Ecology of the brown planthopper in the tropics

V. A. Dyck, B. C. Misra, S. Alam, C. N. Chen,
C. Y. Hsieh, and R. S. Rejesus

Evidence to date suggests that the change to modern rice cultural practices was the major factor causing the upsurge in the density of, and damage by, the brown planthopper (BPH) *Nilaparvata lugens* (Stål) in recent years. The aspects of these practices that have been shown to increase pest abundance are a high tiller number per square meter, flooding of fields, and application of high doses of nitrogenous fertilizer. More evidence is needed to indicate if the cropping pattern, high yielding varieties per se, weeds, natural enemies of *N. lugens,* climate, or insecticides play a critical role in increasing the pest's abundance.

The density and composition of the BPH in the field fluctuate dramatically within one crop period, within a year, and over a period of years. The changes during a crop period are influenced by crop age and the generation pattern, which is rather distinct in a given field. Dispersing macropterous adults invade a field soon after planting, and usually two major generations develop before crop maturity. The highest insect densities occur when nymphs dominate the population, usually about 60 and 85 days after transplanting. Nymphal mortality may be high. Adult wing form may change during a crop period. Adults disperse out of the field mainly near crop maturity. Dispersal flight is close to the ground, and occurs in the early evening hours.

Within a year's time in a double-cropped area, usually there are two population peaks, one near the end of each crop season. Apparently surrounding crops strongly influence pest density, possibly through the size of the dispersing population. The largest peak in a year may occur in either the dry or the wet season.

Sampling the BPH is difficult because of the aggregated distribution that develops in the field. The tiller number per hill appears to be important in improving sampling methodology. The current methods and objectives of sampling are critically reviewed.

THE BROWN PLANTHOPPER (BPH) *Nilaparvata lugens* (Stål) has in recent years become an important insect pest of rice in the tropics. The damage it causes in several countries has increased dramatically within the past 5 years. Numerous authors say the recent increase in damage and in population density may

International Rice Research Institute. Los Baños. Philippines: Central Rice Research Institute. India; Bangladesh Rice Research Institute, Joydebpur, Dacca, Bangladesh; Plant Protection Center, Taiwan; Joint Commission on Rural Reconstruction, Taiwan; and University of the Philippines at Los Baños, Laguna, Philippines.

be related to climate and the growing of the new, high yielding rices with modern technology. This paper reviews critically the known ecology of the BPH in the tropics, and evaluates the various environmental factors that might influence population fluctuations, especially those in the recent outbreaks. It includes information only from tropical countries.

The ecology of the BPH involves the relationship between the insect and its biotic and abiotic environments. The most important factors of the biotic environment are host plants and natural-enemy fauna, those of the abiotic environment are climate and agricultural chemicals. Mochida and Dyck (1976, 1977) reviewed briefly the effect of environmental factors on the BPH. Relevant literature and experimental data are discussed much more fully in this paper.

Because sampling technology is such a basic component of studies of population dynamics, current sampling techniques for *N. lugens* are briefly reviewed. Some aspects of dispersal behavior are also discussed.

EFFECTS OF BIOTIC ENVIRONMENT ON BROWN PLANTHOPPER

Host plants

Rice (*Oryza sativa* L.) is by far the most important host plant of the BPH. Very few BPH have been found on other plants. The observation suggests that other plants provide only a marginal habitat for the insect (Hinckley 1963a; Leeuwangh 1968; Otake and Hokyo 1976; pers. comm. with J. H. Stapley, Ministry of Agriculture and Rural Economy, Guadalcanal, Solomon Islands). However, a few alternate hosts have been noted in the literature: *Eleusine coracana, Leersia hexandra, L. japonica* Makino, *Saccharum officinarum* L., *Zea mays, Zizania latifolia* Turcz., and *Zizania longifolia* (Nasu 1967, 1969; Grist and Lever 1969; Misra and Israel 1970; Anon. 1976b). Pathak (1968) mentions that the availability of food plants affects the population density of BPH.

The dominance of rice as a host plant logically suggests that a fallow period without ratoon rice should reduce the pest population (Dyck 1974b; MacQuillan 1974; Stapley 1975, 1976a; Anon. 1975b; Varca and Feuer 1976). Because rice from stubble can provide a reservoir or even a suitable breeding site for the BPH, stubble management has been suggested as a control measure (Grist and Lever 1969; Ho and Liu 1969 ; IRRI 1972; Soehardjan et a1 1973; Calora 1974; Mochida and Suryana 1975; Sastrowidjoyo 1976). Alternatively, extensive rice areas would increase the pest population (Kulshreshtha et a1 1974; Abraham and Nair 1975; Anon. 1975c). However, speculations in the literature are that increased availability or abundance of nonrice host plants in or near rice fields positively affects pest abundance (Cendaña and Calora 1967; Kulshreshtha et al 1974; Fernando 1975; Varca and Feuer 1976). Experimental data at IRRI suggest that weeds may contribute to an increase in pests as a rice crop nears maturity, possibly by providing an environment with a dense plant stand. However, besides logic, little evidence supports the recommended cultural control measure of "clean cultivation" (Grist and Lever 1969; Chakrabarti et al 1971). MacQuillan (1974) provides some evidence, and Stapley (1975, 1976a) suggests that weeds (for example, *Eleusine indica*) on levees or nearby fields provide an alternative habitat for predators (*Cyrtorhinus* spp.) of BPH. To the degree that they do so, weeds would assist in insect control. More experimental data are needed to clarify the role of nonrice host plants in BPH population dynamics.

Rice

Cropping pattern. The cropping pattern literature has frequently suggested that increasing the number of crops per year on a given plot of land can magnify insect problems (Nickel 1973). Double or continuous cropping, with staggered planting times, contributes to BPH outbreaks. Irrigation and short-duration, photoperiod-insensitive varieties have made possible more than one crop a year. That suggestion is reasonable. The longer a suitable host plant is in the field in a given year, the greater is the chance for pest populations to reach high densities. The insects can easily disperse from one field to another, and spread infestation from old crops to young. The argument appears to have been accepted by many authors (Dyck 1974b; Kalode 1974, 1976; Kulshreshtha et al 1974; MacQuillan 1974; Anon. 1975a; Abraham and Nair 1975; Fernando 1975; Mochida and Suryana 1975, 1976; Stapley 1975; Sastrowidjoyo 1976; Otake and Hokyo 1976; Varca and Feuer 1976; Anon 1977). As a result some have suggested synchronized planting and harvesting as a control measure (Hoppe 1973; Calora 1974).

There are, however. a few cases of hopperburn where only one crop a year is grown in India, Indonesia, and Thailand (Anon. 1975a; Freeman 1976; Mochida and Suryana 1976). Voon Boon Hoe (pers. comm., Agricultural Research Center, Department of Agriculture, Kuching, Sarawak) believes that density of the BPH in Sarawak may be low because only one crop of tall, leafy rice is grown each year. Otake and Hokyo (1976) noted that local varieties in Indonesia, planted synchronously, have low BPH infestations. Despite intensive cropping of high yielding varieties in West Malaysia, the BPH problem is small, possibly because of a break between cropping seasons. Mochida and Suryana (1 976) found that some areas in Indonesia carry two crops per year but have few BPH problems. They concluded that a BPH infestation is highly possible, but not certain, if more than one crop is grown each year. Thus, no really convincing evidence is available to demonstrate that growing more than one rice crop in a single year encourages outbreaks of *N. lugens.* Because of the difficulty of proving that such is the case, the hypothesis, although reasonable, is likely to remain a hypothesis for some time to come.

New high yielding varieties. It is generally accepted that cultivation of high yielding rice varieties increases insect pest problems (Smith 1972; Nickel 1973). Most commonly suggested as a factor associated with recent BPH outbreaks is the introduction of dwarf, high yielding varieties (Banerjee et al 1973 ; Soehardjan 1973; Abraham and Nair 1975; Anon. 1975a, 1977; Pathak 1975; Oka 1976; pers. comm. with J. H. Stapley; pers. comm. with B. Thomas, Kerala Agric. Univ., Kerala, India). Mochida et al (1977) show a rough correlation between the increase in area planted to new varieties in Indonesia, and the increase in pest infestation.

The new varieties are short, have erect leaves, and produce many tillers. The dense plant canopy they form, especially under conditions of high fertility and good water management, no doubt produces a microclimate different from that in fields of traditional varieties. The high-tillering character of the new varieties, possibly combined with dense planting, and the nature of the associated plant canopy have frequently been pointed out to be a critical feature that may affect the insect (Bae 1966; Israel and Prakasa Rao 1968; Chakrabarti et al 1971; Ngoan 1971; Pathak 1971; Das et al 1972; Smith 1972; Pathak and Dyck 1973; Anon. 1975a, c; Diwakar 1975; Fernando 1975; Nishida 1975b; Kalode 1976; Otake and Hokyo 1976; Varca and Feuer 1976).

Some authors have suggested that the new varieties are intrinsically more susceptible to the BPH than are the traditional varieties (Pradhan 1971, 1975; Mochida and Suryana 1975; Way 1976). Diwakar (1975) commented that minor pests are becoming major pests because uniform germplasm is being grown over large areas, and that although the new varieties carry resistance to former major pests, they evidently give new pests an opportunity to develop. However, even though everyone agrees that most new varieties are susceptible to the BPH, some authors have specifically defended them, saying that, in general, they are no more susceptible than the tall indica varieties. Those authors say it is the agronomic practices used with the new varieties that are the crux of the matter (Shastry 1971; Freeman 1976). As a matter of fact, both Pradhan (1971, 1975) and Way (1976) commented that agronomic practices also contribute to pest problems.

Actually we have almost no published evidence that the new varieties themselves contribute to the BPH problem. Some high yielding varieties grown with modern technology have not developed a problem with the pest (Lim and Heong 1976). Also the early maturing of some varieties could reduce the pest problem because fewer generations of the pest can develop on them (Fernando 1975; Varca and Feuer 1976).

Last year at IRRI we tested the effect of old and new varieties on insect populations. Equal numbers of seedlings of each variety were planted at equal spacings in the greenhouse and in the field. The field infestation was high, especially at the peak of the second generation. We found few differences between old and new varieties in the size of the insect population, and even high-tillering varieties did not appear to stimulate the populations to grow larger than on low-tillering varieties. But the differences in tiller number among varieties were not as great as expected. Artificially adjusting the tiller number produced a trend suggesting that more tillers per hill would increase the pest

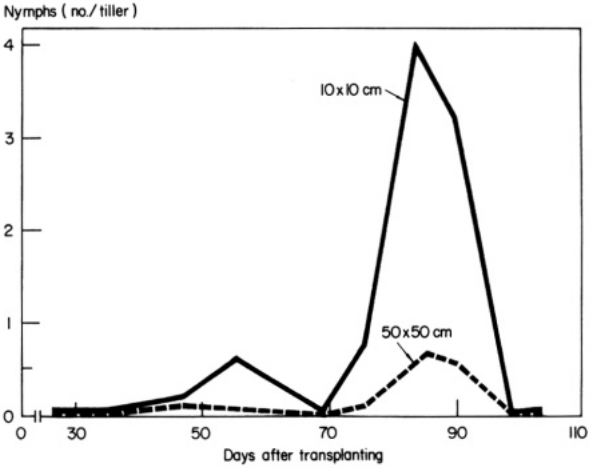
Table 1. Nymphal and adult populations[a] of *Nilaparvata lugens* at peaks of the first two generations per crop on rice cultivars. IRRI greenhouse and field study, 1976 wet season.

Cultivar	Tillers in field (no./hill)	Field population (no./hill)		Caged greenhouse population[b] (no./cage)	
	50 DT	35 DT	63 DT	42 DI	70 DI
Old varieties					
BPI-76 (Nonsensitive)	16	18 bcde	79 bc	593 ab	1290 b
Sigadis	14	24 de	111 bc	–	–
GEB 24	20	27 def	54 b	–	–
New varieties					
IR20	28	16 bcde	85 bc	697 ab	1723 b
IR26[c]	22	14 abcd	28 b	649 ab	212 a
IR36[c]	28	11 abc	4 a	–	–
C4-63G	23	23 de	76 bc	–	–
Peltta I-2	21	33 ef	76 bc	–	–
Mahsuri	26	19 cde	63 bc	–	–
Low-tillering					
H4	22	31 ef	108 bc	484 a	1286 b
IR480	19	17 bcde	46 b	673 ab	1052 b
IR127-80-1[d]	16	39 ef	138 c	–	–
High-tillering					
Peta	23	23 cde	66 bc	547 ab	1747 b
IR8	22	22 cde	73 bc	516 ab	936 b
IR22[d]	20	32 ef	122 c	–	–
Tiller number artificially adjusted					
IR1917-3-17 low no.[e]	5	7 a	32 b	410 a	929 b
IR1917-3-17 mod. no.[e]	15	19 cde	43 b	559 ab	1409 b
IR1917-3-17 high no.[e]	22	28 ef	89 bc	880 b	1734 b
IR1917-3-17 low no.[d]	5	11 ab	116 bc	–	–
IR1917-3-17 mod no.[d]	15	28 def	139 c	–	–
IR1917-3-17 high no.[d]	33	48 f	123[f] c	–	–

[a] In a column any two means followed by the same letter are not significantly different at the 5% level DT = days after transplanting. DI = days after infestation. [b] Populations initiated with 3 pairs of adults/cage at 60 days after seeding (DS). Plants were replaced every 3 weeks with 60-day-old plants. [c] Varieties showing resistance to insect. [d] To increase planthopper density, diazinon granules at 1 kg a.i./ha were applied at 1 and 20 DT, and methyl parathion was sprayed (0.75 kg a.i./ha) biweekly beginning at 35 DT. [e] Greenhouse plants maintained at 4. 8 and 12 tillers/hill for low, moderate, and high tiller densities, respectively. [f] Hopperburned plots

population (Table 1). We could not demonstrate that the new varieties necessarily increase pest populations, but we showed that a high tiller number per hill may be conducive to an increase in pest density. Our earlier studies indicated that short stature did not affect pest populations (IRRI 1973).

Planting method. The number of tillers in an area is influenced not only by the tillering ability of cultivars, but also by the method of planting. Several authors have suggested that close spacing and the consequent dense crop stand increase the BPH problem (Bae 1966: Cendaña and Calora 1967; Ngoan 1971; Das et al 1972; Mammen and Das 1973; MacQuillan 1974; Abraham and Nair 1975; Anon. 1975c; Freeman 1976). High seeding rates for broadcast rice crops may achieve the same effect (Anon. 1975a; Kulshreshtha et al 1974; MacQuillan 1974). The effect on the insect is attributed to a suitable micro-



1. Numbers of nymphs of *Nilaparvata lugens* on short Peta transplanted at spacings of 10 × 10 cm and 50 × 50 cm. IRRI, 1972 dry season.

climate, perhaps a higher relative humidity when plant density is high (Kulshreshtha et a1 1974; Feuer 1975).

Israel (1969) and Kalode (1974) suggested that broadcasting, as opposed to transplanting, may contribute to outbreaks and pest damage. Direct seeding or drilling may reduce the pest problem (Hinckley 1963a; Israel 1969).

Field experiments at IRRI tried to verify such suggestions. One experiment with IR20 showed no significant differences among spacings. At times of peak insect density, however, both short Peta (an IR262 line) and tall Peta had significantly more nymphs per tiller and per square meter at the 10- × 10-cm spacing than at 50- × 50-cm (Fig. 1). In 1976 the BPH populations on plant spacings ranging from 5- × 5-cm to 40- × 40-cm were compared. The number of nymphs per hill and the number of tillers per hill were often positively correlated. The number of nymphs per tiller remained relatively constant over various spacings. There was also positive correlation between nymph number and hill density per square meter and between nymph density and tiller number per square meter. However, the nymph population per square meter was generally low when the number of tillers per hill was high (Table 2). The tiller number increased at the cost of hill density per square meter.

Thus, the BPH population appears to respond positively to a greater number of tillers per square meter, which may be achieved through close spacing or—if the spacing is not affected—a high number of tillers per hill.

In a study comparing broadcast-seeded, row-seeded, and transplanted plots planting method had no apparent effect on the pest number (IRRI 1974).

Plant age. It has often been thought that the age of the rice plant in the field influences pest density. The literature has numerous references to a peak in

Table 2. Populations Of *Nilaparvata lugens* nymphs on rice selection IR1917-3-17 transplanted at several spacings and treated with insecticides.[a] IRRI, 1976 wet season.

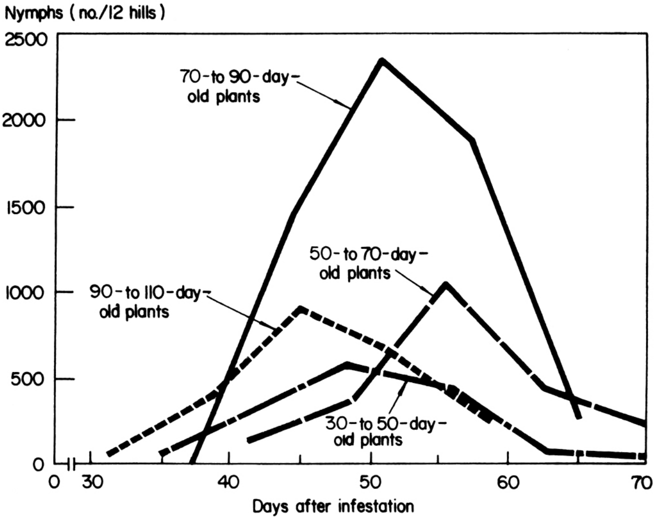
Spacing (cm)	Hills (no./m^2)	7 WT	9 WT				
		Nymphs (no. /m^2)	Nymphs			TIllers	
			(no./m^2)	(no./hill)	(no./tiller)	(no./m^2)	(no./hill)
40 × 40	6	35 a	450 a	72 a	2.8	160 a	26 a
40 × 20	12	32 a	747 ab	60 a	2.7	267 b	22 b
20 × 20	25	77 ab	1,398 ab	56 a	3.7	367 c	15 c
40 × 5	50	205 bc	1,114 ab	23 a	2.5	431 c	9 d
20 × 5	100	467 cd	2,460 b	25 a	3.6	705 d	7 de
5 × 5	400	1,885 d	HB	HB	HB	880[b] e	2[b] e

[a] To increase planthopper density diazinon granules at 1 kg a.i./ha were applied 1 and 4 WT and methyl parathion was sprayed (075 kg ai./ha) biweekly at 6 WT. In a column any two means followed by the same letter are not significantly different at the 5% level. WT = weeks after transplanting. HB = plants hopperburned. [b]One replication only.

the BPH population beyond about 60 days after transplanting, or between the heading stage and harvest, and hopperburn most commonly occurs during this period (Hinckley 1963b; Bae and Pathak 1966; Leeuwangh 1968; Ho and Liu 1969; Chelliah and Subramanian 1973; Pathak and Dyck 1973; Soehardjan 1973; Koya 1974; MacQuillan 1974; Anon. 1976a; Heong 1976; Kalode 1976; Otake and Hokyo 1976; pers. comm. with P. R. Hale). *N. lugens* tended to be more numerous after 60 days, especially in the dry season (Bae and Pathak 1969). Crop age appeared to have a highly significant effect on the insect population (Alam 1971). The two major population peaks within 1 year coincided with the maturation of the main crops at IRRI. Wan (1972) found that the number of planthoppers and leafhoppers (as a group) caught in light traps or in field samples corresponded closely to the percentage of water-soluble protein-nitrogen in the rice plant ($r = +0.9$). The percentage peaked at first flowering. Wan suggests that the protein nitrogen favorably affects the fecundity of the hoppers. Another reason for a peak insect-density near crop maturity is simply that some time is required for the population to increase over a span of two or three generations.

In a critical experiment at IRRI, *N. lugens* was reared in an insectary for three generations on plants of a specific age range. In the second and third generations it was observed that many more insects developed on the 70- to 90-day-old plants than on those of other ages (Fig. 2). When BPH were reared on plants progressing from 10 to 110 days old, the third generation was only one-half the size of that of insects reared on plants kept within the 70- to 90-day period (IRRI 1974). The BPH appears to multiply best on plants in the 20-day period before flowering. Insect density would naturally be greatest following this period.

Young crops can have large infestations and suffer damage, and seedbeds can attract rather large numbers of adults (BPI et al 1974; Mochida et al 1977). Such situations are, however, unusual and occur during outbreaks.



2. Density of the second generation of *Nilaparvata lugens* on IR22 plants of different age ranges in an insectary experiment. IRRI, 1973.

when many adults are dispersing. Most infestations on young plants (Chelliah and Subramanian 1973; Soehardjan 1973; Otake and Hokyo 1976) are small, and occur when normal numbers of macropterous adults multiply in a seedbed or on a young crop.

Natural enemies

The literature contains rather frequent references to organisms that attack BPH. But in most cases the references give no evidence of control of the pest by its natural enemies. Some authors have suggested or believed that the enemies indeed reduced the pest population. Pathak (1968) stated that populations of planthoppers fluctuate according to natural enemies as well as other factors of the environment. On the other hand, Otake and Hokyo (1976) in Indonesia did not notice predators and parasites exerting much control of the BPH, especially in a pest outbreak.

Predators. Studies in greenhouse cages described the activity of several predatory species against BPH (Bae and Pathak 1966, 1968; Dyck and Orlido 1977). B. Thomas (pers. comm.) indicated that in Kerala, India, the BPH population was low recently, partly because of predators. *Cyrtorhinus* spp. reportedly have a depressing or controlling effect on the pest population (Bae 1966; J. H. Stapley 1975, 1976a, b, pers. comm.; Kalode 1976; Murthy et al 1976). *C. lividipennis* apparently prevents the increase of the BPH population in drilled rice fields, but not in transplanted ones (Hinckley 1963a). It appears to be a better predator in cages than in the field. Its peak density occurred at about the same time as that of BPH (Alam 1971).

Spiders apparently play a role in suppressing pest numbers (Chiu et al 1974; Samal and Misra 1975; Kalode 1976). Data by Gavarra and Raros (1975) suggest that low pest densities are caused by high predator densities.

Other predators mentioned in the literature are beetles (Israel and Prakasa Rao 1968; Abraham and Mathew 1975) and ducks (Anon. 1977). Both reportedly controlled BPH effectively in the field.

Two attempts were made at IRRI to demonstrate the real role of predators in the field. Reduced predator populations did not greatly change planthopper density (Dyck and Orlido 1977). However, removing *Nephotettix virescens* Distant significantly increased planthopper density over the control (IRRI 1973). It appears that predators can curtail BPH numbers, but evidence that they do so under normal field conditions is lacking.

Parasites. Little work has been done on parasites of the BPH. Hinckley (1963a) found egg parasitism to be rare in Fiji, but according to Nishida et al (1976) the nonpest status of planthoppers in many areas of Thailand appeared to be due mainly to egg parasitism. In Sri Lanka, parasites were not the only factor limiting planthopper populations; neither did the parasites play a regulative role (Otake et al 1975).

However, recent work in Sarawak, Malaysia, emphasizes the importance of parasites of adult hoppers, especially Strepsiptera and Pipunculidae. Munroe (1974, 1975) states that 20 to 30% of adults are commonly parasitized. He believes that parasites exercise a high degree of natural control over planthoppers in Sarawak. Voon Boon Hoe (pers. comm.) suggests that parasites are harbored by abundant natural vegetation around rice fields of farmers who use low-technology production methods. More evidence is needed to define the role of parasites in BPH control.

Pathogens. There are several records of the killing of BPH by fungi, but the actual contribution of fungi to pest control is unknown. Bae (1966) speculated that an infection of *Entomophthora* spp. helped reduce pest density, but Hinckley (1963a) concluded that fungi were a much less important cause of pest mortality than predators. Dyck and Orlido (1977) attempted to create an epizootic with a fungus in the field, but the pest control achieved was only marginal.

Plant diseases

Preliminary observations in IRRI fields suggested that BPH nymphs preferred hills infected with the grassy stunt disease, of which they are vectors. However, a rearing test in the insectary indicated that population growth was slightly better on healthy plants than on diseased plants (IRRI 1973). The relationship between the disease and the insect needs further study.

Phytophagous insects

No work has been done on competition among BPH, or to see whether the population dynamics of BPH contains a self-regulating component. Hinckley

(1963a) considered the possibility of interspecific competition between *N. lugens* and *Sogatella, furcifera* (Horvath) in Fiji. He concluded that differences in the dominance of the two species during the crop period were due to the effects of crop age and not of competition. Work at IRRI indicated some competition between *N. lugens* and *Nephotettic virescens,* with *N. lugens* as the more successful competitor (IRRI 1973).

EFFECTS OF ABIOTIC ENVIRONMENT ON BROWN PLANTHOPPERS

Climate

Various climatic factors affect BPH development and population dynamics, including outbreaks. The factors suggested include mean temperature, rainfall, and relative humidity. Data collected during the periods of insect population growth or decline implied a relationship between climate and the particular biological parameters measured (Tao 1965; Chou 1969; Misra 1971). However, the data are connected only in a general sense and correlations have to be established. Studies on population dynamics require many years' data. After reviewing the effect of climate on rice insects, Kisimoto and Dyck (1976) cited the need for more proof of relationships between climate and insect biology.

Temperature. Several studies have tried to define the influence of temperature on BPH development. Temperatures between 25 and 30°C are considered optimal for egg and nymphal development (Pathak 1968; Ho and Liu 1969; Bae and Pathak 1970; Chiu 1970; Kulshreshtha et al 1974; Anon. 1975c; Kalode 1976). Temperatures above 30°C, e.g. 33 or 35°C, are unfavorable for insect survival (Ho and Liu 1969; Bae and Pathak 1970; Chiu 1970; Anon. 1975c; Kalode 1976). Eggs have greater tolerance for high temperatures than do nymphs or adults (Bae and Pathak 1970). High temperatures probably influence distribution or even seasonal abundance (Bae and Pathak 1970; pers. comm. with P. C. Lippold, Plant Protection Project, UNDP/FAO, Seoul, Korea). Temperatures below 15-8°C are unsuitable for development (Ho and Liu 1969; Kalode 1974). Overwintering in Taiwan occurs only rarely (Kisimoto and Dyck 1976). Several authors give the time duration of each instar at different temperatures (Ho and Liu 1969; Bae and Pathak 1970; Chiu 1970). Bae and Pathak (1970) reported that fluctuating temperatures had a moderating effect on development.

As expected, the rate of development increases as temperature increases. Misra and Israel (1970) found that the BPH life cycle was shorter in warmer periods than in cooler.

Suggestions that temperature affects the BPH population dynamics are common. High temperatures appear to be associated with high pest numbers (Fukuda 1934; Alam 1971; Hoppe 1973; Anon. 1975a; Tirawat 1975). Narayanasamy (1975), however, found in the field a positive correlation between BPH populations and lower temperatures. Abraham and Nair (1975) suggested that outbreaks may be related to a 20-30°C range of temperature.

Ho and Liu (1969) in Taiwan developed a method of forecasting BPH outbreaks from accumulated data on average temperatures during the winter. If the accumulated temperature was higher than 2,100°C, an outbreak was forecast. The method is probably not suitable for tropical areas, where the insect does not appear to have a resting stage from which the whole population develops according to temperature.

Solar radiation is naturally related to temperature. Alam (1971) suggested that the pest population growth was positively related to hours of sunshine, but Narayanasamy (1975) reported that the population density was higher at a "lower sunshine period." Excessive solar radiation is said to prevent population increase (Pathak 1968: Anon. 1975c).

Except from laboratory studies, we obviously know little about the influence of temperature on population dynamics. Long-term field studies combined with critical experiments in controlled environment facilities are needed to clarify what is really happening in nature.

Relative humidity. It is commonly stated in the literature that a humid environment is preferred by *N. lugens,* and is conducive to its development and population increase (Bae 1966; Cendaña and Calora 1967; Ngoan 1971; Hoppe 1973; Abraham and Nair 1975; Anon. 1975a; Tirawat 1975; Narayanasamy 1975). A range of 70 to 85% relative humidity is optimal for BPH development (Kulshreshtha et al 1974); however, no critical experiments have been conducted to verify the role of atmospheric moisture in population dynamics. Earlier studies at IRRI suggested that constant humidities of 50 to 60% were optimal for population growth (IRRI 1976), but more recent studies using fluctuating humidities indicated that variations within normal field limits were not critical to population increases.

Rainfall. A few authors have found that BPH outbreaks occur during the wet season, or suggest that they are related to rainfall (Grist and Lever 1969; Soehardjan 1973; Anon. 1975a: Huynh 1975; Kurien 1975: pers. comm. with P. R. Hale and B. Thomas). In a portion of central Java, Indonesia, Sastrosoedarjo (1976) found a significant positive correlation (r = 0.907*) between the total yearly rainfall from 1970 to 1975 and the number of infested hectares of rice [log damaged area (ha) = –3.3262 + 2.5545 (mm rainfall)]. As expected, there was a negative correlation between the number of dry months in a year and the area damaged. There was an insignificant tendency toward correlation between the number of rainy days in a year and area damaged (r = 0.838).

More authors, however, suggest the opposite: that outbreaks occur during dry weather, and that relatively low rainfall is conducive to population increase (Fukuda 1934; Bae and Pathak 1966; Pathak 1968; Custodio et al 1973; Narayanasamy 1975; Velusamy et al 1975). In Fiji, Hinckley (1963a, b) found that serious damage occurred in the lower and wetter parts of a field where the insects congregated after a spell of dry weather. In his experience dense populations of BPH were most apt to occur after such a spell. But dry weather, he believed, could not by itself cause a major outbreak, for renewed rainfall may disperse the pest and reduce its density. Heavy rainfall, possibly combined with strong winds, may cause decreased pest numbers (Kulshreshtha et al 1974; Abraham and Nair 1975; Fernando 1975; Varca and Feuer 1976).

Sometimes workers see no specific relationships between rainfall and pest abundance (Leeuwangh 1968 ; MacQuillan 1975 ; Mochida et al 1977). Considering the conflicting and mostly speculative information available, no conclusion can be drawn about the influence of rainfall on the BPH.

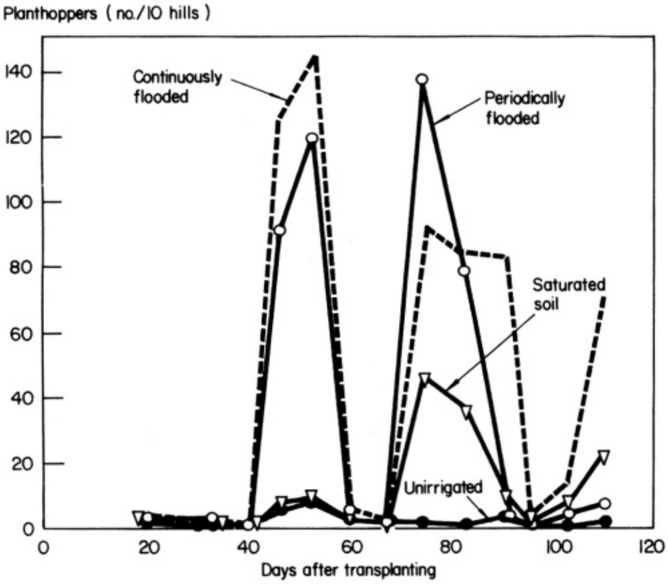
Wind. Feuer (1976) suggested that typhoons could reduce BPH numbers; and the limited air movement within the microhabitat could increase populations (Ngoan 1971; Hoppe 1973; Anon. 1975c).

Microclimate. The dense canopy produced by high-tillering varieties, close spacing and high fertility, combined with continuously flooded fields, produces a microclimate that favors multiplication of BPH (Das et al 1972; Anon. 1975c; Abraham and Nair 1975; Kalode 1976; Alam and Karim 1977). Conditions within the canopy, near the base of the plant, are humid and shaded (Nishida 1975b; Kalode 1976; Varca and Feuer 1976). Such microenvironment is favorable to the pest but is unfavorable to its natural enemies (Nishida 1975b). The halting of irrigation and spreading apart of rows (Dyck 1974b) may represent an attempt to reduce the relative humidity of the microenvironment.

Preliminary observations at IRRI in 1972 indicated that closely spaced plants produced a slightly cooler and more humid microenvironment during the daytime than did widely spaced plants. Lin (1970) made the most extensive observations of the rice microclimate in relation to *N. lugens.* He measured the temperature and relative humidity at 10, 30, 60, and 90 cm above the water surface. The air temperature in the daytime was significantly higher between hills than in the open. The temperature near the water was slightly lower than at higher levels, and became significantly lower when the foliage was greater and provided more shade. Relative humidity was highest near the water surface, and decreased progressively toward the tops of the rice plants. Lin suggests that the theoretically optimum niche for multiplication of the BPH is 10 cm above the water where the relative humidity is high, the temperature is “high,” and the shade formed by foliage is most effective.

Water management

Authors are unanimous in believing that improved irrigation and water standing in the field are conducive to the growth of the BPH population, and probably increase the crop damage (Hinckley 1963a ; Israel 1969; Banerjee et al 1973 ; Pathak and Dyck 1973; Anon. 1975c, 1977; Fernando 1975; Mochida and Suryana 1975, 1976). That is expected in the light of findings with other insects (Smith 1972). To prove the point, pest density at IRRI was monitored during the dry season in plots having varying degrees of standing water or soil moisture. When a plot was flooded continuously or periodically, two large population peaks developed. Only one moderate peak developed when the soil was kept



3. Nymphal populations of *Nilaparvata lugens* on rice variety IR20 with various levels of irrigation. IRRI, 1972 dry season.

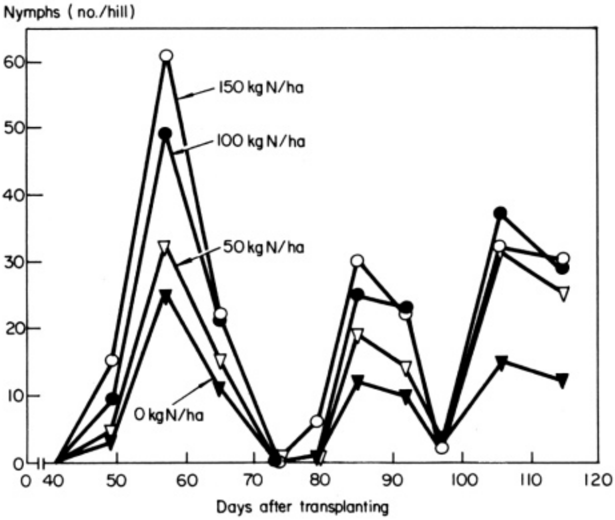
saturated but not flooded; and few insects were found in unirrigated plots (Fig. 3). We can conclude that flooding positively affects pest population increase.

Upland rice fields versus lowland

The conclusion in the section on water management implies that lowland rice fields should have greater pest problems than upland fields. That has generally been true in tropical areas. Stapley (1975, 1976b, pers. comm.) reported that in the Solomon Islands the BPH seldom attacked rice grown "dry," and the insect was never a problem in upland rice. But the change from upland to lowland culture caused the development of BPH as the main rice pest. Wet cultivation of rice leads to more BPH (Wan 1972; Abraham and Nair 1975). However, hopperburn has been observed in upland rice in New Guinea (P. R. Hale, pers. comm.), Indonesia (Sastrowidjoyo 1976), and at IRRI in 1976.

Agricultural chemicals

Fertilizers. It is generally accepted that the addition of fertilizers to crops tends to aggravate pest problems (Smith 1972; Nickel 1973). It is frequently assumed that nitrogenous fertilizers have contributed to the recent increases in the prevalence of BPH (Israel and Prakasa Rao 1968; Pathak 1968, 1971, 1975; Ngoan 1971; Das et al 1972; Smith 1972; Banerjee et a1 1973; Hoppe



4. Populations of nymphs of *Nilaparvata lugens* on rice variety IR22 treated with different levels of ammonium sulfate fertilizer in two doses, 60% at 7 days after transplanting and 40% at 42 days. IRRI, 1971 wet season.

1973; Mammen and Das 1973; Pathak and Dyck 1973; Soehardjan 1973; Kulshreshtha et a1 1974; Abraham and Nair 1975; Anon. 1975a,c, 1977; Nishida 1975b; Velusamy et a1 1975; Freeman 1976; Kalode 1976; Mochida et al 1977; Otake and Hokyo 1976; Varca and Feuer 1976).

Various authors have explained the effect of nitrogen fertilizer on BPH. Several stated that the fertilizer produces a thick canopy (Anon. 1975a; Nishida 1975b) that provides a favorable microenvironment for the insect (Kulshreshtha et a1 1974; Freeman 1976). Others say that nitrogen produces better nourished or more succulent plants (Varca and Feuer 1976).

Some experimental evidence verifies the assumption that nitrogen fertilizer added to rice plants causes an increase in pest population. Abraham (1957) was the first to show in the field that planthoppers were dense on plants treated with a large amount of nitrogen or nitrogen plus P_2O_5. At IRRI greater amounts of ammonium sulfate fertilizer resulted in more planthoppers in the field, on either a per-hill or a per-tiller basis (Fig. 4). Cheng (1971) found that BPH on nitrogen-treated plants produced more honeydew, survived better, and developed a larger population than those on nitrogen-deficient plants. Female BPH reared on plants receiving large amounts of nitrogen fertilizer showed high fecundity (Kalode 1974). Pathak (1975) demonstrated in the greenhouse that increased applications of nitrogen fertilizer improved insect survival and increased the number of progeny.

Considerable evidence shows that the addition of nitrogen fertilizer increases planthopper populations. The reason appears to be more than just a change in the microenvironment, and has something to do with the nutritional status of the plant and the insect's physiology.

Insecticides. Soehardjan (1973) suggests that the frequent application of insecticides is a reason for the increased density of planthoppers. Resistance to insecticides (Fernando 1975) or the rapid breakdown of insecticides (Sethunathan 1971) could be a part of the problem.

Another result of insecticide use could be the unintentional killing of natural enemies of the BPH (Alam 1971 ; Fernando 1975 ; Nishida 1975a.b; Cheng 1976). That has been suggested of predators (Chakrabarti et al 1971 ; Kulshreshtha et al 1974; MacQuillan 1974; Abraham and Nair 1975; Stapley 1975, 1976a,b; Dyck and Orlido 1977; Varca and Feuer 1976; IRRI 1977) and of parasites (Nishida et al 1976).

Stapley (1976a,b) presented field data suggesting that parathion sprayed in the field to kill other pests kills predators of BPH. As a result the BPH soon becomes abundant. Dyck and Orlido (1977) reported that at IRRI high BPH densities frequently followed spray applications of methyl parathion. No doubt, one factor involved was a reduction in the number of predators. Recent experimental data showed that methyl parathion sprays could increase BPH density in upland fields. Other insecticides that have been identified also can aggravate the BPH pest problem (IRRI 1977).

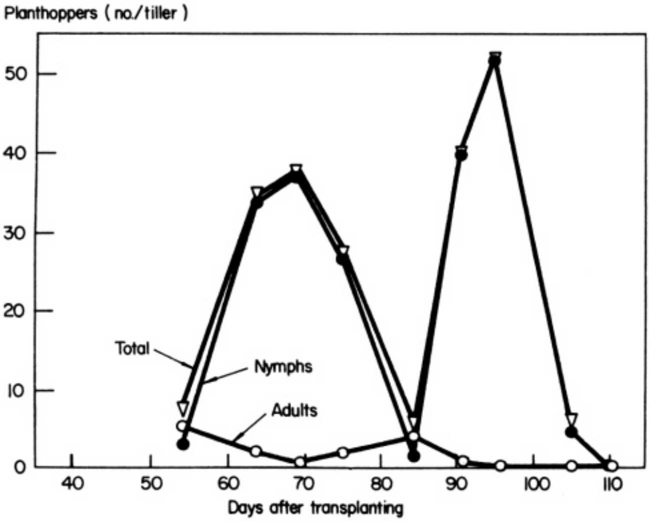
Despite the evidence, there is almost no information on the harmful effects that insecticides may have on beneficial organisms in farmers' rice fields. Given the limited amounts of insecticides used and infrequent applications as a whole, it seems improbable that insecticides could be a major cause of the recent BPH outbreaks. The question warrants further investigation.

POPULATION DYNAMICS OF THE BROWN PLANTHOPPER

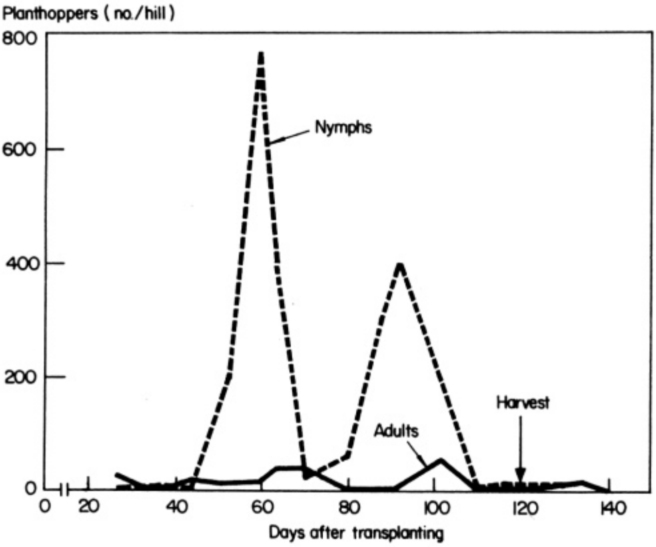
Fluctuations within a crop period

Generation pattern. A few years ago light-trap collection data suggested overlapping BPH generations in the field. But frequent observations revealed that rather distinct generations existed (Pathak and Dyck 1973). Studies at IRRI as early as 1970 show that a regular sequence of nymphs and adults (Fig. 5, 6) markedly changes the planthopper density from week to week, and even from day to day (IRRI 1971, 1972).

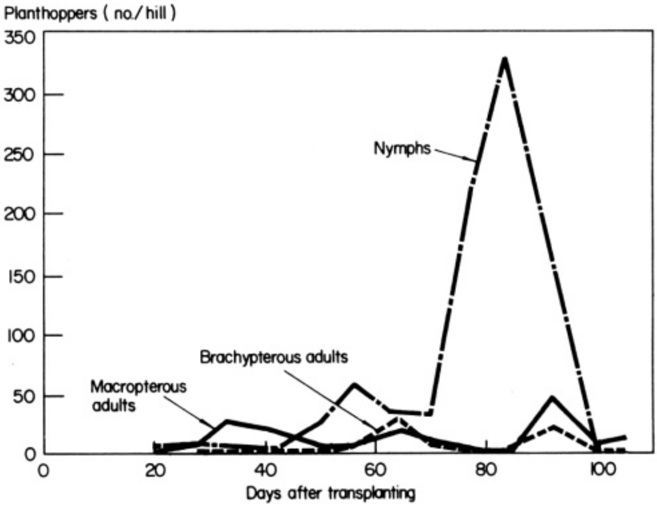
A common pattern is for macropterous adults to invade a crop between 20 and 40 days after transplanting (Fig. 7). The adults scatter randomly in the field (Kalode 1976). The females lay eggs, and nymphs soon appear as the dominant stage. Observations at IRRI some years ago indicated that the nymphs at any one time were in two or three instars. With time the average instar number in the population increased (Fig. 8). When the nymphs developed into adults, some were brachypterous (IRRI 1972). Another generation—sometimes the largest—followed within the crop period. As the crop neared



5. Population of *Nilaparvata lugens* on rice variety IR8. IRRI, 1970 wet season.



6. Population of *Nilaparvata lugens* on rice variety IR20 treated six times with the insecticide diazinon (2 kg a.i./ha). IRRI, November 1970 to March 1971.

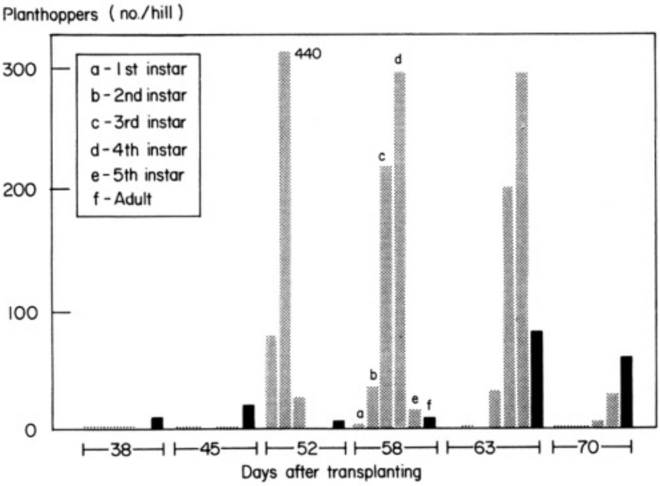


7. Density and composition of a field population of *Nilaparvata lugens* during a crop life. IRRI, 1971 wet season.

maturity, few macropterous adults were collected at the end of this large generation; they apparently had dispersed to new habitats (Fig. 7). The highest number of visible insects within one generation usually occurred when the population was largely in the nymphal stage. Hsieh (1972) found the majority of adults with either wing form were females (Fig. 9).

Hsieh (1972) monitored the adults caught on upright sticky boards at the perimeter of a field. Many adults were caught within the first 15 days after transplanting, but they evidently did not establish a breeding population. A second flight period at around 35 or 40 days, when slightly more adults were caught, started the generation sequence in Figure 7. Sticky-board catches peaked again just after the two adult-emergence periods, about 70 and 98 days after transplanting. Evidently those two flight peaks, even though lower than the first two, represent adults leaving the field (Fig. 9).

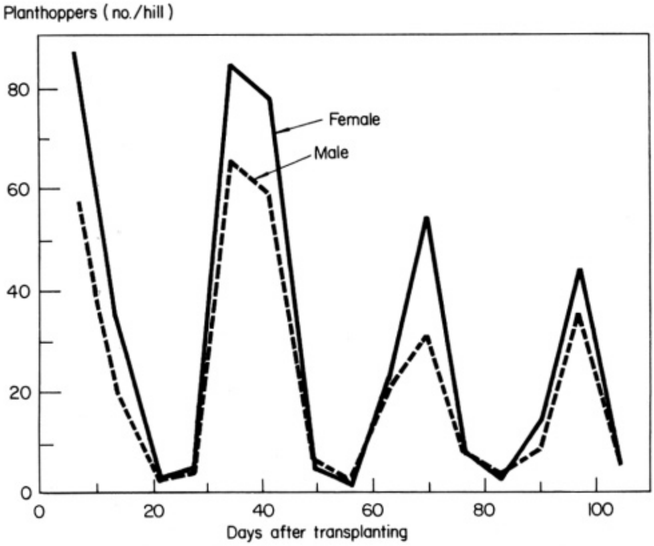
In 1976 at IRRI we attempted to construct life tables for the BPH. Egg, nymph, and adult densities were recorded three times each week. The data (Fig. 10, 11) revealed that the major adult immigration occurred between 20 and 30 days after transplanting. Oviposition followed immediately, and the density of the resultant nymphs and adults peaked at about 50 days. These data probably involved considerable sampling error, for all juvenile stages and adults do not peak at the same time. The emerging adults (more than 50% were female) were numerous. Evidently many soon emigrated, for the next batch of eggs was only slightly larger than the first. The second major



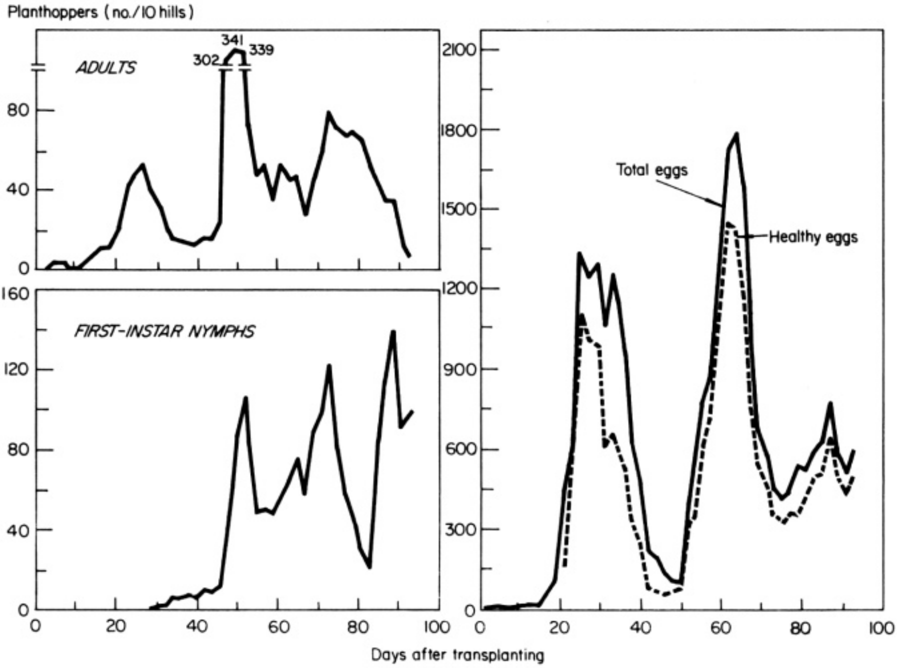
8. Populations in each instar of *Nilaparvata lugens* on rice variety IR20 treated with diazinon insecticide. IRRI, November-December 1970.

generation, as indicated by the density of its third- and fifth-instar nymphs and adults, was much smaller than the first. The reason is unknown.

Egg parasitism during the second oviposition period was about the same or lower than that during the first. For the whole crop period, egg parasitism



9. Numbers of macropterous adults of *Nilaparvata lugens* caught on vertical sticky traps (1 m^2) set on levees facing away from and around a rice field. IRRI. 1971 wet season.



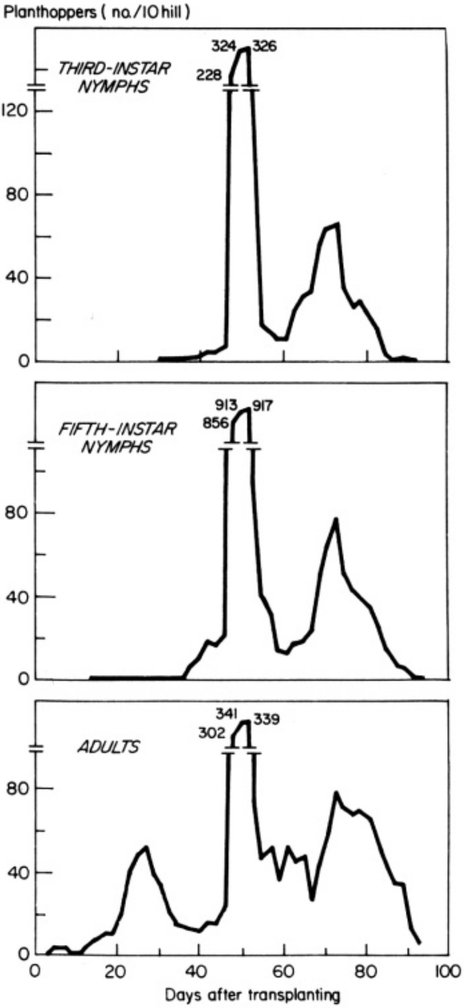
10. Egg, nymph, and adult densities of *Nilaparvata lugens* on rice selection IR1917-3-17 (3-point running av.). IRRI, 1976 wet season.

ranged from 0 to 71% and averaged 24%. Egg predation averaged only 1% (range of 0 to 20%). Adult parasitism was negligible, ranging from 0 to 10% and averaging 0.5%. The last peak in adult population initiated a small third generation that probably was not completed before harvest.

Because of imprecise and inaccurate sampling, and because of the problem of adult dispersion, few conclusions can be drawn regarding the mortality within each generation. The actual percentage of eggs that hatched was also unknown. Ho and Liu (1969) found that only 52% of eggs hatched. However, it does appear that young nymphs have high mortality, possibly from predation, especially in the second major generation.

A similar set of observations, except that no eggs were counted, was made in an upland rice field at IRRI in 1976. Even though sampling was initiated rather late, there evidently were at least two generations, the largest reaching a peak at 50 days after rice emergence (Fig. 12). It is not known why the insects failed to multiply beyond 60 days.

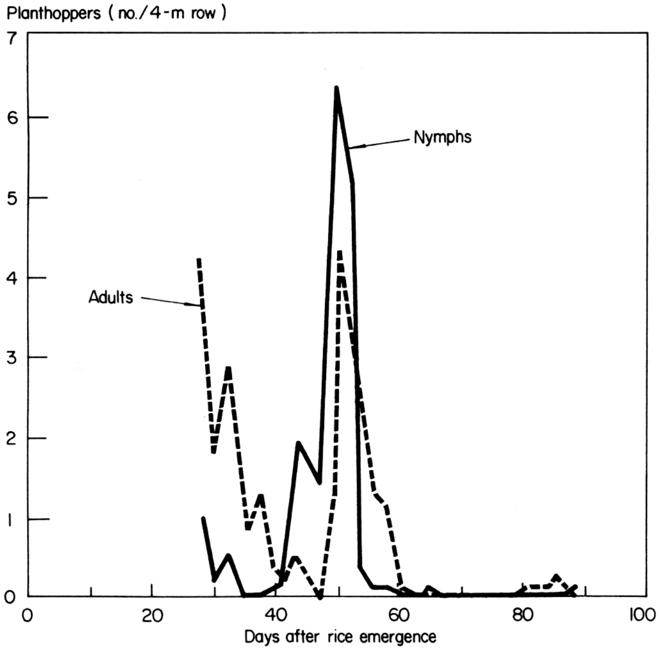
Data collected at IRRI on about 75 irrigated lowland crops over the last 6 years almost always show two or three generations per crop period and only rarely one or four. There may be a small generation during the first 40 days after transplanting, but normally it is negligible. Its peak density occurs at about 30 days. This generation, or even immigrant adults by themselves, can



11. Populations of third- and fifth-instar nymphs and adults of *Nilaparvata lugens* on rice selection IR1917-3-17 (3-point running av.). IRRI, 1976 wet season.

damage the plants if the dispersal flight is large when the crop is first transplanted, and many eggs are laid. Densities of the two major generations reach peaks at around 60 and 85 days after transplanting (Fig. 7). Sometimes the first peak is the largest, sometimes the second. Occasionally a fourth generation develops if the variety is medium or late maturing. The peak density of the fourth generation occurs beyond 100 days, and sometimes is the highest of the entire crop period (IRRI 1971).

There are several literature references to large invasions of newly planted crops by adults, which may damage the crop directly or soon give rise to large



12. Populations of *Nilaparvata lugens* on rice variety Kinanda in an upland field. IRRI, 1976 wet season.

nymphal populations that may kill the plants (Mochida et al 1977; Stapley 1976b; Varca and Feuer 1976). The adults may originate in other fields, or even in seedbeds (Otake and Hokyo 1976). The development of several generations between a crop's planting and harvest, and the occurrence of generation peak densities, have been noted or described by a few authors. Alam (1971) found three peaks per crop in two crops out of three. Pathak (1971) found either the second or third peak was the highest. The peak population generally occurred at or after panicle initiation. Gavarra and Raros (1975) noted peaks at about 60 and 90 days after transplanting. Mochida et al (1977) concluded that there were two generations per crop for short-duration varieties. Das et al (1972) claimed that four to five generations were completed in a cropping season. Grist and Lever (1969) report that in Vietnam there were three or four generations per year, probably meaning per crop. Some authors have reported that peak populations can develop in the middle of a crop's life span (Otake et al 1975; Stapley 1976b), but they more commonly develop toward the end, when the third generation peaks (Hinckley 1963a; Ngoan 1971; Kulshreshtha et al 1974; Anon. 1975a,c; Nishida et al 1976).

Surveillance. The time each generation peaks varies somewhat from crop to crop, possibly according to when the immigrant adults first invade the crop.

However, the peak in each generation can be predicted to some extent by monitoring the dispersing insects with sticky boards, and observing the size and composition of the field population on a per-hill basis. Dyck and Orlido (1977) demonstrated the usefulness of such monitoring to set times for application of insecticides. The strong population fluctuations during a crop's life, due to changing generations, also make it important to select sampling times carefully in field experiments. Treating or sampling at randomly selected times could produce erratic results. Surveillance of pest populations as a tool of effective pest control is gaining acceptance in several countries (Hinckley 1963a; Singh 1975; Yen and Chen 1977; Zotzmann 1976; B. Thomas, pers. comm.).

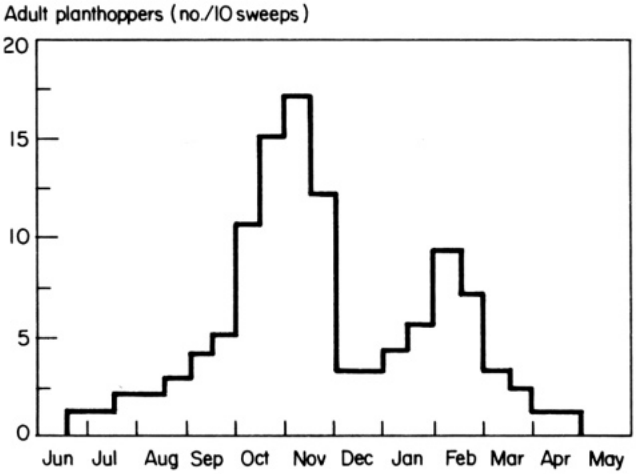
Fluctuations within a year

BPH are active throughout the year in the tropics (Pathak 1968; Ho and Liu 1969; Chiu 1970; Kulshreshtha et al 1974). If generation life is about 1 month, there could be 12 generations per year. In subtropical areas there may be 6 to 7 (Anon. 1977), 10 (Ho and Liu 1969), 11 (Chiu 1970), or 8 to 11 generations per year (Yen and Chen 1977).

Occasionally it has been reported that BPH populations appear to have only one major peak each year. That may be related to the cropping pattern. The period between June and September has been mentioned for areas north of the equator (Lei and Wang 1958; Israel 1969; Fernando 1975; Velusamy et al 1975; Anon. 1977; pers. comm. with N. V. Huynh), and March and April for those south of the equator (Hinckley 1963b).

However, two population peaks usually develop within 1 year, no doubt one for each major crop season (Chiu 1970; Misra and Israel 1970; IRRI 1973, 1974, 1975; Kalode 1974; Kisimoto and Dyck 1976; Diwakar 1975; Heong 1976; Yen and Chen 1977). That is confirmed by light-trap catches and by occasional field data. Sometimes no differences are observed between the two peaks (MacQuillan 1975). In most cases reported north of the equator, the largest peak comes during the last half of the year, during the second crop (Fig. 13; Table 3; Tao 1965; Chou 1969; Lin 1970; Misra 1971; Hoppe 1973; Hsieh and Yen 1975; Alam and Karim 1977; Hsieh 1977). However, in a 1-year study, Alam (1971) found the largest light-trap catch during the first half of the year. Also Ho and Liu (1969) stated that the insect density was greater in the first crop than in the second. N. D. Penny (pers. comm.) in Malaysia found that the greatest catch in a light trap was obtained in July, but that field visual counts were highest in December.

At IRRI we are trying to explain the changes in insect populations from season to season through a rather unusual experiment. Crops are planted almost every month, and the BPH population density and composition are measured weekly. When the data have been collected, the peak nymphal density for each generation for each crop is determined. The first-, second- and third-generation peaks occur approximately at 30, 60, and 90 days after

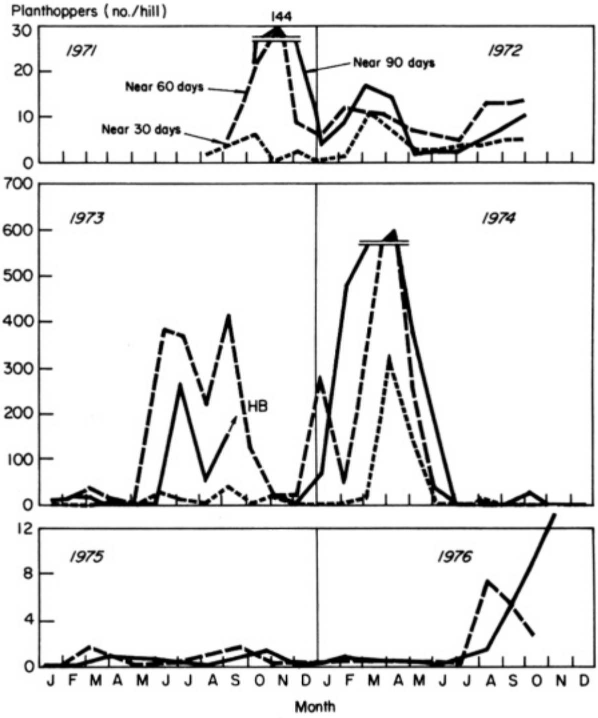


13. Seasonal occurrence of *Nilaparvata lugens* on rice, according to fortnightly observations. Cuttack, India, 1966–67.

transplanting. The peak population density of each generation from many crops has been plotted in Figure 14. The curves indicate the fluctuations in nymphal populations over time, with biases of crop age, generation number or stage, or adult movement excluded. Thus, the effects of season can be observed. In general it was found that there were usually two population peaks

Table 3. Numbers of adult *Nilaparvata lugens* caught in a light trap at Bangladesh Rice Research Institute, Joydebpur, Dacca, 1970–76.

Month	1970	1971	1972	1973	1974	1975	1976
January	–	9	0	0	0	0	8
February	–	2	0	0	14	3	22
March	–	15	3	0	53	47	27
April	92	0	0	0	6	668	51
May	44	0	0	39	27	225	369
June	131	205	0	45	93	122	97
July	193	31	4	67	314	45	102
August	180	29	0	25	1,795	86	684
September	8	1,314	0	8	1,357	254	913
October	408	1,581	341	11	2,726	235	2,381
November	452	1,414	936	134	2,672	3,976	57,875
December	8	0	571	14	49	86	61
Total for 48 weeks	–	–	1,855	343	9,106	5,747	62,590
Total for 52 weeks	1,516	4,600	1,855	361	9,853	6,163	67,497



14. Brown planthopper *Nilaparvata lugens* density on crops of the medium-maturing rice variety IR20 planted monthly or bimonthly at IRRI. Each curve is the insect generation maximum density on crops of nearly the same age, either 30, 60, or 90 days after transplanting. Data are for both nymphs and adults in 1971-72, but only for nymphs in 1973-76. HB = hopperburn.

each year, suggesting that something outside the crop was indeed influencing pest density. At IRRI there are two major crop-periods each year, approximately January-June and July-December. The periods correspond to a dry, hot season and a wet, cooler season. The presence of two population peaks per year strongly suggests that within a year's time period the major influence on insect populations is the surrounding rice-cropping pattern (IRRI 1973, 1975) and not climate, because there are two crop cycles per year but only one climatic cycle. Also, the season with the highest population density is not constant, again suggesting that the climatic nature of the season is not very important in irrigated rice culture. The influence of the cropping pattern probably is related to the size of the dispersing adult-planthopper population.

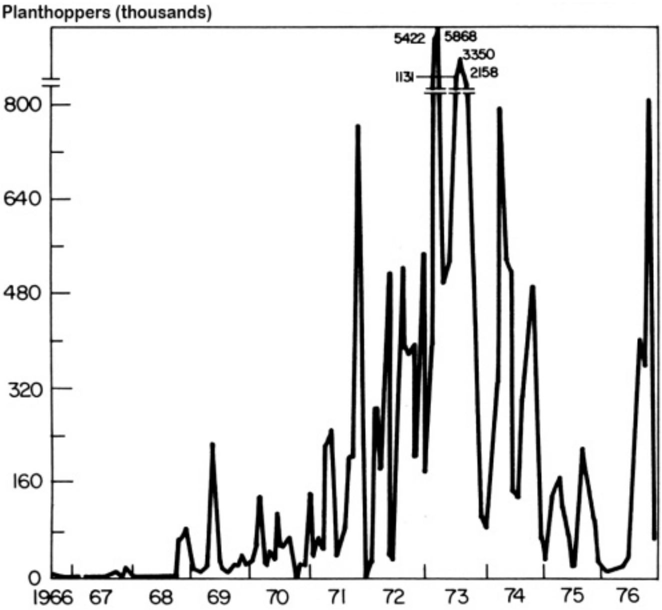
The existence of specific times of year when BPH may be abundant obviously implies that some benefit may be gained from surveillance and forecasting.

Fluctuations over the years

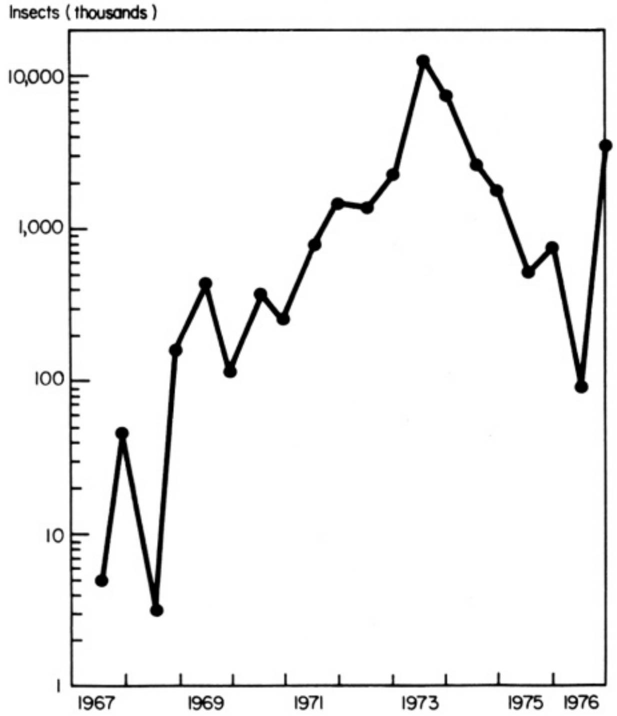
Because the BPH has only recently been a serious pest of tropical rice fields in Asia, there are no long-term records of insect numbers. That makes it difficult or impossible to determine what has actually caused this new pest problem.

Available data are from India, Bangladesh, and the Philippines. Kalode (1974, 1976) reported that light-trap catches in several states of India appear to have increased over the last few years. Catches in Bangladesh since 1970 have fluctuated widely, but considering the very large catch in 1976, the trend is toward higher pest densities (Table 3).

Figure 15 shows the trend in light-trap catches at IRRI during the past 10 years. There was a general increase in the catch size from 1966 to 1973. In 1973 the Philippines suffered severe crop damage from BPH. The pest population declined in 1974 and 1975, but sharply increased again in 1976. The $\log_{10}$ of the population increased gradually and steadily up to 1973 (Fig. 16), suggesting that the cause of the increase was operating with little deviation, which tends to rule out climate as the cause. A scan of records shows that no climatic parameter changed consistently over the years. If seasonal shifts in climate have no important effect on BPH, small changes in long-term climatic trends should have none either. The logical explanation of the increase, then,



15. Numbers of adult *Nilaparvata lugens* caught in 4-week periods in three light traps at IRRI, 1966–76.



16. Numbers of adult brown planthoppers *Nilaparvata lugens* caught in 6-month periods in three light traps at IRRI, 1967–76.

is that rice cultural practices, which have clearly been changing within the past 10 years, in some way encourage growth of the pest population. The components of modern rice culture that might be involved (IRRI 1975) are discussed in the earlier parts of this paper.

A survey of 100 farmers in Laguna province (i.e. around IRRI) showed that there has been almost a total change from traditional to high yielding varieties in the last 15 years. Also during this period the use of fertilizer increased steadily, and there was an increase in the area double-cropped to rice and in insecticide use.

A decline in light-trap catches at IRRI that occurred in 1974 and 1975 (Fig. 15, 16) was probably caused by the widespread growing of BPH resistant varieties around IRRI. And the sharp increase in catches in 1976 (Fig. 15, 16) may be related to a local change in insect biotype, making currently grown varieties more susceptible to the pest.

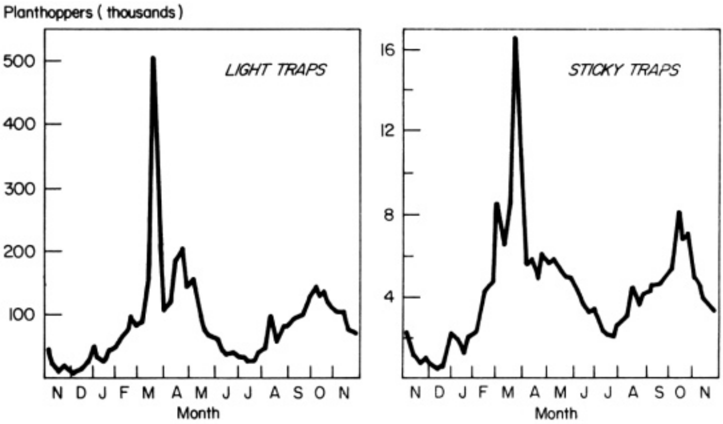
Inspection of Figures 14 and 15 reveals (with minor exceptions such as that in 1974) a rough correspondence between the trends in increase and decrease of pest populations. Despite the fact that light-trap data represent insect fluctuations for a much larger area than do field observations, the comparability of the two trends means that the long-term trends seen in light-trap records can also be observed in fields. Probably, however, field collections are second-hand indicators of changes in pest numbers over a period of years, since the size of the immigrant invasion would play a major role in determining field densities. We must continue light-trap records to maintain continuity of data and to provide for future trend analyses.

DISPERSAL OF THE BROWN PLANTHOPPER

Dispersal in relation to population dynamics

Brown planthoppers move from plant to plant within a field, and adult movement may increase near the end of a crop (Hsieh 1972). However, this section of the paper describes the movement from one field to another of flying macropterous adults. The dispersal permits adults to leave a maturing crop, probably at the end of the third generation, and invade a young crop. Adults may also spread out of a field after the first, or especially the second generation (Mochida et al 1977), but the greatest dispersal is expected while the crop is maturing. MacQuillan (1974, 1975) reported that according to sticky-trap catches maximum dispersal occurred just before harvest; adults were collected throughout the year, however. An experiment at IRRI, where the naturally occurring population was trapped in a field cage at 35 days after transplanting, indicated that dispersal during and at the end of a crop period affects pest density. Near harvest the caged population was much larger than that outside the cage. Assuming that the mortality of caged insects was similar to that of uncaged insects, it appears that the cage prevented dispersal, and the adults continued to breed inside the cage. Our data suggest that because of the two main crops per year at IRRI there are two major dispersal periods, one at the end of each cropping period (Fig. 17). However, dispersal from young crops could occur if the plants are unsuitable because, for example, of hopperburn (IRRI 1974).

Several sources have pointed out that the dispersing insects fly mainly in the early evening hours (IRRI 1972, 1973, 1974; Hsieh 1972; Hoppe 1973; Anon. 1975c; MacQuillan 1975; Kalode 1976, Varca and Feuer 1976). Hoppe (1973) and Kalode (1976) add that the flight occurs in the evenings of hot, humid days. The dispersal flights no doubt occur during the preoviposition period (Hoppe 1973). Figure 9 indicates that more females than males were caught in sticky traps at IRRI, but that probably only reflects the female-to-male ratio in the field. Flight is rather near the ground: catches on sticky boards at IRRI were greatest at 1 m height, less at 4 m, and much less at 8 m. Directional flight is regarded as unlikely, although analysis of sticky-trap records from all around IRRI suggested that more planthoppers flew into IRRI fields from surrounding fields than outward. However, that may only be caused by changing wind direction. Soedarmo (1976) thought that man may accidentally transport planthoppers with seedlings or on vehicles, and



17. Numbers of adult *Nilaparvata lugens* caught in 1-week period in 3 light traps and 12 sticky traps at IRRI, November 1973–November 1974.

that irrigation water and aquatic birds carry the insects. However, such agents of spread are not likely to be important.

Regarding reinfestation, adults apparently enter a field in waves (Fig. 9). However, only the second wave may lead to a nymphal hatch that can be measured (Fig. 7). It may be that seedlings right after transplanting are not preferred by the dispersing adults for oviposition.

Long-distance migration in tropical regions has been studied very little. Kisimoto and Dyck (1976) hypothesized that planthoppers move each year from tropical to subtropical to temperate regions of East Asia. Northward migration is passive, depending on the movement of air masses. Calora (1974) expected that BPH could migrate on air currents from one province of the Philippines to the next. However, Dyck (1974a) doubted that adults can disperse more than a few kilometers in the tropics. There is no need to assume migration because the BPH is always present in tropical areas. There is no known case of a large dispersal flight that is likely to have originated from a great distance.

Wing form

Most work on wing form has been done in Japan, and the resulting ideas have appeared in literature from tropical countries. According to several authors (Grist and Lever 1969; Ho and Liu 1969; Kulshreshtha et al 1974; Laosinchai and Hongsaprug 1974; Kalode 1976), low nymphal density and plentiful food supply cause the development of the brachypterous form; the opposite conditions cause the macropterous form to develop. Kalode (1976) adds that brachypterous forms develop under an optimal temperature regime.

As already mentioned, macropterous forms invade a field and begin the infestation (Anon. 1975c). The second generation may produce some brachypterous forms, which apparently are very fecund (Ho and Liu 1969; Heong 1976). Near the time of crop maturity, macropterous adults again dominate and disperse from the field (Fig. 7; Hsieh 1972).

Some findings vary somewhat from the usual descriptions in the literature. Hinckley (1963a) found that macropterous forms usually made up about 75% of the population, rarely less than 50%. Crowding did not appear to affect wing form. In a 1-year study at IRRI, Alam (1971) never found a high proportion of brachypterous females. Otake et a1 (1975) reported that in Sri Lanka the brachypterous rate increased at the end, not at the middle of the season. More research is needed to clarify the role of wing form in population dynamics.

DISTRIBUTION OF THE BROWN PLANTHOPPER IN RICE FIELDS

Very little research has been done in the tropics to characterize the field distribution of *N. lugens.* Hoppe (1973) and Kalode (1976) suggested that immigrant adults in a field are randomly distributed. The species usually is found near the base of the plants; Hoppe (1973) suggests that is a result of negative phototaxis.

During the crop, aggregation may develop. Otake and Hokyo (1976) noted that adult females often were aggregated in the field. The distribution corresponds to "a mathematical model of (a) negative binomial series with a common k." Chen (1976) recently intensively studied the field distribution, and found that the aggregation index was 1.2888 for all instars of the nymphal stage; 0.8542 for brachypterous adults, and 1.8096 for macropterous adults.

In 1973, at IRRI on several occasions we counted the number of BPH on every hill in a few field plots and studied the distribution patterns. The insects were not distributed randomly within the field as a whole, nor within some of the plots (Gomez 1974). The magnitude of the sampling variance was positively correlated with insect density. There was a tendency for adults and a greater tendency for nymphs to be clustered on certain hills. Nymphal densities on adjacent hills were related. Nymphs tended to distribute themselves over tillers rather than over hills; and the number of tillers per hill partly, but not completely, explained the clustering behavior. The use of "hoppers per tiller" as a unit of measure and the effectiveness of using two or three hills as a sample unit need to be investigated (IRRI 1975). A unit involving hills may be needed in population studies, but a unit involving tillers could be suitable for research on insect damage (IRRI 1971).

SAMPLING THE BROWN PLANTHOPPER

Because complete enumeration of the total population is impossible in regular field studies, a sampling procedure must be devised. Current sampling procedures in ecological experiments are rather ad hoc, and there is little evidence of their accuracy or precision. The percentage coefficient of variation of planthopper estimates in IRRI experiments within 1 year ranged from 1 to 660 (Gomez 1974). As long as ad hoc methods are employed, we must use experimental results with caution.

Sampling individual hills

Sampling individual hills or groups of hills is basic to ecological studies in which the sample unit must be given in terms of a specific land area. (The number of tillers per square meter changes as a rice crop grows, but the number of hills per square meter does not.) Various techniques have been used to count insects on hills: visual estimates, aspirators (Heong 1975; Singh 1975; Otake and Hokyo 1976), striking a hill with or without a catching device (Dyck 1974b; Dyck and Pathak 1974; Anon. 1975c), Kittoor's glass-book technique (Dyck and Pathak 1974), and cages or bags for covering or removing a whole hill.

At IRRI we have used visual counting, including thorough hill-searching, rather extensively because it permits rapid counting without subsequent laboratory work. Both nymphs (as a group) and adults can be counted by experienced observers. The accuracy of visual counting probably decreases as pest density increases. Using 10 or 16 haphazardly scattered healthy hills per plot, we have sampled 1, 2, 3, or 7 times each week. However, healthy hills may give inflated estimates of population densities. Others have used 10 or 20 hills (Chelliah and Subramanian 1973; Mochida and Suryana 1976; Mochida et al 1977; Otake and Hokyo 1976). N. D. Penny (pers. comm.) sampled 100 random hills semiweekly. Hinckley (1963a) counted the insects on one stem on each of 10 hills, and Nishida (1975a) recorded the insects counted within a fixed time, possibly 3 minutes.

Mouth aspirators permit careful collection of nymphal stages in particular. We usually sampled 10 hills/plot each week (IRRI 1971). Although sampling is more tedious and slower than visual counting, the collections are immediately available for identification and counting. On the other hand, motorized suction machines permit rapid collecting but are not suitable for sampling young nymphs (Dyck and Pathak 1974). Alam (1971) collected insects from sample rows and MacQuillan (1968, 1974) sampled hills or 0.3-m-row units. Wan (1972) placed a metal cylinder around individual hills before sampling with a modified vacuum cleaner, and found that the method favored the collection of adult insects. Soehardjan (1973) employed a D-Vac suction machine to collect adults from 1-m^2 units.

Insects knocked off a hill that has been struck are usually counted visually after the pests fall onto the water surface. However, Misra and Samal (1975) constructed a cylindrical cage, into which the planthoppers are tapped from the plants. Gavarra and Raros (1975) each week sampled 30 hills, obtaining insects by holding the plants above a greased wooden paddle and striking them. Hinckley (1963a) clapped an ethyl acetate killing jar against the base of rice hills and ran it upwards, trapping the planthoppers. Wan (1972) says use of the method caught mostly nymphs and few adults.

Das et al (1972) selected three hills at random, cut off all tillers at points below the water line, and placed the tillers in plastic bags; later the collected material was sorted and the insects counted in the laboratory. A similar method is currently being tested at IRRI for life-table studies, but the bag is placed over the hill before the rice is cut.

Counting insects on only 10 or 20 hills/plot lacks precision. A quick calculation of the number of hills required for a precision level of 10 or 20% suggests that several hundred hills should be sampled. Using a formula given by Southwood (1966), Munroe (1974) calculated that 64 hills were required to obtain a 50% precision level, and 1,600 hills to get a 10% level. However, Chen (1976) recently calculated that 50 to 70 hills were adequate at any plant stage for intensive studies needing a 20% level, and 30 to 40 hills for extensive studies to meet a 30% precision level. Chen also developed a plan for sequential sampling at three crop ages; his plan was for use in the field to determine population densities and whether those densities were above or below economic thresholds.

Sweep net

The sweep net has been widely used to sample BPH from seedbeds and rice fields. Its main advantages are speed and convenience. Catches heavily favor adults, however, and are biased by the crop age and nature of the stand, the microhabitat of BPH, the sweeping technique used, and climatic factors. Sweeping can be useful, however, for extensive field surveys (Otake and Hokyo 1976), or when adult comparisons within short time spans are needed and sampling conditions remain uniform.

The number of sweeps per plot varies from 5 to 100 (Hinckley 1963a; Wan 1972; Dyck and Pathak 1974; Nishida 1975a; Mochida and Suryana 1976; Mochida et al 1977; Otake and Hokyo 1976). Bae and Pathak (1969) took sweep samples every 10 days between 0800 and 1000 hours but O. Mochida (pers. comm., CRIA-IRRI, Sukamandi, Indonesia) made sweeps weekly after 0900 or 1000 hours. N. D. Penny (pers. comm.) found it best to sweep at 1000 hours.

Mochida et a1 (1977) tried to correlate sweep net catches with directly counted field densities, and developed the following formulae:

$$Y = 1.2432X + 0.6963 \ (r = 0.8562)$$
$$X = 0.5896Y - 0.2050 \ (r = 0.8562)$$

where X is log [(no. adults + nymphs)/hill + 1] and Y is log [(no. adults + nymphs)/50 strokes of net + 1]. However, Otake and Hokyo (1976) found they could not correlate field counts and sweep samples of macropterous females. Wan (1972) suggested a pooling of net and direct counts.

Traps

The most commonly used traps are those with light (incandescent, fluorescent, or blacklight) as the attraction source (Wan 1972; IRRI 1973; Anon. 1977). Light traps depend on the positive phototactic response of the insects; physiological as well as abiotic environmental factors can influence the behavior (Leeuwangh 1968). The correspondence of light-trap catches to field samples varies from poor to good (Leeuwangh 1968 ; Alam 1971 ; Fig. 14, 15).

Airborne net-traps and yellow-pan water-traps have been used in Indonesia (Mochida and Suryana 1976) to catch dispersing, flying insects. Another trap for flying planthoppers is the sticky trap — boards or cylinders covered with sticky material (IRRI 1972; MacQuillan 1974, 1975). Hsieh (1972) found that sticky traps were useful even in rainy weather. At IRRI the sticky board 1 m above the ground gave a good catch. There was a good correlation between sticky-trap and light-trap catches (Fig. 17). Thus, both light and sticky traps can be used to monitor dispersing insects.

Quadrats

Wire quadrats are useful for counting population densities in seedbeds and broadcast-seeded fields (MacQuillan 1974; IRRI 1976). The quadrat may be 0.06 to 0.25 m^2 (Abraham 1957; O. Mochida, pers. comm.). However, sweeping with a net is probably an appropriate method of sampling seedbeds because the plants are small, and the populations are low and composed almost entirely of adults.

CONCLUSIONS

The density and composition of the BPH population in the field fluctuates dramatically within the lifetime of one crop, within 1 year, and over a period of years. The insect changes during a crop's life are influenced by crop age and the pattern of insect generations, which is rather distinct in a given field. Dispersing macropterous adults invade a field after planting, and two major generations usually develop before the crop matures. Insect density is highest when nymphs dominate the population, usually about 60 and 85 days after transplanting. Nymphal mortality may be high. Most dispersion of adults from the field takes place near crop maturity.

Within a year, there are usually two population peaks, one near the end of each crop season. Surrounding crops apparently influence pest density strongly, possibly by affecting the size of the dispersing population. A year's largest peak may occur in either the dry or the wet season.

Evidence to date suggests that the change to modern rice cultural methods within the past 10 years is the major factor in the upsurge in recent years of BPH populations and of the damage the insect causes. Components of those methods that have been shown to increase pest populations are many tillers per unit area, flooding fields, and applying high doses of nitrogenous fertilizer.

More evidence is needed to indicate whether critical roles in increasing pest populations are played by cropping patterns, high yielding varieties per se, weeds, natural enemies of BPH, climate, or insecticides. If indeed the main cause of the insect problem is man's modern methods of growing more rice, the BPH will probably remain a pest or become an even more serious pest. The solution is not likely to come from reversing the trends of modern agriculture, but from improving our pest management skills.

Sampling the BPH is difficult because of the uneven distribution that develops in the field. Use of the number of tillers per hill appears to be an important step toward improving sampling methodology. We have reviewed the current methods of sampling BPH and discussed the advantages and disadvantages of each. There is little evidence so far to indicate what exactly is the best method for any particular purpose. In ecological studies it is important to sample all stages of the insect on some kind of a hill basis. Traps are useful for monitoring dispersal.

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