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MANAGING TROPICAL RICE PESTS THROUGH CONSERVATION OF GENERALIST NATURAL ENEMIES AND ALTERNATIVE PREY[1]

WILLIAM H. SETTLE,[2] HARTIAHYO ARIAWAN, ENDAH TRI ASTUTI,
WIDYASTAMA CAHYANA, ARIEF LUKMAN HAKIM, DADAN HINDAYANA.[3]
ALIFAH SRI LESTARI, AND PAJARNINGSIH
Indonesian National Integrated Pest Management Programme, Jalan Margasatwa 61, Pasar Minggu, Jakarta Selatan, 12510, Indonesia

SARTANTO
Laboratorium Pengendalian Hama dan Penyakit Tanaman Pangan, Bantul, DIY, Indonesia

Abstract. The cultivation of tropical Asian rice, which may have originated 9000 yr ago, represents an agricultural ecosystem of unrivaled ecological complexity. We undertook a study of the community ecology of irrigated tropical rice fields on Java, Indonesia, as a supporting study for the Indonesian National Integrated Pest Management Programme, whose purpose is to train farmers to be better agronomists and to employ the principles of integrated pest management (IPM). Two of our study objectives, reported on here, were (1) to explore whether there exist general and consistent patterns of arthropod community dynamics related to natural or intrinsic levels of biological control, and (2) to understand how the existing levels of biological control are affected by insecticide use, as well as by large-scale habitat factors relating to differing patterns for vegetational landscapes, planting times, and the length of dry fallow periods.

We performed a series of observational studies and two experimental studies. Abundant and well-distributed populations of generalist predators can be found in most early-season tropical rice fields. We took samples from plants and water surface using a vacuum-suction device, and from the subsurface using a dip net. Our results show that high populations of generalist predators are likely to be supported, in the early season, by feeding on abundant populations of detritus feeding and plankton-feeding insects, whose populations consistently peak and decline in the first third of the season. We hypothesize that since this abundance of alternative prey gives the predator populations a "head start" on later-developing pest populations, this process should strongly suppress pest populations and generally lend stability to rice ecosystems by decoupling predator populations from a strict dependence on herbivore populations.

We experimentally tested our hypothesis of trophic linkages among organic matter, detritivores and plankton feeders, and generalist predators and showed that by increasing organic matter in test plots we could boost populations of detritivores and plankton-feeders, and in turn significantly boost the abundance of generalist predators. These results hold for populations found on the plant, on the water surface, and below the water surface. We also demonstrated the link between early season natural enemy populations and later-season pest populations by experimentally reducing early-season predator populations with insecticide applications, causing pest populations to resurge later in the season.

Overall, these results demonstrate the existence of a mechanism in tropical irrigated rice systems that supports high levels of natural biological control. This mechanism depends on season long successional processes and interactions among a wide array of species, many of which have hitherto been ignored as important elements in a rice ecosystem. Our results support a management strategy that promotes the conservation of existing natural biological control through a major reduction in insecticide use, and the corresponding increase in habitat heterogeneity.

Key words: agroecosystems, tropical rice; biological control; Chironomidae; community dynamics; detritivores and plankton feeders; field experiment; green revolution; insecticide use and pest outbreaks; integrated pest management; Java, Indonesia; rice-field ecology; rice landscape patterns; synchronous vs. nonsynchronous plantings.

1 For reprints of this Special Feature, see Footnote 1, p. 1963.
2 Present address:155 Valencia Rd. Aptos CA 95003, USA
3 Present address: Department of Entomology, Bogor Agricultural University, Jalan Raya Pajajaran, Bogor 16143, Indonesia.

INTRODUCTION

Most biological control programs focus on promoting one or two "premier" natural enemies as agents for the suppression of particular pests. In contrast, we argue that consistently high levels of natural biological control may often result from a complex set of community-level interactions that lead to a far more stable and robust system, vis-à-vis insect pest populations, than has previously been considered. We have arrived at this hypothesis from our own work on pest management in tropical rice agroecosystems.

Ecologists tend to think of agricultural systems as disturbed, depauperate, and evolutionarily recent. Tropical Asian rice, however, is an important exception. Rice cultivation is thought to have originated in northeast Thailand nearly nine thousand years ago (Bray 1986), and has been in Indonesia for at least three thousand years (Tas 1974). This long ecological history, together with extensive geographic distribution and generally warm and wet local climates, has resulted in an agricultural ecosystem unrivaled by any other in the world in terms of ecological complexity. Indeed, the arthropod species richness in many of the rice fields we observed surpasses that of most natural temperate systems. Yet the study of rice from an ecological viewpoint is just now in its infancy.

The dominant pest-control strategy in tropical rice over the past 30 yr has been the use of resistant varieties and especially the use of chemical insecticides, and the vast majority of research related to arthropods in tropical rice has been directed towards only a small handful of "pest" species without examining the biotic linkages to the rest of the system. Considering the paramount importance of rice culture in the world today and in the foreseeable future, systematic investigation into the structure and function of rice-field ecology is long overdue.

We have been working for the past four years within an FAO (Food and Agriculture Organization of the United Nations) and Indonesian National Integrated Pest Management (IPM) program on the Island of Java in Indonesia. In this paper we hope to stimulate some thought and discussion among ecologists and agriculturists by suggesting a mechanism that explains how tropical rice fields are robust and stable in the absence of insecticides as a result of an extremely rich web of generalist natural enemies.

Our principle hypothesis can be divided into two parts. First, we suggest that an early-season peak of detritivore and plankton-feeding insects provides a highly consistent, abundant and well-dispersed alternative food source for a diverse community of generalist predators. This effectively decouples the generalist predators from a strict dependence on rice herbivores, and allows predator populations to develop well in advance of rice-pest populations, thereby consistently keeping pests well below economically damaging levels. Second, we suggest that these in-field community-level patterns can be enhanced or disrupted by large-scale "habitat" factors, thereby affecting the inherent strength and stability of the system. These large-scale factors include area-wide spatial and temporal patterns of the landscape, i.e., planting patterns, water-use patterns, and insecticide-use patterns.

Background

Despite a growing body of scientific and empirical evidence showing that insecticides in tropical rice were a mistaken and counter-productive input, the fact remains that insecticides are still the dominant control tactic today. Worldwide, rice now accounts for more insecticides than any other crop, with =80% of this amount used in Asia (Woodburn 1990). For this reason we feel it necessary to present a brief history of insecticide use in Indonesian rice.

Rice is the staple food for almost half the world's population—roughly 109 people live on small rice farms, the vast majority of which produce rice for local consumption—estimates are that only between 2 and 4% of total global rice production is traded on world markets (Ooi 1991). With >180 X 106 people, Indonesia has the fourth largest national population, with about 112 X 106 people living on Java alone—an island roughly the size of New York State. For Indonesia, a stable and sustainable rice harvest has long been a top national priority

Beginning in the late 1 960s in many countries throughout Asia, rice production was greatly boosted by the introduction of short-duration, high-yielding varieties (HYVs)—the product of research at the International Rice Research Institute (IRRI) together with national research programs in a number of Asian countries. The result of this green revolution in Indonesia was an increase in average yield from ~2 Mg/ha, with one harvest per year, to yields averaging 5-6 Mg/ha for, in many areas, two crops per year (Huke 1991, van der Fliert 1993). For Indonesia the improvements in irrigation and yield potential resulted in a transformation from being the largest rice importer in the world, to being self-sufficient in rice by 1984 (Wardhani 1992), although the past several years have seen Indonesia fall back to being a rice importer.

The green revolution was literally and metaphorically a technology packaged for mass consumption. The package usually included the HYV seeds, nitrogen and phosphate fertilizers, insecticides, and fungicides. In many countries farmers were obliged to use all of these inputs, including calendar-based insecticide applications (van der Fliert 1993). Whereas fertilizers directly affect yields and are required for HYVs to reach their potential yield levels (e.g., Yoshida 1981, Huke 1991), insecticide inputs were based on the assumption that tropical rice yields are limited by insect pests, and that insecticides could control these pests. However, after some 30 yr of farmers applying insecticides on rice, there is no good evidence that farmers' yields have been increased as a result.

Large-scale applications of insecticides in rice in Indonesia began with an attempt by the government to control apparent problems due to stemborers (Mochida 1978, Rubia et al. 1989). In the late 1960s, somewhat prior to widespread use of the HYVs, the government of Indonesia undertook to contract out pest-control activities. Some 800 X 103 ha of rice were treated for yellow stem borers by aerial applications of phosphamidon (Dimecron 50; Ciba Geigy Ltd., Switzerland) from 1968 through 1970 (Mochida 1978). Aerial applications for stemborers by various insecticide firms on contract to the Indonesian government continued well into the 1970s. By 1974 a new pest, the rice brown planthopper, *Nilaparvata lugens* (Stal), was emerging in many of the areas sprayed as a pest far worse than stemborers (Rubia et al. 1989). Prior to 1970 and the mass spraying of phosphamidon, the rice brown planthopper was not reported as a pest in Indonesia. However, the Indonesian government assumed the emergence of the rice brown planthopper was due to the longer rice-growing seasons resulting from irrigation, or the new rice varieties (e.g., Mochida 1978, Dyck and Thomas 1979, Sawada et al. 1991), and decided to solve the problem by promoting even more insecticide use. Specifically, in 1975 the Indonesian government introduced a subsidy plan so that insecticides could be made available to farmers for about 20% of actual cost (van der Fliert 1993). Subsidies for insecticides increased yearly, and by the mid-1980s the annual subsidy averaged U.S.$120 X 106. In spite of (or rather because of) the increasing amounts of chemical insecticides used, in 1977 Indonesia lost—106 Mg of rice to the rice brown planthopper—enough to have fed 2 X 106 people for 1 yr. Overall, during the late 1970s Indonesia is estimated to have lost upwards of U.S.$ 109 worth of rice to the rice brown planthopper, not including the cost of the insecticides, opportunity costs, or the social and health costs of exposure to insecticides (Wardhani 1992).

The sad irony is that rice brown planthopper problems are effectively "self-inflicted wounds." The evidence accumulated over at least 15 yr clearly supports the fact that the rice brown planthopper is an insecticide-induced resurgent pest whose degree of damage is positively correlated to insecticide use (e.g., Aquino and Heinrichs 1979, Chiu 1979, Heinrichs 1979, Chelliah and Heinrichs 1980, Kenmore 1980, Reissig et al. 1982, Peralta et al. 1983, Heinrichs and Mochida 1984, Kenmore et al. 1984, Ooi 1988, Heong 1991).

In response to the rice brown planthopper threat, the IRRI, together with national research institutes, beginning in 1977 multiplied and widely distributed seeds of the variety IR26 which had genes from South Asia that caused the rice to be distasteful to the rice brown planthopper. Yet within three seasons the rice brown planthopper populations in most of East and Central Java were able to feed on IR26 (Kenmore 1991). During the early 1980s, Indonesian scientists developed and released several new high-quality resistant varieties based on the IR36 germplasm mixed with local germplasm. The rice brown planthopper problem subsided for several years, and in 1984 Indonesia attained self-sufficiency in rice production (Wardhani 1992). However, insecticide subsidies continued to increase and increasing amounts of insecticides were applied to rice. In 1986 Indonesia witnessed the dramatic and sudden breakdown in resistance to the rice brown planthopper of all of these varieties that were based on IR36 (Kenmore 1991).

Many researchers now hypothesize that heavy insecticide use actually accelerates the adaptation of pest populations to the resistant varieties. The proposed mechanism assumes a natural genetic diversity within planthopper populations sufficient to provide individuals capable of feeding and reproducing well on the new resistant varieties. Insecticides release planthoppers from high levels of natural mortality by natural enemies, allowing the genetically superior planthopper individuals to outcompete the "normal" individuals and, hence, rapidly become the dominant fraction of the planthopper population (Gallagher 1988, Gould et al. 1991, Gallagher et al. 1994, Heinrichs 1994; P E. Kenmore and D. G. Bottrell, *unpublished manuscript* presented at 1994 Entomological Society of America Symposium).

In 1986 the Indonesian government, threatened by a loss of their newly achieved rice self-sufficiency, took bold steps. President Suharto listened to the advice of national advisors who stated that the massive amounts of insecticides used to try to combat the rice brown planthopper were in fact the cause of the rice brown planthopper problem. In August 1986 President Suharto issued a Presidential Decree that banned 57 types of insecticides for rice. Two years later the government had eliminated the U.S.$150 X 106 per year subsidy on insecticides, and stated in some detail that IPM was to be the official approach to pest control, meanwhile initiating a large-scale program for farmer training in IPM.

The strategy of the Indonesian National IPM program

and the Asian Intercountry IPM Program is to help farmers overcome their insecticide habit by helping them to become better observers, experimenters, and decision-makers in their own fields. To date somewhere around 500 000 Indonesian rice farmers have been trained for one full season. The results are tangible: studies of approximately 5000 farmers show training reduces insecticide use by ~60% (Anonymous 1993; Pincus, *unpublished report* [1991] to the Indonesian National Integrated Pest Management Program, Jakarta, Indonesia). These same studies show IPM farmers have, on average, slightly higher yields, higher overall returns, and lower economic variance (risk).

METHODS FOR DETECTING BIOLOGICAL CONTROL IN THE RICE AGROECOSYSTEM

Our hypothesis regarding generalist natural enemies derives from a suite of observational studies and two experiments, all done in farmer fields and subject to normal farmer practice.

Observational studies: within-field patterns and processes

We haphazardly took samples in a transect across farmer plots on a weekly schedule for 5 wk. and then every 10 d until just before harvest—a total of 10 sample dates, and a minimum of 30 sample units for each field. Agronomic practices—weeding, fertilizer-use, and varietal choice—were left to the farmer to decide; however, farmers allowed us to control the details of insecticide applications.

Samples were taken with a vacuum-suction device powered by an automobile-interior vacuum and a 12-volt car battery, known as a "Farmcop" (Caring et al. 1979). The samples were taken by dropping a 70 cm tall zinc funnel with a 400-cm2 opening at the base over the rice plant. The top of the zinc tube was enclosed by organdy netting. Insects that attempted to fly were first sucked from the netting before moving the suction tube down onto the plant and onto the surface of the water. The vacuum tube was taken over each area several times until no more insects were observable. This took 3–10 min depending on the size of the plant. Samples were then marked, taken to the laboratory and frozen in their original organdy sample bags, and later thawed and put into plastic film bottles containing a 70% alcohol solution for later sorting and identification.

Observational studies: differences among habitat types

We chose to compare two landscape types commonly found on Java: a large-area synchronously planted "rice bowl" in Northwest Java, and a moderately sized, less synchronously planted area in Central Java.

Northwest lava (Karawang district).—This area comprises ~400 x 103 ha divided into four irrigation blocks fed by two dams. Two crops a year are grown in the irrigated areas, with a long, dry fallow period after the second season, lasting 1-3 mo depending on the irrigation block. The timing of water release from the dams is controlled by the government, and water arrival is delayed between adjacent schemes by about 2-wk intervals. Farmers plant nurseries and begin preparing the soil as soon as water is available. Within each irrigation block rice is hand-transplanted, mostly synchronously.

Within each irrigation block are a patchwork of contiguously planted rice fields bordered by villages. As Indonesian villages are planted in trees and gardens, from the air the impression is one of large rice fields surrounded by "forest." These areas of contiguous rice fields (called *hamparan* in Indonesian) vary in size, but in Northwest Java hamparan are large, usually between ~500 and 3000 ha. In one hamparan, several villages and > 1000 farm families may participate in cultivating rice.

The area of Northwest Java that we studied is representative of several large "rice bowls" found elsewhere on Java, characterized by large-scale and synchronous planting patterns and long, dry fallow periods. This landscape pattern resulted from the construction of large-scale irrigation schemes during the late 1960s, which allowed government control of water release and obliged synchronous planting on a large scale by farmers. Government policy on pest control in the area is currently based on the idea that synchronously planted fields, with a long dry-season break in the planting cycle, is the best pattern to help control rice pests and diseases because it will tend to "break the pest cycle." Within this area 1-2 crops of rice are grown during the year—a rainy-season rice crop (November-March) and a dry-season rice crop following immediately after (March-July). The period from August through October is a fallow period, with stubble being burned in small piles, leaving large expanses of dry and barren ground.

Central Java (Bantul district).—The area in Central Java from which we took samples is representative of the older and more traditional rice-production areas of Indonesia. These areas have long histories of cultivation and small-scale, socially complex systems for water control at the village level (Bray 1986). Water from aquifers, rivers, and dams is available almost year-round, and the between-hamparan and even within-hamparan fields are often distinctly non-synchronously planted. Natural, as well as village, vegetation is more closely woven in-between the rice fields. Hamparan are on the scale of tens to hundreds of hectares. In contrast to Northwest Java, the time for which rice fields are fallow and dry is relatively short (1 mo), with a soybean, corn, or vegetable crop often planted as a third season crop after the second crop of rice.

Experiment. organic-matter effects on community dynamics

The principle hypothesis emerging from our observational studies was that generalist predators feed on detritivores early in the growing season. We tested this hypothesis by varying levels of organic matter (OM) in rice fields in order to measure population differences of detritivores, plankton feeders, and generalist predators between the treatment levels.

We took ~1.5 ha of rice land and created 12 plots, 20 x 20 m with a minimum of 5 m between plots. Plot assignments were randomly chosen. The soil was flooded and let stand for 3 mo with an occasional weeding in order to try to reduce the existing levels of OM. We then brought in z2 Mg of composted cow manure to add to half the plots. Manure is sometimes used as fertilizer by rice farmers, but is generally in too short supply to substitute for inorganic fertilizers. Rice (variety IR64) was transplanted 10 d later.

We took weekly samples both on and above the water surface (typical Farmcop samples) as well as from below the water surface, including about 2 cm of the surface of the mud. The below-surface aquatic samples were taken using dip nets and the same zinc funnels with 400-cm2 openings as for the suction samples. A total of 15 suction samples and 5 aquatic samples were taken per plot each week for 5 wk. In order to reduce the effects of disturbance by the sampler, stratified samples were taken from within each of the four corners, and from the center areas of the plots. Within each stratum samples were taken haphazardly. Samples were processed as in the observational-study surveys described above (see *Observational studies: within field . . .).* The experiment was halted halfway through the season as our interest was only in early-season (aquatic) patterns.

Experiment: insecticide effects on rice arthropod communities

We treated three of six plots of IR64 rice with insecticides in a 1.5 ha area owned by one farmer. The choice of chemicals and timing of applications was based on typical farmer behavior in the area. Specifically, we applied two treatments of granular carbofuran 3% active ingredient (a.i.) (Furadan 3g; Food and Machinery Corporation, USA) at the recommended dosage of 17 kg/ha at 15 and 30 d after transplanting (OAT). We also applied two sprays of monocrotophos (Azodrin 15 wsc; Shell International Chemicals, U.K.) at 500 gm a.i./ha at 25 and 37 DAT. Monocrotophos is an insecticide banned for use on rice, but, nevertheless, often used by farmers. All other agronomic practices remained the same, based on local farmer practice.

A total of 48 samples were taken at each sample date over the course of the growing season. Samples were taken weekly for 5 wk. then every 10 d for a total of 10 sample dates. Processing of samples was done in the same manner as with the farm surveys detailed above (see *Observational studies: within field . . .).*

Classification by "functional groups"

In four years of taking samples from irrigated rice on Java we have catalogued ~765 species of arthropods. Such diversity obliged us to seek a means to reduce the complexity while creating an understanding of structure and function. We feel that functional groups are an appropriate means of classifying arthropods in Indonesian rice fields for two reasons: (1) the goal of our analysis is a comparative look at the structure and function of a single crop ecosystem; whatever arbitrariness exists in the designation of functional groups will at least be consistent across rice habitats; and (2) the intuitive nature of defining a classification scheme based on where an arthropod lives within the system, and what, and how it eats, works well in farmer-training exercises. Therefore, we use functional groups as a heuristic tool that varies to some extent depending on location, ecological factors, and cultural and educational differences.

RESULTS AND DISCUSSION

Detritivores and plankton feeders: indirect contributors to natural biological control

A tropical rice field, once flooded, is a rich "soup" of organic materials, originating from several sources including residues from the previous crop cycle, organic wastes brought in by irrigation water from villages, and algal growth (Roger et al. 1991). Bacteria and phytoplankton are the base of the aquatic food web in tropical irrigated rice, both being fed upon by zooplankton. Indeed, phytoplankton (as opposed to the residues from higher plants) may be the dominant source of energy at the base of many fresh-water aquatic systems (Hamilton et al. 1992). Populations of small to intermediate-sized zooplankton and phytoplankton are, in turn, fed on by plankton feeders such as mosquito larvae and chironomid midge larvae. While we classify them as plankton feeders, many species of chironomid larvae also feed on detritus. Of the 765 species of spiders and insects currently catalogued in our collection from Indonesian lowland irrigated rice, roughly 19% of the total are detritivores or plankton feeders (compared with 16% herbivores) (Fig. 1). The role of this group in the functioning of tropical rice ecosystems

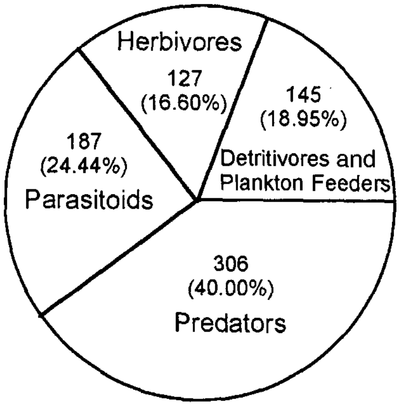

FIG. 1. Of the total number of species catalogued in our collection from lowland irrigated rice in Indonesia, a majority are natural enemies. Detritivores and plankton feeders represent an important contribution to the total diversity. The numbers represent species catalogued within each trophic level; percentages of the total collection are in parenthesis.

has been almost entirely ignored. A few species have been looked at as possible occasional pests of rice, and the tendency has therefore been to lump them all as "pests " .

The larvae of two fly families—Chironomidae (true midges) and Culicidae (mosquitoes)—feed on aquatic plankton. In our studies, the true midges vastly outnumbered the mosquitoes; in fact, mosquitoes were rarely captured in samples. In the agricultural literature we reviewed, chironomids were mostly considered potential pests. Work in California has focused on three genera that apparently can cause local sporadic damage to the newly emerged roots of rice seedlings when rice is broadcast-seeded (Clement et al. 1977), although no measurement of actual yield loss was made. In Asia, Heong et al. (1991) lumped all the chironomids as "root feeders" under the heading of "phytophagous" insects. However, this generalization does not accord with our observations or the general literature on aquatic insects (Wirth and Stone 1956, Coffman 1978, Pinder 1986, Hilsenhoff 1991). Also, we know of no reports from tropical Asia implicating a chironomid species as causing serious damage to rice. Given abundances commonly seen of up to several thousand per square metre, it is likely there would be a noticeable effect on the rice crop if the chironomids we commonly observed were feeding on rice roots. The lumping of all chironomids as "pests" is probably a simplification that overlooks the positive contribution of these insects to the rice ecosystem.

Ephydrid flies and collembolans were among the dominant groups of detritivores captured in our samples. We found 19 species of Ephydridae and 5 species of Collembola. Of the ephydrids, *Ochtera sp. is* a predator, and *Hydrellia philippina is* a leaf miner. The remaining species are detritivores (Reissig et al. 1986). *H. philippina* mines the rice leaves that remain resting on the water surface after transplanting. While considered a "pest" (Manandhar and Grigarick 1983), Shepard et al. (1990) demonstrated that rice plants can tolerate up to ~60% damage without any reduction in yields, and that damage greater than 60% causes only slight reductions in yield. As with the Chironomidae, it is probably inaccurate to represent this family as containing predominantly pest species.

We suggest that detritivore and plankton-feeding insect populations provide a consistent and abundant source of food for large and diverse populations of generalist predators, up to halfway through the season. The patterns of emergence (Figs. 5 and 6) show that populations of detritivores and plankton feeders (in large part made up of chironomids) peak at about 30 d after transplanting (DAT), and then decline over the rest of the season, whereas rice herbivore populations only begin to emerge much later in the growing season (50-60 DAT). This suggests that chironomids are unlikely to interfere with generalist predators feeding on pests. Note that this early-season peak in "others" is mirrored—with a slight delay—by the predator populations (Fig. 5a). These data gave us our first hint that predators might be feeding on detritivores and plankton-feeding insects early season.

High early-season abundances of plankton feeders and detritivores, together with abundant populations of generalist predators, have been observed by W. H. Settle in Vietnam, India, Bangladesh and The Philippines, and Central China. To check for a general trend in our data from Java we compiled data from six locations in the form of cumulative distribution functions—that is, with trophic categories calculated for each date as a proportion of their overall seasonal sum (Fig. 2). These patterns show predator populations temporally developing after populations of plankton feeders and detritivores, but before populations of herbivores. This is consistent with our hypothesis that generalist predators are supported in the early season by decomposers and plankton feeders. (We exclude parasitoids for clarity, but they follow after herbivores.)

Do general predators eat detritivores and plankton feeders?

We found evidence from both observational and experimental studies to support the idea that predators are actually feeding on the detritivores and plankton feeders:

Behavioral observations.—In both the field and in aquarium studies, we have frequently observed a number of different generalist predators feeding on the larvae and adults of midges and ephydrid flies, as well as

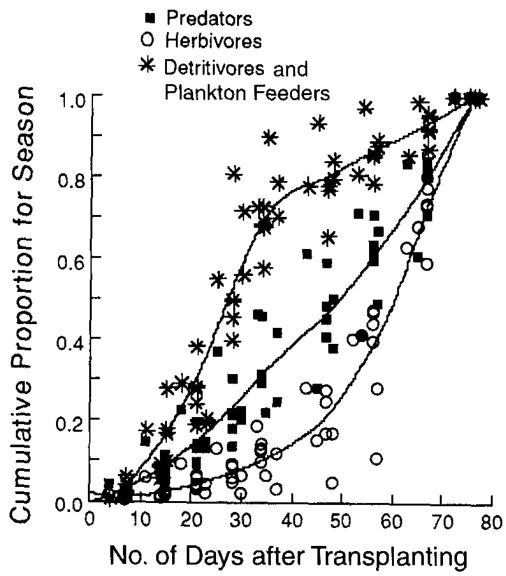

FIG 2. The cumulative proportion of total seasonal abundance of three trophic levels over one season, compiled from six locations in Java. Curves represent Loess fits, tension = 0.5. Note that populations of detritivores and plankton feeders emerge earliest, followed by predators, and finally by herbivores. This supports the hypothesis that predators are feeding on populations of detritivores and plankton feeders.

collembolans. In our future work we plan to quantify linkages and per capita interaction strengths, *sensu* Paine (1992).

Likelihood of encounter.—From our weekly vacuum samples from six locations we calculated the likelihood of co-occurrence of detritivores and plankton feeders vs. herbivores, given that a plant has a predator on it (Fig. 3a). Predators have roughly 25-35% greater likelihood of finding an adult detritivore or plankton feeder than of finding an herbivore. In certain areas this likelihood of predators encountering detritivores and plankton feeders in the early season is quite high (Fig. 3b).

Experimental results: organic matter affects predator numbers.—The results from our organic matter (OM) experiment provide strong support for our hypothesis, by showing that plots with high levels of OM have higher populations of detritivores and plankton feeders and higher populations of predators—both below and above the water (Fig. 4). A detailed analysis of effects on specific functional groups remains to be done.

Experimental results: insecticide-treated vs. untreated rice.—The results of our second controlled experiment, comparing treated vs. untreated fields in Northwest Java, show a classic pattern of insecticide resurgence (Fig. 5b). The resurgent peak in the treated plots is due almost entirely to the rice brown planthopper. Note how natural enemy populations in the untreated plot "mirror" the population peak of detritivores and plankton feeders, and then rise again, above and in advance of the late-season rise in herbivores; whereas, in the insecticide-treated plots the natural enemy populations are suppressed during the early season. Although predator populations are ultimately higher at

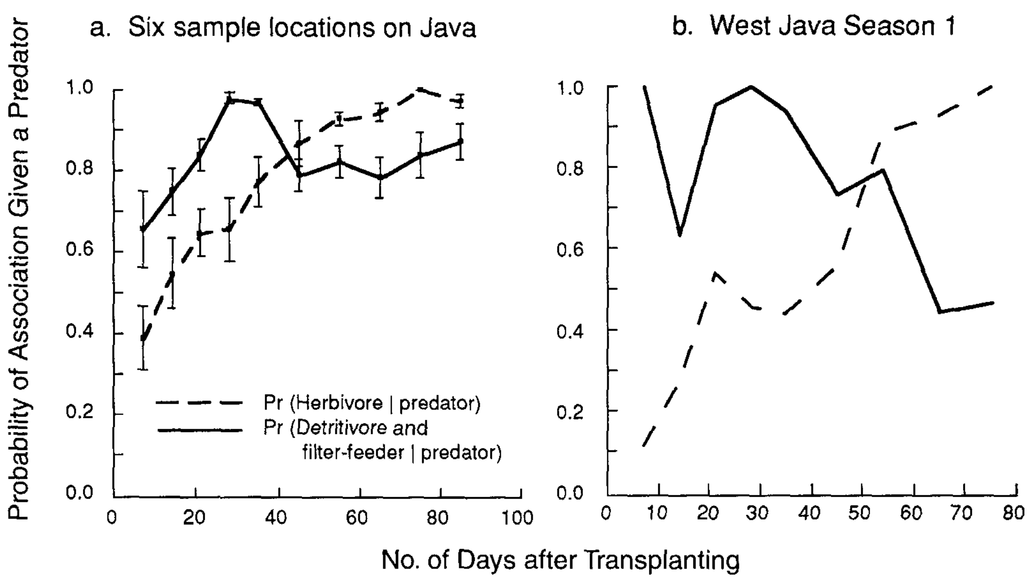

FIG. 3. The conditional probability of a predator co-occuring on the same plant with a detritivore or plankton feeder vs. co-occuring with an herbivore, given the condition that a predator is present. (a) For six sites on Java; error bars are ±2 SE. (b) Certain locations have high likelihoods of predators co-occuring with detritivores and plankton feeders in the early season.

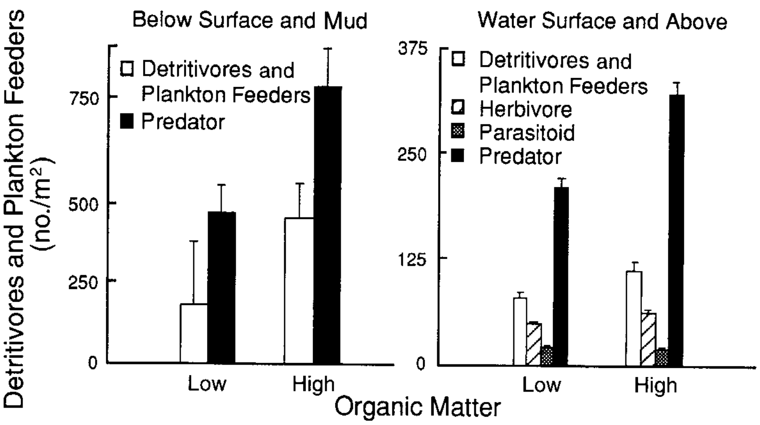

FIG. 4. Number of detritivores and plankton feeders (mean +1 SE) in Indonesian rice fields as a function of organic-matter (OM) levels, in six replicate plots each 20 × 20 m.

the end of the season in the treated plots, these populations are effectively "too late" because they develop behind and below the populations of herbivores.

The insecticides we used had the largest negative effect on the functional group of surface-dwelling predators (Veliidae, Mesoveliidae, and Hydrometridae) (Fig. 5c and d). This observation, coupled with the fact that insecticide-treated plots exhibited resurgence of brown planthopper populations, supports previous conclusions that surface-dwelling predators are an important functional group in naturally suppressing populations of the rice brown planthopper (Kenmore et al. 1984, Nakasuji and Dyck 1984, Kuno and Dyck 1985).

Insecticide-treated plots showed higher populations of detritivores and plankton-feeders (Fig. 5e and f). Specifically, plankton feeders (Chironomidae) exhibited a large increase in numbers in the insecticide plots, most likely due to reduced predation pressure. Resurgence of chironomids due to insecticide applications in rice has been noted elsewhere by Takamura (1993). Any direct effect of insecticides on chironomids may have been mitigated by their known resistance to pollutants and insecticides, see Pinder (1986) for a review.

In contrast to the plankton feeders, populations of detritivores (principally surface-dwelling Collembola and ephydrid flies) were significantly reduced in the treated plots (Fig. 5e and f). Note the similarity with our previous results for the surface-dwelling predatory Hemiptera. This leads us to conclude that this particular insecticide treatment has strong negative effects on the surface-dwelling fauna in general. This makes sense if we think of the water surface as a boundary layer between air and water that physically lends itself to the buildup of insecticide sprays.

What is the role of synchrony and scale in the dynamics of tropical rice communities?

Rice is grown under widely varying conditions throughout the world, and whatever intrinsic patterns may tend to exist are likely to be influenced by external, large-scale factors. As detailed above, we characterized Northwest Java as "large-area synchrony with long, dry fallow period," and Central Java fields as "moderate-area synchrony with short, dry fallow period." Unfortunately, the variables of hamparan (contiguous rice field) size, planting synchronicity, and length of dry season are confounded, making it difficult to separate out their relative effects on arthropod community structure.

The promotion of synchronous planting as a means of controlling pests can be frequently found in the literature (e.g., Dyck et al. 1979, Oka 1979, Loevinsohn et al. 1993), and is in fact one of the IPM tactics promoted by the Indonesian Department of Agriculture. The assumption is that non-synchronous planting patterns promote pest problems because they give the rice pests a constant source of food. That analysis, however, is based solely on a plant-herbivore model, and does not take into consideration natural enemies and alternative prey. Earlier studies have questioned the validity of this tactic. Researchers examined patterns of the rice brown planthopper outbreaks in Northwest Java from March 1986 to March 1991 (Sawada et al.1991) clearly showing that the rice brown planthopper outbreaks are more prevalent and more serious in the synchronously planted areas when compared with the non-synchronously planted ("staggered") areas nearby. They attributed these differences to higher levels of pest mortality due to natural enemies in the staggered areas. Similar results were found in Malaysia (Wade and Salleh 1992).

Fields in the Northwest Java rice-bowl area are synchronously planted on the scale of several thousand hectares, virtually al1 of which is barren and dry during the preceding long fallow period. Examination of trophic level differences between fields from Northwest Java and Central Java for the first rice-growing season, suggests that predators are late coming into the fields in

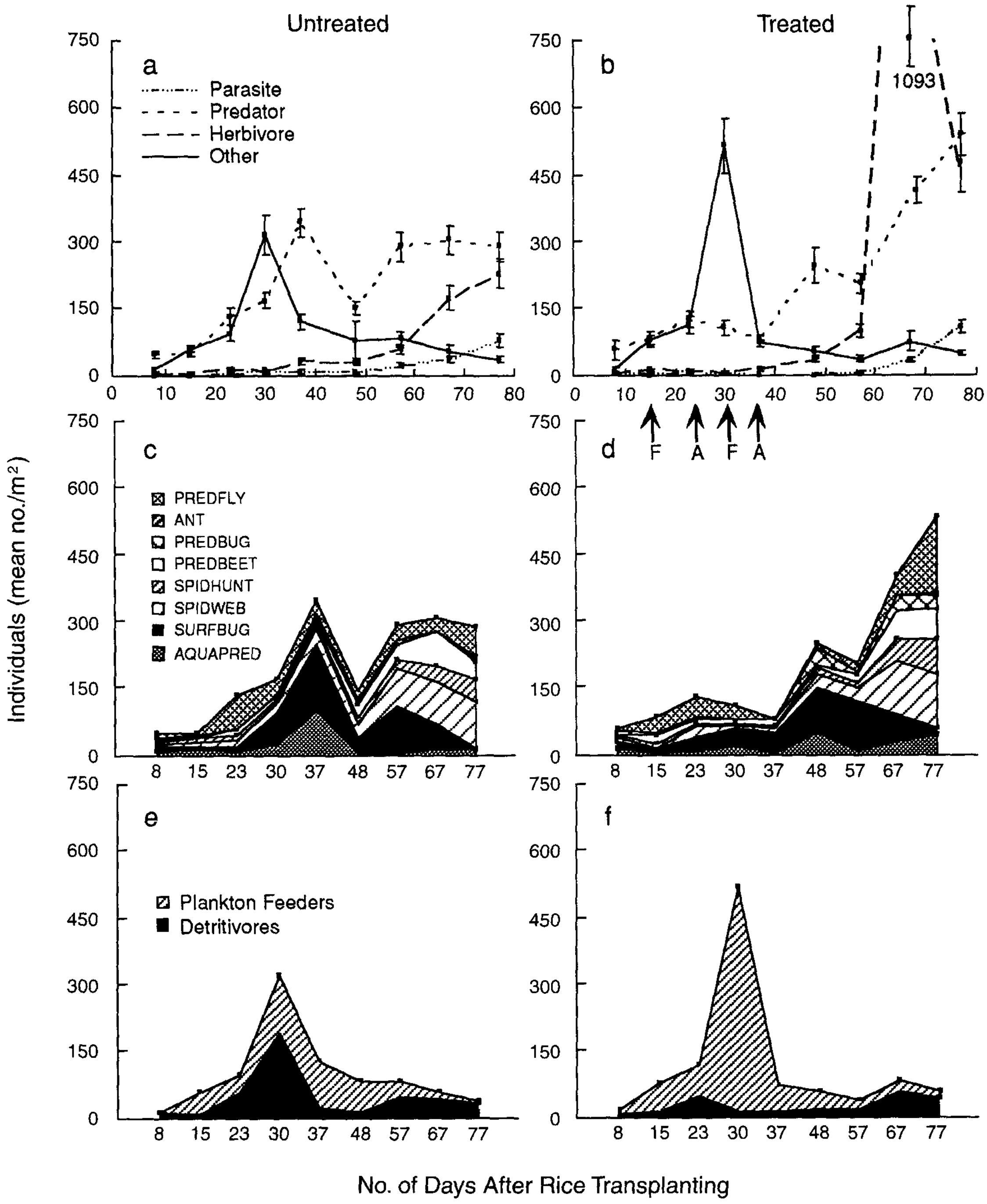

FIG. 5. Community profile during the second growing season (dry; March-July) from experimental rice field plots in Northwest Java, treated vs. untreated with pesticides. Data are means + sr. (a) Note that detritivore and plankton feeders peak early in the season, followed closely by predator populations at a time when pests are virtually absent. (b) Insecticide applications caused suppression of predators early in the growing season, causing the resurgence of pests later in the season. F = Carbofuran 3% active ingredient (a.i.) and 17 kg formulation per hectare; A = monocrotophos (Azodrin) 500 gm/ha a.i. Arrowheads show dates of pesticide applications. (c) Untreated plots are relatively higher in the functional groups for surface-dwelling predators ("surfLug") and aquatic predators ("aquapred"), compared with treated plots in (d). (e) and (f) insecticides cause suppression in detritivores, but resurgence in plankton feeders, in part due to their habitat locations (water surface vs. under water or in the mud).

Northwest Java compared with Central Java (Fig. 6a and b). Indeed, it requires almost 65 d after transplanting for predator populations in Northwest Java to reach the levels—both in density and dispersion—that are reached in Central Java after only 11 d (Fig. 7a and b).

The large-scale synchronous planting of a second rice crop in Northwest Java proceeds directly after the first. Predators that have built up during the preceding rainy-season crop clearly carry over into the next season (Fig. 7a and c). Although we are unable to partition the contribution made by each factor, these data indicate that large-scale synchronous plantings having long, dry fallow periods are, in some sense, "weaker" systems than the less synchronous areas in Central Java. This conclusion is further supported by an analysis of functional-group differences.

Functional-group differences between synchronous and less synchronous areas

Functional-group comparisons show that the less synchronous, more vegetationally diverse plots in Central Java have a substantially greater abundance of spiders and predatory flies for the first growing season, especially early in the season, compared with Northwest Java for either season (Figs. 5c and 6c vs. Fig. 6d). The dominant predator guild in the weakest location (Northwest Java season 1) is the terrestrial predatory beetles (Fig. 6c).

The largest difference among predator functional groups between seasons one and two for Northwest Java is the early-season peak in aquatic and surface-dwelling hemipteran predators, which are far more abundant the second season (Fig. 5c vs. Fig. 6c). Also for Northwest Java, both web and hunting spiders are poorly represented in the first, and early in the second season, but become abundant by the end of the second season. Spiders and surface-dwelling predators are known to be critically important factors in the control of the rice brown planthopper (Kenmore 1980, Nakasuji and Dyck 1984). Their relative impoverishment in Northwest Java indicates a serious weakness in the system

CONCLUSIONS

From observational data we constructed an hypothesis suggesting why species-rich, abundant, and well distributed populations of generalist predators can be found in many early-season rice fields. We showed that these populations are likely to be supported by feeding on abundant populations of detritus-feeding and plankton-feeding insects, whose populations consistently peak and decline in the 1st third of the season. We further hypothesized that since this abundance of alternative prey gives the predator populations a "head start" on later-developing pest populations, this pro cess should strongly suppress pest populations and generally lend stability to rice ecosystems by decoupling predator populations from a strict dependence on herbivore populations. We experimentally tested our hypothesis of trophic links among organic matter, detritivores and plankton feeders, and predators, by showing that by increasing organic matter in test plots we could boost populations of detritivores and plankton feeders, and in turn significantly boost the abundance of general predators. These positive relationships held true for populations found on the plant, on the water surface, and below the water surface. We also demonstrated the link between early-season natural enemy populations and later-season pest populations by experimentally reducing early-season predator populations with insecticide applications, causing pest populations to resurge later in the season. Overall, these results demonstrate the existence of a mechanism in tropical, irrigated rice systems that supports high levels of natural biological control. This mechanism depends on season-long successional processes and interactions among a wide array of species, many of which have hitherto been ignored as important elements in a rice ecosystem.

Natural biological control

There are at least two ways in which the processes that support naturally high levels of biological control are commonly disrupted:

1) Natural enemies are kept down by early-season applications of insecticides. Our experimental results add to the already large number of studies showing that insecticide applications in tropical rice are the most likely cause of pest problems. However, two new implications of our study are: (a) if aquatic invertebrates—detritivores and plankton feeders—are indeed important elements in a robust rice ecosystem, then pesticides (including herbicides) should be examined for negative effects on these animals. Certain herbicides may negatively affect phytoplankton and zooplankton, which may indirectly negatively affect the health of predator populations. For example, the herbicide atrazine (Gesaprim 80 wp; Ciba Geigy Ltd., Switzerland) at a concentration of 1.33 g/L has been shown to prevent development of certain *Chironomus* species (Pinder 1986).

2) Unfavorable landscape design and water-use patterns weaken the system. In rice landscapes characterized by synchronous and large-scale planting patterns and preceded by long, dry fallow periods, the arrival of natural enemies is severely delayed. A secondary but important effect of this delay is that generalist predators will arrive too late to take advantage of the peak in alternative prey provided by detritivores and plankton feeders. Some of our recent work in these "weak" habitats is aimed at helping farmers find ways to

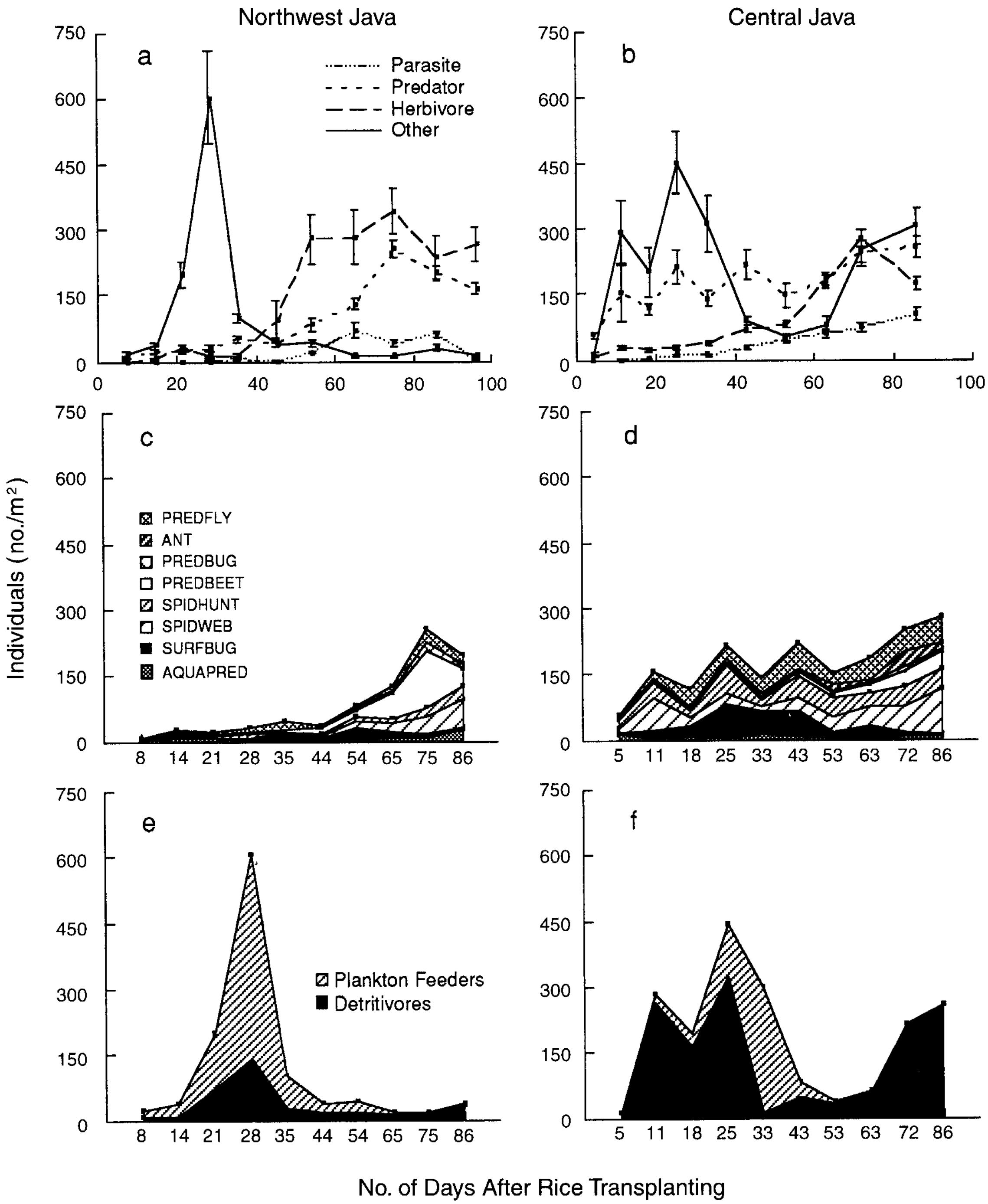

FIG 6. Community profile in observational rice-field plots for Northwest Java vs. Central Java for season one (after the dry fallow period). Fields in Northwest Java are planted synchronously on a scale of > 1000 ha and have a 3-mo dry fallow period, whereas the Central Java fields are planted synchronously on a scale of tens to hundreds of hectares with only a l-mo dry fallow period. (a) and (b) Note that populations of natural enemies are delayed early in the season in Northwest Java. Data are means +2 SE. (C) and (d) Predator functional groups are especially weak the first 65 d in Northwest Java, probably due to long re-immigration times associated with large-scale synchronous planting and long dry fallow periods. (e) and (f) Plankton feeders dominate the Northwest Java fields, whereas detritivores dominate the Central Java fields. This is probably a reflection of the relatively small amounts of organic matter found in Northwest Java fields after farmers burn their straw, and of the longer dry fallow period.

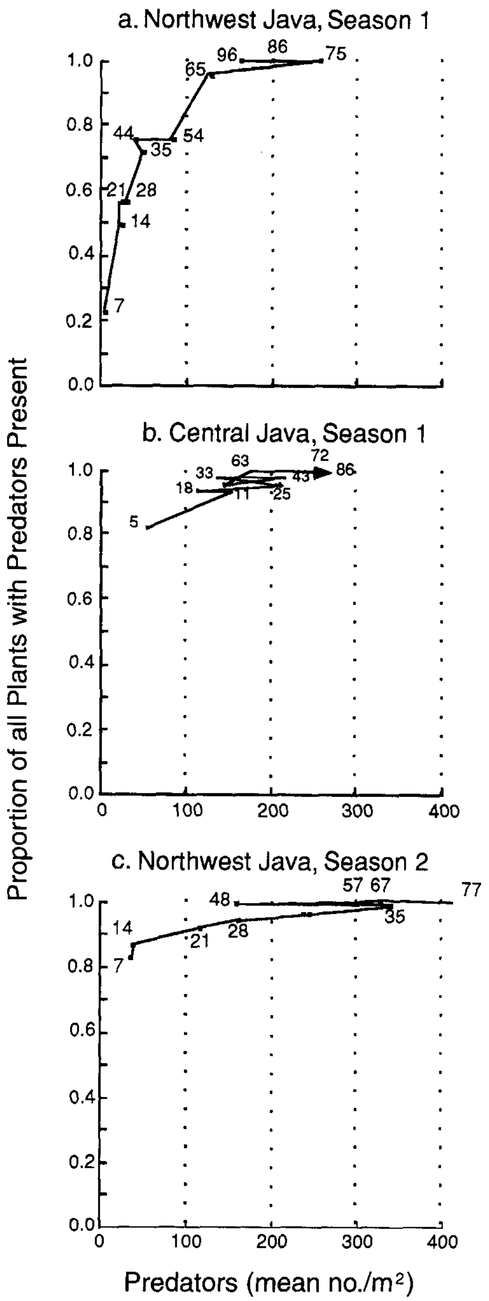

FIG. 7. Dispersion as a function of density for predators in Indonesian rice fields. Line numbers represent days after transplanting (DAT). Note the delay in arrival of predators in Northwest Java season 1 vs. Central Java season 1. No such delays exist for the second season in Northwest Java.

"bridge" natural enemies across long, dry fallow periods by planting dry-season crops, such as soybeans or green manures, or promoting the conservation of straw mulch piles.

While crop-protection scientists may change their ideas on the need for insecticides in tropical rice, the fact still remains that tens of millions of farmers throughout Asia have become habituated to using insecticides. The question no longer is whether insecticide use should be drastically reduced, but rather, what the best mechanism is for bringing about this reduction and getting farmers "off the habit." Unfortunately, the misunderstanding among farmers (and, indeed, many government workers) concerning the use of insecticides is not related to just a single concept, but rather, to a suite of related concepts. Farmers commonly feel: (1) that all insects in their fields have the potential to do damage to their crops; (2) that any amount of loss to the plant leaves and stems will cause a concomitant loss in yield; and (3) that insecticides are a kind of "medicine" that helps the plant be healthy in the same way that immunizations protect humans.

Ignorance engenders fear, and an uneducated, fearful, and passive farmer population will continue to try to rely on insecticides. To turn this around is difficult. The mechanism of insecticide-induced resurgence is not obvious as it involves indirect effects and an inherent delay of ~ 1 mo between the cause (insecticides) and effect (outbreak).

On the bright side, we have seen convincing evidence that a decentralized, participatory educational approach, such as embodied in IPM Farmer Field Schools ongoing in many countries in Asia, has succeeded in helping farmers overcome the old misconceptions by helping them demonstrate for themselves the ecological cause-and-effect relationships associated with insecticide use. The four fundamental principles of IPM within this program are: (1) grow a healthy crop; (2) observe the field weekly; (3) conserve natural enemies; and (4) farmers must become experts.

In light of the robust mechanism supporting high levels of natural biological control, the best strategy for biological control in tropical rice is for farmers to conserve the diversity of existing species through major reductions in pesticide use, to keep dry fallow periods short, and to maintain the heterogeneity of small scale rice landscapes.

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