Studies on the population increase and the movements of soybean aphid, *Aphis glycines* MATSUMURA.

I.   On the two types of population increase[1].
II.   On the movements from plant to plant[1].

Y o s h i a k i I t o

In recent years there have been many experimental studies on the multiplication of insects, which has led to the understanding that under specific conditions the growth of an insect population follows the logistic curve as proposed by Verhurst and Pearl. In addition, many mechanisms for this phenomenon have been posited. According to Uchida (1949), insect population growth follows an S-curve rather than being linear because as the population density increases, the adverse effects of high population density, such as reduced fecundity and increased mortality or the mutual interference by individuals as in the case of the *azuki* bean beetle (*Callosobruchus chinensis*), intensify.

However, because all of these experiments were carried out in environments which can be considered 'self-sustaining' systems, limited both in space and in amount of plant material, it is not known if the same mechanisms occur in nature. Morishita's (1950) observations show that different mechanisms do occur in nature; the many experiences of pest-control attest to the differences between controlled and natural environments.

This study attempts to clarify this point by investigating the pattern of population growth of insects that are allowed a certain freedom of movement in a semi-open environment. We would like to express our appreciation to Tou Kawata, Yuasa, Shizuo Kato, Shuji Ishikura (Technical officers of the Agricultural Technology Research Institute, Entomology Section), for their guidance and support, Prof. Toshiro Uchida (Dept. of Agricultural Sciences, Kyoto University), and Shoji Hashiguchi, for his instruction on calculating saturation population density (K) using all data points rather than the traditional four points.

I. The two patterns of population growth

Materials and Methods

Kagawa no.13 soybeans were planted into pots (diameter 13cm, height 12cm) filled to 80% with a mixture of unfertilized field soil (3 parts) and sand (1 part). Except for watering and propping, no special maintenance was conducted; branches from the 3rd, 4th,

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[1] Presented at the 1951 *Nihon-Konchu-Gakkai-Taikai* [National Conference of the Japanese Entomological Society]. Although the first section of this paper represents the first investigation of aphid multiplication, due to various circumstances, it was published after a second paper reporting on the same experiment on wheat (1952), and another paper which includes discussion of this experiment (1952a). Please refer to these other papers.

and 5th leaves[2] were retained, and the others pruned. (There is a pilot study in which the cultivar *Itachi* was used). One juvenile aphid from a batch of aphids borne from a single alate vivopara that was captured on June 10th, was placed on each of 4 leaves of each soybean plant, and the subsequent multiplication was investigated. Each pot was covered with a glass case (height 50cm, diameter 25cm) and placed on the roof; the number of aphids on each leaf was counted at regular intervals. Description of the environmental conditions of the experiment are omitted here as they were nearly identical to ambient conditions for the duration of the study (September ~ November, 1950; pilot study July and August).

Results

One- to 2-day-old juvenile aphids were placed on the upper surface of each of four leaves of each soybean plant as the leaves began to open (September 5th). One to 3 days after successful colonization of the leaf, the juvenile aphids developed into apterous vivopara and began to bear young (Figures 1 and 2). The aphids continued to spread to higher leaves as soon as they emerged, up to the seventh leaf. The aphid population increased as seen in the figures. The population maximum was reached while the seventh leaf was young (September 28th ~ 30th). At this point, the populations ranged from 30 to 150, and the average saturation density (K) was an estimated to be 100 aphids. The population of the 7th leaf stopped increasing at about September 30th, and either remained static or began to decrease. At the same time, aphids spread almost instantaneously to leaves 1 ~ 6, which for the most part had not yet been colonized. This migration occurred nearly simultaneously, and was a mass event distinctly different from a small-scale chance occurrence. The movement of aphids on the plants is described in table 1. Of course, because the aphids moved along the stem, in some cases it was possible to see a peak stem population lagging the peak on the 7th leaf, which was followed by dispersal onto the lower leaves. The migration included both adult and juvenile aphids; however, the ratio is not clear. Over-saturation of the 7th leaf was resolved in this manner, followed by a secondary population increase on the other leaves. Although there were slight deviations due to differences in leaf area, in general, this population increase followed the logistic growth curve. The population growth on each leaf slowed as the population reached 400 ~ 800, depending on the leaf size, and eventually reached zero-growth. At this point, the leaf area was no longer increasing, and so the upper asymptote was reached. It bears pointing out that at this time, numerous apterous vivopara were seen descending the stem and fleeing the plant, and either ambled around in the glass case or escaped through openings. It is believed that this escaping was a significant cause of the decreasing per-plant population growth rate.

The per-leaf saturation densities are given in table 2. The host plants missing from the table were sprayed with TEPP, and thus, saturation populations were not reached. Although there is substantial variation according to this table, the K-ratios of all the leaves show the same tendency. Although the leaf areas were not measured in this experiment, results from the second report indicate that the per-area-of-leaf saturation densities are less variable.

Implications of the results

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[2] Leaves are numbered from the bottom, excluding the cotyledons.

Morisihita (1950) investigated the per-area-of-water density and migration of adult water slider, *Gerris lacusris D.* in nature, and discovered that the equilibrium of population growth was not maintained by adjustments in fecundity and mortality, which had been the conclusion drawn from all previous experiments carried out in unnatural experimental environments, but rather by the relatively unrestricted movement of insects. In the case of the water slider, although newly arriving insects were not prevented from immigrating to ponds with high population density, as population densities increased, greater numbers of insects moved to ponds with lower densities, resulting in an averaging of population densities. Morishita suggested three patterns of population growth: (I) low density pattern, in large ponds comprising areas which are not inhabited by the water slider, in which saturation density of the pond as a whole is never achieved; (II) saturated density pattern, in ponds providing optimal conditions for the insect, in which saturation populations are achieved early in the season; (III) special pattern, in ponds that provide suboptimal conditions for the insects and are therefore not inhabited in the beginning of the season, but are invaded later in the season as the insect populations in more optimal ponds reach saturation.

The results of my study clearly show that the mechanisms for maintaining population density equilibrium of soybean aphids on soybean plants are the same as those of the water slider in nature. In other words, super-saturation of a host is prevented by emigration of insects, rather than by changes in mortality or fecundity. The 7th leaves, on which saturation densities were first reached, can be thought of as pattern II suggested by Morishita; and the lower leaves, to which the aphids migrated *en masse*, can be thought of as pattern III. The super-saturation of the pattern II leaves was avoided by mass-migration of aphids to the pattern III leaves.

Although it is speculated that the equilibrium density of each plant as a whole (totals of figures 1 and 2) is similarly maintained by emigration of aphids, future experiments will test this.

For the reader's information, the results when the plants are sprayed with TEPP are presented in figure 3. According to this figure, the population remained dispersed even after the total population was reduced, which contradicts the results of the second experiment. This issue requires more detailed investigation. On the plants that were not sprayed with TEPP, there was no yield due to infestation of the pods by aphids; the plants sprayed with TEPP yielded soybeans, because although the aphid populations increased a second time, by that time the pods had already hardened and did not become infested.

II. Plant to plant migration

In the previous experiment the author observed that equilibrium population density on leaves was maintained by movement between leaves, and speculated that the equilibrium population density on plants was maintained by emigration from plants. The following experiment was conducted to test the latter hypothesis.

Materials and Methods

The soybean cultivar *Norin* no.2 was used as a host. The aphids used were progeny of a single alate vivopara collected from a soybean field in the experimental station in early May, 1951. Sets of 6 (no. 1, 2) and 5 (no.3, 4) soybeans were planted 30 cm apart into 4 wooden planters (length 80cm, width 60cm, depth 15cm) containing field soil; the pots were covered by a 60 x 80 x 60 cm mesh enclosure, preventing escape of the aphids

to the outside. The multiplication of aphids was observed. Aphids were placed on the 1st and 2nd leaves of each plant as the 2nd leaf emerged. The planters were identified by number (no.1 ~ 4); the plants within each planter were identified by letter (A, B~F); leaves were identified by roman numeral (0, I, II, …) as in the previous experiment. The experiment was conducted from June to August, 1951.

Results

1) Migration routes: as in the first report, the aphids inoculated on the 1st and 2nd leaves moved to new leaves as they emerged and continued to multiply. Saturation population density on the 4th leaf was reached around the eighth day after inoculation. In the 1950 experiment at this point, aphids moved back to the older leaves; however, in this experiment, aphids moved to the 4th or 5th leaves of the other 4 (or 5) plants. In this manner, the equilibrium population of the first leaf was maintained. Subsequently, saturation population density was reached on the new leaves of all of the plants, at which point the aphids moved to the lower leaves. Multiplication was occurring on all leaves 12 to 16 days after inoculation. The migration to new leaves of other plants, the subsequent movement to lower leaves observed in this experiment is thought to be qualitatively different from the occasional movement occurring at low population densities. (table 3)

2) Multiplication on Individual Plants: On plants that were inoculated, migration originated from the 1st and 2nd leaves; and on plants to which aphids migrated, migration to older leaves originated from the 3rd and 4th leaves. However, the subsequent pattern of multiplication was the same on all plants; the only difference being that the migration to older leaves on the inoculated plants occurred 2 days earlier than on the other plants. The plants in this experiment were inoculated earlier than in the previous study, and the plants were still growing when the mass migration to older leaves occurred. Thus, aphids were also observed moving to newer leaves. In addition to population densities of newer leaves being greater than older leaves, their leafstalks were also infested, resulting in a bell-shaped population growth curve. This pattern is the same as for the single-plant experiments in the previous study, and demonstrates that population density equilibrium is being maintained.

3) Saturation Density: the saturation densities of the plants in the 3rd and 4th planters are presented in table 5. The densities are averages of the five plants within each enclosure; the average density per $10cm^2$ of leaf was 260, with no significant differences between plants or leaf level. The plants in planters 1 and 2 began to senesce before saturation densities were reached and therefore no saturation densities could be calculated.

    Although the relation of saturation densities to nutrient status and climate has been demonstrated in previous studies (Terao and Tanaka, 1928), saturation densities in open ecosystems are influenced by the densities of adjacent areas; for example, if there is low density in surrounding areas, a low-density equilibrium, with a good deal of non-infested space, will be maintained. Although it is not expected that the saturation densities presented here will occur in all situations, these densities along with those from the first study may serve as a reference level for the holding capacity of a leaf.

    The same calculations on a per-plant basis yield the following results: planter 1: 16,500 insects; planter 2: 18,500; planter 3: 23,000; and planter 4: 30,000. The theoretical population growth curves drawn from these numbers are conspicuously

skewed to the left compared to the actual growth curves. It is thought that this is primarily due to the increase in leaf area over the course of the experiment.

These results provide evidence in support of the hypothesis that equilibrium population density is maintained by plant-to-plant movement.

III. Discussion of the two experiments

Up to now, the view that biological communities are closed-systems has been held strongly among ecologist, and has led to extrapolation to natural ecosystems of inferences about population density dynamics garnered from laboratory studies. However, Imanishi (1949a) equated such a view to environmental determinism, and asserted that [in nature] organisms are not so strongly bound to an environment, react rather flexibly, and in fact actively choose their environments. As mentioned earlier, Morishita's (1950) study, which was based in this theoretical framework, demonstrated that the population equilibrium a community was maintained by active selection of environments, depending on the quality and population densities of adjacent environments, and not by decreases in fecundity or increase in mortality.

The results of the two studies presented here demonstrate that the mechanism described by Morishita of maintaining population equilibrium of adult insects can also be seen in insect communities in the process of multiplying. Within an individual plant, the over-saturation of new leaves is avoided by movement of insects to older leaves, which have previously not been utilized; and the equilibrium population on plants as a whole is maintained by movement of insect between plants.

However, that is not say that decreases in fecundity did not occur. In both studies, as the populations reached high densities, the average size of the aphids decreased noticeably, and it is believed that the number of progeny decreased as a consequence. Yet, during both within plant and between plant movement it was not possible to identify an obvious decline in fecundity in the overall population growth curves. Thus it is reasonable to believe that the equilibrium population was maintained for the most part by movement of insects (the results of the 1951 study are presented in figure 5).

Incidentally, as can be seen in the 1950 experiment, the insects did not move from plant to plant when saturation densities were reached on a single plant after movement of insects from newer to older leaves, but rather the insects first moved to new leaves of other plants, and only moved to older leaves after the new leaves of all the plants had become saturated. The fact that the adjacent plants were spaced 30cm apart suggest that the insects moved first to new leaves of adjacent plants because they presented a more favorable, or 'higher value' environment. However, as the population densities of the new leaves increased, the relative 'value' of the new leaves decreased; the insects began moving to older leaves when the relative value of the new and old leaves became equal.

The above factors should be taken into consideration when thinking about the multiplication of insects in natural environments. For example, it would be useful to take into account the fact that a given population of insects interacts with adjacent environments and the insect communities inhabiting them when thinking about plant protection. Up to now, there has been only one study that investigate these factors: Voute (1937) reported that in *Kokuzou* communities the speed of insect movement was higher in areas of high population density. Many more experiments need to be conducted with different kinds of insects – including *in situ* experiments. Correlation between the appearance of migratory alate forms of soybean aphids (Shands and Simpson, 1948) and population density, and the appearance of alate forms of *Unka* (Delphacidae) at high

population densities (Miyake and Fujiwara, 1951) may be related to the mechanism of equilibrium population maintenance proposed here.

III. Summary

1. The multiplication of soybean aphids on different leaf levels of individual soybean plants grown in pots was observed: the aphids first multiplied on the young, central leaves and when saturation population densities were achieved on these leaves, moved to the older leaves, which had not yet been infested, in this manner, the population equilibrium of the central leaves was maintained.
2. In the second experiment, several soybeans were planted 30cm apart; one plant was inoculated with a single aphid, and the subsequent multiplication observed. When saturation population density of the central leaf was reached, the aphids moved *en masse* to the central leaves of adjacent plants. Only after saturation population was reached on the central leaves of all the plants did the aphids move to the older leaves.
3. There were no significant differences in the pattern of population growth by leaf level and movement between leaves in the two experiments.
4. In these experiments, it was shown that the per-10cm^2-leaf-area saturation density population was 250 aphids.
5. The population growth pattern of aphids on the central leaves can be thought of as following pattern II used by Morishita (1950) to describe population growth of the water slider *Gerris lacustris D.*; the pattern on the older leaves which receive aphid immigrants can be thought of as following pattern III.

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