Evaluation of Mortality Factors with Special Reference to Parasitism of the Green Rice Leafhopper, *Nephotettix* *cincticeps* UHLER (Hemiptera : Deltocephalidae)

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A superficial comparison of the numbers in a population killed by different mortality factors is by itself misleading. This arises from the fact that each mortality factor seldom acts alone but has interactions with each other either sequentially or contemporaneously. Since we have no information on the relationship among mortality factors within the egg stage of the green rice leafhopper, several assumptions about their modes of interactions were made to measure the amount of mortality that each factor would cause if it were operating alone.

In every hypothetical case, the proportion of eggs parasitized increased with the increase of egg density. This suggests that the egg parasite operated density-dependently against the host density. This tendency was quite evident in the early and mid-season paddy. From field and laboratory experiments it follows that the egg parasite was able to respond positively to host density.

Feasibility of the successful use of egg parasites for the integrated control of the green rice leafhopper was discussed in relation to annual changes of leafhopper population and of percentage of eggs parasitized in the field that received no insecticidal treatment for five years.

INTRODUCTION

KIRITANI *et al.* (1970) have suggested that the population density of the green rice leafhopper, *Nephotettix cincticeps* UHLER, is regulated through several density-dependent processes which operate at different levels of the population density. From the viewpoint of population regulation, the mortality factors should be evaluated first by their degree of dependency on the population density, secondly by their order in the sequence of mortality agents and finally by their interactions with other factors (SOLOMON, 1964; MORRIS, 1965).

It has been stated in a previous report (KIRITANI *et al.*, 1970) that the occurrence of egg mortality was density-dependent. The major mortality factors during the egg stage may be named as follows: failure to hatch, parasitism and fungus diseases. As these mortality factors operate contemporaneously or one after another at the egg stage, the measurement of apparent mortality may provide only a poor index of the real effect of the individual factors on egg survival and population trends. Since little information is available on interaction and sequence among them, hypothetical cases were considered in order to evaluate the effect of each egg mortality factor from results obtained by periodical field surveys. On the other hand, the response of the egg parasite to its host density was measured experimentally in the field.

On the basis of these results, it was assessed to what extent these factors were responsible for regulating the population of the green rice leafhopper.

METHOD

The design of experimental fields and the method used in estimating egg density have been fully described in a previous paper (KIRITANI *et al.*, 1970), so that only a brief account is given here.

1. Description of experimental fields

In Kochi Prefecture, various varieties of rice which differ in sowing time are cultivated, but the cultivating system of rice is almost fixed in the respective locality. Accordingly, paddy cultivating areas in Kochi Prefecture may be classified into two types: early-paddy area and mid-season-paddy area. In the early-paddy area, rice is usually cropped twice a year; the mid-season paddy together with the early and late paddy are cultivated. The early paddy is sown toward the middle of March. Whereas, in the mid-season-paddy area, rice is cropped once a year and sowing is usually made in early May.

Two representative areas, Nangoku and Ino, were selected for the present study. Nangoku and Ino districts are located in the early-paddy area and the mid-season-paddy area, respectively. In total, 24 and 12 life tables for eggs were constructed for the periods of 1966–68 in Nangoku and of 1968–71 in Ino, respectively.

2. Estimation of egg density and sorting of mortality factors in the egg stage

Eggs are deposited *en masse* on a leafsheath of the rice plants and the mean number of eggs per mass varied from 5 to 18 according to the generation of the insect (SASABA and KIRITANI, 1971). Egg masses, except those which had already hatched or for which mortality factors were identified, were kept in a glass tube (4.5×1.0 cm) with a piece of moistened filter paper for further examination. Mortality factors were classified into failure to hatch, parasitism by an egg parasite, *Japania andoi* ISHII, fungus diseases and unknown causes. Thirty to 50 quadrates (10×10 cm each) were placed on nursery beds and the number of eggs in each quadrate was examined by dissecting the seedlings. After transplantation, the egg density of leafhoppers was assessed weekly in the following way until harvest. During the first 3 weeks after transplantation, random samples of 100–150 hills were dissected. Afterwards, one stalk taken from each of 100–600 hills, which were selected randomly, was cut off at its base to examine the eggs of leafhoppers. The eggs which had hatched remained in their egg shells in the tissues of leafsheaths and the parasitized or diseased ones could easily be determined by their coloration or by the formation of hyphae.

Since eggs are recognized by their egg shells even after they are hatched, the egg density inclusive of the hatched and unhatched ones increased in a cumulative manner reaching a maximum density which roughly corresponded to the end of the oviposition period for the generation concerned. Thus each local peak of the oviposition curve was regarded as the density of eggs for the generation concerned.

3. Response of egg parasites to host density

Twenty, 40, 80, 160 and 320 pairs of the leafhoppers collected from a paddy field in Nangoku, on July 13th, 1967, were respectively introduced in five field cages ($60 \times$

60 cm in area and 120 cm in height), each containing 5 hills of the rice plant, and they were allowed to oviposit for 3 days. The rice plants were then transplanted in 25 quadrates located in an early paddy field following the Latin square arrangement and were exposed to the attack of egg parasites. After one week's exposure, all the rice plants were brought back to the laboratory to examine the response of egg parasites to host density.

RESULTS

1. The life tables for the egg stage

The life tables in Nangoku and in Ino area given in Tables 1 and 2, respectively. The percentage mortality of eggs increased almost always with the rise in egg density. Among the mortality factors, parasitism played the most important part. On the basis of these life tables, we were able to go into further detailed analysis on the interactions between individual mortality factors and host density.

2. Intensity of various mortality factors in relation to host density

It has been argued that the effect of any mortality factor on the population trend is likely to be influenced by other factors which act simultaneously or successively. One line of thought on successive mortalities is presented by SOLOMON (1964), who calculated theoretically the final survival by varying the order of action of different types

Table 1. THE LIFE TABLES FOR THE EGG STAGE OF *N. cincticeps*, IN NANGOKU

Cultivation system	Early paddy			Mid-season paddy			Late paddy	
Generation	1st	2nd	3rd	2nd	3rd	4th	4th	5th
1966								
No. of eggs/hill	4.68	109.09	564.69	69.60	679.72	666.11	47.60	177.22
Failure to hatch (%)	44.0	17.8	10.1	73.7	24.3	16.6	37.1	21.4
Egg parasite (%)	29.1	49.4	67.8	2.0	42.3	55.6	15.3	35.7
Fungus diseases (%)	0.0	1.7	0.0	0.0	24.2	10.6	29.5	10.2
Unknown (%)	22.8	0.0	0.0	0.0	0.0	0.0	1.7	18.3
Total (%)	95.9	68.9	77.9	75.7	90.8	82.8	83.6	85.6
1967								
No. of eggs/hill	3.61	85.70	544.32	29.04	1,014.40	306.98	94.36	271.04
Failure to hatch (%)	45.0	15.2	11.3	39.6	22.3	8.4	33.6	16.1
Egg parasite (%)	10.0	14.2	36.9	13.2	42.5	71.0	12.9	35.0
Fungus diseases (%)	0.0	29.5	4.3	8.9	16.7	5.2	30.1	22.4
Unknown (%)	0.0	0.0	3.3	4.2	1.8	0.0	3.1	0.5
Total (%)	55.0	58.9	55.8	65.9	83.3	84.6	79.7	74.0
1968								
No. of eggs/hill	0.36	34.93	339.02	5.27	680.65	720.93	125.55	280.20
Failure to hatch (%)	43.8	23.5	13.4	21.5	45.0	23.1	37.9	16.1
Egg parasite (%)	0.0	8.4	29.2	0.0	28.0	57.9	54.6	49.4
Fungus diseases (%)	0.0	17.3	1.5	0.0	8.8	2.6	7.5	0.0
Unknown (%)	0.0	0.0	6.3	17.7	2.2	0.0	0.0	0.0
Total (%)	43.8	49.2	50.4	39.2	84.0	83.6	99.9	65.5

Table 2. THE LIFE TABLES FOR THE EGG STAGE OF *N. cincticeps*, IN INO

Cultivation system	Mid-season paddy		
	2nd	3rd	4th
1968			
No. of eggs/hill	99.27	830.32	909.30
Failure to hatch (%)	19.6	15.5	17.5
Egg parasite (%)	0.0	25.4	44.9
Fungus diseases (%)	29.3	2.5	0.4
Unknown (%)	4.4	0.0	0.0
Total (%)	53.3	43.4	62.8
1969			
No. of eggs/hill	57.27	189.81	673.70
Failure to hatch (%)	20.7	11.9	6.8
Egg parasite (%)	1.2	51.9	51.5
Fungus diseases (%)	12.3	0.0	1.9
Unknown (%)	1.3	2.2	2.7
Total (%)	35.5	66.0	62.9
1970			
No. of eggs/hill	164.02	581.44	455.15
Failure to hatch (%)	32.2	7.3	2.1
Egg parasite (%)	1.0	61.8	83.7
Fungus diseases (%)	20.8	2.6	0.0
Unknown (%)	0.0	0.2	0.0
Total (%)	54.0	71.9	85.8
1971			
No. of eggs/hill	52.08	147.42	447.39
Failure to hatch (%)	29.7	6.6	3.7
Egg parasite (%)	16.3	73.0	80.1
Fungus diseases (%)	14.2	4.2	0.0
Unknown (%)	0.8	0.0	0.0
Total (%)	61.0	83.8	83.8

of mortality factors, *i.e.*, density-dependent and density-independent factors and one causing constant-number deaths. Another line of thought on the interactions of the contemporaneous mortality factors was developed by MORRIS (1965), who emphasized the importance of the interaction coefficient among the factors. In the present study, due to the lack of information on the interaction among the mortality factors, some hypothetical cases concerning the interactions were assumed to measure the amount of mortality that each factor would cause, (1) when individual mortality factors are mutually exclusive, and (2) when they operate independently from each other.

(2-1). *Eggs affected by one factor are invulnerable to the other factors*

It is conceivable that contemporaneous mortality factors may operate in a mutually exclusive manner. In this case, eggs affected by each mortality factor are for some reason invulnerable to the action of all the other contemporaneous mortality factors. In other words, contemporaneous mortality factors may act in succession as the sequential mortality factors. The results were analyzed assuming the following two extreme

cases; one mortality factor operates first and is followed by the others, or the first comes last. In the case where any specified mortality factor was assumed to come last, the egg density referred to the one saved from the other two preceding factors. Therefore, the percentage mortality should become greater than otherwise when any mortality factor comes last.

The relationship between the number of eggs per hill and the percentage parasitism is presented in Figs. 1 and 2. In either case the mortality for the egg parasite increased, generally, with the increase of egg density. There are several exceptional cases. In early paddy in 1966, in which parasitism comes last, the percentage parasitism became the highest at the lowest egg density. This would result from the fact that the proportion of eggs that failed to hatch was so high that the number of eggs exposed to attack of egg parasites was small. Another exceptional case can be seen in mid-season paddy in 1967. The linking of seriated points goes somewhat counter-clockwise, suggesting a delayed density-dependent action of the parasites. This would be caused by the fact that the parasites could not respond promptly to the high host density in the previous generation, *i.e.* 1,014 eggs/hill.

(2-2). *Eggs affected by one factor are as vulnerable as unaffected eggs to others*

There is another sort of interaction where the contemporaneous mortality factors operate in an independent manner. In this case the eggs affected by one factor are

Fig. 1 Percentage of eggs parasitized in relation to the number of eggs per hill in the experimental field in Nangoku.

—•— : The egg parasitism comes first and contemporaneous mortality factors operate in a mutually exclusive manner. ○---○ : The egg parasitism comes last and contemporaneous mortality factors operate in a mutually exclusive manner.

Fig. 2. Percentage of eggs parasitized in relation to the number of eggs per hill in the experimental field in Ino.

•—• : The egg parasitism comes first and contemporaneous mortality factors operate in a mutually exclusive manner. o---o : The egg parasitism comes last and contemporaneous mortality factors operate in a mutually exclusive manner.

as vulnerable as unaffected eggs to other factors. A simple preliminary model is as follows:

$$S = (1 - M_{\text{fail.}})(1 - M_{\text{para.}})(1 - M_{\text{fung.}}),$$

where S = survival rate of eggs,

$M_{\text{fail.}}$, $M_{\text{para.}}$, $M_{\text{fung.}}$ = rate of the number of eggs attacked by any specified mortality factor to total number of eggs, if every mortality factor was the only factor operating. fail., para. and fung. refer respectively failure to hatch, parasitism and fungus diseases.

In the absence of evidence on the frequencies of eggs affected simultaneously by more than two mortality factors and by interactions between them, two hypothetical cases could be put to test by calculation were considered; the most dominant factor is parasitism followed by failure to hatch and fungus diseases in the decreasing order and vice versa. As regards the former case, for example, when eggs affected by parasites contemporaneously with either or both of the factors, they invariably result in parasitism; and when eggs affected by failure to hatch coupled with the fungus diseases, they will be sorted as failure to hatch.

(a) When the decreasing order of dominance is as follows: parasitism, failure to hatch and fungus diseases.

$$M_{\text{para.}} = m_{\text{para.}}$$

$$M_{\text{fail.}} = m_{\text{fail.}} + M_{\text{fail.}} \cdot M_{\text{para.}}$$

Hence,

$$M_{\text{fail.}} = \frac{m_{\text{fail.}}}{1 - M_{\text{para.}}}$$

$$M_{\text{fung.}} = m_{\text{fung.}} + M_{\text{fung.}} \cdot M_{\text{para.}} + M_{\text{fung.}} \cdot M_{\text{fail.}} - M_{\text{para.}} \cdot M_{\text{fail.}} \cdot M_{\text{fung.}}$$

Hence,

$$M_{\text{fung.}} = \frac{m_{\text{fung.}}}{1 - M_{\text{para.}} - M_{\text{fail.}} + M_{\text{para.}} \cdot M_{\text{fail.}}}$$

(b) When the decreasing order of dominance is as follows: fungus diseases, failure to hatch and parasitism.

$$M_{\text{fung.}} = m_{\text{fung.}}$$

$$M_{\text{fail.}} = \frac{m_{\text{fail.}}}{1 - M_{\text{fung.}}}$$

$$M_{\text{para.}} = \frac{m_{\text{para.}}}{1 - M_{\text{fail.}} - M_{\text{fung.}} + M_{\text{fung.}} \cdot M_{\text{fail.}}},$$

where m = observed rate of the number of eggs attacked by any specified mortality to total number of eggs.

The percentage mortality caused by each mortality factor was calculated in both cases. Obviously in the formulae mentioned above, M should be equal to or greater than m . The corrected percentage mortality caused by the egg parasite ($100 \cdot M_{\text{para.}}$) was shown in Figs. 3 and 4. Generally $100 \cdot M_{\text{para.}}$ increased with the increase of host density, suggesting the density-dependent process is operating.

Fig. 3. Percentage of eggs parasitized in relation to the number of eggs per hill in the experimental field in Nangoku. The contemporaneous mortality factors are operating with overlapping in an independent manner.

●—● : The egg parasitism acts as the dominant mortality factor followed by failure to hatch and fungus diseases. ○---○ : Fungus diseases act as the dominant mortality factor followed by failure to hatch and egg parasite.

Fig. 4. Percentage of eggs parasitized in relation to the number of eggs per hill in the experimental field in Ino. The contemporaneous mortality factors are operating with overlapping in an independent manner.

●—● : The egg parasitism acts as the dominant mortality factor followed by failure to hatch and fungus diseases. ○---○ : Fungus diseases act as the dominant mortality factor followed by failure to hatch and egg parasite.

3. Response of egg parasites to host density

To make clear the response of parasites to host density, rice plants with eggs of various densities were prepared by confining rice plants together with leafhoppers in a cage, and these plants were transplanted in the experimental field, and the eggs were exposed to egg parasites from 16th July for one week. The number of eggs per stalk, which was deposited by introduced females in the cage, ranged from 2.5 to 80.

Though the result was not clear cut, the percentage parasitism within a parasite generation increased with increasing egg density. It was estimated by a census that the egg densities per stalk on 17th and on 26th July were 4.5 and 13.4, respectively. It is more realistic, therefore, to analyze the relationship between percentage parasitism and egg density within the range of egg density actually observed in the field, i.e. from 4 to 14 eggs per stalk. The number of parasitized eggs per stalk (ordinate) is plotted against the number of eggs per stalk (abscissa), both in a logarithmic scale (Fig. 5). If egg parasites did act as the density-dependent mortality factor, the slope of the regression line should be greater than unity. The slope of the actual regression line was greater than unity (2.03); the response was superproportional (HASSELL, 1966), that is, the host eggs suffered higher mortality at a higher egg density than at a lower one.

Fig. 5. Regression of the number of eggs parasitized in log. on the number of eggs in log. in the range of egg density of 4 and 14. For further explanation see text.

DISCUSSION

Since we have no information on the relationship among mortality factors within the egg stage of the green rice leafhopper, several assumptions on the interactions among them were made to measure the amount of mortality that each factor would cause if it were operating alone. In every hypothetical case, the proportion of eggs parasitized increased with the increase of egg density. It is conceivable, therefore, that egg parasites operate as the density-dependent mortality factor, though several assumptions adopted in this paper would not represent the realistic interactions among the three mortality factors.

In order that the parasite operates as the density-dependent mortality factor, it has to respond positively to host density. Female parasite, *Japania andoi* laid about 35 eggs on an average in the laboratory (25°C, 70% R.H.), and the number of eggs laid by the green rice leafhopper rarely exceeded 100. The number of days taken from egg to reproductive adult development was about 21 days in this parasite, and about 40 days in the green rice leafhopper under comparable conditions. Assuming that both host and parasite reproduce in an exponential manner, with a power of 100 and 35 respectively, the parasite may increase 11.25 ($35^2/100$) times as many as the host after about 40 days. The superiority of parasites in the reproductive rate over their hosts would make parasites respond numerically to the increase of hosts.

With regard to the functional response to host density, HASSELL (1966) subdivided this response into two components. One is that the number of eggs laid per parasite is constant but the parasite attacked regions of high host density resulting in aggregation (*i.e.*, aggregation response). Another is that there is no aggregation but the number of eggs laid per parasite is proportionally greater where host density is higher (*i.e.*, individual response). As shown in Fig. 5, the parasite responded super-proportionally to host density, through aggregative and/or individual responses.

It is believed that, since 1952, leafhoppers have increased rapidly following the widespread application of synthetic insecticides, such as, DDT, BHC and parathion etc. This situation was accounted for by the fact that BHC was not only very effective

Fig. 6. Annual changes in the percentage of eggs parasitized in the experimental field in Ino. The field received no insecticides for 5 years.

against the rice stem borer, *Chilo suppressalis*, but also against the natural enemies of leafhoppers, whereas it proved to be less effective against leafhoppers. As shown by KAWAHARA *et al.* (1971), the LC_{50} dose of leafhopper for BHC was about 50 times greater than that of *Lycosa* which is one of the most important predators of leafhoppers. Though it remained unexplained to what extent the parasite was affected, it is reasonable to assume that the parasite was equally susceptible to insecticides as spiders were. It is conceivable, therefore, that rapid increase of the green rice leafhopper depended chiefly upon the destruction of the natural enemy populations by the use of synthetic insecticides.

The parasitism of eggs has been studied for 4 years in a experimental paddy field, in Ino, about 700 m² in area, where no insecticides have been used for a successive period of five years since 1967. The percentage of eggs parasitized increased year by year (Table 2, Fig. 6). The maximum number of spiders per hill was 2.5, 8.3 and 22.9 in 1969, 1970 and 1971, respectively (KIRITANI *et al.*, unpublished). On the contrary, the maximum number of eggs per hill throughout the season decreased year by year; 909.3, 673.7, 581.4 and 447.4 in 1968, 1969, 1970 and 1971, respectively (Table 2). These facts suggest that the population density of leafhoppers was reduced annually more and more by biological control factors, which had long ceased to operate as effective controlling factors by the use of non-selective insecticides.

For the purpose of establishing an appropriate control program of leafhoppers, experimentations with selective insecticides have been conducted with satisfactory results (KAWAHARA *et al.*, 1971; KIRITANI *et al.*, 1971; KIRITANI *et al.*, 1972). It was shown in these papers that the spiders may prevent the resurgence of leafhoppers after treatment with selective insecticides. Namely, application of selective insecticides improved the balance between the spiders and leafhoppers in favour of spiders. It remains to be solved as to how the egg parasites can be made to contribute to contain the leafhopper population density after treatment with selective insecticides. It is conceivable, however, that the egg parasite would play an important role in the integrated control program of the leafhopper as for reasons mentioned above. Accordingly, the conservation of parasites and predators is a pre-requisite for the integrated use of chemical and biological agents in controlling the green rice leafhopper.

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REFERENCES

- HASSELL, M. P. (1966) Evaluation of parasite or predator response. *J. Anim.Ecol.* **35** : 65-76.
- KAWAHARA, S., K. KIRITANI and T. SASABA (1971) The selective activity of rice-pest insecticides against the green rice leafhopper and spiders. *Botyu-Kagaku* **36** : 121-128.
- KIRITANI, K., N. HOKYO, T. SASABA and F. NAKASUJI (1970) Studies on population dynamics of the green rice leafhopper, *Nephotettix cincticeps* UHLER: Regulatory mechanism of the population density. *Res. Popul. Ecol.* **12** : 137-153.
- KIRITANI, K., S. KAWAHARA, T. SASABA and F. NAKASUJI (1971) An attempt of rice pest control by the integration of insecticides and natural enemies. *Gensei* **22** : 19-23.
- KIRITANI, K., T. INOUE, F. NAKASUJI, S. KAWAHARA and T. SASABA (1972) An approach to the integrated control of rice pests: Control with selective, low dosage insecticides by reduced number of applications. *Jap. J. appl. Ent. Zool.* **16** : 79-86.
- MORRIS, R. F. (1965) Contemporaneous mortality factors in population dynamics. *Can. Ent.* **97** : 1173-1184.
- SASABA, T. and K. KIRITANI (1971) Factors responsible for the variation of egg-mass size in the green rice leafhopper, *Nephotettix cincticeps* UHLER. *Kontyu* **39** : 54-60.
- SOLOMON, M. E. (1964) Analysis of processes involved in the natural control of insects. *Adv. Ecol. Res.* **2** : 1-58.