THE INFLUENCE OF THE QUALITY OF THE FOOD ON THE EGG-PRODUCTION IN SOME INSECTS.

By

Dr. J. K. DE JONG

(Buitenzorg, Java).

INTRODUCTION.

In studying the gradation of insect populations, the economic entomologist has to face three problems, viz. the status of parasites, the climatic environments and the food conditions.

Although nearly every author on gradation in insect pests is fully aware of the fact, that the food must play an important role, it is nevertheless curious to see, how little work, compared with that carried out on the effect of temperature or of parasites, has been done in this line of research.

Now the investigation of the influence of food conditions upon the gradation in nature is not so easy. Not only is it necessary to take into account the quantity and the quality of the food-supply, but we must know further which part of this food can be utilized by the insects. If we take three insects, a bug, a beetle and a caterpillar feeding on the same leaf, the chemical analysis of this leaf will say us next to nothing of its influences on the rate of reproduction. Generally speaking the bug will only use the contents of the phloem, the beetle grinds up the whole leaf, but much of the contents of the different cells will pass the intestine not or only slightly digested, and again in caterpillars only those cells are used, that have been cut into two by the mouth-parts.

But here the chain of the different possibilities does not end. If we rear a plantbug and an aphid on the same leaf, we may assume, that the food they suck in both cases is the same. Nevertheless the result may be quite different. The aphid will thrive, when the food is high in carbohydrates, the bug shows its greatest fertility when the food is rich in albuminoids, thus showing that the same quality of the food may have a different effect on different species.

The quantity of the food although of prime interest in such animals as *Cimex,* plays in most cases only a role as soon as food is growing short, that is to say, when the damage has been done. The aim of the economic entomologist is to prevent such a calamity and what occurs afterwards is, as a rule, of small interest to him. In some cases however it may be necessary to know, which are the effects of shortage of food on the gradation in the following generations.

In tropical countries as a rule, we need not consider the quantity of the food. In many cases food is plentiful throughout the year; in other cases only during very definite periods in which the crop is grown or the seed ripens, but really devasted areas, where 100 % of the food available has been used by the insects, although they do occur, are very rare.

Field observation revealed the fact, that even adjacent plots might differ considerably in their liability to insect attack. The planter used to ascribe this to differences in the health of the plants. If we translate health by composition of the insect food, we may say that he is right.

The question then arises, which peculiarity in the composition of the insect food makes, that one plot is heavily infested, whereas another close by may be not or only slightly infected.

We know that the manuring will change the chemical composition of the leaf, thus another still more important question occurs to us; are we able to change the conditions for the food-plants to such an extent, that the liability to insect attacks diminishes. In other words, is it possible to combate insect pests by cultural measurements.

The literature on this subject, mainly dealing with the influence of manuring and tillage on the intensity of insect (and fungous) attack has quite recently been reviewed by BRAUN (1937), so that it is not necessary to discuss the different papers here. Some of them will be mentioned in connection with the experiments described hereafter.

The chief aim of this work was to ascertain if the influences of the quality of the food on the egg-production of insects, with the exclusion of the differences which are inherent to the use of different food-plants, could be large enough to be of interest to the economic entomologist. It is naturally divided in two parts, the first one deals with the behaviour of the insects on unmanured plants, the second with the effect which manuring of the plants ultimately has on the egg-production of the insects. The second aim was, if possible, to investigate the nature of these influences.

In this paper the behaviour of the insects on the unmanured plants are described.

The work was carried out at the Treub-Laboratory of the Botanical Gardens at Buitenzorg. Grateful acknowledgements must be paid to the Director

of these Gardens, Dr. K. W. DAMMERMAN, for putting a working table at the disposition of the author. Investigations with *Helopeltis* took place at the Tea Experimental Station Buitenzorg during the years 1932-34. Part of the results were published in the Archief voor de Theecultuur.

METHODS and MATERIALS.

When studying the influence of the variations in the quality of the food on insects, one should take care of an adequate control of all other conditions. That is to say, climatic and environmental conditions should be eliminated as factors affecting the egg-production or other phenomena that are likely to be studied.

Thus stress should be laid on the absolute necessity of allowing the food to vary only, the other conditions must remain as much the same as possible.

Unfortunately it was not possible to carry out the different experiments under exactly the same conditions. Temperature could not be kept constant, indeed it fluctuated from 25 to 30 degrees Celcius in the course of the day. Light conditions were apt to vary considerably. Only the relative humidity was kept constant at about 100 %.

For these reasons experiments taken at different times of the year could not be combined. Only a comparison between those run during the same period was allowed.

As a rule the insects were kept in glass vessels which were placed before a north window of the laboratory in such a way, that the direct sunlight could not enter them (in the months of May-August). The leaves which served as food were changed every morning between 8 and 10. A thoroughly wettened piece of cotton-wool was put on the base of each leaf to prevent it from loosing its turgor. In the case of *Helopeltis* small bottles were used, wherein the tea-shoots were placed. The vessels were closed, so that the living leaf combined with the wet piece of cotton-wool soon made the relative humidity rise to saturation.

In this way conditions other than food were the same for every individual insect included in the experiment. For every individual the temperature would vary in the same way and to the same degree. Table 1 *) shows the temperature during the months of September and November 1936.

Light conditions would only differ slightly. The relative humidity was always about 100 %.

This high humidity as a matter of fact is a distinct drawback in rearing insects. An absolute 100 % saturation, if it could be maintained long enough, might even proof fatal to a great number of insects. Specially troublesome was the high humidity when rearing larvae of *Helopeltis*. Working with caterpillars, the wet cotton-wool had to be left out in the fourth and fifth stages. The insects

*) **For table 1, 4 - 9, see the end of this paper.**

being then very susceptible to an excess of moisture. In one case larvae of *Euchromia horsfieldi* MR. were fed with leaves of *Ipomoea arborescens* DON. which were wettened by the rain that had fallen over night. Of the about 200 larvae only three gave moths.

Nevertheless it was thought necessary to keep the relative humidity high, because otherwise it would escape all observation. The evident disadvantages in rearing had to be taken into the bargain.

The leaves were always offered abundantly, so that the larvae or the imagines had not to shift for themselves in obtaining their food and could eat as much as they liked.

Another factor which is very important, is the effect of crowding upon the fertility of the insects. It was therefore absolutely necessary to use the same number of insects in glass vessels of the same form and of the same solid content.

Thus the only difference between the various vessels in one experiment was the quality of the food they contained.

The insects used in the experiments were *Helopeltis theivora* WATERH.; *Epilachna* sp. feeding on *Datura fastuosa* L.; *Tinolius eburneigutta* WLK.; and *Diacrisia strigatula* WLK.

To make things as simple as possible only one kind of food-plant was used in every experiment. In the case of *Helopeltis, Thea assamica* MAST. was used. *Epilachna* was fed with the leaves of *Datura fastuosa* L., *Tinolius* and *Diacrisia* got leaves of *Thunbergia grandiflora* ROXB.

The differences in quality were obtained by taking leaves of different age, by selecting different plants of the same species and by technical methods.

The first kind of food was the fresh full-grown leaf taken from the plant every day about 7.30 a.m.

Only one third of the leaves plucked were given as food to the insects under observation immediately. In the experiments it is indicated as leaf I.

One third was kept with the stalks in a glass jar with water over night and given to another collection of insects the following day. This is leaf II. The rest was kept for two days and given to still another collection of insects as leaf III.

The leaves that were kept aside to serve as food for the insects at the end of 24 or 48 hours after picking were placed on a table at a distance of at least two meters from the window. Here CO_2 assimilation was practical nil, and as respiration continued uninterruptedly, a constant decrease of the carbo-hydrates took place.

In this way we obtained three kinds of food differing chiefly from one another by the quantity of the carbo-hydrates. This being the highest in leaf I, the lowest in leaf III. Other chemical changes which might have taken place were not taken into account.

Apart from the full-grown leaves, half grown and very young leaves were used. They were always given in a fresh state. In the experiments they are indicated as leaf M and J.

In the case of *Helopeltis* only young tea shoots of a maximal length of about 15 cm could be used as food, so that the differences between old and young could not come into consideration. Here an other quality of the food was made, by cutting away in a full circle the bark of a branch at its base. This prevents the carbo-hydrates formed in the leaves to travel down to the roots. After some time the wood of the branch is full of starch. This has a very definite influence upon the young shoots growing above, as the formation of young leaves almost comes to an end apparently as soon as the quantity of carbo-hydrates reaches a definite level. Leaves from these branches are quite full of starch. In the experiments they are indicated as leaf A.

Experiments with *Epilachna*.

Imagines of *Epilachna* were captured in the Botanical Gardens on *Datura fastuosa* L. and made to oviposit on leaves of this plant in the laboratory. There was hardly any mortality in the egg-stage, the only trouble sometimes was the voracity of the newly hatched larvae. Even if fresh food was available, they showed more or less cannibalistic tendencies and ate the neighbouring eggs, which had not yet hatched. The high relative humidity may have favoured these tendencies.

190 of these larvae were placed in glass-vessels of 400 cc solid content, containing 9 or 10 larvae each. 95 of them were fed with fresh leaves of *Datura fastuosa* (leaf I), the others with leaves which had been kept for one day in the laboratory (leaf II). The first imago appeared 19 days, the last one 26 days after the larvae had hatched. The duration of the pupal stage was 4 days, thus the larval developmental period ranged from 15 to 22 days. The temperature during this period is shown in table 1.

Owing to the less favourable environmental conditions (the excessive humidity will have played an important role), the mortality during larval development was high. Only 38,6 % and 39,8 % respectively on leaf I and II reached maturity. These differences, only slightly in favour of leaf II, indicate that the quality of the food did not affect the mortality.

If we look at the duration of the larval period, we find a not very pronounced difference between the two lots. The mean developmental period is lengthened from about 21 days on leaf I to 22 days on leaf II. If however we take into account the great variability in the length of this period, ranging from 19 to 26 days, we cannot attach much importance to a mean difference of 24 hours.

The results of this experiment are computed in table 2.

Table 2.

		Duration of development from larva to imago Days								Mean developmental period
		19	20	21	22	23	24	25	26	
	Number of ♂	5	3	7	2					20.35 days
	Number of ♀		3	8	3	2	1			21.80 „
A.	Total number of both sexes	5	6	15	5	2	1			21.14 „
	Number of ♂	1	1	4	5	5	6	1	1	22,62 „
	Number of ♀		2	6	2	2	2	0	1	22,00 „
B.	Total number of both sexes	1	3	10	7	7	8	1	2	22.38 „

Duration of development of *Epilachna* larvae, from the hatching of the eggs to the emerging of the imagines. A. on leaf I. B. on leaf II.

We will not discuss the influence of the quality of the food on the duration of the larval period in general any further. In *Helopeltis*, the only difference was an increase of the larval mortality, whereas in caterpillars a definite lengthening of the period from egg to imago could be stated. We will see these results in the subsequent experiments, but as no general rule could be detected the mere mentioning of these facts must suffice.

We will now turn to the imagines reared in the foregoing experiment. They are of two kinds, those fed on leaf I and those grown on leaf II. As a matter of course they were kept separate. Half the number of the females originating from larvae kept on leaf I were fed with leaf I, the other half with leaf II. The females of the other lot were dealt with in the same way. At the end of the experiment it became evident, that in this case the quality of the larval food did not have any influence on the longevity and the fecundity of the adults. We will not therefore consider them separately here.

To these females were added 10 females from another stock, fed with fresh leaves, which were given leaf III as food, so that at the beginning of the experiment we had:

15 females kept on leaf I
16 „ „ „ „ II
10 „ „ „ „ III

Each female was placed in a glass vessel, such as had been used in rearing the larvae, and was allowed to mate. If the male died before the female, it was replaced by another one, so that cessation of oviposition, or sterility of the eggs could not be attributed to the absence of males. *Epilachna* copulates frequently in nature as well as in captivity, and continues to do so to the end of life.

Oviposition (in captivity) commenced as a rule on the 11th to 16th day of imaginal life and might go on uninterruptedly till death. Normally the eggs were laid once a day about the first hours of the noon. Their number ranged from 1 to 46.

For some reason as yet unknown a couple of females did not oviposit. We find such individuals in nearly every experiment. Perhaps they ought to be excluded when computing the results. If it had been done in this case, the differences between I and II would have been still more striking.

As it might be possible that the unability to oviposit was due to the sterility of the male, these were replaced in such cases by other males that had already successfully mated with other females.

In table 3 we find in a condensed form the results of this experiment, while in figure 1 egg-production is shown grafically.

The complete figures are given in table 4.

Table 3.

	Quality of the food		
	leaf I	leaf II	leaf III
Mean total number of eggs	356.—	261.75	134.—
Mean number of egg-cluster	20.5	16.55	13.41
Mean duration of imaginal life (in days)	36.2	40.6	39.7
Mean number of days on which the ♀♀ oviposited	17.6	15.8	10.—

Results of rearing *Epilachna* on different kinds of food (computed from the figures given in table 4).

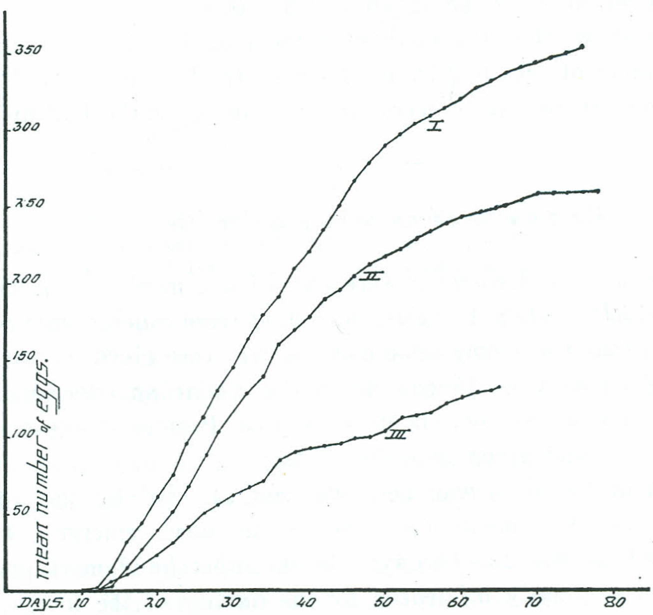

Fig. 1. Mean numbers of eggs laid by *Epilachna* when fed with: I fresh leaves, II 24 hours old leaves, III 48 hours old leaves.

We find that the duration of imaginal life is not or hardly affected by the quality of the food. Neither is the number of days elapsing from the beginning of oviposition towards the end of life. On the contrary, the number of days on which the female really oviposits diminishes from a mean of 17 and 16 days on leaf I and II to 10 on leaf III. In the same time the number of eggs laid dayly decreases from a mean of 14.8 and 10.1 to 5.7. The same is true for the number of eggs laid by one female. It may range from 1 to 46 a day, but the means on the different kinds of leaf are 20.5, 16.55 and 13.41 respectively.

Full evidence of this decreasing fertility is given by the total number of eggs. On leaf I this is 356, on leaf II this number is 262, whereas on leaf III it is only 134. The absolute numbers range on leaf I from 0 to 1149. On leaf II from 0 to 560 and on leaf III from 11 to 391.

The course of the egg-production is plotted in figure 1 where the mean subtotals of every second day are given.

During the first twenty days of oviposition there is not much difference between I and II, I being always a two-days egg-production in advance of II. But then gradually the differences become more and more pronounced and the result is, that the females fed with the fresh leaves yield some 36 % more eggs than those on one day old leaves. Looking at the curve, which represents the egg-production of the animals on leaf III, we see at a glance, that fertility is greatly reduced.

In conclusion we may add, that the eggs laid by the females on I and II all hatched, whereas on leaf III the number of dumb eggs gradually increased. The first twenty days of oviposition a certain number of eggs would hatch, but thereafter no larvae could be obtained from them.

These results show, that the quality of the food had a very definite influence on the number of eggs laid by the females. In this case these differences in quality were mainly due to a decreasing amount of carbo-hydrates in the leaves.

Experiments with *Helopeltis*.

The experiments with *Helopeltis* were carried out much in the same way as those with *Epilachna*. Only the glass jars used were much larger (4000 cc) owing to the fact, that the young tea-shoots, which were given as food, had a total length of at least 10 or 15 cm. As in the *Epilachna* experiments fresh material and one or two days old shoots were used. Besides shoots were taken from ringed branches and given in a fresh state.

The duration of larval development was not affected by the quality of the food. In all the experiments the time of the larva emerging from the egg to the last ecdysis was 12 - 14 days. On the other hand mortality during the larval period was greatly influenced by the quality of the food.

Helopeltis larvae are rather susceptible to high relative humidity, so mortality, even in cultures with the most suitable kind of food, often exceeded 30%.

If fed on leaf II, this percentage would go up to 70 or even 90 and on leaf III in every case it was 100. No larvae could be reared on tea-shoots that had been kept for 48 hours in the laboratory. On leaf A the mortality was about 50%.

The quality of the food as offered by leaf II and III thus proved to be unsuitable for rearing the larvae. But not only the larvae died on these leaves. The imagines too succumbed in due course. Fed on leaf III they would die within 10 days, without laying any eggs. Fed on leaf II duration of life was maximal 23 days, but the number of eggs would still be small. Only in one kind of experiment better results could be obtained.

Very soon after the last ecdysis copulation takes place and the mature female may even start ovipositing on the third day, continuing to do so to the end of life.

As a rule the first eggs are laid on the sixth day or even later still. By means of an ovipositor the eggs are sunk into the tea-stalk, and only two tiny hairs arising from the surface betray its place. Temperature records are much the same as in the experiments with *Epilachna*, so there is no use to give them here.

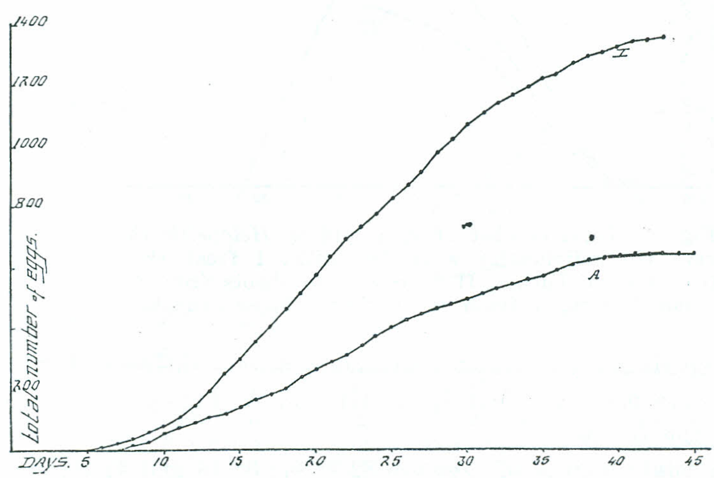

Fig. 2. Total number of eggs by *Helopeltis theivora* (13 individuals each) when reared on: A. tea-shoots from ringed branches; I fresh shoots form normal bushes.

In figure 2 the egg-production is given from *Helopeltis theivora* feeding on leaf I and leaf A. The curves are computed from the data given in table 5. The mean number of eggs was 104 and 50 respectively, the mean longevity 34.8 and 28.8 days.

We see that an increase of the quantity of carbo-hydrates in the food results in a definite decrease of the total number of eggs and even in a decrease of the duration of life.

Another experiment, the data of which are given in table 6 is shown grafically ni figure 3. Here three kinds of leaf were used, viz. leaf I, leaf A and leaf II. As in the foregoing experiment leaf I yielded better results than leaf A. On leaf II egg-production was very poor. The mean total number of eggs was

64.1, 41.8 and 23.25 on leaf I, A and II respectively. Duration of life in the same order 24; 20.6 and 15.2 days.

Compared with leaf I, leaf A has a greater, leaf II a smaller amount of carbo-hydrates. We find, that in both cases egg-production as well as duration of life decreases. An explanation of this phenomenon is only possible if we also take into account the available amount of albuminoids.

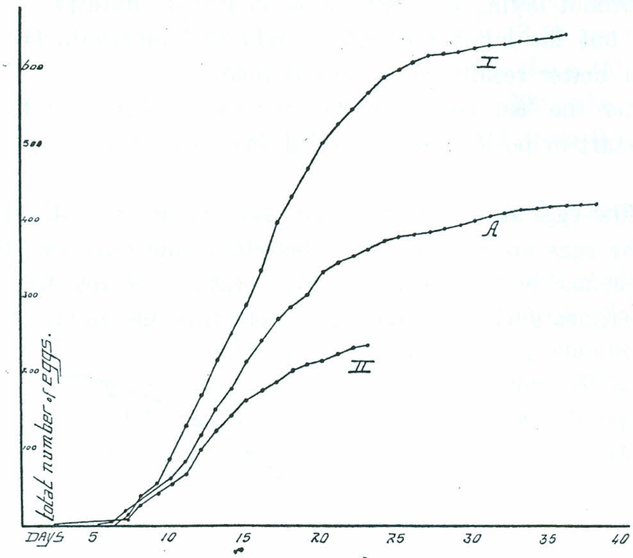

Fig. 3. Total number of eggs laid by *Helopeltis theivora* (10 individuals) when fed with: I fresh shoots from normal bushes, II 24 hours old shoots from normal bushes, A fresh shoots from ringed branches.

A third experiment yielded at first sight entirely different results. Four kinds of leaf were used, viz. leaf I, II, III and A. Figure 4 compiled from table 7 shows the results.

The mean total numbers of eggs are 82.7; 111.6; 18 and 42.4 respectively, the longevity 25.7; 36.3; 15.6 and 26.6 days. In the other experiments it was always leaf I that gave the best results in rearing *Helopeltis,* but here we find that leaf II is much better than leaf I and even that leaf III is not so bad as might be deduced from the other experiments.

To a good understanding of these facts it is necessary to enter into some details. The quality of the tea-shoots offered as food to *Helopeltis* is apt to vary considerably throughout the year. These variations are partly due to the changing of the monsoons, but for the greatest part they find their origin in changes which occur in the bushes themselves.

Every second year the tea-bush is pruned down. The picking of the leaves used for the manufacturing of tea is started some months after this pruning and continues until the bushes become too high, thus are ready for the following pruning. It is evident that the intensity with which the picking of the leaves takes place, must exert some influence on the tea-bush. Eventually, when the plucking were too severe the bush would die in the long run. On the other hand if leafpicking was stopped for some time, the bush is not stimulated to form new off-shoots and will then proceed to form starch reserves in the wood of roots and stems. This was the case in our experiment where four kinds of leaf were included. The shoots, with the exception of leaf A, originated from un-

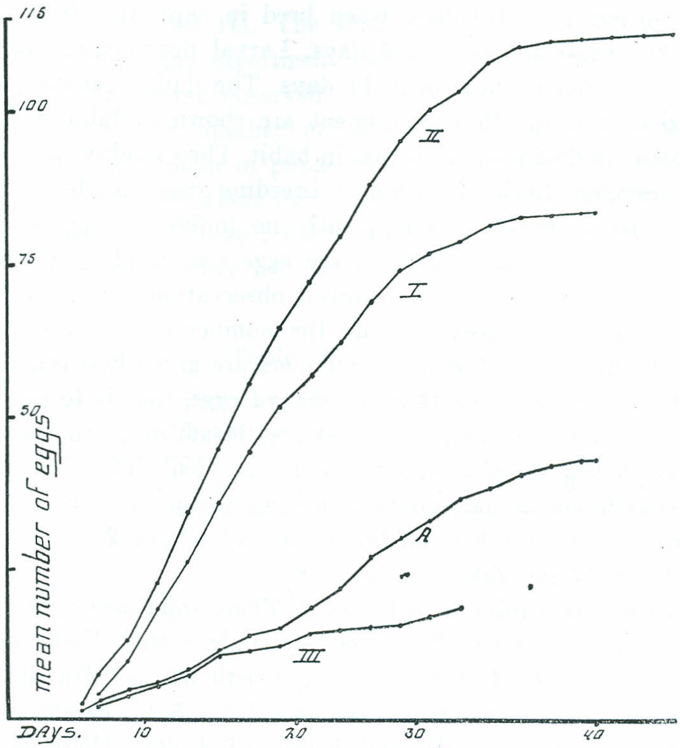

Fig. 4. Mean number of eggs laid by *Helopeltis theivora* when fed with: A fresh shoots from ringed branches, I fresh shoots from unplucked bushes, II 24 hours old shoots from unplucked bushes, III 48 hours old shoots from unplucked bushes.

plucked bushes, thus giving quite another quality of food to *Helopeltis* than those from normally plucked gardens.

In the experiments with *Epilachna* we found, that a decreasing amount of carbo-hydrates in the food resulted in a decreasing fertility of the adults. Here we are acquainted with a new fact. Starting from what we might call an optimum of the carbo-hydrates a decrease as well as an increase of the quantity of the carbo-hydrates results in a decrease of the total number of eggs. The second fact is important from the economic point of view. We found that rearing *Helopeltis* on shoots taken from bushes which were left unplucked for some time gave results, that differed entirely from those obtained on leaves originating from normally plucked bushes.

This is an indication that the differences in insect attack, which we sometimes observe even in adjacent plots may be due to differences in the plants, that is, in the composition of the food they offer to the insects.

The experiments with *Tinolius* and *Diacrisia* will show us other examples of this kind.

Experiments with *Tinolius*.

Tinolius offers no difficulties when bred in captivity. In Buitenzorg the duration of the egg-stage is 5 or 6 days. Larval development takes place in 26 - 48 days. The pupal stage lasts 14 days. The daily maximal temperatures during the period of the first experiment are shown in table 8.

The moths are distinctly nocturnal in habit. They readily mate and oviposit soon after emerging. Lack of sufficient breeding cages made it impossible to keep the females separately; consequently no individual egg-counts could be carried through. The absolute total of the eggs was divided by the number of females. Individual variation thus escaped observation. After the females had died, the abdomen was dissected and the number of ripe eggs it contained, counted. In the different tables these numbers are given between brackets. The other figures give the absolute total number of eggs, that is to say, the number of eggs found in the abdomen of the females is added to the number of eggs laid by them. A few females were killed by accident. This explains the great number of eggs found in the abdomen in some instances (table 10).

The caterpillars were kept in large glass vessels of 2500 cc solid content, containing 16 or 17 individuals each.

As food were used full grown leaves of *Thunbergia grandiflora* ROXB., with a minimum length of 14 cm. As in the experiments with *Epilachna* they were used in the qualities I, II, III. Besides a fourth and a fifth quality was included by using half grown leaves ranging from 5 to 10 cm in length and very young leaves with a maximal length of 4 cm. These are the leaves M and J.

In contradistinction with the results obtained in the experiments with *Epilachna* and *Helopeltis* we find here a very definite influence of the quality of the food on the duration of the larval development. We need not be surprised at this. Most caterpillars are very susceptible to changing conditions whatever they may be, and the length of the larval developmental period consequently is very variable. Even in lots where circumstances were likely to be much the same a fortnight might elapse between the first and the last moth emerging from the cocoon.

It is not improbable that crowding has played an important role here.

Table 9 shows the number of moths that emerged each day. There is not much difference between J, M and I, although if plotted graphically, J would show a slight retardation compared with I and M, II and III show a very definite lengthening of the developmental period of about 5 to 6 days. Experiments with *Diacrisia* showed similar results. There leaf II gave the shortest developmental period. It turned out in every experiment with *Tinolius* as well s with *Diacrisia,* that the food that gave the highest egg-production showed t the same time the shortest developmental period. For the present we will onfine ourselves to the mentioning of these facts and refrain from a further iscussion.

Turning now to the egg-production of the female moths, we find (table 11), hat there is not much difference between M and J. Same as in *Epilachna* we ind a decrease towards II and III. The smallest number occurs in J. The quality of the food used in this experiment had no influence on the hatching of the eggs. No dumb eggs were observed.

In order to compare the number of eggs laid in captivity with that produced in nature a great number of pupae was collected from the same food-plants on exactly the same spot where each day the leaves were plucked, which were used in the experiments. These pupae yielded 21 females together laying 11616 (114) eggs. (For the number between brackets see table 10).

Table 10.

Quality of the food						
J	M	I	II	III	B	B'
0	12	5	10	0	0	25
0	109	0	0	0	52	72
0	7	0	17	0	0	3
0	0	10	1	0	24	0
0	0	0	5	0	0	0
0	1	0	12	9	0	0
0	0	0	0	7	19	0
0	21	2	0	3	0	0
0	0	0	0	0	0	0
0	200	11	0	0	0	0
	97	2	0	0	0	0
	165	0	11	35	11	0
	193	0	1	4	1	1
	147	0	0	0	7	0
	0		0	23	0	6
	3		0	8	0	0
	0			7	0	0
	0			0	0	0
				0	0	3
				0	0	0
				0	0	
				0		
				0		
				0		
				0		
0	955	30	57	96	114	110

Number of ripe eggs found in the ovary after dissecting the abdomen of the dead females. B = moths from pupae found in the *Thunbergia* hedge, B′ = moths from pupae found on normally growing plants.

Table 11.

Quality of the food	Number of ♀♀	Total number of eggs	Mean number of eggs per ♀
J	10	1667	167
M	18	6010 (955)	344
I	14	4598 (30)	329
II	16	4193 (57)	262
III	24	5048 (96)	210

Number of eggs laid by *Tinolius* on different kinds of food. For the numbers between brackets see table 10.

This is 552 for each female or about 200 more than in the most favourable food-conditions in the laboratory. It may be due to several causes, more suitable climatic circumstances and better food. (The chemical composition of the leaves probably changed immediately as soon as they were separated from the plant). The chief reason however will be, that captivity had a very marked effect on the rate of food consumption. The amount of food taken by the caterpillars in captivity, living under experimental conditions is appreciable much less than in nature.

Towards the end of this experiment I came across the original stand of *Thunbergia* in the Botanical Gardens, where the plants were allowed to climb high up into the trees. The leaves which were used in the experiments were gathered from *Thunbergia* growing as a hedge which was pruned down as soon as it grew too high.

It looked as if the plants on the original stand were far less affected by *Tinolius* than the hedge-plants. A more careful examination seemed to confirm this first impression, because there were far more injured leaves on the hedge than here. As it was too late to include the leaves into the experiment, a great number of cocoons was collected. From 20 of these emerged females, which in due course laid 8255 (110) eggs, giving a mean of 418 eggs for each female. This is 139 less than the number of eggs laid by the moths feeding on the hedge. It is hardly possible that the micro-climatic differences could account for this. The places where the plants grew were only 200 m apart, the diversity in temperature and in relative humidity could only be slight. The insolation of the hedge was more intense, but it is highly improbable that these direct climatic influences on the caterpillars were large enough to affect the egg-production on such a scale. Thus the most probable explanation was to assume a marked diversity in the quality of the leaves. Experiments with *Diacrisia* subsequently proved that this assumption was right.

The following experiments merely confirmed the results which were obtained in the first one. As a rule leaf M yielded slightly better results than leaf I, but not always. Table 12 shows an experiment where feeding with leaf I gave more eggs. The difference as a whole is small and not very convincing. On the very young leaves only one female emerged from the pupae. This is not due to an extremely high mortality, but to the fact, that the 11 other moths were males.

Table 12.

Quality of the food	Number of ♀♀	Total number of eggs	Mean number of eggs per ♀
J	1	100 (61)	100
M	8	1887 (76)	236
I	5	1220 (90)	244
II	13	2385 (218)	183
III	7	1071 (412)	167

Number of eggs laid by *Tinolius* on different kinds of food (27-X-37); numbers between ( ) are the eggs found in the ovary after the moth had died.

Experiments with *Diacrisia*.

The experiments with *Diacrisia* were run in exactly the same way as those with *Tinolius*. The caterpillars are rather polyphagous. They feed also on *Thunbergia*, but whereas *Tinolius* is found on the younger leaves, *Diacrisia* prefers the older ones.

Experiments were started with some 200 eggs found on a leaf of *Thunbergia grandiflora* in the Botanical Gardens. After hatching the larvae were kept on fresh full-grown leaves for 12 days. Then they were divided into 5 lots containing 40 caterpillars each and kept in glass vessels of 2500 cc solid content. The five different kinds of food were again I, II, III, M and J leaves from *Thunbergia grandiflora*.

No difficulties in rearing were met with, excepting the caterpillars kept on leaf J. Indeed of the 160 caterpillars kept on leaf I, II, III and M 159 gave moths. Rearing on leaf J was not so successful. When most of the caterpillars of the other groups had pupated, these had only reached half the size of the full-grown larvae. Therefore, on the 33 day after hatching, the food was changed again into fresh fullgrown leaves. Of the 40 caterpillars only 27 pupated. 18 of these pupae gave moths. The retardation in the development amounted to 10 or 11 days.

Working with *Diacrisia* is very convenient. The moths are completely nocturnal in their habits, simulating death in daytime even when they are touched and moved from one vessel to another. They copulate and oviposit freely in captivity and the total number of eggs will perhaps exceed one thousand if the caterpillars are kept on suitable food in proper conditions.

In the Buitenzorg climate the egg-stage lasts 5 to 6 days. Larval development takes place in 25 to 35 days, whilst the pupal stage takes 11 to 12 days.

As in the experiments with *Tinolius* no individual egg-counts could be made. After the females had died the abdomen was dissected and the ripe eggs in the ovary counted. In the different tables their numbers are placed between brackets. During the first experiment many moths were put into the alcohol by mistake. The animals simulated death so completely, that the error appeared only when it was too late.

Table 13.

Quality of the food	Number of ♀♀	Total number of eggs	Mean number of eggs per ♀
I	27	13810 (708)	511,5
II	17	10638 (495)	625,8
III	18	9888 (876)	549.3
M	20	9167 (855)	458.3
J	7	1689 (706)	241,3

Number of eggs laid by *Diacrisia* on different kinds of food (8-X-37). The number between ( ) are the eggs in the ovary after the death of the female.

The results of this first experiment are shown in table 13. During the first 12 days of larval life the caterpillars were fed with fresh full-grown leaves. In the following experiment the different kinds of food were given immediately after the hatching of the eggs. As could be expected from the results of the first experiment, rearing on leaf J was impossible. But not only leaf J, leaf M also proved to be very unsuitable as food for the young caterpillars. Mortality directly from the beginning was very high and eventually from the 50 larvae only 8 pupated, but gave no moths.

On the leaves I, II and III also rearing was not so successful as it had been in the first experiment. As a matter of fact more than 50 % of the caterpillars died before they were able to pupate. This was due to a change in the climate. During the first experiment temperature had been rather high and relative humidity low. Then a change occurred and the next two months a rather wet period was experienced, with a temperature that was approximately 1½ or 2 C^0 lower than in the proceeding period. The high relative humidity combined with very turgescent leaves, which were not completely dry on the surface, made the caterpillars very susceptible to fungous attack.

The results as to the total number of eggs are rather poor. The differences between I, II and III are still more striking than in the foregoing experiment. But they are computed from a much smaller number of individuals and therefore not so convincing.

Table 14.

Quality of the food	Number of ♀♀	Total number of eggs	Mean number of eggs per ♀
I	11	3137 (489)	313.7
II	8	3824 (183)	478.—
III	15	4313 (1280)	287.5

Number of eggs laid by *Diacrisia* on different kinds of food (22-XI-37). The numbers between ( ) are the eggs contained in the ovary after the female had died.

If we compare the results with those obtained in rearing *Tinolius*, we find a striking difference. In *Tinolius* the best results were obtained on the young and on the full-grown leaves, whereas *Diacrisia* could not or hardly be brought to maturity on the young and half-grown leaves. This is about what could be expected from the differences in the life habits of the caterpillars in nature. *Tinolius* being found on the young leaves, *Diacrisia* on the older ones. That however in *Diacrisia* leaf II and not leaf I should turn out to give the best results was rather something like a surprise. Looking at the figures of table 13, we find that not only II gives more than 100 eggs more than I but that even III surpasses I with a mean of 38 eggs.

Table 14 shows us slightly different results in so far that now I gives 26 more eggs than III. The differences between II and I are still more striking. It is remarkable that in III 2 moths evidently failed to oviposit and that 4 more only laid a certain part of their eggs. The number of eggs contained in the ovary of each individual moth are: 294, 324, 184, 202, 204, 72, 13, 15, 7, 3, 0, 0, 0, 0, 0. This is very exceptional. Although in every group of individuals we may find one or two with one hundred or more eggs, the majority have none or only very few. The cause of this phenomenon is unknown. As a result of these two experiments (and a third merely confirmed them) we find that the best kind of food for the caterpillars of *Diacrisia* is offered by leaf II. When fed with leaf I or with leaf III the number of eggs falls down sharply. Between these two kinds of food there is not much difference. In the first experiment leaf III gave the better results; in the second one feeding with leaf I gave more eggs.

About the same time as the second experiment a large scale experiment was run, including some 600 caterpillars divided into 6 different lots. This experiment was started a fortnight earlier, so that the young caterpillars did not suffer from the extreme wetness, that proved so fatal to many larvae some 20 days later. The change of the weather did not affect the half-grown caterpillars to such an extent, alhough in one case mortality was as high as 31 %.

As mentioned in the description of the experiments with *Tinolius* the female moths reared from pupae collected in nature from a *Thunbergia* hedge gave appreciably more eggs than those collected from the free growing *Thunbergia* plants. Leaves of the hedge-plants and of the normally growing plants were included into one experiment, and as lack of suitable glass vessels did not allow me to use more than 6 different kinds of food, the half-grown leaves (M) were omitted. The results are shown in table 15. A represents the leaves taken from the hedge, B those from the free-growing plants.

Table 15.

Quality of the food		Number of ♀♀	Total number of eggs	Mean number of eggs per ♀
	I	31	13880 (529)	447.7
A	II	40	21329 (811)	533.2
	III	37	15523 (767)	419.5
	I	39	14352 (485)	368.—
B	II	41	18020 (680)	439.5
	III	29	14231 (533)	490.7

Number of eggs laid by *Diacrisia* on different kinds of food (8-XI-37). The numbers between ( ) are the eggs contained in the ovary after the female had died.

In A we find the same results as in the two foregoing experiments. Here again I gives slightly more eggs than III. II is distinctly better.

B shows us quite different results. Compaired with A, I and II show a decrease of the mean number of eggs. In I this is about 80, in II more than 90. Considering the behaviour of the moths of *Tinolius* on these two plants, we might have expected such a decrease. If we look however at the number of eggs laid by the female moths grown upon leaf III we find instead of a decrease a very definite increase of the mean number of eggs. III reaches nearly the same level as II in the A series.

In B we find an increasing number of eggs from I to III, whereas in the other experiments this order was III-I-II or I-III-II. The experiments in B thus give us results, that are just the reverse from what we found in *Epilachna* and in *Tinolius*. There a decreasing quantity of carbo-hydrates gives an increasing number of eggs, here a decreasing quantity gives an increasing number of eggs. The other experiments with *Diacrisia* show agreement with those with *Helopeltis*, where we found that a decrease in the quantity of the carbo-hydrates gave at first an increase of the number of eggs, followed by a decrease. The successive series II-I-III in *Diacrisia* is the same as I-A-II in *Helopeltis*.

Discussion.

If we review briefly the results described above, we find, that the differences in fertility are in most cases very pronounced. These differences are entirely due to the changing quality of the food.

The first conclusion therefore is, that the influence of the quality of the food under experimental conditions is large enough to be of interest to the economic entomologist.

Are these differences also large enough in nature?

We are allowed to answer this question in the affirmative.

In our experiments the following facts were brought to light.

In *Tinolius* we found a difference of about 150 eggs between the individuals feeding on the same kind of food-plants, but which were growing on different localities. The like was found true when rearing *Diacrisia* on the same kinds of leaf.

In *Helopeltis* we saw, that in some cases leaf I, in other cases leaf II would give the better results. These leaves came from quite different plots in the garden, the one being plucked normally, whereas the other was left unplucked.

We might further draw attention to the work of Mahdihassan on lac. Although not procuring exact data on the correlation between the food and the fertility of the insects, it is quite obvious that the quality of the food is the most important factor in lac-production.

It is possible to cite a great many more authors on economic-entomological subjects, all supporting the idea, that the food may have played an important role in the gradation of the pest. The few examples however will have made it clear enough, that the differences in the total number of offsprings are so great, that they will account for nearly every change in the total number of individuals of the insect populations, that may occur in nature. We will not pretend that these changes in every case will be due to food-effects, but in many cases they are.

At any rate we come to the conclusion that the plants growing on different localities (be they even adjacent), may have a distinctly different food value for the animals feeding on them, so that consequently the concerning insects show great diversity in their fertility.

Considering our figures, they warn us, that we must be very careful with the interpretation of field observations. So in many localities in Java during the dry season different kinds of mealy bugs increase their numbers to an astonishing amount. As a rule it is thought, that this is due to climate influences, viz. higher temperature and lower relative humidity, but as the plants themselves undergo the influence of the dry monsoon too, we have the same right to ascribe the flourishing of the mealy bug family to favourable food conditions e.g. higher carbo-hydrate content. It is obvious that in such cases only careful laboratory experiments can tell us which part is due to the direct climatic influences and which part to food-effects.

Another point we may draw attention to is the fact, that different species react differently on the same kind of food. In our experiments we saw already one example in the cases of *Tinolius* and *Diacrisia*. As in nature the first species shows a preference for the younger leaves, the latter for the older full-grown ones, it was not very surprising that *Tinolius* was most fertile on young leaves (leaf M) and *Diacrisia* on older ones. If we only take into consideration the leaves I, II, III, we find that *Tinolius* shows decreasing fertility in this order, whereas in *Diacrisia* (in one instance) the total number of eggs increased using the same leaves in the same order.

Another example of this is found when rearing *Toxoptera aurantii* B. D. F. on tea. If we compaire the life habits of this species with those of *Helopeltis* we find, that they both feed on the same kind of leaves, that is to say on the young shoots and even on the expanding buds. Nevertheless we seldom find the two species together on the same plant.

In one experiment *Toxoptera* was reared simultaneously with *Helopeltis* and on exactly the same kind of food. The results for *Helopeltis* have been discussed above, they are shown in figure 4 and in table 7.

In table 16 the mean totals are given again, together with those obtained when rearing *Toxoptera.*

Table 16.

Quality of the food	Mean number of offsprings *Helopeltis*	*Toxoptera*
A	42,4	46.6
I	82,7	46,6
II	111.6	12.2
III	18,—	0.—

Mean total number of offsprings of *Helopeltis* and of *Toxoptera* grown on four different kindts of tea-shoots.

The fertility of the insects on the different kinds of food disagrees in every point, excepting perhaps that the lowest fertility in both cases is found on leaf III.

As the two species are found on exactly the same spots in the tea-bushes and thus probably suck the same kind of juices, this example clearly shows us, that every species reacts on the different food-qualities in its own specific way.

If we now turn our attention to the differences in the quality of the food, we will for the present rule the young and the half-grown leaves (J & M) out and confine ourselves to the leaves I, II, III and A.

Leaf I was taken every morning from plants growing in the garden and given as food to the insects immediately. Part of the leaves plucked were kept in the laboratory for 24 or 48 hours, before they were used as food, thus giving the leaves II and III. Leaf A was obtained by ringing a branch and using the leaves growing above this wound as food.

Starting from leaf I as the normal kind of food, leaf II and leaf III differed from it by a diminishing content of carbo-hydrates. Whatever might be the chemical composition of leaf I, leaf II always contained less carbo-hydrates and in leaf III this quantity was still smaller. On the other hand, leaf A as compared with leaf I always showed an increase of the carbo-hydrates content. In the experiments where these four kinds of leaf were used we had consequently a series of food with diminishing quantities of carbo-hydrates from A via I to III.

If we pass under review the results of our experiments in regard to the carbo-hydrate content of the leaves, we find:

1) In *Tinolius* a decreasing fertility when using the leaves I-II-III.
2) In *Epilachna* a decreasing fertility when using the leaves I-II-III.
3) In *Toxoptera* a decreasing fertility when using the leaves A-I-II-III.
4) In *Diacrisia* an increasing fertility when using the leaves I-II-III.
5) In *Helopeltis* an increasing, after that a decreasing fertility when using the leaves A-I-II-III.
6) In *Diacrisia* an increasing, after that a decreasing fertility when using the leaves I-II-III.

Or in other terms:

when the quantity of the carbo-hydrates in the food diminishes the fertility of the insects:

1) decreases in *Epilachna, Tinolius, Toxoptera.*
2) increases in *Diacrisia.*
3) increases, after that decreases in *Helopeltis* and *Diacrisia.*

It is clear, that if we try to explain these facts, it is absolutely necessary to take at least into consideration the available amount of albuminoids. It will be seen by the discussion of the manuring experiments (in a subsequent paper) that the ratio between the carbo-hydrates and the albuminoides in the food plays an important role, although things are largely complicated because the quantity of the food taken by the insects is not the same when using different kinds of leaf.

For the present we will simply draw attention to the fact, that the available amount of carbo-hydrates plays an important role, and that somewhere there seems to be an optimum, different for each separate species, on which the insects thrive best.

Buitenzorg, February, 1 1938.

LITERATURE.

ANDERSEN, K. TH. Der Einflusz der Umweltbedingungen (Temperatur und Ernährung) auf die Eierzeugung eines Insekts (*Sitona lineata* L.) mit postmetaboler Eientwicklung und langer Legezeit. Z. angew. Ent. 20 1933, p. 85 - 116.

BRAUN, H. Die Aufgaben des Pflanzenschutzes. A. Kulturmasznahmen. In SORAUER's Handbuch der Pflanzenkrankheiten VI, 1937.

ERGLE, D. R. Carbohydrate content of cottonplants at different growth periods and the influence of fertilizers. J. Am. Soc. Agron. 28 1936, p. 775 - 786.

HERFORD, G. M. Observations on the biology of *Bruchus obtectus* SAY with special reference to the nutritional factors. Z. angew. Ent. 22 1935, p. 26 - 50.

HOFFMANN, C. Der Einflusz von Hunger und engem Lebensraum auf das Wachstum und die Fortpflanzung der Lepidopteren. Z. angew. Ent. 20 1933, p. 51 - 84.

MAHDIHASSAN, S. Predisposing factors and infection by lac and other scale insects. Z. angew. Ent. 23 1936, p. 265 - 280.

MAHDIHASSAN, S. The range of host-selection and the specific differentiation of lac and other parasites. Arch. Naturgesch. N. F. 5 1936, p. 1 - 22.

PARK, F. Studies in population physiology VI. The effect of differentially conditioned flour upon the fecundity and fertility of *Tribolium confusum* DUVAL. J. exp. Zool. 73 1936, p. 393 - 404.

REH, L. Düngung und Insektenbefall. Z. angew. Ent. 3 1916 p. 133.

TITSCHACK, E. Experimentelle Untersuchungen über den Einfluss der Massenzucht auf das Einzeltier. Z. angew. Ent. 23 1936, p. 1 - 64.

VICKERY, H. B.; PUCKER, G. W.; LEAVENWORTH, C. S. & WAKEMAN A. J. Chemical investigations of the tabaccoplant. V. Chemical changes that occur during growth. Connecticut Agric. Exp. St. Bull. 374, 1935.