Ecology of the brown planthopper in temperate regions

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The population of the brown planthopper *Nilaparvata lugens* (Stål) in temperate regions is characterized by discrete periods of seasonal appearance, low initial density, steep and steady growth, clumped spatial distribution, and violent fluctuations from year to year. *N. lugens,* a temporary inhabitant, arrives from long distances barely in the rice-growing season. Its high potential fecundity, high adaptability to its host in various stages, and high tolerance to crowding cause its uneven, clumped spatial distribution within a field. These characteristics also cause the steep and steady growth in population that enables the insect to increase to destructive levels despite its low initial density. The fluctuations in density of initial migrant populations, which are governed by unstable factors, largely cause the violent year-to-year fluctuations in population. The relevance of these characteristics to the strategy for efficient control of the brown planthopper is discussed.

NILAPARVATA LUGENS (Stål), commonly known as the brown planthopper (BPH), is widely distributed in tropical, subtropical, and temperate regions of Asia, where occasional outbreaks seriously injure cultivated rice. There seems to be a distinct difference between the ecology of the BPH in tropical areas where the population may remain in the paddy field throughout the year and that in temperate regions where BPH cannot survive the winter season and is replaced every year by immigrants from southern regions. Such a difference results in different patterns of pest damage and correspondingly different strategies for efficient control.

This paper outlines the ecology of the BPH population in such temperate regions as Japan and Korea on the basis of field population studies conducted mainly in Japan. For comparison, it also describes results of work on the whitebacked planthopper, *Sogatella furcifera* Horvath, whose biology is similar to that of *N. lugens,* particularly in Japan and Korea. The major characteristics of the BPH population are:

- discrete period of seasonal appearance,

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- low initial density,
- steep and steady population growth,
- clumped spatial distribution, and
- violent density fluctuations from year to year.

Those characteristics obviously result from combinations of the physiological properties intrinsic to the insect and the environmental (climatic, biotic, or cultural) conditions of temperate regions.

DISCRETE SEASONAL APPEARANCE

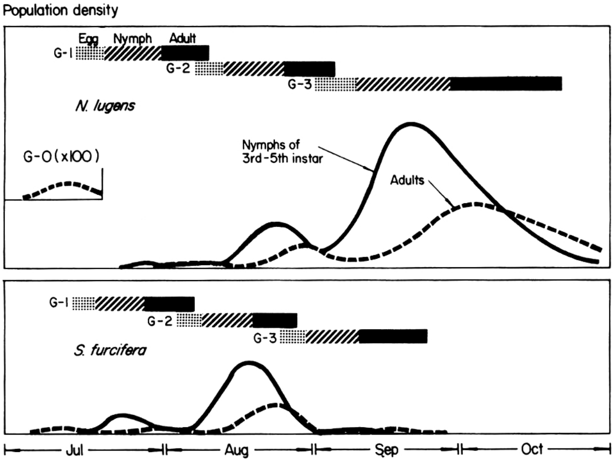
The term *discrete* is used here in two senses. First, the history of the BPH in temperate areas may be called discrete in that its population is seen during only part of each year. In most districts of Japan and Korea, rice is usually grown only from June to October. The initial *N. lugens* population (and that of *S. furcifera*) appears as immigrants soon after the crop is planted.

The population grows for some generations, then disappears after the end of the rice growing season. Extensive land and sea surveys together with experimental analyses of flight activity, now confirm that the initial immigrants in Japan (and probably in Korea) are long-distance migrants, moving from the continent over the East China Sea (Kisimoto 1971, 1976a,b ; Ohkubo 1973). Although some authors have suggested a diapause-like phenomenon in the egg stage (Miyake and Fujiwara 1962; Okumura 1963), a large number of field observations so far indicate that because of the low temperature and lack of alternative host plants, at no developmental stage can the insect normally survive the winter in Japan. The BPH in temperate regions is thus regarded as a temporary inhabitant.

Second, discrete generations can be seen in the population pattern. Each of the usual three generations during the season has a distinct population (Fig. 1), although the generations overlap to a certain extent (Kisimoto 1965; Kuno 1968). Some recent studies indicate the same can also be said of Korea (Lee and Park 1976: Hokyo et al 1975). Undoubtedly, the reason is that the initial invasion usually occurs within a limited period because of the specificity of weather conditions that bring about the migration (Kisimoto 1976a). Also, the rather short lives of the adult insects contribute to the discreteness of generations.

LOW INITIAL DENSITY

A notable feature of BPH populations in temperate regions is the low density of the initial immigrant population, which later sharply increases. The average density of the initial generation in an unsprayed paddy field at the Kyushu Agricultural Experiment Station (Fukuoka, Kyushu Island, Japan) between 1961 and 1968 was about 0.0l/hill (Table 1). That is about one-tenth of the *Sogatella, furcifera* population and is also much smaller than the initial densities



1. Idealized representation of population patterns of *Nilaparvata lugens* and *Sogatella furcifera* during a rice-growing season (G = generation) (from Kuno 1968). Based on data from Kyushu Agric. Exp. Stn., Chikugo, Fukuoka, Japan.

of two other coexisting leafhoppers, *Laodelphax striatellus* and *Nephotettix cincticeps.* In Korea, Hokyo et al (1975) recorded a peak of 0.016 *N. lugens*/hill (at Suweon), which is also much smaller than the 0.25 hill for *S. furcifera.*

The initial density, however, varies widely among different districts of the same country. As anticipated from the specificity of the migration pattern

Table 1. Population growth of *Nilaparvata lugens* **and** *Sogatella furcifera* **in an unsprayed paddy field, 1961–1968. Kyushu Agric. Exp. Stn., Japan.**

Insect species and population factor		Generation			
		Initial (G-0)	First (G-I)	Second (G-II)	Third (G-III)
N. lugens					
Population density (no./hill) [a]	N + A	0.0105	0.586	4.98	19.51
	A	0.0105	0.162	1.38	5.40
Range during 1961 to 1968 [b]	N + A	0.0022 ~ 0.0497	0.122 ~ 3.52	0.532 ~ 48.19	3.35 ~ 214.8
Reproduction rate [c]			15.40	8.50	3.92
Population growth rate			513		
S. furcifera					
Population density (no./hill)	N + A	0.121	0.625	1.65	0.115
	A	0.121	0.187	0.494	0.034
Range during 1961 to 1968	N + A	0.0089 ~ 0.603	0.0330 ~ 5.78	0.0600 ~ 40.18	0.0093 ~ 1.17
Reproduction rate			1.55	2.64	0.07
Population growth rate			4.09		

[a] The density is the average for the period corresponding to each generation (For details of calculation, see Kuno and Hokyo 1970b). N + A: Sum of adults and 3rd–5th instar nymphs; A. Adults only. [b] The range from the minimum to the maximum density observed during 1961–1968. [c] The rate was calculated based on the density of adults

described by Kisimoto (1976a), the initial population in Japan tends to become lower as one moves from southwestern to northeastern districts in the direction of the air-mass movement at the time of invasion (e.g. Suenaga and Nakatsuka 1958). A similar gradient for the initial population was also observed in Korea (Hokyo et a1 1975).

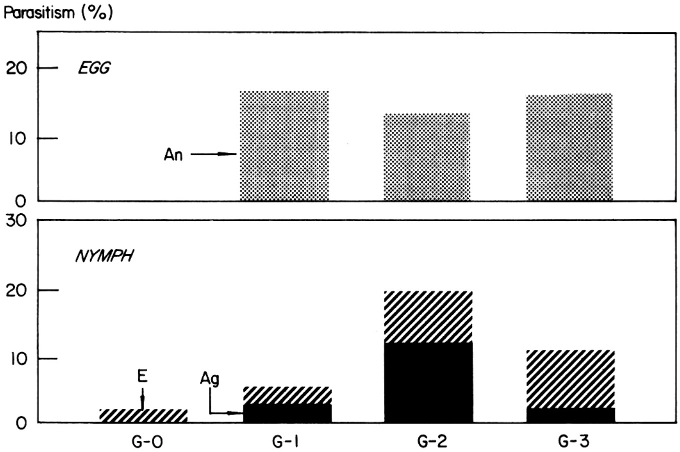
STEEP AND STEADY POPULATION GROWTH

Obviously, the capability for steep and steady population growth makes BPH one of the most important pests of rice despite its low initial numbers. The population growth results from steady multiplication during three generations, which contrasts with the growth of the whitebacked planthopper population, which stops at the second generation and crashes thereafter (Table 1). The initial BPH population multiplies more than 500 times, bringing about an eightfold increase per generation. As a result, a destructively high density of more than 200 nymphs and adults per hill was attained in an outbreak year. In contrast, the whitebacked planthopper has a much lower rate of population growth; it multiplies only 4.1 times, or about two times per generation. That may explain why unlike BPH, it cannot be a serious pest in temperate regions, despite its much higher initial population.

Fecundity

The high rate of the BPH population growth is primarily due to its high fecundity. Suenaga (1963) reported that the number of oocytes per female is about 2,000 on potted rice plants. Kuno (1968) observed 805 to 908 eggs/female in the three generations. On field-grown rice covered with a nylon net, Kusakabe (unpubl.) found nearly 1,000 eggs/female. Those values seem to represent the potential fecundity of the insect in the field. A number of authors (e.g. Suenaga 1963; Mochida 1964) on the basis of laboratory experiments in which either cut plants or seedlings were used have often reported much smaller fecundity values of some hundreds or less. By no means may such conditions be optimum for sap-sucking insects.

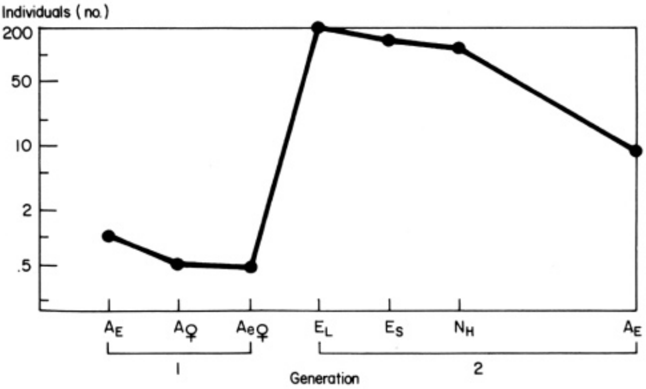
Like other planthopper species, a few days after emergence, BPH adults copulate and begin to lay eggs, then continue to oviposit at a roughly constant rate. The high potential fecundity described above usually cannot be realized in the field because the adult insect's life is shortened by various factors. Kisimoto (1965), for instance, observed a life span of about 9 days for brachypterous females of the first generation. Kuno and Hokyo (1970a,b) estimated that first-generation brachypterous females live 8.1 days as adults and each unparasitized female lays 429 eggs, the egg-laying being less than half the potential. Ichikawa and his collaborators (e.g. Ichikawa 1976a,b) recently found that these planthoppers have an elaborate system of mating communication. It is likely, however, that in the initial low-population generation, fecundity occasionally is reduced because of insufficient chances to mate.



2. Average parasitism of *N. lugens* generations (from Kuno and Hokyo 1970b). Data obtained 1965–68 at Kyushu Agric. Exp. Stn. An = *Anagrus* sp.; E = *Elenchinus japonicus;* Ag = *Agamermis unka.*

Survival of immature stages

A variety of mortality factors operate during the egg and nymphal stages. The egg, which is laid into the tissue of the leafsheath or leaf of rice, is attacked by a mymarid parasite, *Anagrus* sp., whose biology has been studied in detail by Ôtake (1967, 1968, 1969, 1970, 1976). According to a study at Kyushu Agricultural Experiment Station, parasitism by *Anagrus* sp. of the BPH was lower than its parasitism of the other planthoppers and fairly stable throughout the season, varying somewhere between 10 and 20% on the average (Fig. 2). The egg mortality due to other factors. such as predation by the widely distributed mirid *Cyrtorhinus lividipennis* Reuter, or parasitism by some fungi, was observed. Among the mortality factors for nymphs, predation by spiders seems to be of great importance, although few quantitative data have so far been obtained on the actual rate. Among various species of spiders found in paddy fields (Kobayashi 1961; Lee and Park 1976), several species belonging to Lycosidae (*Lycosa pseudoannulata* Boes. et Str., *Pirata subpiraticus* B. et S., etc.), and micryphantidae (*Oedothorax insecticeps* B. et S., *Gnarhonarium dentatum* Trider, etc.) are usually most plentiful both in Japan (Kuno 1968; Kiritani et al 1972) and Korea (Lee and Park 1976; Hokyo et al 1975). Their peak populations sometimes exceed 10/hill. The planthopper nymph is attacked also by some parasites belonging to three taxa: a nematode, *Agamermis unka* Kaburaki et Imamura; a Strepsiptera, *Elenchinus japonicus* Esaki and Hashimoto; and some species of Dryinid wasps (Esaki and Hashimoto 1937). Their parasitism at the Kyushu Agricultural Experiment Station tended to become high in the second BPH generation. The parasites leave the host's body at its



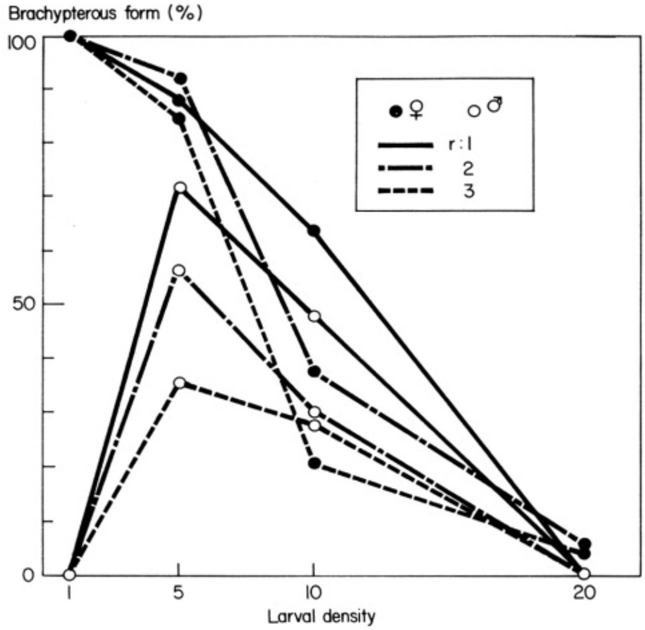
3. Reproduction-survival in the field starting from one first-generation adult of *N. lugens* (from Kuno and Hokyo 1970b). The data were obtained in 1968 at Kyushu Agric. Exp. Stn. A_E = adults emerged; A ♀ = female adults emerged; Ae ♀ = unparasitized female adults; E_L = eggs actually laid; E_S = eggs survived; N_H = nymphs hatched (= E_S – eggs parasitized).

adult stage; thus, although they attack nymphs, their effect is classified as adult mortality or a decrease of reproductive females (their parasitism entirely spoils the host's reproductive ability). Some 50% of the BPH population at the Kyushu Station is lost to egg and nymphal parasites before third-generation adults emerge although individual parasitism rates in each generation are generally rather low (Fig. 2). A number of physical and biological mortality factors may also affect the nymphal stage, as yet there is little information about them.

A presumably typical example of the reproduction-survival curve for the BPH is shown in Figure 3. The high fecundity of the species gives rise to a high rate of increase (about eightfold per generation in this case), notwithstanding a rather low survival rate, especially in the nymphal stage.

Adult wing forms in relation to population growth

The BPH, like many other Delphacids, has two adult wing forms. Kisimoto (1956, 1965) concluded that the macropterous form is migratory and adapted to finding a new habitat for the species, and the brachypterous form is sedentary and adapted to breeding in a suitable habitat. Under experimental conditions the proportion of the macropterous females can vary from 0 to 100%. Poorer living conditions (e.g. dense populations) during the nymphal stage mean more macropterous females. For the male, however, there is apparently an optimum density range that stimulates the appearance of the brachypterous form; the male becomes a macropterous adult at both low and high densities (Fig. 4). Generation-to-generation changes of the proportions of adult forms in the field are shown in Fig. 5. The initial population is naturally composed

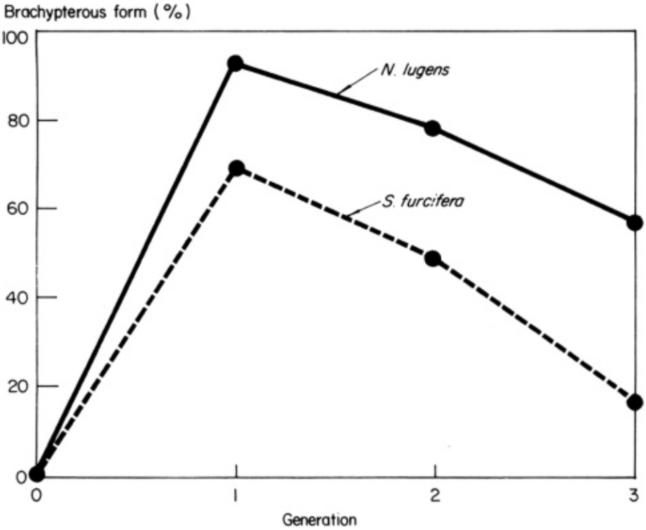


4. Percentage of brachypterous forms in both sexes of *N. lugens* from a rearing experiment in which the initial density and the interval of renewal of the food and the container size (r) were varied (from Kisimoto 1965).

exclusively of macropterous adults. In contrast, most females of the ensuing first generations are brachypterous. The proportion of brachypterous females then tends to decrease toward the last generation as population density increases and the host plants mature. The decrease is much slower than in whitebacked planthopper, however, and most second-generation females are brachypterous although the proportion varies from year to year depending on the population density (Kuno and Hokyo 1970b). Figure 5 thus clearly shows that BPH, in contrast to whitebacked planthopper, has a high tolerance for crowding and a high adaptability to different stages of the host, so that active dispersal from the field does not usually take place until the third or last generation. That may be an important reason for the steady BPH population growth during the rice growing season.

CLUMPED SPATIAL DISTRIBUTION

Clumped or patchy distribution of individuals within a field is another important characteristic of the BPH in temperate regions. Other rice leafhoppers usually show much more uniform population distributions (Kuno 1963,

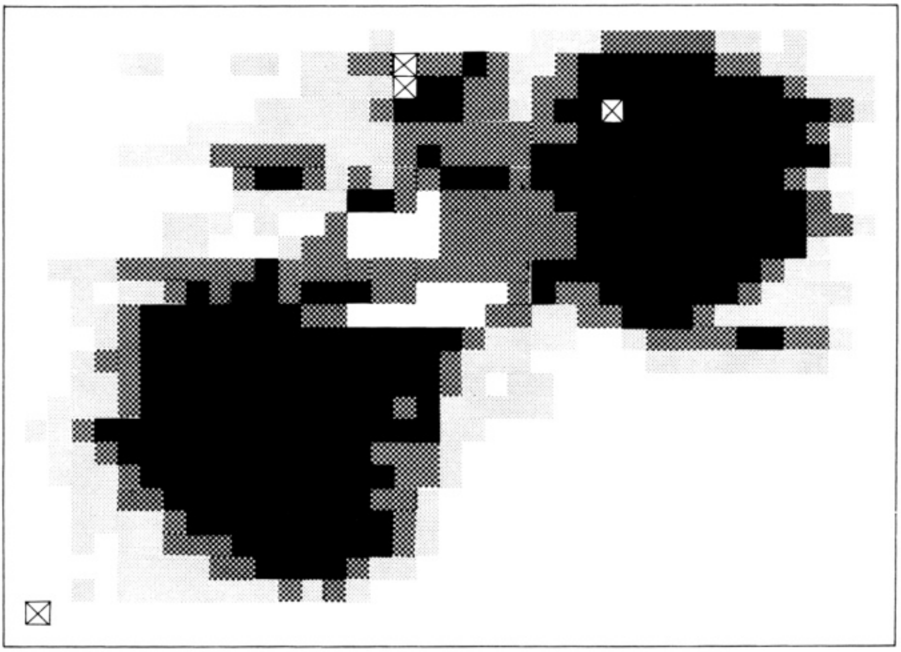


5. Percentage of brachypterous form in females in the field population of *N. lugens* at each seasonal generation (from Kuno 1968). The data were obtained from 1961 to 1966 at Kyushu Agric. Exp. Stn.

1968)—a topic to be described only briefly, because it has been discussed elsewhere (Kuno 1976).

The initial immigration population is distributed nearly at random within a field, as might be expected from the process of its establishment. Its clumped distribution later is the result of growth of a population that has limited ability to travel (Kisimoto 1965; Kuno 1968). It may be regarded as the random distribution of colonies formed from the original immigrants. Mathematically, the number of individuals per hill of rice in the initial population can usually be described by the Poisson distribution, and that in the later breeding population by the negative binomial distribution. That fact can be used to develop efficient sampling plans for making population estimates (Kuno 1976).

In temperate regions, the injury of BPH is usually in the form of patches of hopperburn in a field, each patch drawing a distinct margin (Fig. 6). Such a pattern obviously results from a clumped distribution. That will be confirmed from Figure 7, which shows the relation of the range from minimum to maximum number of individuals on 50 sampled hills to the mean population on successive sampling dates. The range is wide in relation to the mean density, reflecting the clumped spatial distribution. At the time of highest population (278/hill), for example, the range was 10 to 1,274 adults and old nymphs. The maximum value was much more than enough to result in destruction of the hill concerned, while the minimum was far below the injury threshold. The insect's high tolerance for crowding is also evident in the clumped pattern of spatial distribution.

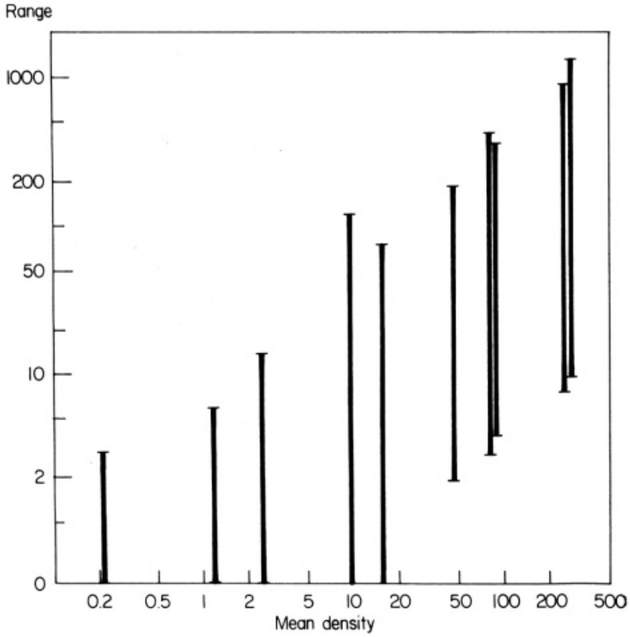


6. An example of the distribution map of hills injured in various degrees by *N. lugens* (from Kisimoto 1965). Small square represents each hill; plain areas are hills not injured; squares shadowed by small dots are hills in which the damage was detectable but none of tillers were killed; squares with large dots are hills some tillers of which were killed; black squares are hills entirely killed; squares crossed are missing hills.

I have shown (1968, 1976) that the degree of aggregation or clumpedness of distribution is closely negatively correlated with the density of the initial population in each year. It may follow that in tropical regions the distribution is usually much less clumped because the population of immigrants established in each field will be much higher. That inference is supported by Otake and Hokyo's field data (1976) taken in Malaysia and Indonesia.

VIOLENT DENSITY FLUCTUATION FROM YEAR TO YEAR

In temperate regions like Japan or Korea, the BPH (and the whitebacked planthopper) is known as a typical outbreak-type pest whose population fluctuates violently from year to year (e.g. Suenaga and Nakatsuka 1958; Paik 1976). For instance, from 1961 to 1968 the maximum population density of the third generation was about 64 times the minimum density (Table 1).



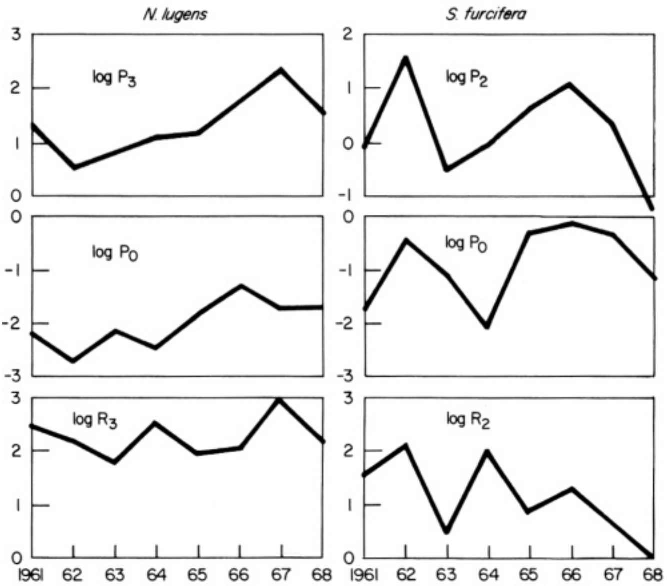
7. Relation of the range of the number of *N. lugens* on a hill to the mean density of *N. lugens* on 50 hills on each sampling date. Based on successive samples from July to October 1967. Data from Kyushu Agric. Exp. Stn.

Thus, while serious rice yield losses occur throughout a region in outbreak years, no great loss may be observed in other years in many parts of the same region.

To analyze such a violent fluctuation, one can first express the density of the third generation, P_3, using its two components, the initial density P_0 and the overall population growth rate R_3 as

$$P_3 = P_0 R_3 \text{ or } \log P_3 = \log P_0 + \log R_3.$$

Figure 8 compares year-to-year fluctuations of both these components with that of log P_3. The density of the initial population itself fluctuates widely, greatly influencing the density of the later third-generation populations, although the rate of population growth also shows considerable variation from year to year. Such large fluctuations of P_0 can be anticipated because of the possible uncertainty in the two factors determining it—the population density at its unknown premigration origin, and the synoptic weather conditions while it is migrating. The coefficient of determination of log P_0 (in terms of the squared value of the coefficient of correlation with log P_3) was 0.58; that of log R_3 was 0.36. Thus, it may be said approximately that in this case 60%

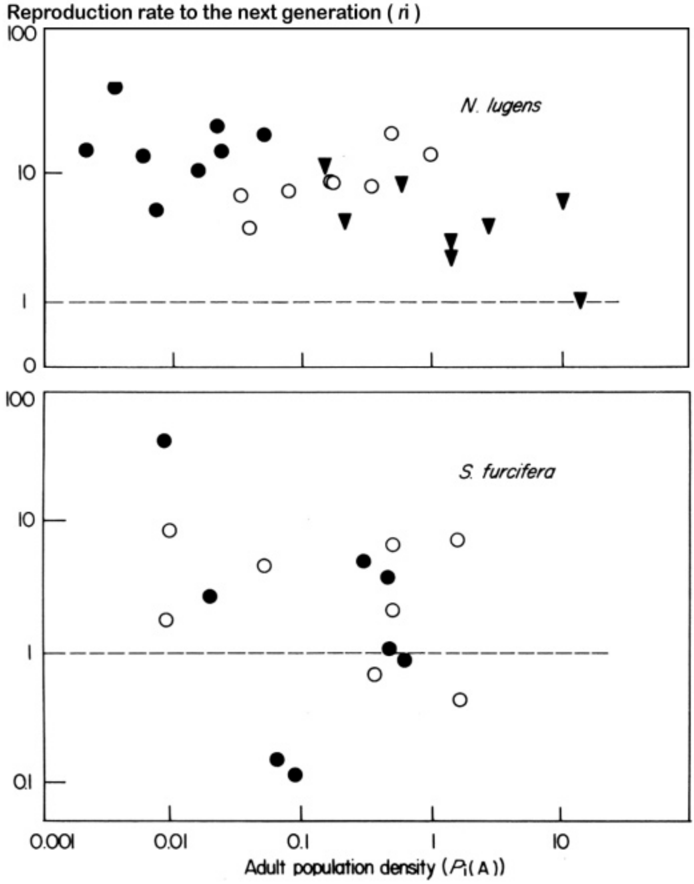


8. Graphical comparison of the year-to-year fluctuation of the population density at the peak generation (third for *N. lugens* and second for *S. furcifera*) and those of its two components, the initial density (P_0), and the overall population growth rate (R_3 or R_2). The data were obtained at Kyushu Agric. Exp. Stn.

of the fluctuation of the third-generation population density could be accounted for by the density of the initial immigrant population, and 40% by the fluctuation of the population growth rate in the field.

Further separation of the population growth rate into three subcomponents, r_1, r_2, and r_3, representing the reproduction rate at each generation ($\log R_3 = \log r_1 + \log r_2 + \log r_3$). reveals the fairly high contribution of r_1, indicating the relatively important effect of early-season reproduction on the overall population growth rate. Kuno and Hokyo (1970b) and Kuno (1968) concluded from various analyses of the numerical relationship between rice leafhoppers and their natural enemies that neither predators nor parasites can be key factors governing such fluctuations of the overall population growth rate. There are few data from which to assess the factors responsible for the fluctuation, but some weather factors seem to be important, especially in their effect on host-plant conditions. Kisimoto (1976b) has made clear the importance of host-plant conditions for *N. lugens.* There may also be cases in which the variation of mating rate of the initial generation — inverselydependent on population density — has some effect on the fluctuation of the population growth rate, because the female adult does not copulate until its ovaries mature, i.e. until established in the field after migration in the case of initial population (Katayama 1975).

The whitebacked planthopper's situation is somewhat different; the relative



9. Relation between the population density (P_i) and the reproduction rate to the next generation (r_i) for each of the successive seasonal generations. The data were obtained from 1961 to 1968 at Kyushu Agric. Exp. Stn. ● = G-O ($i = 0$); o = G-I ($i = 1$); p = G-II ($i = 2$).

influence of initial density on peak density (i.e. the density of the second generation) is rather lower (the coefficient of determination was 0.34), because the reproduction rate of the species in the paddy field is far less stable than that of BPH. Figure 9 shows that reproduction rate is not only far lower on the average, but also much more variable than that of BPH. Figure 9 may thus confirm the robustness of the BPH as well as its high tolerance for crowding.

SUGGESTION FOR OUTBREAK FORECASTING

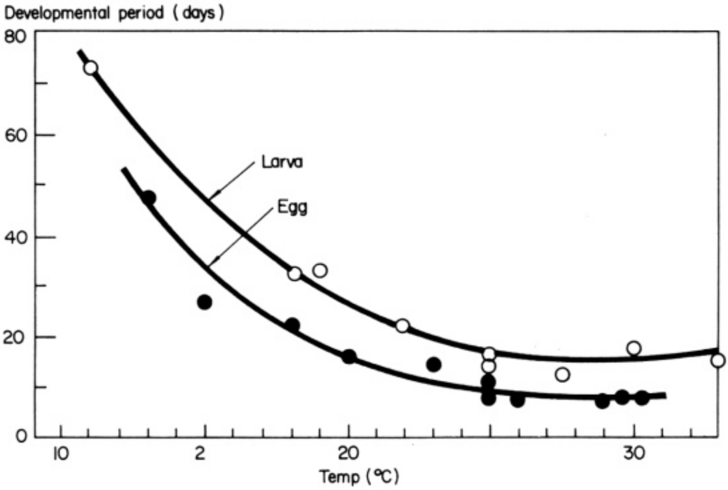
From the knowledge reviewed above, it is now possible to derive a basic strategy for the prediction of BPH outbreaks in temperate regions. Such characteristics of the insect as its sharply defined life cycle originating with low-density immigrants, and its steady population growth over several generation make prediction feasible.

Because there is no way of determining the premigration population, the practical first step in forecasting is to know the time of appearance and the density of the invading initial population as exactly as possible. The time the insects appear may be used in predicting the time later generations occur on the basis of the speed of development in relation to temperature (Fig. 10). As seen in Figure 8, the initial density itself fairly highly correlates with the density of the later third-generation population in question. Thus if initial density can be estimated precisely, the third-generation density may be predicted with considerable certainty as early as 2 or 3 months before the rice is damaged.

Table 2 shows the coefficients of correlation between the densities of the peak of generation (third for *N. lugens;* second for *S. furcifera*) and each preceding generation from 8 years of studies at Kyushu Agricultural Experiment Station.

Precise estimation of the initial population over a wide area, however, usually requires a large amount of labor because of the low density involved. For alternative or additional use, net traps or yellow-pan water traps set in the field are recommended (Kisimoto 1976b).

Although subject to possible disturbance by weather conditions, light trap data are also valuable for assessing the initial population level. For example, I found a high correlation of $r = 0.90$ between the initial density of BPH in the field and the sum of light trap catches (Kuno 1968).



10. Average egg period and nymphal period of *N. lugens* at various temperatures (from Kisimoto 1965).

Table 2. Coefficients of correlation between densities of the peak generation (third for *Nilaparvata lugens,* second for *Sogatella furcifera*) and each preceding generation.[a]

	Generation		
	Immigrant	First	Second
N. lugens	0.761	0.854	0.889
S. furcifera	0.478	0.851	–

[a] Based on an 8-year study at Kyushu Agric. Exp. Stn., Fukuoka, Japan.

In the first generation, which appears about early August, the correlation with the third-generation population, of course, rises further and prediction becomes more precise (Table 2), although injury usually occurs after two generations. Sampling also becomes somewhat less laborious as the population increases. For most efficient control of the BPH, it is therefore advisable to make intensive population censuses of the first generation (Kisimoto 1965; 1976b; Kuno 1968). In the second generation, it is still practicable to predict third-generation density and reliability increases, but in outbreak years injury sometimes begins to occur in this generation.

For the whitebacked planthopper, predictions of the second generation population does not become reliable until the first generation in early August (Table 2) because of the unstable reproduction in the paddy field. But special effort to forecast outbreaks of this species seems pointless in most of the temperate regions because the ability to multiply on rice is so low that serious injury may rarely, if ever, result (Fig. 9).

Attempts to develop a practical system of forecasting BPH outbreaks are now being made in Japan. Kisimoto (1976b), for example, proposed 0.3 to 0.5 females/hill as the critical first-generation population level that will be followed by hopperburn in the autumn. He also designated a tentative threshold in the initial population to discriminate between mass and minor immigration catches of 10 individuals in a net trap and 50 to 60% in water trap. Early control of the population is recommended when a mass immigration is detected. Ideally, threshold values for each generation should be determined for each district because the population growth rate may differ from district to district according to environmental and cultural conditions.

In a system of outbreak forecasting like the one I have discussed, it is indispensable to obtain an objective population estimate with a precision appropriate to the generation being studied. For that purpose I have discussed elsewhere (Kuno 1976) field-sampling techniques adapted to the characteristic spatial distribution of the BPH.

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