

COMPARATIVE ANALYSIS OF THE POPULATION DYNAMICS OF
RICE LEAFHOPPERS, *NEPHOTETTIX CINCTICEPS* UHLER AND
NILAPARVATA LUGENS STÅL, WITH SPECIAL REFERENCE
TO NATURAL REGULATION OF THEIR NUMBERS

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INTRODUCTION

In southwestern districts of Japan, four species of rice leafhoppers, *Nephotettix cincticeps*, *Nilaparvata lugens*, *Sogatella furcifera* and *Laodelphax striatellus*, often cause serious damage to the cultivated rice either directly by sap-sucking or indirectly as the vector of some virus diseases.

Since 1961, a long-term population study on these four species has been conducted in this station to reveal the basic features of the dynamics of their populations in paddy fields and thereby to prepare an ecological basis for the effective control of these important insect pests which had not yet been established.

On the basis of the 8-year results of this study, we describe here the outline of the population properties of the first two species of the above four, *Nephotettix* and *Nilaparvata*, that are predominant in abundance. The description covers the two aspects of population dynamics, temporal changes and spatial structure; and the results are discussed with particular reference to the comparison of the situation as to natural population regulation between these two species.

Our main conclusions in this paper are fundamentally consistent with those that were derived from the 6-year results (1961-1966) in a previous paper (KUNO 1968) dealing with all the four species, but they have become more confirmative by addition of the data for both 1967 and 1968. The general methods of sampling and data-analysis for this study have also been described in detail in the previous paper, so that they will be mentioned here only briefly.

THE INSECTS

Taxonomically, *Nephotettix cincticeps* belongs to Cicadellidae, and *Nilaparvata lugens*, to Delphacidae of the order Hemiptera. The following is a brief summary of their general biology which has so far been made clear at length (e. g. SUENAGA and NAKATSUKA 1958; NASU 1963; SUENAGA 1963; KISIMOTO 1965; MIYAKE 1966; KUNO 1968).

These leafhoppers are multivoltine insects. Their populations in paddy fields are

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established usually in July, soon after the planting of rice seedlings, by the adults invading from the outside, and then propagate there passing several generations until October. The adults have high fecundities which often amount to several hundreds per female. The eggs are laid into stem (leaf-sheath) (*Nephotettix*) or either stem or leaf (*Nilaparvata*) of the host plant in masses each consisting of several (*Nilaparvata*) or some 10 or more (*Nephotettix*) eggs on the average. The nymphs pass through five instars till their emergence as adults. In summer, roughly speaking, it takes about one week for the eggs to hatch, and about two for the nymphs to emerge as adults. Both the nymphs and adults live and feed on the rice plant. In *Nilaparvata*, as in other delphacid leafhoppers, the adult has two wing-forms; macropterous form which can fly by wing and brachypterous one which cannot. Among adult females, the proportion of the former becomes high when the living conditions, such as the population density during nymphal stage or the physiological stage of the host, are not suitable; so that this form is regarded as the type adapted for migration from unsuitable to suitable habitats, whereas the latter form, as that adapted for reproduction under suitable conditions. Meanwhile, no such polymorphism is known in *Nephotettix*, its adult being always of macropterous or normal-winged type. In late autumn after rice plants were harvested from the field, *Nephotettix* remains in the fallow or nearby areas as nymphs, where it overwinters and passes the following generation in spring on gramineous weeds such as *Alopecurus aequalis*. *Nilaparvata*, in contrast, usually disappears from the field or nearby areas by winter until it again appears at the beginning of the next rice-growing season; and where and how it survives this off-season period remain mostly unknown.

With respect to the status as the pest of rice plant, it is well known that these two species are distinctly different from each other. *Nilaparvata* is a typical example of the outbreak-type pests, causing destructive damage at the time of occasional outbreak; and the injury ("hopperburn") usually occurs in autumn as the result of collective sap-sucking by a great number of individuals. *Nephotettix*, on the other hand, does not cause any remarkable injury by sap-sucking alone at least under ordinary circumstances; and the economic importance of this species arises chiefly from its early-season transmission of the rice dwarf virus, an important disease of the rice plant.

SOURCE OF DATA

The Field

A fixed plot of paddy field having the area of about 250 m² (11 m × 23 m) was used for the routine population census. The planting and subsequent cultural management were performed in accordance with a standard procedure in this district except that no pesticides were applied throughout the year. The whole plot contained the regularly spaced 4250 hills of rice plants (variety Hôyoku) each originating from several 35-day-old seedlings planted on June 28 every year. The plants were harvested early in

November.

Census Methods

The routine census of population density was conducted throughout the rice-growing season (July — October). The sampling unit adopted was a hill of rice plant. The hills to be sampled on each census date were determined systematically so as to disperse them evenly over the whole plot. For the initial population which consists exclusively of invading adults, 500 or more hills usually were examined each time at 5 days intervals during July by means of direct counting in the field. In the later generations where the leafhoppers increase in number and the plants grow large in size, the sample size was reduced to 50; and the census was made by using a suction machine with 1h. p. gasoline engine in such a way that nearly all the leafhoppers (including both nymphs and adults) on each hill could be collected. The samples thus obtained were brought back to the laboratory, dried in an incubator, and then examined under binocular microscope to count the number for each species. This census covered the period from late July to late October at intervals of 7-12 days.

By statistical examination of all the data thus obtained, it was proved that in either of the two species the standard error for population estimation ranges in most cases from some 10 to 30% of the mean at the time of peak density for each generation. The level of precision in our data therefore seems to be satisfactory for the purpose of detecting the basic features of population dynamics.

FEATURES OF POPULATION CHANGES

Method of Analysis

In multivoltine insects like these leafhoppers, the populations at different generations within a year are subjected to different environmental conditions (weather, physiological stage of the host plant, natural enemies, etc.). In this sense, a given seasonal generation for such insects may be analogous to a given developmental stage for univoltine species. In view of this, we analyzed the pattern of population changes from the two different angles; the seasonal generation-to-generation changes for each year and the year-to-year fluctuation for each seasonal generation.

Fig. 1 shows a typical pattern of seasonal prevalences in the paddy field for *Nephotettix* and *Nilaparvata* on the basis of our 8-year data. It is evident that in the field both species have usually three (and a partial fourth occasionally) generations after their initial invasion though in *Nephotettix* the majority of the last generation do not give rise to adults in that year owing to the onset of nymphal diapause in autumn. These generations are in most cases fairly discrete with each other. For convenience, they are called here simply as the first (G-I), second (G-II) and third (G-III) generations in order of succession, regardless of the generations passed before the invasion into paddy field. Also, we use the term "initial generation" or G-O to indicate the initial invading population from which the first generation ensues.

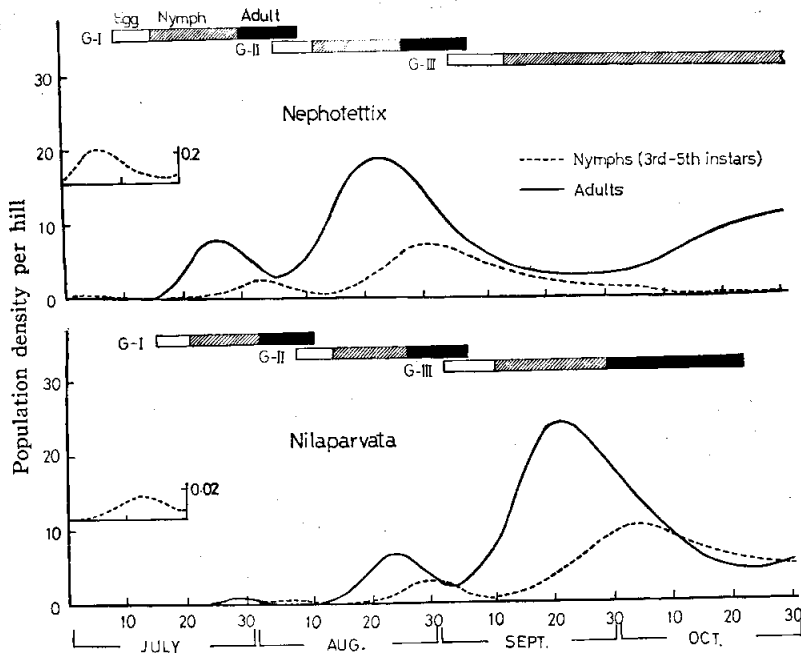


Fig. 1. Typical pattern of seasonal prevalences in the field during the rice growing season.

By examining the census data for individual years, it was found that in both *Nephrotettix* and *Nilaparvata* the time of peak incidence for each of these successive generations varies from year to year to lesser or greater extent, depending largely on the two factors; the time of incidence of G-0 adults and the trend of temperature during subsequent periods of the season. On the basis of this fact, we plotted the population trend for each year not on the calendar date but on the physiological time in terms of accumulated amount of day-degrees above 12°C from July 1 on, and then adopted the procedure shown in Fig. 2 to calculate the representative population density (as the sum of 3rd-5th instar nymphs and adults) for each generation. The value of D , the amount of day-degrees necessary for the completion of both egg and nymphal stages, for use in this calculation (see Fig. 2) was estimated by regression analysis of the experimental data that had been obtained under natural temperature conditions; it was 292 for *Nilaparvata* and 332 for *Nephrotettix*, when the threshold temperature for development was fixed for convenience as 12°C . As the value of L which represents the time-lag between the respective peaks for emergence and oviposition, we used a tentative value of 100 day-degrees for both species, since there were no data available for its concrete estimation. The time of peak incidence for the initial invading generation was determined by the eye from the incidence curve for that year. The population estimates thus obtained for individual generations were then transformed to logarithm for the following quantitative analyses.

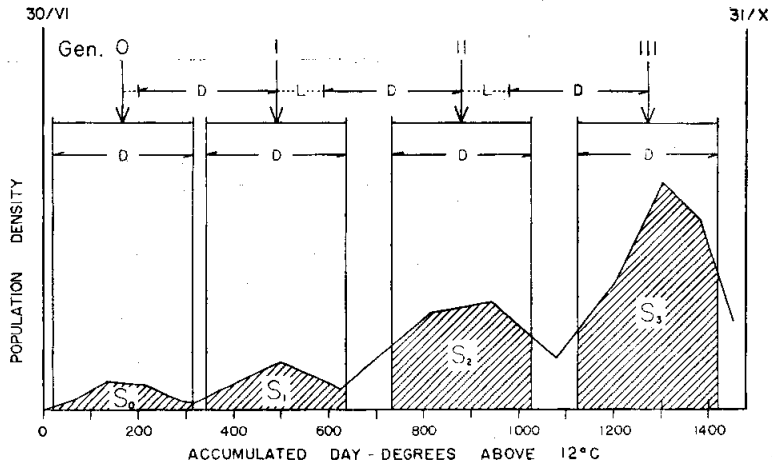


Fig. 2. Illustration of the procedure to calculate the representative population density for each of the successive seasonal generations. D: The amount of day-degrees above 12°C necessary for the species concerned to complete the whole immature period; L: The amount of day-degrees corresponding to the time-lag between the peaks of emergence and oviposition. The density for the i th generation is calculated as $P_i = S_i/D$.

Pattern of Seasonal Population Changes

The 8 years' average of the log population density for each of the four successive generations (G-O—G-III) was plotted in Fig. 3 (solid line). The pattern of seasonal

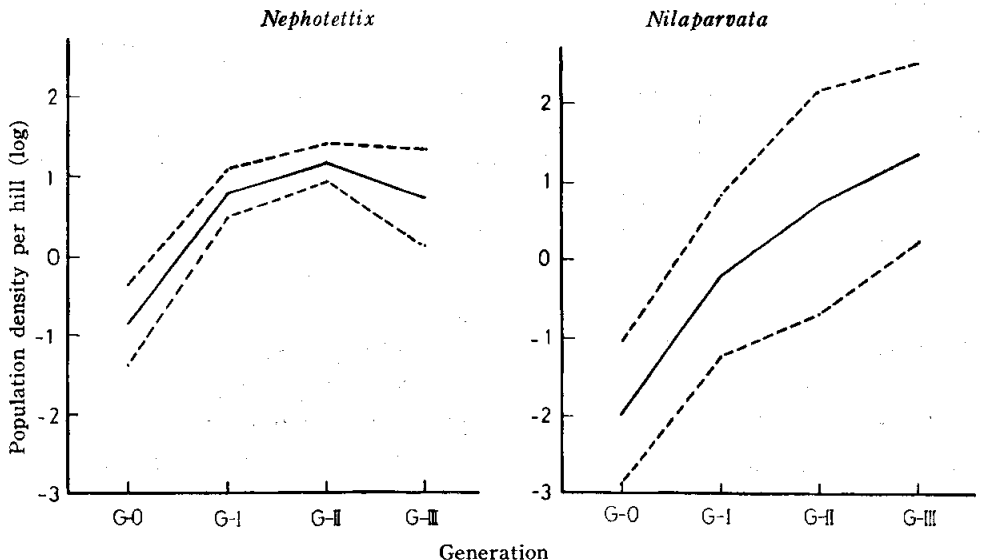


Fig. 3. Basic pattern of the seasonal generation-by-generation trends of population density (solid line) and the magnitude of annual population fluctuation at each generation (broken lines). The former is based on the annual average of population density for the 8-year period, and the latter, on the range of mean ± 2 S.D. (S.D.: standard deviation).

population changes apparently shows a clear difference between the two species concerned. Particularly, it is worthy of note that the maximum population density within a year is attained at G-II and G-III in *Nephotettix* and *Nilaparvata*, respectively, each of which we refer to hereafter as the "peak generation" or G-P for each species.

To analyze the pattern of population growth in the paddy field, let us first formulate it as

$$P_p = P_0 R_p = P_0 r_1 \cdots r_p$$

or

$$\log P_p = \log P_0 + \log R_p = \log P_0 + \sum_{i=1}^p \log r_i \quad (1)$$

where P_p = population density at the peak generation; P_0 = population density at the initial generation; R_p = overall rate of population growth from the initial to peak generation; r_i = rate of reproduction from the $(i-1)$ th to i th generation (P_i/P_{i-1}); p = number of generations passed until the peak generation (*i. e.*, $p=2$ in *Nephotettix* and $=3$ in *Nilaparvata*).

Table 1 presents the antilog mean values of the variables in (1). Although the values of \bar{P}_p (mean population density at the peak generation) for both *Nephotettix*

Table 1. Mean values of the variables in formula (1) to characterize the pattern of seasonal population growth as the annual average. The values are shown as antilogarithms.

	\bar{P}_p	\bar{P}_0	\bar{R}_p	\bar{r}_1	\bar{r}_1^*	\bar{r}_2	\bar{r}_3
<i>Nephotettix</i>	15.20	0.138	109.7	44.5	7.84	2.47	—
<i>Nilaparvata</i>	19.51	0.0105	1855	55.7	15.4	8.50	3.92

* The value of \bar{r}_1 corrected to make it comparable with \bar{r}_2 or \bar{r}_3 ($r_1' = r_1 \times (\text{proportion of adults in } P_1)$).

and *Nilaparvata* are of similar level, there are remarkable differences between both species in the values of the independent variables composing it. The mean population level at the initial generation (\bar{P}_0) in *Nephotettix* is higher by more than 10 times than that in *Nilaparvata*; but, instead, the overall rate of subsequent population growth (\bar{R}_p) of the former is less than one-tenth as low as that of the latter. Comparison of either \bar{r}_1 or \bar{r}_2 indicates that the population of *Nephotettix* is less prolific than that of *Nilaparvata* irrespective of the generation. Meanwhile, it is a common feature for both species that the rate of reproduction is highest at the initial generation and gradually decreases thereafter. This means that the contribution of the reproduction early in the season to the overall population growth rate is considerably great in either of the two species.

Pattern of Annual Population Fluctuation

The value of standard deviation (square root of variance), *S. D.*, based on the log-transformed population density for each year can be used as an adequate measure

of the magnitude of year-to-year population fluctuation at each generation, because it is directly comparable to $C.V. (=s/m)$ for the untransformed density and hence is free from the effect of population level. The range for mean $\pm 2 S.D.$ calculated from the 8-year data are shown in Fig. 3 (broken lines) for each of the successive generations. It is apparent that in all the generations from G-O to G-III the population of *Nephotettix* is much more stable from year to year than that of *Nilaparvata*. For example, the actual ratio of the highest to the lowest year during 1961-1968 was only 2.4 for the second or peak generation of the former, whereas in the latter this ratio amounted to 90.6 for the same generation. It thus became evident that the magnitude of annual fluctuation is another fundamental feature to characterize each species' population beside the basic pattern of seasonal changes mentioned before.

In Fig. 4 the year-to-year trend of the population density at the peak generation for each species is shown in relation to the trends of its individual components in formula (1). By this graphical presentation we attempted to evaluate the relative importance of each of these components upon the resultant population fluctuation at the peak generation. This procedure is comparable to VARLEY and GRADWELL (1960)'s method of key factor analysis proposed for life table studies. In the case of *Nilaparvata*, it will be recognized from the figure that the population level at the third or peak generation is governed primarily by P_0 , the population level at the initial invading generation, and secondarily by R_p , the overall rate of subsequent population growth, in each year. In fact, the value of the coefficient of determination, r^2 , (r : correlation

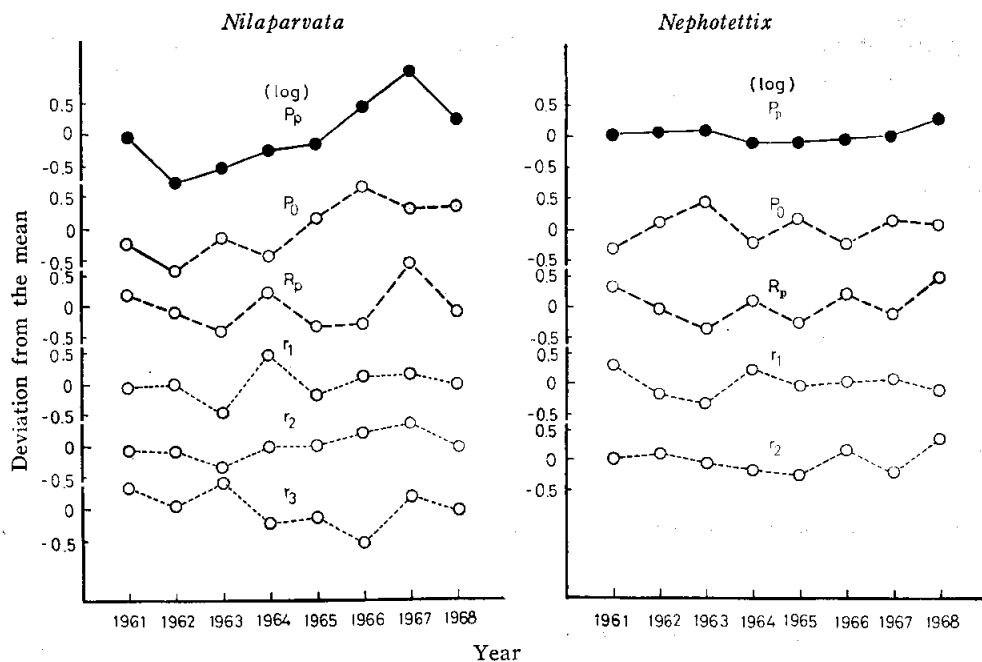


Fig. 4. Graphical comparison of annual fluctuations for the population density at the peak generation (solid line) and its components in formula (1) (broken lines).

coefficient with P_p) was 0.58 for P_0 , and was 0.36 for R_p , indicating that P_0 and R_p account for some 60 and 40%, respectively, of the variation in density at G-III, the peak generation. Comparing the fluctuation of R_p with that of each of its three components r_1 , r_2 and r_3 , we find that r_1 or the reproduction rate from the initial to first generation most significantly correlates with R_p , though both r_1 and r_2 also vary to some extent from year to year. It thus may be stated as an important suggestion

Table 2. Correlation of the population densities (log) between different seasonal generations of the same year.

	<i>Nilaparvata</i>			<i>Nephotettix</i>		
	G-I	G-II	G-III	G-I	G-II	
G-O	0.849	0.798	0.761	G-O	0.574	0.309
G-I		0.986	0.854	G-I		-0.169
G-II			0.889			

for the population forecasting of *Nilaparvata* that the level of its population at the third or peak generation in a given year has been largely determined by early August, the time of occurrence of its first generation. This will be numerically confirmed from Table 2 where the correlation of population densities between different generations was examined. On the other hand, in *Nephotettix* neither P_0 nor R_p shows any apparent correlation with P_p , the values of r^2 being 0.10 and 0.04, respectively. Obviously this is because R_p fluctuates in such a way that it almost completely compensates the annual variation of P_0 to yield remarkable stability in P_p . Also, we cannot find out any distinct difference between r_1 and r_2 with respect to their degrees of contribution to the fluctuation of R_p . These facts for *Nephotettix* result inevitably in rather low degrees of correlation between the population densities of different generations (see Table 2). It should be noted that such apparent invalidity of the result for this species arises from the mutual dependence among the individual components of P_p , and that in such a case, as MOTT (1966) stated, the assessment of their relative importance on the basis of correlation becomes rather problematical. By examining Fig. 4 in detail, one might suggest the existence of similar phenomenon, though being far less conspicuous, in the case of *Nilaparvata* also. It seems that such mutual correlation among the individual components of P_p is of ecological importance in itself, because it may have some close relation to the nature of population changes in terms of the density-dependent population regulation which will be analyzed below by different approach.

Natural Regulation of Population Density

Following SOLOMON (1964)'s definition, we mean here by "population regulation" the stabilization of population density through density-dependent processes. The simplest, straightforward method for detecting the existence of regulatory processes that is applicable to multivoltine species like these leafhoppers will be to compare the magnitude of annual population fluctuation among successive seasonal generations within a year; the smaller magnitude of fluctuation at a given generation than at

the preceding one may indicate the existence of regulatory process in the relevant period. The theoretical basis of this method is that, since the log population density at a given generation is the sum of both the density at the preceding generation and the rate of subsequent reproduction ($\log P_i = \log P_{i-1} + \log r_i$), the variance also is expected to increase from the preceding to the current generation by the amount corresponding to the variance of the log reproduction rate if the reproduction proceeds independently of the population density. Examining Fig. 3 on the basis of this criterion, we can suggest the existence of population regulation for the following three cases; the reproduction from G-O to G-I and from G-I to G-II in *Nephotettix* and that from G-II to G-III in *Nilaparvata*.

Population regulation or stabilization as detected above is of course the outcome of the density-dependence in reproduction. This is clearly shown in Fig. 5 where the reproduction rate from a given generation to the next was plotted against the population density at the former for each of the three successive generations, G-O, G-I and G-II. Namely, in *Nephotettix* there consistently exists a strong tendency for the reproduction rate to decrease with increasing population density in the whole

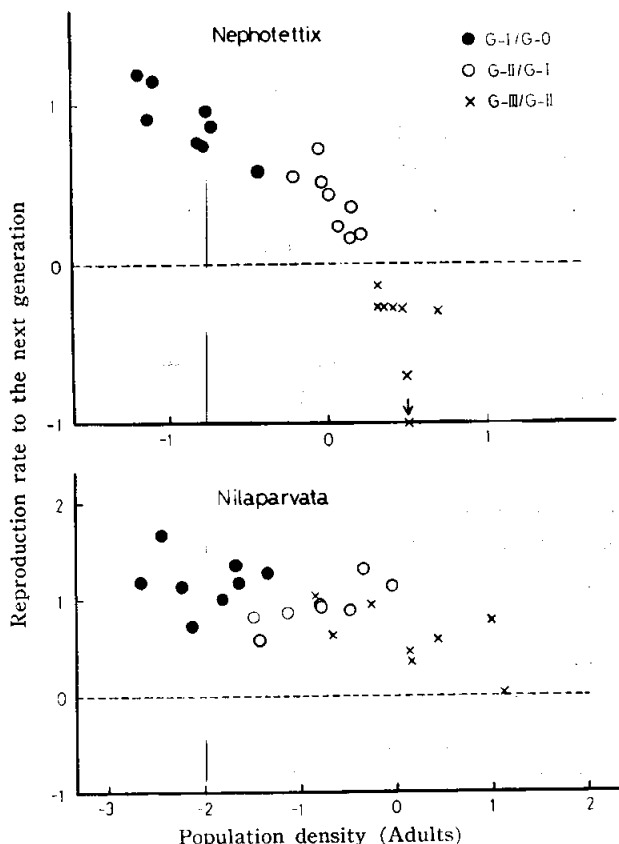


Fig. 5. Relation of the rate of reproduction to the population density for each of the successive seasonal generations (log).

process of population growth from G-O to G-II, the peak generation of this species; but, in contrast to this, we cannot find for *Nilaparvata* any such tendency in these earlier generations, and the density dependence can be seen only in the reproduction from G-II to G-III. For statistical examination of these results, we adopted the test proposed by MORRIS (1963) by using the value of the slope b in the regression of log population density at a given generation on that at the preceding one. As seen in Table 3, the result gives numerical confirmation to the above conclusion from Fig. 5, the b -values being fairly smaller than unity in all the above-mentioned three cases. We may also note from the last column of Table 3 that while in *Nephotettix* the overall rate of population growth from the initial to peak generation eventually shows strong dependence on the density at G-O, such is not the case with *Nilaparvata*.

Table 3. Values of the slope b (with the confidence interval for $P=0.95$) in the regression equation for log population densities between successive seasonal generations for detecting population regulation.

	G-I/G-O	G-II/G-I	G-III/G-II	G-P/G-O
<i>Nephotettix</i>	0.308 ± 0.438	-0.158 ± 0.923	0.103 ± 2.410	0.155 ± 0.477
<i>Nilaparvata</i>	0.968 ± 0.602	1.344 ± 0.228	0.710 ± 0.365	0.946 ± 0.805

G-P: Peak generation for each species (=G-II in *Nephotettix* and =G-III in *Nilaparvata*).

In order that the above results be statistically valid, the sampling error in population estimation at each generation should be sufficiently small relative to the net magnitude of year-to-year population fluctuation, or at least be roughly of the same level for different seasonal generations. This requirement proved to be generally satisfied in our present data for either of the two species (KUNO 1968).

The next problem is to assess the equilibrium population level in each species towards which the regulatory process as detected above is at work. Tentatively, this level can be estimated from the regression equation between the population densities for both the peak generation and the preceding one by putting both the variables equal to each other. The equilibrium density thus obtained was 13.5 in *Nephotettix* and 572 in *Nilaparvata*, each expressed as the antilog value of the total number of both adults and 3rd-5th instar nymphs per hill. These estimates may not themselves be fully reliable on account of the probable error due to extrapolation, but at least it is evident that the equilibrium level of *Nephotettix* population is much lower than that of *Nilaparvata*'s.

It thus may be concluded that: (1) In either of the two species, *Nephotettix* and *Nilaparvata*, there exists a distinct process of natural regulation of population density. (2) But there is a wide difference between both species with respect to the consistency in the action of regulatory process; namely, in *Nephotettix* population regulation occurs far more consistently than in *Nilaparvata* as a result of the much lower equilibrium population level in this species.

INTERPRETATION OF THE FEATURES IN RELATION
TO THE FACTORS THAT DETERMINE THEM

Next to the comparative description of the pattern of population changes for both *Nephotettix* and *Nilaparvata*, we shall assess here how such distinct differences between the two species as revealed above could be brought about, although the data available for us are as yet insufficient for full explanation of the processes involved.

Rate of Reproduction and Its Seasonal and Annual Variations

Generally, the rate of reproduction in each generation is determined by the four components; (1) potential fecundity characteristic of the species, (2) proportion of the fecundity realized in the field, (3) percentage hatching of eggs deposited, and (4) survival rate of nymphs from hatching till emergence as adults.

It has already been shown by KUNO (1968) that *Nilaparvata* has much higher fecundity than *Nephotettix*. In the outdoor experiments using potted rice plants, the fecundity under confined condition amounted consistently to 800-900 eggs per female in *Nilaparvata*, but at best to some 400 in *Nephotettix*.

In these leafhoppers the longevity of adults, together with the daily rate of oviposition, is closely related to the actual fecundity realized in the field, because the females begin to lay eggs some days after emergence and the oviposition continues through rather long period thereafter. In 1968 we attempted to estimate the adult longevity in the census field for both the species by applying HOKYO and KIRITANI (1967)'s method which enables us to evaluate the natural daily survival rate on the basis of percentage incidence of the pre-mature females within a generation (see HOKYO and KUNO 1970; KUNO and HOKYO 1970 for details). Table 4 presents the result of estimation of the realized fecundity at the first generation of 1968 based on these data. It can be seen that in *Nilaparvata* the realized fecundity also is far higher than in *Nephotettix* by about 10 times, and that this is a combined result of both the longer life span of adults and the higher rate of daily oviposition.

Table 4. Estimates of the realized fecundity and related parameters for the field population (1968: G-I) based on HOKYO and KIRITANI's method.

	Pre-oviposition period (days)	Daily survival rate	Mean longevity (days)	Mean oviposition period (days)	Daily oviposition rate	Mean fecundity per female
<i>Nephotettix</i>	2.9 ^a	0.758	4.13	1.85	25.7	47.6
<i>Nilaparvata</i>	2.5 ^a	0.876	8.08	5.79	74.0 ^a	429.0

^a Determined experimentally by rearing adults on potted rice plants.

The survey of the egg and nymphal parasitism in the census field was conducted every year from 1965 to 1968. In Fig. 6 shown are generation-by-generation trends of the average value of total percentage of parasitism for each stage during this 4-year period. As the egg parasites of *Nephotettix*, two species of wasps were found;

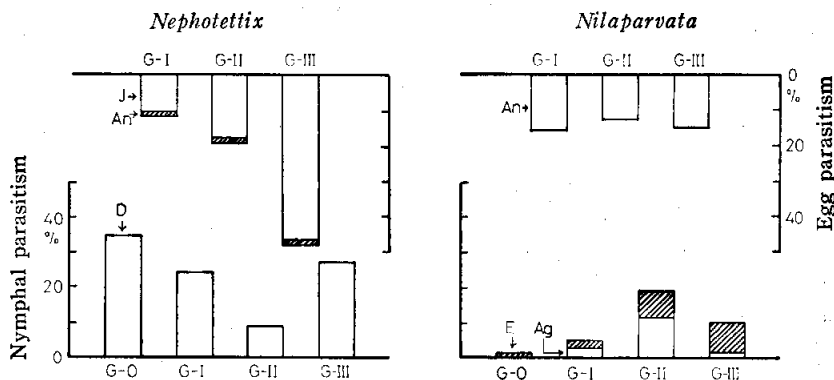


Fig. 6. Average percentages of parasitism in the egg and nymphal stages at each seasonal generation (1965-1968). J: *Japonia*; An: *Anagrus*; D: *Dorilaidae*; E: *Elenchinus*; Ag: *Agameremis*.

a trichogrammatid, *Japonia andoi*, and a mymarid, *Anagrus* sp., the latter being far less dominant than the former; and the total percentage of parasitism increased gradually from G-I (about 10%) towards G-III (about 50%). In the egg of *Nilaparvata*, *Anagrus* sp. was the only parasite detected; and the percentage parasitism remained low (12-15%) throughout the season (see Fig. 6). At the time of examining egg parasitism, those eggs that had died due to other causes were also observed sometimes in considerable percentages (particularly in *Nilaparvata*). It seems that several factors, such as infertility, predation by *Nabis* spp., and parasitism by some fungi or bacteria, are responsible for these deaths; but in this study we could not trace the real cause for individual cases. The nymphs of *Nephotettix* are parasitized by dorilaid flies (mainly *Alloneura orizaetora*), and those of *Nilaparvata* chiefly by both a Strepsiptera, *Elenchinus japonicus*, and a Nematoda, *Agameremis unka*. In either case, the parasites usually leave the host's body in its adult stage, and the parasitism results in sterilization of either sex of the hosts attacked. As seen in Fig. 6, the percentage of parasitism in *Nephotettix* shows gradual decrease from G-0 to G-II but increases again in G-III. Conversely, the percentage parasitism in *Nilaparvata* is very low at G-0, shows some increase towards G-II, and then decreases again in G-III. In both egg and nymphal stages, we can see from Fig. 6 that the population of *Nephotettix* suffers from the parasitism more heavily, as a whole, than that of *Nilaparvata*.

Both the nymphs and adults of these leafhoppers are attacked by a variety of predators also, of which several species of spiders such as *Oedothorax insecticeps*, *Lycosa pseudoannulata*, *Theridion octomaculatum*, and so on, are predominant in abundance. As KOBAYASHI (1961) and Itô *et al.* (1962) showed on the basis of their studies on the after-effect of insecticidal application upon insect pests of rice, their total pressure against the population growth of either species seems to amount, on the average, to fairly high degree every year, though we could not evaluate here it numerically.

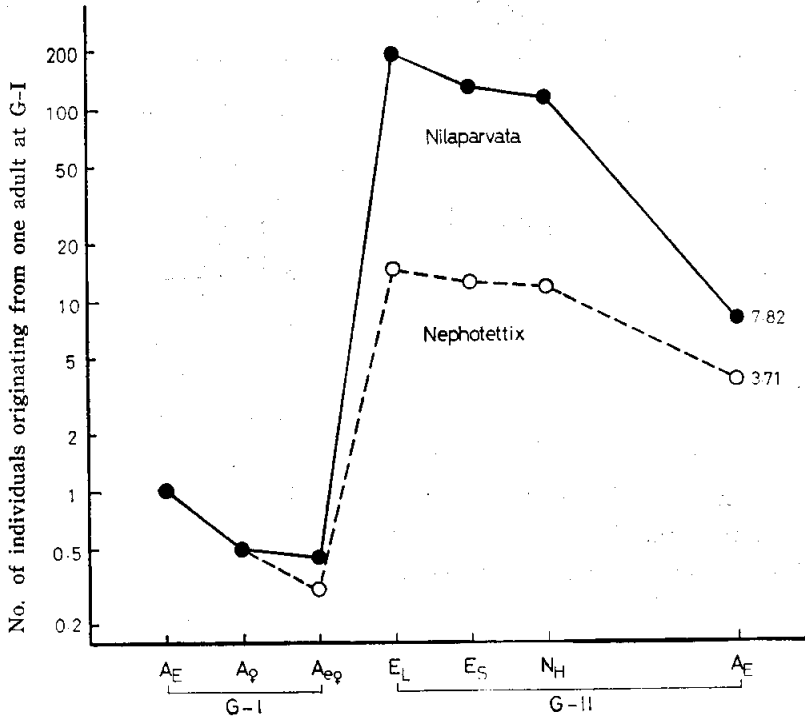


Fig. 7. Comparison of the reproduction-survivalship curve from G-I to G-II of 1968 in the field between the two species. A_E: Adults emerged (being put as 1 for G-I); A_♀: Female adults emerged; A_♀: Effective or unparasitized females; E_L: Eggs laid in the field; E_S: Eggs survived; N_H: Nymphs hatched (=E_S-Eggs parasitized).

As an example for comparative illustration of the process of reproduction, Fig. 7 shows the reproduction-survivalship curve from G-I to G-II obtained in 1968 for both species. This is based on the two kinds of data mentioned before; one from the analysis of adult survival by HOKYO and KIRITANI (1967)'s method for estimating the total emerging population and the fecundity realized in the field (e.g. Table 4; see also HOKYO and KUNO 1970; KUNO and HOKYO 1970, for details), and the other from the survey of the egg and nymphal parasitism in the field. Obviously, there is a notable difference between the curves for both species: The curve for *Nilaparvata* comes above that for *Nephrotettix* at A_♀ (effective or unparasitized female adults) owing to the lower percentage of nymphal parasitism in this species; at the subsequent step to E_L (total eggs laid), this difference is enlarged further by its much higher fecundity realized in the field (see Table 4); and then it is reduced again by the lower survival rate for nymphal stage in this species, though the curve still maintains the level being nearly twice as high as that for *Nephrotettix* at the last step, A_E for G-II, representing the net reproduction rate from G-I to G-II.

From the results described above, it may be said that, in comparison with *Nephrotettix*, the high rate of population growth characterizing *Nilaparvata* is the

combined result of high original fecundity, high proportion of the fecundity realized in the field and low percentages of parasitism in both egg and nymphal stages, which compensates more than enough for its rather low survival rate in the nymphal period.

As shown before (Table 1), the reproduction rate in both species has a general tendency to decrease with the progress of generation. This may largely be explained by the fact that the habitat conditions for both reproduction and survival of these leafhoppers become increasingly unsuitable towards later period of the season as a combined result of both the seasonal maturing of the host plant and the increase of population density. In *Nilaparvata* whose adult has two wing-forms, brachypterous and macropterous, it was found that the proportions of both forms change seasonally with the following pattern: The adults of G-O are the immigrants from the outside, and hence composed exclusively of macropterous individuals; but at G-I most of the females are of brachypterous form, and the proportion of this form in females gradually decreases towards G-III (see Fig. 10). This clearly reflects such gradual deterioration of the habitat conditions as mentioned above.

The magnitude of annual fluctuation of population growth rate may in the first place depend upon the sensibility of that population to the annual variation in environmental conditions of the habitat. In the case of *Nilaparvata*, we have already shown that r_1 or the reproduction rate from the initial to first generation most critically correlates with the fluctuation of R_p (overall rate of population growth till the peak generation) (see Fig. 4); it therefore may be stated that the large magnitude of fluctuation of R_p in this species arises largely from the high sensibility or vulnerability of its population to varying environmental conditions of the paddy field during such an early period of the season. As shown later (Figs. 8 and 9), it is considered that neither the parasites nor the predators are responsible for such a large annual variation in the rate of population growth. Accordingly, it may be reasonable to consider that the "key factor" for annual variation of R_p in this species is either direct or indirect effect of the weather conditions early in the rice-growing season, though the definite causal pathway concerned remains yet unknown.

Another important causal component of the variation of population growth rate will be the intensity of the tendency for population regulation. In fact, as shown before (Fig. 4), R_p for *Nephotettix* fluctuates in such a way that it compensates the annual variation of P_0 , the level of initial population. Thus, it would be impossible to give full explanation to the remarkable stability of *Nephotettix* population at its peak generation, unless such strong density-dependence in the reproduction of this species is concurrently taken into consideration in addition to its low sensibility to varying environmental conditions.

Processes of Population Regulation

There are two kinds of processes that are capable of causing density-dependent changes in reproduction rate: the attack by natural enemies and the intra-specific

competition or interference. We shall first examine the mode of action of the parasites and predators upon the populations of these leafhoppers in relation to their overall possibility of regulating the prey populations.

The result of analysis of the parasites' mode of action is given in Fig. 8 on the basis of log rate of survival from parasitism. Left graphs of the figure illustrate to what extent the annual variation in R_p , the overall rate of population growth, can be accounted for by either individual or total action of the egg and nymphal parasites. It may be apparent that in either of *Nephotettix* and *Nilaparvata* the effect of parasitism as a whole is rather stable from year to year relative to R_p , and as a result cannot explain most part of the annual variation in R_p . The right graphs show annual trends of the intensity of attack by these parasites in each of the three cases where regulation was detected (two for *Nephotettix* and one for *Nilaparvata*) in relation to those of

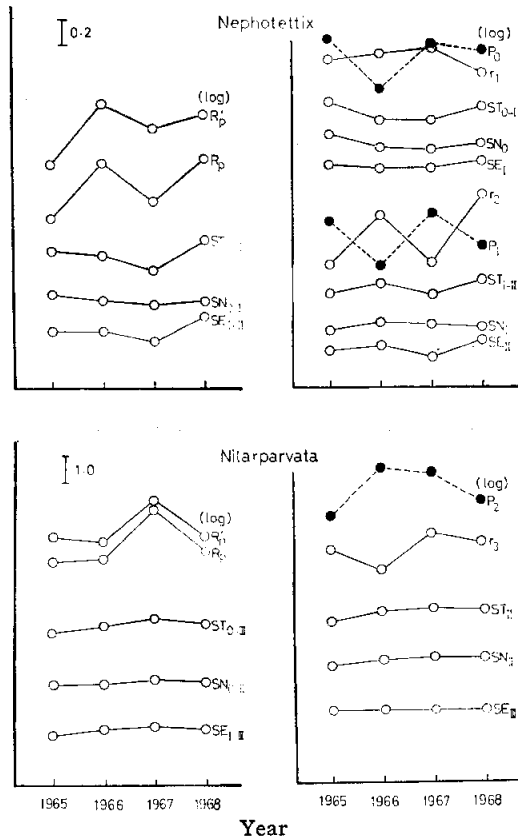


Fig. 8. Annual fluctuation of the rate of survival from parasitism (\log) in relation to the fluctuation of reproduction rate. ST: Total rate of survival from both egg and nymphal parasites; SN: Rate of survival from nymphal parasitism; SE: Rate of survival from egg parasitism (For example, $SE_I = SE$ at G-I; $ST_{0-II} = SN_0 \times SE_I \times SN_I \times S_{RII}$). R_p' indicates the value of R_p after all the effects of parasitism were eliminated (For example, R_p' for *Nephotettix* = R_p / ST_{0-II}).

the population density at the preceding generation. The only case that shows density-dependent changes is the egg parasitism at G-I for *Nephotettix*; but even in this case the variation remains far from sufficient to account for the overall fluctuation of r_1 . It thus may be concluded that the parasitism cannot be the main factor causing population regulation in either of the two species concerned.

With respect to the effect of predation by spider populations, we have no data available for its direct evaluation; but the fundamental mode of their action can be assessed indirectly by analyzing the census data for the spiders that were concurrently obtained in the routine sampling for leafhopper populations. As mentioned before, several species of spiders simultaneously occur in paddy field, and their total population gradually increases towards autumn. For quantitative analysis of the relationship between spiders and leafhoppers, we took the period from July 20 to October 25 and divided it into three subperiods, July 20–August 15 (period I), August 16–September 15 (period II) and September 16–October 25 (period III), which roughly correspond to G-I, G-II and G-III for the leafhoppers, respectively. Then, following the procedure similar to that adopted before, we calculated the representative population density of the spiders as total of all the species detected (including both young and adults) for each of these three periods of each year, and plotted it in Fig. 9 against the total population density of the four species of leafhoppers (sum of 3rd–5th instar nymphs and adults) for the corresponding period. It can be seen from Fig. 9 that: (1) In period I there is no distinct numerical correlation between the densities of predator and

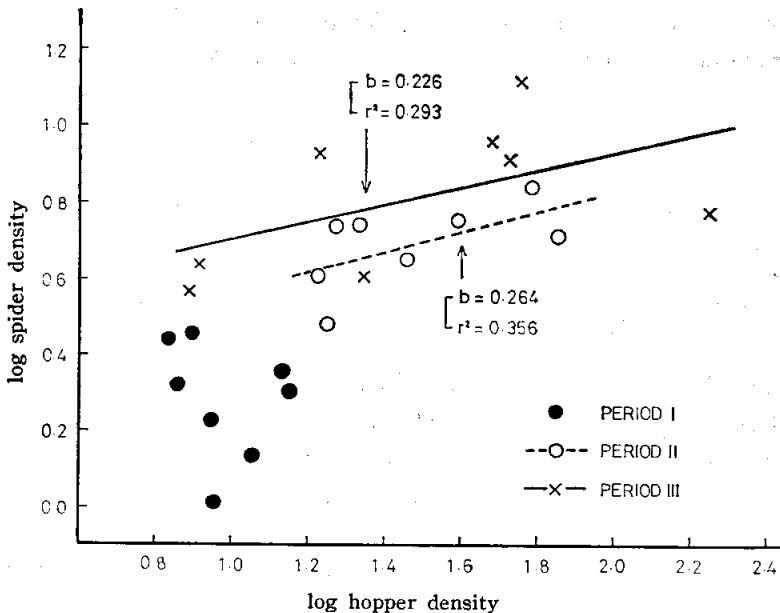


Fig. 9. Relation of the total population density of spiders to that of leafhoppers for different years. Period I: July 20–August 15; Period II: August 16–September 15; Period III: September 16–October 25.

prey populations; (2) In periods II and III, however, the former shows a notable tendency to increase with the latter; and (3) The slope b in the regression of predator density to prey density takes the value considerably lower than unity in either case of these two periods. The first of the above findings indicates that initial invasion of spiders into paddy fields occurs independently of the density of prey populations existing there at that time; while the second, that the rate of subsequent growth in the spider population depends more or less on the density of leafhoppers as the prey. The third finding, on the other hand, clearly shows that this "numerical response" of predator population to prey density is by no means linear but of "saturation" type, and hence that the mortality imposed on the leafhopper population by these spiders is fundamentally "inverse density-dependent". Obviously, this is because the spiders can neither propagate nor disperse themselves with such a high rate as to allow them the prompt correspondence to rapid population changes in the leafhoppers. In fact it is known that all these spiders require much longer periods than the leafhoppers to complete one generation (KOBAYASHI 1961). In addition to this fundamental limitation, their habit as polyphagous predators may result in a further reduction in the effectiveness of predation as a controlling factor for individual prey species. It thus may be said that the spiders, as well as the parasites, cannot act as the influential regulator of the leafhopper populations, nor as the key factor for their annual fluctuations, whatever considerable losses may they cause *on the average* against the latter. A further confirmation to this may be given by Table 6 which shows that in either case of *Nilaparvata* and *Nephotettix* there is a positive, instead of negative, correlation between the overall rate of population growth till the peak generation and the average density of total spider population during the corresponding period.

Table 5. Relation of the overall rate of population growth (R_p) (in log) to the average density of total spider populations during the corresponding seasonal period (in log).

	Corresponding period	Correlation coefficient
<i>Nephotettix</i>	Periods I-II	0.817
<i>Nilaparvata</i>	Periods I-III	0.423

We are thus led to the conclusion that in either of the two species the natural regulation of population density here detected may be largely attributable to the intra-specific competition or interference. As shown before, there is a wide difference between both species in the population level about which regulatory processes are in operation. This fact clearly indicates that the contents of intra-specific mechanisms leading to population regulation are quite different between these two species.

According to our experimental results using potted rice plants (HOKYO and KUNO in preparation), the carrying capacity of the plant in August for *Nephotettix* population amounts to more than several hundreds per hill (as the number of emerging adults).

It is therefore evident that the actual level about which the population is regulated (see Fig. 3) is far lower than the absolute capacity of the host; even in 1968, the highest year, the population level at its second or peak generation is less than one-tenth as low as the carrying capacity, being about 35 individuals per hill as emerging adults (see Table 6). In such a situation, deaths due to the direct effect of competition are not likely to occur and hence may not explain the density-dependent reduction of reproduction rate at all. Support to this is given by Table 6 where the width of head capsule in adults of G-II was compared between the individuals collected from the field and those experimentally reared on potted rice plants at different parental densities: The head-capsule width for the field population did not significantly differ from the values for the experimental ones at parental densities 3

Table 6. Comparison of the width of head capsule between field and experimental populations (1968: G-II). The latter was reared on potted rice plants under confined, outdoor condition.

		Eggs laid per hill	Adults emerged per hill	Percen- tage emerged	Head-capsule width in adults (mm; $\times 20$)	
					female	male
Experimental population	A	108	137	(100)	29.57 \pm 0.12 ^a	24.89 \pm 0.09 ^c
	B	306	251	82	29.41 \pm 0.15 ^a	24.90 \pm 0.13 ^c
	C	801	461	58	28.72 \pm 0.11 ^b	23.67 \pm 0.13 ^d
Field population		136	35*	26	29.34 \pm 0.17 ^a	24.45 \pm 0.16 ^c

* Estimated by HOKYO and KIRITANI's method.

Note: A, B and C for experimental population indicate parental densities 3, 9, and 27, respectively, each with two replications. The values of head-capsule width shown are averages of 50 individuals with the confidence intervals for $P=0.95$. Different letters attached indicate significantly different values ($P=0.05$).

and 9 where the nymphal mortality remained low; but it was significantly larger in either sex than the value for parental density 27 in the experimental population at which the nymphal mortality due to crowding was rather high. It is noted that the data compared here are those that were taken in 1968 when the population density at G-II was highest during the 8 years. It therefore may follow that the regulation of population density in *Nephotettix* is brought about principally by the density-dependent changes of realized fecundity (including the effect of dispersal) due to direct or indirect interference among adults. The finding that the proportion of the fecundity of this species realized in the field is fairly low (see Table 4) seems to indicate the reality of this inference. Also, in a previous paper (HOKYO and KUNO 1970) we have already obtained the data directly suggesting that the apparent longevity of adults in the field tends to decrease with increasing population size of emerging adults.

The population regulation in *Nilaparvata*, on the other hand, is rather easy to interpret, since in this case equilibrium population level proved to be high enough to cause considerable deterioration of the host plant conditions and in fact it was

detectable only in the reproduction from G-II to G-III when the density could attain fairly high levels. One of the probable mechanisms for population regulation in this species is the varying proportions of different wing-forms among parental adults, because most of the macropterous females that emerged in the field become emigrants and do not participate in the reproduction at that place. The left graph of Fig. 10 shows the relation of the apparent percentage of brachypterous form in female adults to the population density (as sum of 3rd–5th instar nymphs and adults) at that generation on the basis of the 8-year data. It can be seen that the year-to-year variation of the percentage of brachypterous females for G-II, as well as that for G-III, is clearly

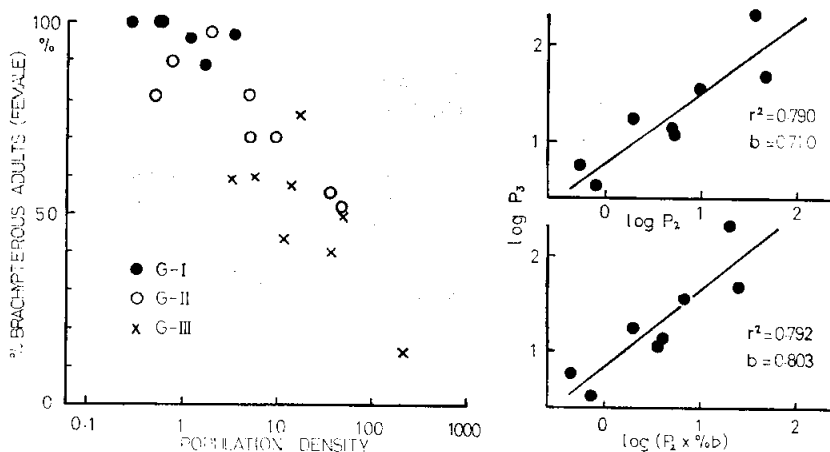


Fig. 10. Relation of the percentage of brachypterous females to the population density at that generation for different years (left) and evaluation of the role of this factor as a regulatory mechanism (right) in *Nilaparvata lugens*.

density-dependent. In the right graphs of the same figure, we examined to what extent this factor contributes to the density-dependent changes of r_3 , the reproduction rate from G-II to G-III, following the method of MORRIS (1963). Apparently, removal of the effect of this factor by replacing the original independent variable ($\log P_2$) by $\log (P_2 \times \%b)$ ($\%b$: % of brachypterous females at G-II) did not cause notable change on the value of r^2 , the coefficient of determination in the regression; but it resulted in some increase in the slope b (from 0.71 to 0.80). This indicates that the density-dependent variation of $\%b$ at G-II cannot be a key factor for explaining the annual variation of r_3 , but that it apparently makes some contribution to the regulatory process involved. However, it should be noted also that the slope b still took the value somewhat lower than unity even after the effect of $\%b$ was eliminated; this suggests the concurrent existence of other mechanisms for population regulation. Consequently, it may be reasonable to consider that the population regulation in *Nilaparvata* is brought about by the combined action of three mechanisms; increasing proportion of macropterous adults or emigrants, decreasing fecundity in the remaining adults,

and decreasing rate of survival in the ensuing nymphs, with increasing population density.

COMPLEMENTARY INFORMATION ON OTHER ASPECTS OF POPULATION DYNAMICS

The foregoing descriptions have been concerned with the specific population properties for each species as revealed by analyzing temporal changes of the mean population density over the field. In this section, the information on two other aspects of population dynamics is briefly discussed since it seems to help concrete interpretation of the dynamics and the processes involved. The first of these two aspects is the spatial structure of population which indicates the mode of existence of individuals within the whole habitat, and the second, the inter-species interaction or the influence of coexisting other species' population(s) upon the population behaviour of each species.

Spatial Structure of Population

The data on which our analysis of spatial distribution of the leafhopper populations are mainly based are those that were obtained from routine population censuses and expressed as frequency distributions of the number of individuals per hill of rice plant.

As described in detail by KUNO (1968), it was proved for both *Nephotettix* and *Nilaparvata* that: (1) Distribution of the initial immigrant populations has a general pattern being somewhat contagious but rather close to the random or Poisson distribution; and (2) In the later generations the distribution tends through reproduction to show marked departures from the Poisson towards the direction of aggregation and can be described most successfully by the negative binomial distribution.

Despite such similarity in the general type of distribution, there proved also to exist a notable difference between both species (except in the initial generation) when the quantitative property of distribution was compared in terms of the degree of aggregation. The parameter we adopted here to measure aggregation is C_A -index¹ ($= (\sigma^2 - m)/m^2$) proposed by KUNO (l.c.), which equals zero in the Poisson distribution and takes larger values with increasing degree of aggregation. Table 7 presents the weighted mean values of this index for the two species (for total counts of 3rd—5th instar nymphs and adults) in each of the 8 years from 1961 to 1968. On the basis of the finding that in these leafhoppers the value of C_A for a given species is relatively stable within the same year (KUNO 1963, 1968), we calculated its weighted mean for each year by BLISS and OWEN (1958)'s regression method to estimate the reciprocal of "common k " of the negative binomial. It is concluded from the table that the population of *Nilaparvata* consistently shows larger value of C_A , i.e. higher degree

¹ Formally, C_A is equivalent to $1/k$ in the negative binomial, but it can be used for any other types of distribution alike as a valid measure of aggregation (KUNO, l.c.).

Table 7. Weighted estimate of the C_A -index measuring aggregation ($C_A = (\sigma^2 - m)/m^2$) for each of the 8 years, 1961—1968.

	1961	1962	1963	1964	1965	1966	1967	1968	Annual average
<i>Nephotettix</i>	0.315 ±0.076	0.210 ±0.040	0.211 ±0.086	0.308 ±0.168	0.233 ±0.056	0.221 ±0.054	0.328 ±0.152	0.244 ±0.076	0.255
<i>Nilaparvata</i>	1.950 ±0.374	2.906 ±0.936	1.410 ±0.524	3.368 ±1.136	1.206 ±0.322	0.445 ±0.086	0.824 ±0.194	0.811 ±0.186	1.328

The values are given as mean \pm 2S.E. for total counts of both adults and nymphs (3rd—5th instars).

of aggregation than *Nephotettix*'s, though in either species (particularly in the former) the value tends somewhat to vary from year to year.

Obviously, this distinct difference in the spatial population structure indicates that the populations of the two species would necessarily be placed in quite different situations as to the actual status of crowding for individuals even when their mean densities are at the same level. To confirm this, the relation of mean crowding to mean density for the peak generation was shown in Fig. 11 for both *Nephotettix* and *Nilaparvata*. "Mean crowding" is the parameter proposed by LLOYD (1967) to represent

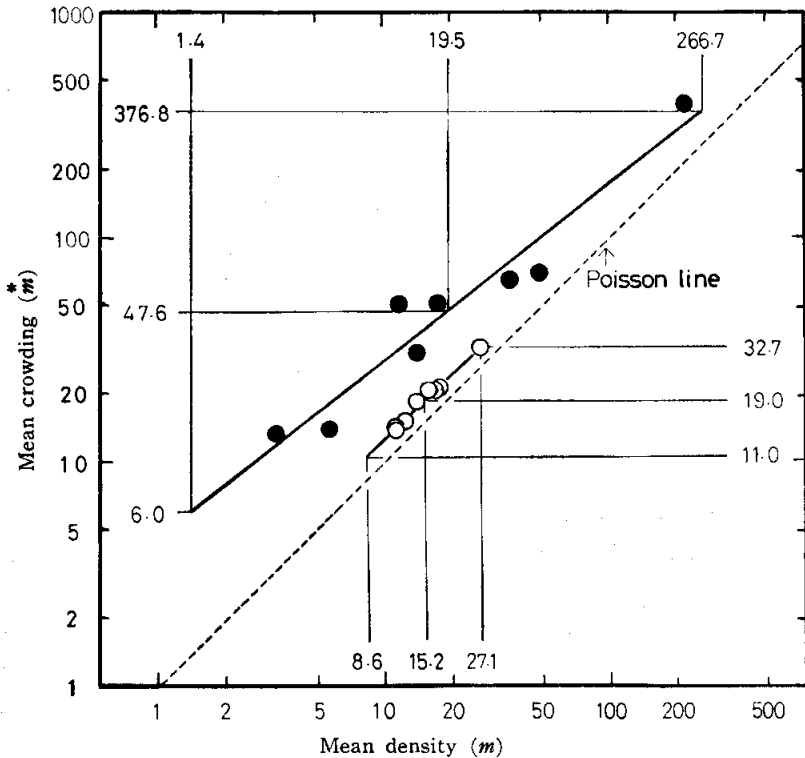


Fig. 11. Relation of mean crowding to mean density at the peak generation for each species for different years (—○—*Nephotettix*; —●—*Nilaparvata*). The range indicated by the regression line for each species corresponds to the range of annual average \pm 2S.D. for $m(P_p)$ obtained before (Fig. 3).

the mean number per individual of other individuals in the same quadrat, and is written as

$$\bar{m}^* = m + \frac{\sigma^2}{m} - 1 = m(C_A + 1)$$

As is evident from the definition, \bar{m}^* , unlike m itself, is an appropriate index to measure the absolute intensity of crowding for individuals. For calculating the value of \bar{m}^* for the peak generation of each year, we used here both the value of C_A in Table 7 and that of m obtained before for the analysis of temporal population changes. From Fig. 11 it can be seen that the actual intensity of crowding is remarkably higher in *Nilaparvata* than in *Nephotettix* over the possible ranges of annual fluctuation of m for both species. At the same density of 20 (per hill), for example, the mean crowding takes the values of about 50 and 25 in *Nilaparvata* and *Nephotettix*, respectively, the former being twice as large as the latter. In a preceding section, it has been shown that the equilibrium population level about which the density at the peak generation is regulated is much higher in *Nilaparvata* than in *Nephotettix*. In connection with this fact, Fig. 11 is of further interest as it indicates that this wide difference in the equilibrium density becomes enlarged still further if we use mean crowding, a more realistic index, instead of mean density to express the level. That is, the real difference of the tolerance for crowding between these two species is regarded to be still wider than is indicated by the comparison in terms of mean density.

As KUNO (1968) made clear with the aid of a simulation study using simplified models of the distribution-generating process, the low degree of aggregation in *Nephotettix* is the inevitable outcome of both the high population level at the initial generation and the high activity of individuals for dispersion during the later generations in this species, whereas quite reverse the situation is the case with *Nilaparvata*. To date we have no data for these leafhoppers to examine if the rate of dispersal of individuals from a given hill depends upon the local population density at that place. More important, however, will be the fact that the spatial dispersion tends by itself to homogenize or stabilize the local density over the whole habitat and hence may be called "regulatory" in its effect, regardless whether the process is really density-dependent or not. It thus may be concluded that *Nephotettix*, as compared with *Nilaparvata*, has a highly consistent tendency to regulate or stabilize its own population not only in time but also in space.

Interaction between Species

In paddy fields, the populations of both *Nephotettix* and *Nilaparvata* (and also the other two species here not concerned) do not live separately but almost invariably coexist feeding on the same food, the sap of rice plant. To know whether or not the behaviour of either species' population is notably influenced by the coexisting other species, we made two sorts of analyses. First, the relation of the overall rate of population growth (R_p) to the seasonal average of population density of the other species during the corresponding period of that year was analyzed. The result is

Table 8. Correlation of the overall rate of population growth (R_p) with the average density of coexisting other species' population(s) during the corresponding seasonal period.

log density of log R_p of	<i>Nilaparvata</i>	<i>Nephotettix</i>	3 species in total
<i>Nephotettix</i>	+0.290	—	+0.223
<i>Nilaparvata</i>	—	+0.190	+0.182

that in either case the correlation coefficient took positive, but rather low values of 0.2 or so (Table 8). Second, the correlation viewed from the aspect of spatial pattern was examined by analyzing the joint distribution of both species on the basis of COLE (1949)'s non-parametric index. As shown in Table 9, the correlation value tended to become positive rather than negative, but it was so low on the average that the situation virtually resembles the mutual independence.

Table 9. Frequency distribution of the value of COLE's correlation index for the joint distribution of *Nephotettix* and *Nilaparvata*, based on all the available data from routine censuses during the 8-year period.

Range of the index	-1.00	-0.80	-0.60	-0.40	-0.20	0.00	0.20	0.40	0.60	0.80	Total	Mean value
	~	~	~	~	~	~	~	~	~	~		
Frequency (No. of samples)	0	0	0	5	13	25	25	5	1	0	74	0.141

Note: In making the 2×2 table to calculate this index, we adopted here "whether or not the number of individuals in the unit (hill) concerned exceeds the median number for that sample" as the criterion for grouping the sampling units for each population into two classes, instead of "whether at least one individual is present there or not". By this treatment, the effect of mean density level on the value of the index will be reduced greatly.

Both these results indicate that: (1) There essentially exists little competitive or repulsive interaction between the two species, at least during the majority of the period for their population growth; and (2) In effect their populations behave rather independently of each other. The latter point will be recognized from Fig. 4 (p. 160) as well in which no distinct parallelism can be detected between both species in the annual trends of either P_0 or R_p ; and this evidently reflects the fact that the main factors governing the population changes are quite different between *Nephotettix* and *Nilaparvata*.

DISCUSSION

From the results outlined above, it has become evident that the two species of rice leafhoppers here concerned exhibit a striking contrast to each other in each of the fundamental features of their population dynamics. These differences may be summed up by saying that the population of *Nephotettix cincticeps* is kept far more stable or homogeneous than that of *Nilaparvata lugens* in both temporal changes and

spatial structure. To realize how widely both species differ in the population stability, it seems sufficient to compare the magnitude of year-to-year population fluctuation for each of them with those for a number of other insects that were presented by SOLOMON (1964) based on a variety of field population data. By this comparison one may find that the magnitude for *Nephotettix*, being only $\times 2.4$ for the 8-year period at the second or its peak generation, is smaller than that for any species there presented, whilst the comparable value, $\times 90$, for *Nilaparvata* indicates rather violent fluctuation in comparison with many of other insects.

The causal relation to account for this overall difference between the populations of both species has also become clear in some detail. Basically, the stability of a population is a reflection of the consistency of the action of regulatory processes in nature; so that much greater stability in the population of *Nephotettix* is explicable by the following two conditions both of which contribute together to the consistency of population regulation in this species: (1) Unlike the population of *Nilaparvata*, it is rather insensible to the annual variation in environmental conditions such as weather. (2) The population level about which regulatory or density-homogenizing mechanisms intensely operate is far lower in this species than in *Nilaparvata* because of its much weaker tolerance for crowding and much higher activity for spatial dispersion.

Seasonal behaviour of the populations of these leafhoppers during the period from late autumn to the next early summer which lacks the cultivated rice plant is as yet not known in detail (particularly for *Nilaparvata*); but at least we know that *Nephotettix* obviously is a sedentary species whose population is bounded to the same area throughout the year, whereas *Nilaparvata*, a typical migratory species whose population movement at the time of habitat-alternation covers great distances. In this study we have shown that a considerable part of the violent annual population fluctuation in *Nilaparvata* is attributable to the instability in the abundance of initial immigrants. It thus will be evident that the pattern of seasonal life history characteristic of each species eventually has a close causal connection with the fundamental features of its population in paddy fields by affecting both the level and variability of the density of initial population.

The relation of these population properties to the actual status as the pest is similarly evident. As mentioned earlier, there is a clear difference between *Nilaparvata* and *Nephotettix* in their features as the pests of rice plant, despite the fact that both species are similarly common in paddy fields of this district. Obviously, this difference can be fully explained if the population properties here revealed are compared in terms of the overall population stability in both time and space. For example, let us tentatively assume 100 individuals per hill to be the minimum population level for causing destructive damage to the cultivated rice. Then, it can be seen from both Figs. 3 and 11 that the population of *Nephotettix*, unlike that of *Nilaparvata*, has virtually no possibility to attain this threshold level in paddy fields *even locally*, despite

the fact that its average level at the peak generation is nearly the same as that for *Nilaparvata*. In fact, the characteristics of *Nilaparvata* population, such as high but vulnerable reproductive power, high tolerance for local crowding, large-scale migration at the time of habitat alternation coupled with low dispersive activity after its establishment, and so on, apparently indicate that this species is, as is really the case, a typical example of epidemic or outbreak-type pests. On the contrary, the population characteristics of *Nephotettix* that are quite the reverse in all these points endorse its actual status as a chronic or non-outbreak-type insect pest whose economic importance arises chiefly from transmission of the rice dwarf virus, not from direct injury.

It would be apparent from the above discussion that the basic features of population dynamics here described are not only a clear reflection of the species' ecological mode of life but also a prime determinant of its specific status or features as the pest, and as a whole represent the essential characteristics of the species at the level of *population*. Of course, we should note also that since these population characteristics are closely connected with the specific environmental conditions for the population under study, they cannot be constant at all but are to show greater or lesser variations in response to different situations. A general principle to account for such variations will be that overall stability of the population as well as its average level is gradually decreased towards the northern fringe of the whole distribution area of the species, on account of the decreasing consistency of the action of regulatory processes along with the increasing effects of weather conditions upon the determination of population changes. In fact some evidence to support this inference for these leafhoppers can be found in the extensive light trap records covering many districts of Japan which were presented by SUENAGA and NAKATSUKA (1958).

The significance of regulatory processes in the dynamics of natural populations has long been a central theme of animal population ecology upon which many arguments have been focused. By historical review of these arguments, at least two opposing lines of thought may be found; one claiming that there must ultimately be a real regulation of numbers by feed-back mechanisms for any population to maintain itself in nature (e.g. NICHOLSON 1933, 1954; SOLOMON 1949, 1957; KLUMP 1962), and the other, that at least in most cases such apparent balance as seen in natural populations is attributable to the combined action of various environmental factors that are essentially unconcerned with such mechanisms (e.g. THOMPSON 1939, 1956; ANDREWARTHA and BIRCH 1954, 1960; MILNE 1957). But the current situation as to this controversy seems to us to be that the theoretical soundness of the former opinion against the latter has become increasingly evident through logical arguments such as KLUMP (1962)'s. Also, not a few empirical proofs or suggestions in favour of these arguments are now being accumulated through recent field population studies on various kinds of insects (e.g. WATT 1963; CLARK 1964; KLUMP 1966; AUER 1968; WAY 1968).

As we have seen, the present study proved the existence of density-dependent

processes to stabilize annual population densities in both of the two species of rice leafhoppers studied, regardless whether the suspected main factors to determine the time-to-time population changes are biotic (*Nephotettix*) or abiotic (*Nilaparvata*). Apart from such direct proofs, there still exists another kind of empirical evidence indicating the same thing: This is the well-known fact that the population of either species in a given district tends to preserve a characteristic mean level of abundance together with a restricted magnitude of fluctuation—Without feed-back mechanisms the probability for such a phenomenon to occur should virtually be equal to zero, as Klomp (1962) clearly proved by using simplified models. The populations of these leafhoppers thus seem to present concrete examples to show fundamental importance of the regulation of numbers in population dynamics.

In particular, the case of *Nephotettix cincticeps* will be worthy of special attention for three reasons: (1) The regulatory mechanisms operate so consistently that the resultant annual stability of population density at the peak generation is strikingly high as insect as compared with most other cases so far reported; (2) The equilibrium population level towards which such feed-back mechanisms operate is by far lower than the absolute capacity of the host plant; and (3) The action of regulatory mechanisms is distinctly species-specific, being little disturbed by the coexistence with other species of leafhoppers. It is often argued that intra-specific mechanisms causing self-regulation of populations come into operation only at extremely high levels of population density and hence rarely become important in nature (e.g. ANDREWARTHA and BIRCH 1954; MILNE 1957). An important implication of the above finding on this species will be that it offers factual evidence against this seemingly plausible argument and exemplifies potential universality of the self-regulation of numbers in natural insect populations.

At present stage, however, there are many points remaining yet unconfirmed in respect to the detailed mechanisms to account for such a sensitive feed-back process in the population of *Nephotettix*. To clarify these points, more elaborate research is required which includes both intensive life-table study and experimental analysis particularly for the population behaviour in adult stage. It is noted that a close study along such a line is now being carried out at Kochi Prefectural Institute of Agricultural and Forest Science in Shikoku, as well as at our station. Their first report, in which one of us (HOKYO) had joined as a collaborator, is appearing in the same issue of this journal (KIRITANI *et al.* 1970). The results described in the paper appear to lend confirmation to several basic conclusions we have derived here about the population regulation of this species, such as the existence of consistently operating feed-back mechanisms and the critical importance of the adult stage in the process of regulation.

SUMMARY

1. Population dynamics of the two species of rice leafhoppers, *Nephotettix cincticeps* and *Nilaparvata lugens*, were analyzed comparatively on the basis of the

8-year data taken in a fixed plot of paddy field in Kyushu Agricultural Experiment Station.

2. These leafhoppers invade paddy fields just after the planting of rice, and then propagate through three discrete generations during the rice-growing season (July—October). Description of the features of their population changes was made from the two different angles; seasonal changes within each year and annual fluctuation for each of the successive seasonal generations.

3. The two species have the patterns of seasonal population changes that are quite different from each other. The population of *Nephotettix* attains its peak at the second generation, whereas that of *Nilaparvata*, at the third or last generation. The density of initial immigrant population is much higher in the former species. Instead, the rate of its subsequent population growth is much lower than in the latter; and as a result both the species attain, on the annual average, roughly the same level of population density at the peak generation for each species. In *Nilaparvata* the fecundity (both potential and realized) proved to be much higher and the percentage killed by the egg and nymphal parasites to be rather lower than in *Nephotettix*, and this accounts for the wide difference in the overall rate of population growth between the two species.

4. In the magnitude of annual fluctuation of the population density at each seasonal generation, there also is a remarkable difference between *Nephotettix* and *Nilaparvata*, the former's population being consistently less variable than the latter's. At the second generation, for example, the latter's population varied 90 times during the 8-year period, but the former's, only 2.4 times, from the lowest year to the highest.

5. Analysis of the annual density relationships between successive seasonal generations revealed that in both the species there exist density-dependent processes to stabilize their populations towards the peak generation for each species, but that the consistency of the operation of such processes is widely different, being much higher in *Nephotettix* than in *Nilaparvata*. In the former the estimated equilibrium level towards which annual densities at the peak generation are regulated was in fact far lower than in the latter (and also than the carrying capacity of the host plant), indicating that the tolerance for crowding is much lower in the former than in the latter. Coupled with the difference in the sensibility to annual variation of the environmental conditions, this gives an adequate explanation to the wide difference in the magnitude of annual population fluctuation between the two species.

6. The mode of action of the natural enemies upon the leafhopper populations proved to be such that neither the predators (spiders) nor the parasites can substantially cause density-dependent stabilization of the density for each species. The regulation of numbers in either species is thus attributable chiefly to the effects of some intra-specific mechanisms. The mechanisms that were assessed by indirect evidence to be of prime importance are, for *Nephotettix*, the reduction of realized fecundity in adults due to

their mutual interference (either direct or indirect), and, for *Nilaparvata*, the increase of macropterous form in emerging female adults together with the decrease of survival rate in either nymphs or adults. Analysis of the population interaction between these two species confirmed that operation of such regulatory mechanisms is species-specific, being little disturbed by the other species' population.

7. A notable difference between the two species was observed in the spatial population structure also, the population of *Nephotettix* being distributed much more homogeneously than *Nilaparvata*'s in the field. It follows from this that the real difference in the tolerance for crowding between both species is still wider than was indicated by the comparison based on the mean density over the whole plot.

8. To sum up, the population of *Nephotettix* is consistently kept far more stable or homogeneous than *Nilaparvata*'s in both time and space; and this is because it has much weaker tolerance for crowding coupled with much higher activity for spatial dispersion. *Nilaparvata* is known to be a typical example of migratory, outbreak-type insect pests, whereas *Nephotettix*, to be a pest of sedentary, chronic type. It is therefore evident that the features of population dynamics as revealed here have a close causal relation with the specific status of the species as the pest of rice plant as well as with its specific mode of life throughout the year, and that as a whole they represent the essential characteristics of the species.

9. Some implications of above-mentioned results concerning the general significance of regulatory processes in the dynamics of insect populations were discussed.

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水田におけるツマグロヨコバイおよびトビロウソウの個体群の動態

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九州農業試験場の無防除水田において8年間にわたって行なった個体群センサスのデータにもとずいて、稲ウンカ・ヨコバイ類の主要な2種、ツマグロヨコバイ *Nephotettix cincticeps* とトビロウソウ *Nilaparvata lugens* の個体群動態の基本的特性を比較・記載し、特に個体数の自然制御 (Natural regulation) の問題との関連においてその生態学的意義を考察した。

両種ともに水田には田植後間もない7月に飛来・侵入し、その後10月までの間にふつう3世代を経過して増殖する。この季節的増殖の基本パターンは両種間で著しく異なる。すなわち、密度が年内の最高に達する世代 (ピーク世代) がツマグロヨコバイでは侵入2世代後 (G-II) であるのに対してトビロウソウでは3世代後 (G-III) であり、また、これらピーク世代に至るまでの増殖経過も大きく異なっていて、侵入世代 (G-O) の個体群密度はツマグロヨコバイの方がずっと高いが以後の各世代の増殖率は逆にトビロウソウがはるかに高い。そして結果的にはピーク世代における密度の年次平均値は両種ほぼ同じレベルになっている。増殖率がこのように異なるのは、トビロウソウではツマグロヨコバイに比べ成虫の産卵数をはるかに多くしかも卵・幼虫の寄生率が低いためである。

この両種は各世代における個体群密度の年次変動の大きさという点でも著しい対照をなしており、個体群の安定度はツマグロヨコバイの方がはるかに高い。たとえば G-II での密度の最高年と最低年の比 (8年間) はトビロウソウの 90 に対しツマグロヨコバイではわずかに 2.4 であった。各世代密度の年次変動の内容を種々の角度から分析した結果、両種どちらの場合にもピーク世代に向かって個体数の自然制御、つまり密度依存過程による密度の安定化という現象が実際に起こっていることが示された。もっともその作用の強さあるいは一貫性の度合いは両種間で大きく異なり、ツマグロヨコバイの場合の方がはるかに顕著で、推定された平衡密度もトビロウソウに比べてはるかに低い値を示した。因みにこの平衡密度 (株あたり20頭足らず) は寄主植物の carrying capacity に比べてもむしろずっと低い値である。ツマグロヨコバイの個体群が年々著しく安定に保たれているのは、結局本種がこのように精密な制御機構を具えているためであるといえる。

この両種の個体群に対する天敵の作用のしかたを分析した結果、寄生者、捕食者 (クモ類) のどちらも有力な制御要因として働いている可能性は否定され、個体数の制御は両種どちらの場合も主として種内の個体間相互干渉によって起こっていることが示唆された。なお互いに共存するこの両種間において競争ないし拮抗的相互作用はほとんど見られず、制御機構が種特異的に働いていることも明らかとなった。この種内機構の具体的内容には不明の点が多いが、種々の点からトビロウソウの場合は寄主条件の悪化にともなう成虫の長翅型率の増大と幼虫生存率の低下、ツマグロヨコバイの場合は成虫期の直接・間接の個体間干渉にもとづく移動率の増加や産卵数の低下が主要な役割を果たしていると推論された。

この両種の個体群はその空間構造 (分布様式) においても著しい相違を示しており、ともに集中分布ではあるがその集合度はツマグロヨコバイの方がずっと低い。このため同じ平均密度であっても各個体にとっての実際のこみあい度はトビロウソウの方がずっと高いという結果になる。

このようにツマグロヨコバイとトビロウソウは個体群動態の種々の側面で互いに著しい対照をなしているが、これらの相違を要約すれば、前者の個体群は後者に比べて時間的にも空間的にもはるかに安定・均一に保たれているということであり、これは基本的にはこみあいに対する感受性とそれにも関連する分散活動力の相違に帰因している。トビロウソウは寄主転換時に長距離移動を行なう典型的な非定住型、そして大発生型の害虫であり、一方ツマグロヨコバイは定住型、非大発生型の害虫として知られている。したがってここに示された個体群動態の特性は、個体群の時間的、空間的安定度というその集約された形においてそれぞれの種の生活史の特徴や害虫としての性格と密接につながっており、種の特性として重要な意味を持つと考えられる。