Studies on the Population of the Apple Leaf Miner

Phyllonorycter ringoniella MATSUMURA

(Lepidoptera : Lithocolletidae)

III. Some Analyses of the Mortality Factors Operating upon the Population¹

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Based on the life table studies for the apple leaf miner, *Phyllonorycter ringoniella* MATSUMURA, five mortality factors which played important roles in reduction of larvae were chosen and the characteristics of their operations were analyzed on the following two points; (1) changes of the mortality rates in accordance with the changes of the numbers of the living larvae per leaf and (2) frequency distribution of deaths per leaf in comparison with the binomial series.

Mortality during the sap feeding stage was dependent on density per leaf. This was mainly due to the cannibalism. Operations of other factors were independent of the numbers of larvae per leaf.

Distributions of deaths due to unknown factors operating upon the sap feeding and tissue feeding stages and those of the parasitism of *Sympiesis* sp. were nearly fitted to the binomial series, which suggested that reductions of larvae due to these factors occurred independently of each other in a given leaf. Distributions of parasitisms of *H. testaceipes* and those of deaths due to cannibalism did not follow the binomial series.

INTRODUCTION

The apple leaf miner, *Phyllonorycter ringoniella* MATSUMURA, spends its larval and pupal stages in a mine made on the underside of the leaf. The eggs are laid on the lower surface of the leaves. On hatching, the larva enters the leaf and extends its mine by shearing through spongy mesophyll cells adjacent to the lower epidermal cells. In its earlier stage, the mine appears as a silvery-green spot of irregular shape on the lower surface of the leaf. As the larva develops, it feeds towards the upper surface chewing out palisade cells as far as epidermis on the upper side. This results in a greenish-white appearance on the upper surface of the leaf.

In this paper, we do not classify the larval stages into instars, but following our custom, we call the younger larvae which feed the spongy mesophyll cell "sap

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feeder" and the older ones which feed the palisade cells "tissue feeder". Such a classification is especially convenient in the field surveys since it saves much labor without a great loss of information.

In extending the mines, when two or more mines meet, competition among the sap feeders occurs. POTTINGER and LEROUX (1971) have observed and described a similar phenomenon for the related species *Lithocolletis* (=Ph.) *blancardella*: one larva attacks the others and kills them by piercing the body in the region of the thorax and abdominal segments. They called this competition cannibalism as the victor imbibes blood from the vanquished. Although we have not made observation in any detail on this process, as our larva has the same basic morphological form and performs similar mining habits to theirs, we believe their explanation will also be applicable in our case. It is probable that the chance of the sap feeding miners crossing each other is greater at high population density than at low density. The chance will be further magnified if the adult lays its eggs with less tendency for spacing-out, or if a specific part of the leaf or specific leaves in a tree are vulnerable to oviposition. But if the adult has judicious behavior in oviposition to space out its eggs or if every part of the leaf or every leaf in the tree is equally vulnerable to oviposition, the chance of waste due to cannibalism will be lessened.

As the larva does not move out of a leaf and remains in a tightly delimited space, the pattern of the death due to parasitism will inevitably be different from that of other free living insects. It will be reasonable to think that the chances of being attacked are greatly influenced by the number of larvae confined in a specific leaf.

These mortalities bring about a reduction of survivors in the leaf and change the distribution pattern of the larvae among leaves from time to time according to the intensity and pattern of actions of the mortality factors.

The problems mentioned above are the subject the present paper deals with.

MATERIALS AND METHODS

Large numbers of apple leaves were collected from an orchard with an area of some 20 ares near the Experiment Station, Aomori Prefecture, in October, 1976. This was the time when the majority of the living insects of the 4th generation reached the pupal stage at which they spend the winter in leaves on the ground.

The mines were carefully opened under the binocular microscope and the contents were recorded for each leaf. Whenever the living larva was found, it was inspected for the presence of internal parasites by dissection.

Other details of the methods will be given in each relevant section.

RESULTS AND DISCUSSIONS

(1) *Life table*

The apple leaf miner, *Ph. ringoniella*, spends its larval and pupal stages in a solitary mine. As POTTINGER and LEROUX (1971) stated in their study on the leaf miner, *L.* (=Ph.) *blancardella*, this results in;

- 1) if it dies at any immature stage, the remains of the body will be secured in the mine and can assure the stage of death,
- 2) the presence of larva, pupa, the cast pupal exuviae or cocoon, or the pre-

sence of larval faeces readily ascertains the kind of parasite which killed the host, and

3) the presence of the cast pupal exuviae partly protruding out of the mine, or, if they are dislodged, the complete absence of any proof of death will indicate the success of adult emergence of the leaf miner.

These characteristics facilitate estimates of the density of specific stages and the degrees of importance of each mortality factor operating upon the population at any one time by a single observation.

To make certain what role each mortality factor played in the studied orchard, the life table was constructed and shown in Table 1. The mean density of initial entrance was 7.7 on the basis of a leaf. In the sap feeding stage about 0.8 and 0.3 larvae per leaf died due to the cannibalism and unknown causes, respectively. Amongst 6.6 larvae which reached the tissue feeding stage, 3.6 were killed before reaching the pre-pupal stage. The main causes of mortality were the parasitism of *Sympiesis* sp. and *Holcothorax testaceipes* and unknown causes accounting for deaths of 0.5, 2.0 and 1.1 larvae per leaf, respectively. The second parasite, *H. testaceipes*, which is poly-embryonic, lays its egg into the host egg (TACHIKAWA, 1966). The parasitized host develops as normal but is suddenly mummified at the end of its feeding period. About ten individuals emerge out of a host on an average. The chalcid, *Sympiesis* sp. is an external parasite. It lays its egg piercing its ovipositor into the mine. Although we have only circumstantial evidence it seems that the chalcid kills the host prior to its oviposition. The number of deaths listed under unknown causes was remarkable. Although the true cause is far from evident in our present knowledge, it seems prob-

Table 1. THE LIFE TABLE FOR THE APPLE LEAF MINER,
Ph. ringoniella, IN THE 4TH GENERATION^a

Stage	No. entering stage	Mortality factor	No. dying
Sap feeder	767.76		
		Cannibalism	77.34
		Unknown	32.28
		Total	109.62
Tissue feeder	658.14		
		<i>H. testaceipes</i>	197.81
		<i>Sympiesis</i> sp.	46.86
		<i>Apanteles</i> sp.	1.08
		Cannibalism	5.99
		Unknown	109.86
		Total	361.60
Pre-pupa	296.55		
		Failure at pupation	8.45
		Total	8.45
Pupa	288.10		
		Unknown	2.11
		Total	2.11
Pupa entering hibernation	285.98		

^a Number per 100 leaves.

able that: (1) the parasite wasp stings the host but does not lay its eggs for some reason, (2) the larva is weak physiologically, or (3) the larva dies due to some unidentified disease. Amongst 3.0 pre-pupae, some 0.1 failed to reach pupal stage. As a result, more than 37 per cent of the larvae which entered the leaf went into hibernation.

The trend of survivorships presented here was basically similar to those for other generations at the same place, or for all generations at other places (YAMADA et al., unpublished). In this study it was not possible to analyze the mortality for the egg stage. Many of the life tables obtained by us until present show, however, that it lies within the range of 0 to 3 per cent and never exceeds 5 per cent irrespective of the egg density. For this reason, it may not be worth serious consideration here. The surprisingly high rate of total survival in this insect is undoubtedly attributable to the absence of dispersal behavior in the hatchlings and the protection effect through its mining behavior.

Based on this life table we picked up two mortality factors in the sap feeding stage and three in the tissue feeding stage for the special consideration which follows below.

(2) *Changes of the distribution on leaves and the pattern of actions of each mortality factor*

The frequency distribution of the number of the miners per leaf for each developmental stage was given in Fig. 1. The histograms are the observed distributions

Fig. 1. Frequency distributions per leaf of the apple leaf miner for each developmental stage. Histograms represent observed data, solid lines theoretical values of the 0-truncated negative binomial, broken lines those of the negative binomial and chain lines those of the Poisson.

A; sap feeder, B; tissue feeder, C; pre-pupa, D; pupa and E; pupa entered hibernation.

Significant test: P_n is for the negative binomial, P_0 for the 0-truncated negative binomial and P_p for the Poisson.

and the curves are theoretical ones as indicated in the captions of the figure.¹⁾

The distribution just after mining leaves was approximately fitted to the negative binomial distribution for the whole histograms and 0-truncated negative binomial distribution for the histograms without 0-term but did not fit to the Poisson distribution (Fig. 1. A). This indicates that the distribution pattern of larvae was not random but aggregative. Since the mortality in the egg stage is very low as mentioned in the preceeding section, the aggregative tendency may reflect directly the pattern of adult oviposition.

At the tissue feeding stage, the pattern changed to the one shown in Fig. 1. B. This was basically identical to the pattern which we obtained before for the same stage (YAMADA et al., 1971) and did not fit any longer to the theoretical ones examined in this study, i.e., the negative binomial, the Poisson and the 0-truncated negative binomial series. This change is caused by deaths due to cannibalism and the unknown (cf. Table 1).

Distribution pattern for the pre-pupal stage changed as was given in Fig. 1. C. This change was caused by the deaths due to parasitisms of *H. testaceipes* and *Sympiesis* sp. and due to the unknown. As the mortality during the tissue feeding stage was severest, the change was drastic in the shapes of the distributions between the tissue feeder and pre-pupal stages. Changes of distribution after the pre-pupal stage were very small (Fig. 1. D and E).

IWAO (1968) and IWAO and KUNO (1971) proposed an index to analyze the density relationship in distribution:

$$\tau = \frac{\frac{m^*}{(1-p)^*}}{\frac{m}{m_o}} = \frac{m^*}{m_o} \cdot \frac{m_o}{m},$$

where p is the average mortality rate; m and m_o , the mean and the mean crowding in the initial population, respectively; and m and m^* , those after the operation of mortality. According to them, the value of τ becomes unity if the operation of mortality is independent of local density, less than unity if it is density-dependent and greater than unity if it is inversely density-dependent or if all-or-none type random mortality operates upon colonies.

In Fig. 2, estimated values of the mean crowding were plotted against the corresponding means for all the developmental stages. Inset is the changes of τ values. It was suggested from this result that the decrease of living larvae in numbers during the sap feeding stage occurred depending on numbers of larvae confined in a leaf; the decrease during the tissue feeding stage occurred either inversely density dependently or in an all-or-none type way, while the decreases during the other stages were density-independent.

Fig. 2. Relation of the mean crowding to the mean at each developmental stage. Inset is the trends of τ between two successive stages.

s; sap feeder, t; tissue feeder, P_p ; pre-pupa, P; pupa and P_h ; pupa entered hibernation.

¹ Calculated with an aid of FORTRAN programs of SHIYOMI (1970 and 1974).

Fig. 3. Changes in the mortality rate in relation to the number of the sap feeders per leaf. Triangles are the rate of parasitism of *H. testaceipes*, crosses the rate of death due to cannibalism and solid circles that due to unknown.

Fig. 4. Changes in the mortality rate in relation to the number of the tissue feeder per leaf. Solid circles are the rate of mortality due to *H. testaceipes*, open circles due to unknown and crosses parasitism of *Sympiesis* sp..

As was shown in the life table, deaths during each developmental stage are not caused by a single factor but more than one mortality factor are operating at a given stage. To detect which factor or factors were responsible for the density relationships suggested above, the average mortality rate due to each factor operating upon the sap feeder was presented in Fig. 3, and that for the tissue feeder in Fig. 4 in relation to the number of miners confined in a single leaf.

Obviously the density dependent mortality in the sap feeding stage was explicable by the cannibalism, because the mortality rate by the cannibalism increased with the increase of numbers of larvae in the leaf, while the mortality rate due to the unknown remained almost constant throughout the wide range of larval numbers in the leaf. On the other hand, the supposed process of inverse density dependence during the tissue feeding stage was not proved by the graphic presentation for each mortality factor (Fig. 4). Although, the death rate due to the parasitism of *H. testaceipes* plotted against the number of sap feeders, which reflects the initial oviposition by this parasite, seemed bimodal (triangle in Fig. 3), such a trend was not detected by the plots against the number of tissue feeders which reflect the realized mortality rate during the tissue feeding stage (solid circle in Fig. 4).

(3) Distributions of deaths per leaf

Assume there are N_i leaves in numbers containing i living larvae before the operation of a mortality factor ($i=0, 1, 2, \dots, i_{\max}$), then after its operation, the N_i leaves will be divided into $i+1$ subclasses depending upon the numbers of deaths j ($j=0, 1, 2, \dots, i$). Denote the number of leaves thus newly classified as n_{ij} , i.e., n_{ij} stands for the number of leaves in a newly formed subclass which contains j deaths after the operation of a certain mortality factor on N_i leaves which contained i individuals before the operation. Then, if i individuals in a leaf are exposed independently

of each other's fate to a certain mortality factor, the frequency distribution of n_{ij} results in the binomial series;

$$n_{ij} = N_i \binom{i}{j} p_i^j (1-p_i)^{i-j},$$

where

$$p_i = \frac{\sum_{j=0}^i n_{ij} \cdot j}{N_i \cdot i}.$$

To test whether reduction of living larvae in numbers was occurring independently of each other, the observed frequencies of n_{ij} was compared with the relevant theoretical distribution for a fixed i . The numbers of classes tested were 13 for each mortality factor (i.e., $i=2$ to 14). Distributions due to parasitism of *H. testaceipes* were also compared with those of 0-truncated binomial distribution. For obtaining the 0-truncated binomial distribution, the probability of death (p_i) was estimated by the maximum likelihood solving for p_i which maximized the following equation:

$$L = \prod_{j=1}^i \frac{\binom{i}{j} p_i^j (1-p_i)^{i-j}}{1 - (1-p_i)^i}.$$

The reason we adopted the latter is that in the distribution of the mortality due to parasitism, the frequencies of leaves having zero deaths (we call it 0-term) may consist of leaves of two different natures which we can not distinguish from each other by appearances; the one is that of the leaves which in fact have been absolutely outside of parasite visits for one reason or another, and the other is that of the leaves which have really been subjected to the parasite visits but no host has been attacked.

Evaluation of fitness was made by chi-square test on the sets of the observed and expected distributions to check if it was reasonable to fit the binomial series to the observed frequencies as the statistical treatment. Having obtained the expected frequencies, the last few subclasses were combined so as to reach an expectation of at

Table 2. RESULT OF THE CHI-SQUARE TEST^a FOR FITTING THE FREQUENCY DISTRIBUTIONS OF THE SUBCLASSES TO THE THEORETICAL DISTRIBUTION

Initial No. of Larvae (i)	<i>H. testaceipes</i>		Cannibalism Binomial	Unknown/Tissue Binomial
	Binomial	0-truncated		
2	— ^b	—	—	—
3	$p \ll .005$	$.005 < p < .01$	—	—
4	$p < .005$	$.20 < p < .30$	—	—
5	$p < .005$	$.05 < p < .10$	—	$.10 < p < .25$
6	$.005 < p < .01$	$.30 < p < .50$	—	$.25 < p < .50$
7	$p \ll .005$	$.05 < p < .10$	—	$.75 < p < .90$
8	$p \ll .005$	$.30 < p < .50$	$.01 < p < .05$	$p < .005$
9	$p \ll .005$	$.10 < p < .30$	$p \ll .005$	$.25 < p < .50$
10	$.01 < p < .025$	$.10 < p < .30$	$.01 < p < .025$	$.10 < p < .25$
11	$p \ll .005$	$.10 < p < .30$	$p \ll .005$	$.75 < p < .90$
12	$p \ll .005$	$.10 < p < .30$	$p \ll .005$	$.10 < p < .25$
13	$.025 < p < .05$	$.025 < p < .05$	$.025 < p < .05$	—
14	$.01 < p < .025$	$.01 < p < .025$	—	—

^a Having obtained the expected frequencies, the last few classes were combined so as to reach an expectation of at least 5.

^b The chi-square test was not practiced due to the lack of the degrees of freedom.

Fig. 5. Examples of the frequency distributions of deaths for each mortality factor (histograms). Solid lines are for the binomial and broken line for the 0-truncated binomial. Numeral under the right end of the horizontal axis indicates the number of larvae before the operation of the mortality factor (i. e., i), besides the number of deaths per leaf. Significant test: P_0 for the 0-truncated and P for the binomial.

least 5. Results of the chi-square tests were summarized in Table 2 for each set of three mortality factors, *H. testaceipes*, cannibalism and the unknown of the tissue feeder. For the rest of the mortality factors, insufficiency of the degrees of freedom did not allow of the test.

Examples of the frequency distributions of deaths were shown in Fig. 5 for the case which can represent the pattern of each relevant mortality factor (i.e., $i=8$ for all mortality factors excepting the case for the unknown of the tissue feeder in which $i=7$ was chosen).

Holcathorax testaceipes

As mentioned above, *H. testaceipes* lays the egg into the host egg. Here, however, the host mortality during the egg stage was ignored and the frequencies of deaths were made based on the numbers of the sap feeder per leaf.

Annihilation of the host due to this parasite was observed in a small proportion of leaves that contained less than 6 hosts, but in the leaves which contained six or more hosts such a drastic case was not observed. The maximum parasitism per leaf did not exceed 8 in number. This partly explains the fact that the rates of the parasitisms did not increase in proportion to the host increase per leaf (Fig. 3). It was revealed that the distributions of deaths per leaf did not follow the binomial series. Compared to it the observed distributions were higher in the 0-terms and in the terms of the right-hand tails in all the cases.

All but three of the cases tested fitted the 0-truncated binomial distributions. Here, however, the observed frequencies were so persistently higher than the expected in the 1-terms and in the terms of right-hand tails that the observed variances were greater than the expected ones, which suggested that the deaths due to the parasitism

did not occur independently of each other but that some processes which produced contagiousness were laid behind.

From the life table for the 3rd generation in this orchard (SEKITA et al., unpublished), it was estimated that the emerged adult females of *H. testaceipes* amounted to as many as 25 per cent of the numbers of apple leaves. This suggests that, no matter how considerable proportion of the parasite adults had been lost for one reason or another, many leaves were visited by more than one individual of the parasite. Thus, the deaths on a certain leaf might result from the attacks due to consecutive parasite visits.

Therefore, for deeper understanding of the distributions of deaths per leaf, we should take into account 1) the host attack by the parasite at its single leaf visit and 2) the frequency of parasite visits on the leaf. Concerning the first point, SUGIMOTO (1978) has performed laboratory experiment for *Kratochviliana* sp. which parasitize the Ranunculus leaf mining fly, *Phytomyza ranunculi* SCHRANK. He found that 1) the female parasite visited its host larvae without discrimination between the presearched and unsearched mines, 2) the frequency of host visits was independent of the host density per leaf, 3) the probability that the parasite attacked living hosts changed according to the physiological condition of the female parasite and 4) the parasite attacked the host at random at a single leaf visit. Based on these observation, he formulated a model of host attack by this parasite at its single leaf visit. Such an analytical approach on each component involved in the parasite-host relationships is left for future studies.

Cannibalism

The distributions of deaths due to the cannibalism did not follow the binomial distribution. The observed distributions were higher than the expected one in the 0-terms and in the right-hand tails.

The more or less fixed forms of the mine cut out by the sap feeding larvae is delimited by the size of the veins. Thus, although the larvae are able to cleave small veinlets, they are not able to cleave larger ones. When they meet larger ones, rather than cleave their way they change their course along the vein until they meet another large vein or cross vein. Through such repeated processes, the more or less definite form of mine is constructed.

Thus, in the occurrence of the cannibalism, the two basic conditions must be met simultaneously: (1) the eggs are oviposited so close to each other that the resulting mines situate within the span of overlapping, and (2) there is not any obstructive vein between the eggs. As mentioned in the previous section, there is an aggregative tendency in the distribution of the sap feeding larvae on the leaf. This may increase the chance of occurrence of mutual contact of the mines. On the contrary, however, the 0-terms were conspicuously higher than the other terms within the range of normal density per leaf (i.e., $i \leq 8$). This suggests that some mechanisms are working effectively in averting the fulfillment of the two conditions mentioned above. We think that the presence of the veins in the leaf which delimits feeding area of the larvae is playing an important role.

Death from unknown causes in the sap feeder

Amongst the mortality factors tested, the mortality rate due to the unknown in

the sap feeding stage was the smallest. The chi-square test was not applicable for any set because of the insufficiency in degrees of freedom. In many sets, however, the observed frequencies were very close to the theoretical ones, suggesting that the occurrence of death was independent of each other.

Sympiesis sp.

The frequencies of deaths due to *Sympiesis* sp. were made based on the number of larvae per leaf which reached the tissue feeder stage. The evaluation of fitness to the theoretical distribution was not possible because of insufficient degrees of freedom for the chi-square test. In many sets (i.e., $i=2, 3, 5, 6, 8, 11$ and 14), however, discrepancies from the binomial series were very small.

From the life table for the 3rd generation, it was estimated that the proportion of the number of adult females to that of apple leaves was less than 5 per cent. Comparing this figure to that of *H. testaceipes*, it was very low. Hence, it might be very low in probability that a certain leaf had been subjected to more than one parasite visit. If this assumption is acceptable, the observed distributions reflect the number of eggs laid by a single visit. This implies that the parasite attacked the host at random per visit.

Death from unknown causes in the tissue feeder

In many cases tested, the deaths due to the unknown fitted the binomial series. This indicated that the deaths amongst the individuals in a certain leaf occurred independent of each other's fate. This finding is very important and will become a starting point for a clarification of true cause of the unknown. Thus, amongst three kinds of possibilities given in an earlier section (p. 140), we can at least make light of (3) or death due to diseases which will have a strong contagious nature.

CONCLUSION

Compared to the survivorship curves of other herbivorous insects, the following two points are characterized in *Ph. ringoniella*; (1) the rate of survival is higher in its earlier stages and (2) the rate of total survival from egg to adult is also higher, even if we take into account its relatively low fecundity (around 40 eggs per female).

In most free living herbivorous insects there are very vulnerable stages in their earlier stages. During this period, many hatchlings are lost due to failure in their establishment to feed or owing to the attacks of predators (e.g. DEMPSTER, 1975). Hence, the first characteristic may be attributable to the fact that risks attendant on the dispersal behavior (i.e., failure in the establishment and/or danger of being attacked by predators) are almost absent in *Ph. ringoniella* because the hatchling enters the leaf immediately after hatching to feed.

The second point is attributable to the protection effect through its mining behavior especially against predators and dispersion, because in many free living insects a noticeable amount of larvae fall a victim not only to parasite but also to predator during their feeding period and in some others the larvae crawl about for the sites of feeding, pupation or hibernation and many fail to find their requirement. On the other hand, deaths of feeding larvae due to the predator, if any, never reach noticeable amount in *Ph. ringoniella*, and they are completely free from any risk of dispersion.

The characteristics mentioned here must be important for this insects in maintaining high population levels throughout the apple growing areas in Japan.

The female moths tended to lay the eggs aggregatively on the leaf. This ought to increase the mutual contact of the mines but such a tendency was not observed. This suggests that some mechanisms reducing the chance of mutual contact of mines are working effectively. In the citrus leaf miner, *Phyllocnistis citrella*, the risk of mutual contact is averted through the adult oviposition behavior (MURAI, 1974). On the other hand, in the present insect, the presence of the veins which delimit feeding area of the larvae seems rather important.

The aggregative tendency arising from the oviposition persisted throughout all the stages (Fig. 1) although different kinds of mortality factors were operating in different ways upon them (Fig. 3 to 5). This was because of that, amongst the mortality factors, none excepting one, the cannibalism in the sap feeding stage, was operating density-dependently and even the cannibalism was not strong enough to change the distribution pattern from the contagious to random.

The characteristics of the mortality factors considered in the section (2) and (3) were summarized as below:

Mortality factor	Density relationship	Randomness
<i>H. testaceipes</i>	independent	no
Cannibalism	dependent	no
Unknown in sap feeder	independent	yes
<i>Sympiesis</i> sp.	independent	yes
Unknown in tissue feeder	independent	yes

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