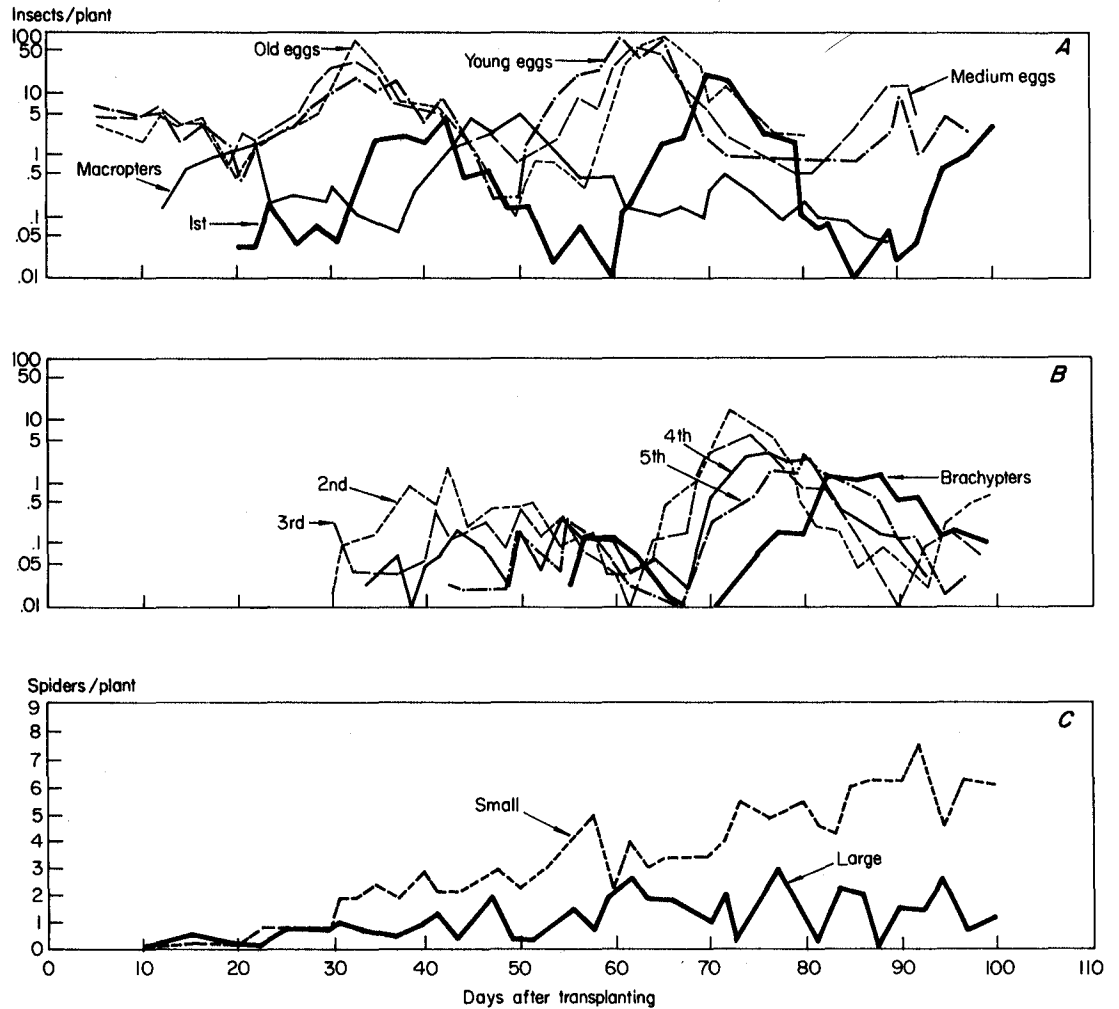


Fig. 2. Population changes of all stages of *N. lugens* and size classes in an insecticide-free rice field planted with the susceptible variety IR 1917 in the Philippines September–December 1977. (A) Macropters (primarily immigrants), 3 egg stages, and 1st instar nymphs showing major mortality between last egg stage and first nymphs. (B) 2nd–5th instar nymphs and brachypters showing fairly constant stage to stage survival. (C) Small and large spiders, showing steadily increasing density which then levels off.

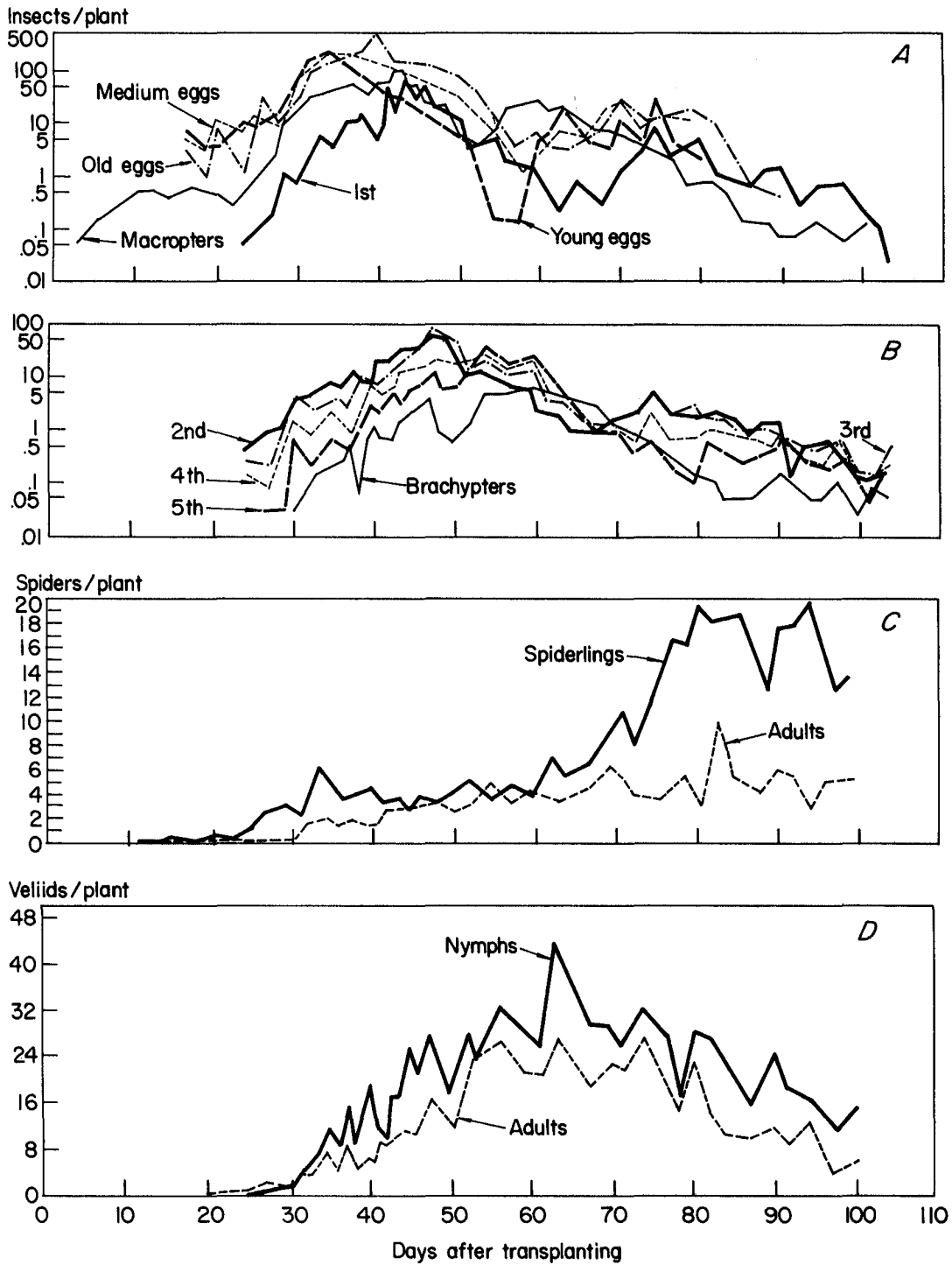


Fig. 3. Population changes of all stages of *N. lugens*, spiders and veliid predators in an insecticide-free rice field planted with the susceptible rice variety IR 1917 in the Philippines, January to April, 1978. (A), (B), (C) as in Figure 2; (D) Veliid predators showing mid-season peak densities higher than *N. lugens* prey densities.

**Table 1.** Stage to Stage and Cumulative Fractional Survival of BPH (*N. lugens* Stål) eggs, nymphs, and preovipositioning adult females in seven Philippine rice crops as calculated by the method of Kiritani and Nakasuji (1967) and Manly (1977).

Stage	Late Wet Season 1977 <sup>1</sup>		Late Wet Season 1977 <sup>1</sup>		Dry Season 1978 <sup>1</sup>	
	First generation	Second generation	First generation	Second generation	First generation	Second generation
Egg						
Young	.80	.71	—	—	.83	.76
Medium	.68	.77	—	—	.72	.72
Old	.39	.59	—	—	.42	.44
% Parasitization (Mean ± Std. Error)	(27.2 ± 4.93)	(35.1 ± 5.26)			(20.8 ± 5.96)	(29.6 ± 5.75)
Total egg	.21	.30	—	—	.25	.24
Nymph						
1st	.45	.54	.16	.73	.82	.64
2nd	.46	.54	.30	.44	.74	.58
3rd	.61	.60	.40	.56	.61	.39
4th	.60	.65	.53	.52	.59	.43
5th	.57	.54	.65	.52	.34	.40
Total nymphs	.04	.06	.007	.049	.07	.025
Total Pre-Adult	.009	.018	—	—	.018	.006
Stage	Dry Season 1979 <sup>1</sup>		Dry Season 1979 <sup>1</sup>		Early Wet Season 1978 <sup>2</sup>	Early Wet Season 1978 <sup>2</sup>
	Not Treated with Insecticide	Insecticide Treated			IR1917 Susceptible Variety	IR26 Partially Resistant Variety
Egg						
Young	.51	.88			.58	.52
Medium	.60	.91			.57	.64
Old	.39	.88			.35	.47
% Parasitization (Mean ± Std. Error)	(27.9 ± 7.62)	(23.9 ± 2.25)			(42.2 ± 2.73)	(37.2 ± 2.88)
Total egg	.12	.703			.12	.16
Nymph						
1st	.85	.91				
2nd	.78	.79			.72	.65
3rd	.67	.75				
4th	.77	.71			.49	.52
5th	.81	.52			.51	.64
Total nymphs	.28	.20			.18	.21
Total Pre-Adult	.025	.141			.021	.034
Pre-ovipositioning females	.74	.92				

<sup>1</sup>IRRI Farm, College, Laguna, Philippines.

<sup>2</sup>Farmers' Field, Bay, Laguna, Philippines.



measured), and death around the time of hatching. Many newly emerged nymphs were seen falling onto the water and then being attacked by veliids.

Nymphal mortality was evenly distributed across instars, probably reflecting the importance of general predators able to kill any stage nymph. Parasitization by dryinids, strepsiptera, and fungal pathogens was never higher than 5% as estimated by visual appearance of dead preserved specimens. Higher rates of nymphal parasitization would have been detected by other sampling techniques such as live collections and rearing (Chandra, 1979; Chua and Dyck, 1982 and Aguda *et al.*, 1981). Table 2 presents data and correlation analyses (using ranks) of average nymphal survivorship with peak nymphal densities per crop. There is a significant negative correlation across the six crops between these two ( $R_s = -.943$ ,  $p < .05$ ).

Macropterous adults outnumbered brachypterous adults at all times in untreated fields. As the number of nymphal survivors was not high enough to account for these

densities of macropterous adults, and as light trap catches showed patterns similar to those of macropterous adults in the fields, we conclude that most of the observed macropterous adults were immigrants, especially during the early weeks of each crop.

Spiders: Spiders, especially lycosids and micryphantids, were commonly seen feeding on adults and nymphs of BPH and *Sogatella furcifera* (Horvath), the whitebacked planthopper (WBPH). Planthoppers were also regularly seen in the webs of spiders, especially, micryphantids and tetragnathids. The most abundant spider genera were *Lycosa*, *Callitrichia*, *Tetragnatha*, *Araneus*, *Argiope*, and *Oxyopes*. Age classifications of spiders were more difficult than for planthoppers. The "spiderlings" described below were certainly smaller than the adults of the same genus but, particularly for non-gravid female adults, the distinction between large spiderlings and adults was arbitrary. Most of the following argument, however, is equally applicable to size classes as to age classes particularly as small spiders including small adults migrate readily by ballooning on silk strands (Kawahara, 1975).

**Table 2.** Summary and Spearman's rank correlation analyses of density-dependence in brown planthopper (*N. lugens*) nymphal mortality and spider numerical response across six crops, Laguna Province, Philippines, 1977-1979.

Field Study (ranked by spider saturation density)	Peak <sup>1,2</sup> Spider Density	Peak <sup>1,3</sup> BPH Density	Nymphal <sup>2,3</sup> Survival (season) (long) (average)	Peak <sup>4,5</sup> Spider Density (biomass)	Peak <sup>4,5</sup> BPH Density (biomass)
Dry season, 1979 <sup>6,7</sup>	6	4.1	0.28	4	1.7
Early wet season, 1978 <sup>8,9</sup>	6	9.5	0.21	4.25	3.1
Early wet season, 1978	8	16.5	0.18	5.25	12.9
Early wet season, 1978	8.5	46.5	0.05	5.5	6.4
Late wet season, 1977 <sup>6,7</sup>	16	461	0.028	9.0	105.0
Dry season, 1978 <sup>6,7</sup>	22	228	0.047	13.0	108.0

<sup>1</sup>Spider Peak Density and Peak BPH Density,  $R_s = .929$  ( $p < .05$ ).

<sup>2</sup>Spider Peak Density and Average Nymphal Survival,  $R_s = -.900$  ( $p < .05$ ).

<sup>3</sup>Peak BPH Density and Average Nymphal Survival,  $R_s = -.943$  ( $p < .05$ ).

<sup>4</sup>Spider Biomass weighting =  $\frac{1}{2}$  spiderlings + adults, while BPH Biomass weighting =  $\frac{1}{3}$  nymphs + adults. These weightings are approximate.

<sup>5</sup>Biomass weighted Spider Peak Density and BPH Peak Density,  $R_s = .943$  ( $p < .05$ ).

<sup>6</sup>IRRI Farm.

<sup>7</sup>Susceptible variety (IR1917 or IR20).

<sup>8</sup>Farmer's field, Bay, Laguna.

<sup>9</sup>Partially resistant variety, IR26.

As shown in Fig 2c, 3c, and 7c, spider population densities tended to increase steadily until equilibrating at a level related to prey abundance. Table 2 shows how these level spider densities were significantly correlated across crops with peak BPH density ( $R_s = .929$ ,  $p < .05$ ).

In the five crops with highest BPH densities spiderling population changes from one ten-day period to the next (spiderlings/plant-spiderlings/plant  $t+10$ ) were positive in 83% of cases. The remaining 17% were small negative changes after levelling off. This meant spider populations increased steadily across fields showing a 70-fold range of prey densities, levelling off in each case at a density significantly correlated with peak prey abundance. In the sixth crop (Fig. 5), prey densities were so low that spider population densities fluctuated and on the whole declined from period to period. This may have reflected

the effects of cannibalism (observed occasionally), starvation, and emigration as well as low reproduction.

Increases in the densities of spider populations were associated with prey availability. Using the same 10-day intervals, we regressed the *change* in spiderling density per adult (or per large spider) on prey availability (estimated as the natural logarithm of total adult planthopper density + 1 per adult or large spider). Planthoppers in this case included *N. lugens* and *S. furcifera* because spiders were normally observed to eat both.

Results given in Fig. 4 and Table 3 shows that as prey availability increased, spiderling population growth, relative to adult spider densities at the start of each interval, increased. Fields with higher adult BPH peak densities also had significantly higher rates

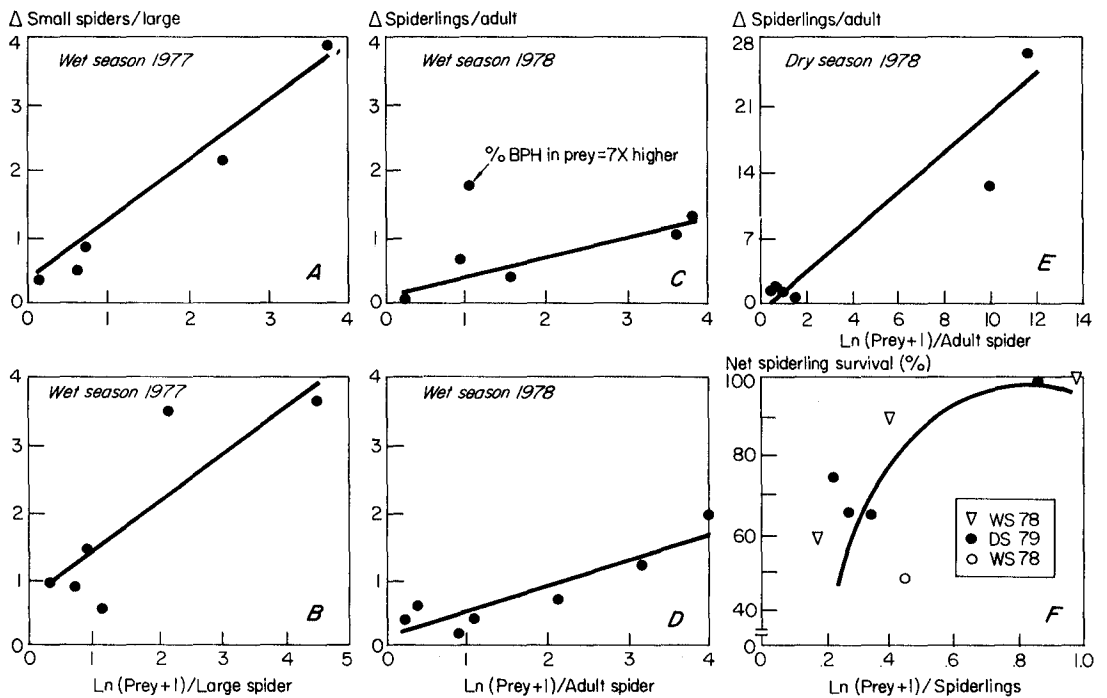


Fig. 4. Numerical responses of spiders (the change in small or spiderling density per adult or large spider) to prey availability (the natural log of planthopper densities per adult spider) over 10-day intervals in insecticides-free Philippine rice fields (see Table 3). (A) and (B) Two separate fields planted with susceptible IR1917 on the IRR I Farm; (C) Planted with IR1917 in a farmer's field, Bay Laguna, the outlying datum was not included in the regression analysis because prey composition was atypical; (D) Planted with IR26, resistant to "biotype 1" phenotype of *N. lugens* in a field adjacent to (C); (E) Planted with susceptible IR1917 on the IRR I Farm; (F) Percentage change in spiderling survival over the same 10-day intervals when prey were limiting.

**Table 3.** Spider numerical response to prey: a summary of regression statistics of  $\Delta$  spiderlings/adult on  $\ln$  (adult planthoppers + 1)/adult spider. See Fig. 4.

Fields	Slope <sup>6</sup>	Intercept	r <sup>2</sup>	t(H <sub>0</sub> : b ≠ 0)	BPH density (Rank) <sup>6</sup>
Dry Season 78 <sup>1,2</sup>	1.810	1.044	.939	7.832	1
Wet Season 77 <sup>1,2</sup>	0.849	0.405	.908	6.286	3
Wet Season 77 <sup>1</sup>	0.572	0.760	.659	2.780	2
Wet Season 78 <sup>3</sup>	0.391	0.056	.810	4.614	5
Wet Season 78 <sup>3,4</sup>	0.271	0.113	.870	4.476	4
Dry Season 79 <sup>1,5</sup>	(Not sig. different from 0)	—	—	—	6

<sup>1</sup>IRRI Farm.<sup>2</sup>Previous season without insecticides on the field.<sup>3</sup>Farmer's field, Bay, Laguna.<sup>4</sup>One sample date excluded from regression as the proportion of immigrant BPH among all species planthoppers was seven times higher than other sample dates, causing exaggerated numerical response (see Fig. 4).<sup>5</sup>Not included Fig. 4.<sup>6</sup>Slope (i.e. rate) of numerical response vs. BPH density, Spearman rank correlation coefficient  $R_s = .886$  (prob < .05).

(i.e. slopes) of spiderling production per unit prey availability to adult or large spiders ( $R_s = .886$ ,  $p < .05$ ). This means that adult spiders responded numerically to increased food by producing more spiderlings and/or that the *net* immigration and subsequent survival of spiderlings increased with prey availability to adult spiders. The spiderlings were perhaps better fed themselves and thus less likely to be eaten by adult spiders. The two fields with highest rates of spiderling production also were the only two fields which had not been treated with insecticide the previous season. This suggests that density of reproducing female spiders was higher to begin with (see discussion).

The above results show the relationship of spider population growth to prey availability. Spiderling populations declined in a few cases from one 10-day period to the next. Fig. 4f shows how spiderling survival was higher in those cases when prey availability to spiderlings increased. Lower apparent survival can include the effects of emigration as well as cannibalism and starvation.

In addition to the dependence of spider population growth on planthoppers, Table 2 shows that the survival of BPH nymphs was

significantly and negatively correlated with the level attained by spider densities across six crops ( $R_s = .900$ ,  $p < .05$ ). Spider's numerical responses therefore had direct impact on pest survival from stage to stage.

**Veliids:** These very active general predators were commonly observed attacking planthopper nymphs and occasionally adults which were on the water surface including those we observed falling onto the water. They attacked any potential "prey", including fallen rice anthers at dehiscence. *Microvelia* and *Mesovelia* were the most abundant genera. Veliid populations were not as closely correlated with BPH populations as were spider populations. Veliid population densities were similar in two untreated fields with over a 100-fold difference in BPH densities (Fig. 3d and 5d). This does not, however, mean these predators are not important in controlling BPH, only that their populations can grow in the absence of large densities of BPH, perhaps by shifting to other prey species.

#### Insecticide Check

**Crop Damage:** About one third of the plants in the field treated with insecticides showed severe hopperburn symptoms. The

yield of that field was 3.9 tons/ha as contrasted with 5.8 tons/ha in the untreated control field.

**Egg Production of BPH:** Figure 1 shows that egg production per BPH female in the insecticide treated field was about double that expected for the observed density of BPH females. There were two reasons for this. First, over half the females sampled were brachypterous, the only case in any of our field studies when this proportion was so high. Brachypterous females often have higher egg production than macropterous females (Kisimoto, 1981). Second, laboratory studies on colony-reared BPH at IRRI showed increase of 2.5 fold after treatments with outbreak-inducing insecticides (Chelliah and Heinrichs 1980, and Chelliah *et al.*, 1980). The observed increase in per capita oviposition nearly matches this estimate and could be due to reproductive stimulation.

**Phenology:** Comparing the treated field with untreated fields, especially the one planted the same day as a control, shows the following major features (Fig. 5):

- i) Very low early BPH densities rising steadily after treatment to a single peak late in the season, in contrast to multiple peaks or one early to mid-season peak without treatment.
- ii) Early season predominance of brachypterous adults in the treated fields. These survived much longer in treated than in untreated fields and contributed to the observed surge of eggs in the treated field.
- iii) The later predominance of macropterous forms as very high BPH density, resulting from treatment, influenced wing morph development. The rapid drop in egg density 20 days before adult density declined suggests most of the macropterous adults in the treated field were emigrating without laying eggs. This drop in apparent egg production could also be a nutritional effect brought on by pest density-related plant stress or aging of the plant.

- iv) Similar levels of egg parasitization regardless of treatments. The mean percentage parasitization of 23.9% in the treated field was not significantly different from 4 of the 7 untreated generations compared in Table 1. This probably was due to the parasite inside BPH eggs being protected from insecticides by rice plant tissue.

#### Survivorship

The final column of Table 1 shows the stage to stage survivorship of BPH in the treated field. Survival from the young egg stage to the first nymphal instar was  $2\frac{1}{2}$  to 3 times higher than in any untreated field. Subsequent survival from 1st through 5th nymphal instars was 3 to 30 times higher than in the three untreated crops with similarly high BPH densities and nearly equal to that in the low density crops. Total egg to adult survival was 5.6 times higher than in the matching untreated control and 3.5 times higher than in any other untreated crop. We compared survival of the preovipositional females only with the matching untreated control, and found about 1.3-fold higher survival for this two-day period. If this is extended for the normal 14-day physiological life span we found in laboratory studies of field collected newly emerged females (Kenmore, 1980 and unpublished), this represents potentially a 6.3-fold increase in female density.

It is possible to distinguish population factors leading to an outbreak as they acted in sequence. A 2.5-fold increase in egg production followed by a 5.6-fold increase in egg to adult survival equals a 14-fold increase in emerging adult density; this is followed by a 6.3-fold increase in female survival for a total of 88.2-fold increase in density per each generation. As this apparently (Fig. 5) operated for about 30 days or 1.5 times the normal generation length of BPH in the Philippines, an 830-fold increase ( $88.2^{1.5}$ ) over the control field is expected. Comparing numbers of nymphs, to avoid the influences of immigration and emigration, we obtained, as an average of ratios on the 10 sample dates during which nymphs developed under sprayed conditions, approximately a 790-fold

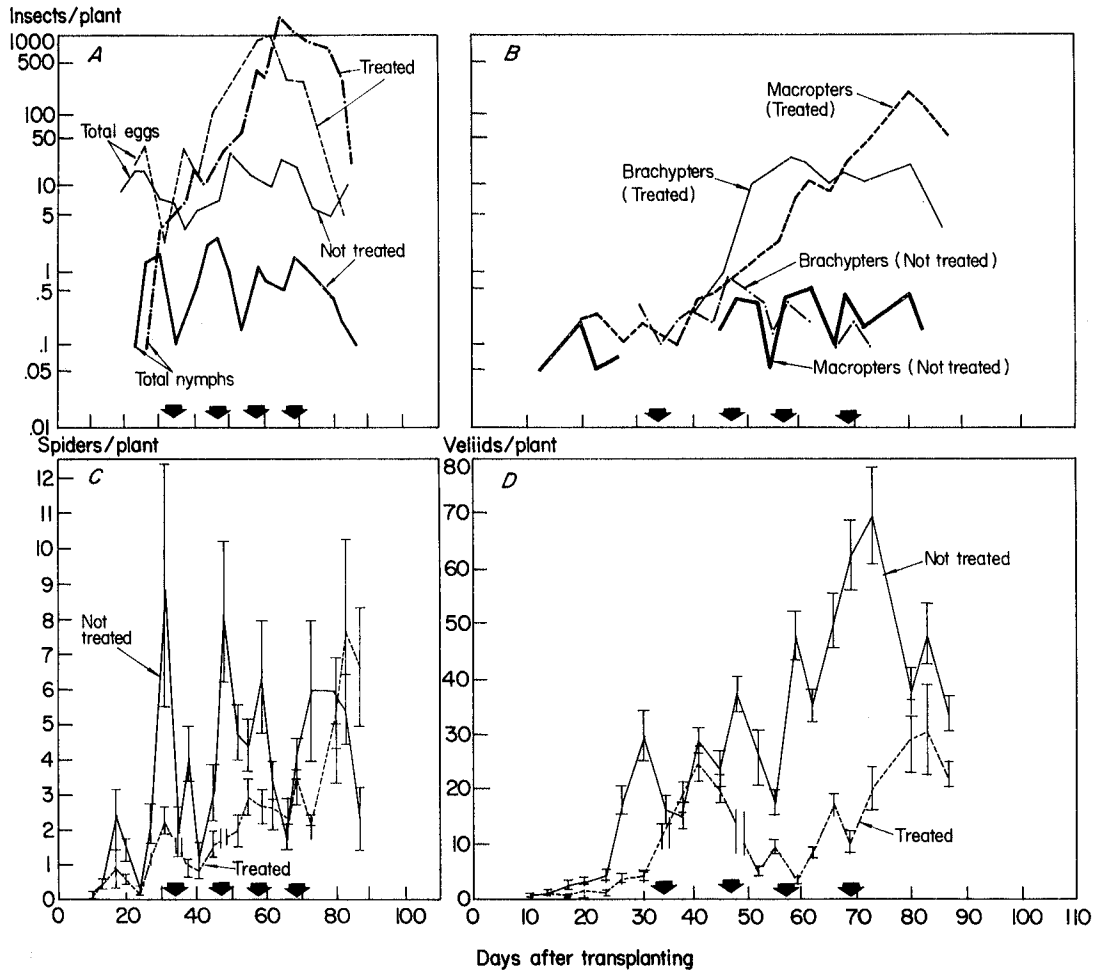


Fig. 5. Insecticide check: Population changes of *N. lugens*, spiders, and veliid predators in a rice field treated with insecticides at indicated dates (arrows) and a control field left untreated in the Philippines, February to May, 1979. (A) Eggs and nymphs, showing over 100-fold average increase in the treated vs. the untreated field; (B) Adults, showing earlier increase in brachypters due to enhanced survival, followed by macropters as high nymphal density induced development of macropters which usually emigrated without laying eggs (compare peaks of eggs and macropters); (C) Spiders, showing no higher and even significantly lower densities in the treated field despite much higher prey availability until after treatment was stopped (bars give  $\pm$  standard errors of the mean); (D) Veliid, showing rapid responses to latter 3 insecticide treatments and failure to reach densities of untreated populations despite much high prey availability (bars give  $\pm$  standard errors of the mean).

increase. While this only demonstrates that the order of magnitude of the combination of the separately estimated components is close to that observed, the *relative* importance of the three, adult female survival  $\geq$  pre-adult survival  $>$  increased physiological egg production, is more significant than their magnitudes. Survival from egg to the first instar seems more important than survival from first through fifth instars, despite the

similar levels of egg parasitization in treated and untreated fields and the near absence of apparent egg predation in both control and treated fields. This suggests that mortality near the time of hatching is one critical factor.

**Natural Enemies:** As expected, densities of spiders and veliids (Fig. 5c, d) were both reduced by insecticide treatments. Both showed a tendency to increase between

treatments and a pronounced rise after treatments stopped. Although spider densities in untreated fields were significantly correlated with BPH densities, they were unable to increase in the treated field despite very high prey densities. Spider densities in the treated field remained below those of the control field, which had very few BPH, until after the final insecticide treatment. This also contributed to the failure of nymphal density dependent regulation—artificially lower spider numbers were unable to affect nymphal survival, in contrast to untreated fields with equally high nymphal densities but much lower survival. After the treatments ceased spiderling populations increased as the spiders were able to feed on the immense supply of food *and* survived to reproduce.

Veliid densities were clearly suppressed by the treatments (Fig. 5d) but showed a greater relative recovery between treatments than spider densities. Nymphal densities were

apparently more affected than adult densities, perhaps because adults were able to immigrate steadily, but neither nymphs nor adults were able to reach the densities achieved in the control field. These artificial reductions in predator density permitted increased BPH stage to stage survival both near hatching (probably due to veliid suppression as compared with the control crop because veliids prey heavily on BPH 1st instars) and across all nymphal instars (probably due to spider suppression as compared with the three higher density treated crops).

### Predator Exclusion

An average of 1.6 BPH per day per cage (or 0.4/plant) were trapped leaving the cages. As shown in Fig. 6a, in the open cages BPH density declined from 25/plant to about 5 per plant over 15 days, then increased with the hatch of nymphs to about 50/plant in the next 15 days. In the closed cages BPH density

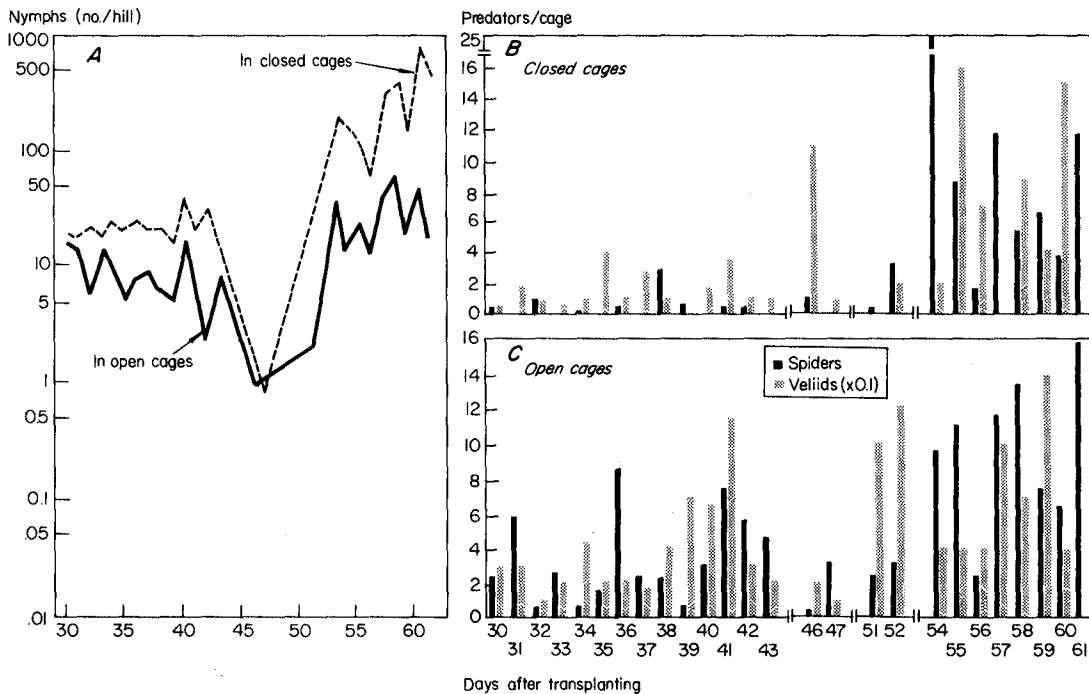


Fig. 6 Predator exclusion: Population changes in *N. lugens* and predators in closed and opened field cages after initially removing all arthropods and stocking with 25 1st instar *N. lugens* nymphs per rice plant. (A) Nymphs per plant, showing 12-fold increase in closed cages protected from predators; (B) and (C) Predator populations in closed and open cages, showing initially lower densities in closed cages which increased to equal those in open cages in response to much higher prey densities inside the cages.

remained at 25 per plant for 15 days, then increased steadily to over 600 per plant in the next 15 days. There was a 12-fold increase in caged BPH density over the exposed control during the 30 days when they were protected from natural enemies. No stimulation of egg production was involved as no chemicals were used.

Fig. 6b shows the numbers of predators caught together with BPH in the first 15 days of each treatment. Veliids were the most numerous in the open cages, followed by spiders. *Cyrtorhinus* was not present in most cages. Invading predators were also found in closed cages, generally at densities well below those in the open cages. Predator densities in the closed cages grew to equal and sometimes exceed those in the open cages during the second 15 days. This response to higher prey abundance in the closed cages suggests that veliids as well as spiders show a positive numerical response to prey availability.

### Varietal Resistance

Fig. 7a shows the numbers of BPH eggs were higher on susceptible IR1917 than on partially resistant IR26. Comparison of nymphal densities, however, (Fig. 7b) shows less difference between varieties. This suggests, as further supported in Table 1, that BPH egg to adult survivorship on IR26 was *higher* than on IR1917. In fact, on IR26 it was the highest of all untreated crops. As it is known that IR26 was not resistant to all BPH phenotypes in the Laguna population (Pathak and Heinrichs 1982), we conclude that those BPH able to reproduce on IR26 remained on it and thrived. One factor leading to higher survivorship was lower predator density in IR26. Fig. 7c and 7d show how densities both of spiders and veliids were lower in the IR26 crop than the IR1917 crop. This was probably due to lower prey abundance and led to higher prey survival on the partially resistant variety. Predators' density-dependent numerical

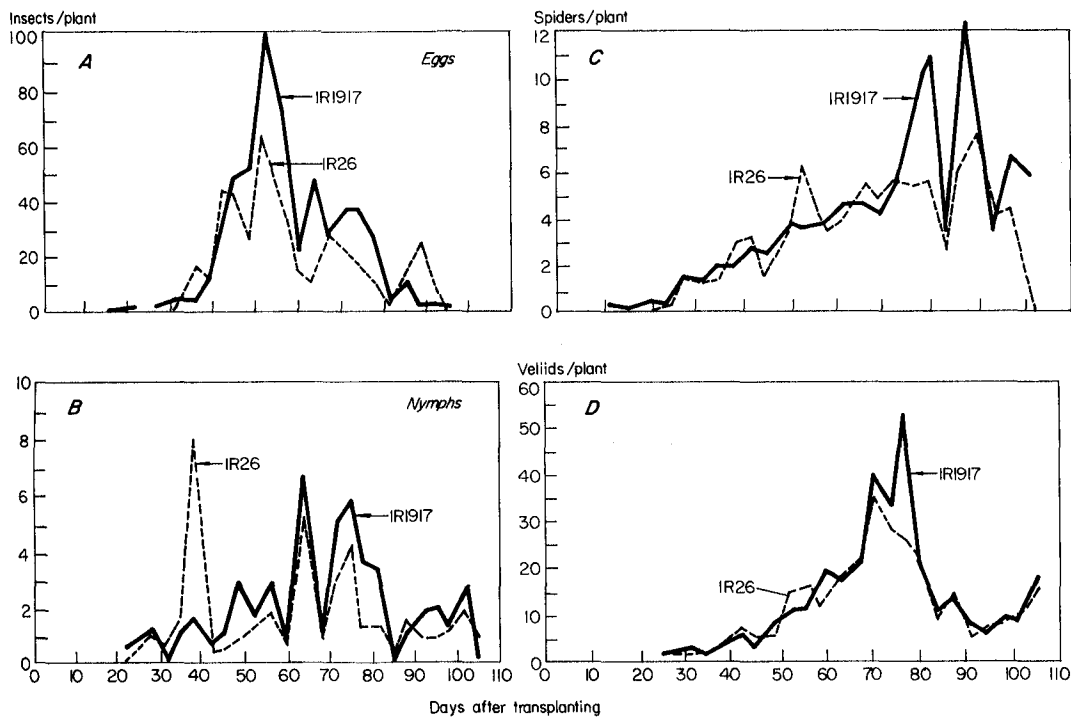


Fig. 7. Natural control compensating for lack of partial rice varietal resistance to *N. lugens* in Philippines, June to September, 1978. (A) Higher egg densities on susceptible IR1917 than partially resistant IR26; (B) Similar nymphal densities show effected *higher* survival of egg and immatures on partially resistant IR26; (C) and (D) Higher numbers of spiders and veliids on susceptible IR1917 show numerical response to higher prey numbers and suggest lower standard on the susceptible variety was due to predators.

response in the susceptible field compensated for a lack of host plant resistance. These results also suggest that strong varietal resistance might reduce prey abundance enough to suppress predator populations under field conditions.

### DISCUSSION

Our results show that tropical BPH population outbreaks can be induced when population regulating factors are disrupted, especially by insecticides. This occurred primarily because BPH survival was much higher when predators were not allowed to respond numerically to BPH densities and secondarily because physiological egg production may have been higher in insecticide treatment than in non-treated females. Egg production still seemed to respond negatively to female density, however, as even in the insecticide treated crop egg production did not reach the highest levels observed when females were at a low natural density in the field. The effects of stimulated physiological egg production were confounded in the field by female survival and wing morph proportions—when females lived twice as long they might have produced twice as many eggs without stimulation. When proportionately more brachypterous females survived, they were able to produce more eggs, due to their intrinsically higher fecundity, than when their proportion was as low as in untreated fields.

The major explanatory gaps left by this study are due to the relatively imprecise sampling methods used, the failure to clearly discern the dynamics and role of migration *among* fields, and the failure to investigate the effects of cropping intensity (all data were taken from environments with 2 or more crops/year). More precise sampling of field populations will produce real understanding of low density dynamics where natural enemies might play a different role, especially when prey densities are so low as might release their growth from natural enemies. Work in progress by Perfect, Cook and associates (Perfect and Cook, 1982 and Rosenberg, 1981) will greatly advance our understanding of the influence of migration of pests and

natural enemies on population dynamics, especially at the more common lower BPH densities.

While wing morph ratio and hence the production of emigrants is considered the key factor regulating Japanese BPH populations (Kuno and Hokyo 1970; Kisimoto 1965) there may be genetic differences between Japanese and Philippine populations. Our results showed *higher* proportions of macropterous adults than Kuno and Hokyo (1970) at the same densities of field-collected individuals. This might have led us to overestimate indigenous adult density and underestimate pre-adult mortality. On the other hand, the BPH colony at IRRI is nearly all brachypterous regardless of density suggesting that artificial selection operated on a genetically controlled wing polymorphism. In any case, emigration only reduced BPH densities in the insecticide treated field after hopperburn had begun.

It is logical and probable that high enough immigration can overwhelm natural enemies, although per capita egg production of BPH should still be reduced due to high female density, and that an increased number of rice crops per year will permit more population growth and potentially more immigration if the BPH is sufficiently released from its within-field regulating factors. Work in progress by Loevinsohn and associates (Loevinsohn *et al.*, 1982) will greatly advance our understanding of how regional cropping intensity affects BPH abundance. They have used light trap data to show significant increases of BPH catches with increased rice cropping intensity.

Recent evidence from large scale monitoring of BPH immigration with yellow pan water traps showed a positive association with cropping intensity over several hundred hectares. It was not possible, however, to relate the level of BPH immigration to subsequent BPH population density in the fields being monitored, probably because of the rate of immigration of natural enemies and their impact on BPH population growth (Perfect and Cook in IRRI, 1983).

Riechert and Lickley (1984), reviewing spiders as biological control agents,



distinguished aggregational and reproductive numerical responses of spider populations to prey densities. We did not distinguish the respective contributions of these mechanisms. We frequently found small ballooning spiders in the air above the crop canopy, gravid females or females with egg sacs in the crop, and considerable spider movement on the paddy water surface. Our regressions are based on food available to large or adult spiders; this suggests a reproductive mechanism (more food leading to more offspring) but the other mechanisms could have been equally responsible. More food may have led to lower competition and higher survival of less robust, smaller individuals.

Certainly their conclusion that the entire community of spiders responds numerically to prey density was supported by this study. We would further add that the community of generalist predators on the water surface, velliids, mesovelliids, and probably gerrids also responds to prey densities, but not so clearly to planthopper densities (see Nakasuji and Dyck, 1984).

Moving beyond population dynamics to pest management, our most significant result was that over a range of apparent immigration rates up to 80 per plant, BPH densities were kept below hopperburn levels without insecticides or varietal resistance. In contrast, even when immigration was apparently *minimal*, the use of insecticides caused an outbreak by blocking the numerical response of predators. Further evidence of the practical role of predators was found in the varietal comparison where survival on a partially resistant variety was *higher* than on the adjacent susceptible variety, because of the higher natural enemy densities on the latter.

Nearly every recorded outbreak of BPH in the tropics has been associated with prior use of insecticides (Kenmore, 1980). Dozens of compounds from three major classes of insecticide have now been found to increase BPH densities after treatment (Reissig *et al.*, 1982). Neither varieties *per se* or fertilizer levels have been shown to induce BPH

outbreaks; the role of cropping intensity is still under study. Yet destruction of natural enemies by insecticides consistently induces BPH outbreaks if sufficient numbers of BPH are active in the vicinity.

Tropical BPH dynamics are similar to those of other previously secondary pests of crops such as cotton and citrus, where regulation by natural enemies is disrupted by insecticide use and populations explode (van de Bosch, 1978; van den Bosch *et al.*, 1982; and DeBach, 1974). Whenever BPH populations are present, good management *must* include judicious, minimal, need-based use of insecticides.

The senior author has compared crops with no insecticide used and neighboring crops with regular insecticide use in Central Luzon, Leyte, Mindanao, Sumatra, West Malaysia, and Southern India. In every case, the treated fields had less than half the population densities of natural enemies of untreated fields and more BPH. The determining factor was not which insecticide was used, but how large is the available population of BPH which can multiply once the natural enemies are eliminated. Once an outbreak is in progress, the amount of crop damage sustained seems to be influenced by crop age and climate as well as variety and BPH feeding intensity (Kenmore, 1980).

The mainstay of BPH control technology is varietal resistance where effective. When a variety exhibits resistance to the local BPH phenotypes, is otherwise acceptable to farmers and is economically rewarding to grow, it eliminates the need for insecticides in BPH control. Resistance also can dampen the rate of population growth during induced outbreaks so that only 10-fold increases occur rather than the hundred or more-fold found on susceptible varieties (Aquino and Heinrichs, 1979). It is possible, however, to experience hopperburn on otherwise resistant varieties when heavy BPH flight activity, as from earlier harvested fields, matches a time of natural enemy destruction by insecticides, as on IR36 in farmers' fields in Mindanao, Philippines (Peralta *et al.*, 1983). Resistance cannot therefore protect against

insecticide misuse. Conversely, resistance can amplify the effectiveness of individual predators, by weakening BPH through inadequate feeding so they more easily fall prey (Kartohardjono and Heinrichs, 1984). Varietal resistance and natural enemies seem thoroughly complementary; the only theoretical problem comes when resistance suppresses BPH populations so much that the food supply for general predators disappears. They may not then be numerous enough to control *S. furcifera* immigrants or BPH of another phenotype preadapted to the otherwise resistant variety. Rapid pest immigration may overwhelm the natural enemy populations kept low by lack of food. This possibility has not yet been directly investigated, but the *S. furcifera* population did increase in our treated field between 10 and 100-fold more than in the control field and is therefore probably under the same sort of natural control as BPH.

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