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THE EFFECT OF THE RATE OF SUCCESSFUL DISPERSAL OF A PHYTOSEIID MITE, *PHYTOSEIULUS PERSIMILIS* ATHIAS-HENRIOT (ACARINA : PHYTOSEIIDAE) ON THE PERSISTENCE IN THE INTERACTIVE SYSTEM BETWEEN THE PREDATOR AND ITS PREY

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INTRODUCTION

Stability of predator-prey systems has been one of the most controversial topics in population and community ecology. Recent studies in this field include many theoretical approaches to elucidate the relationship between stability and the spatial variation in prey density among patches in predator-prey systems (e. g. ROYAMA, 1970; HASSELL and MAY, 1973; MURDOCH and OATEN, 1975).

However, few experimental studies have been conducted to test this problem. HUFFAKER's (1958) famous experimental study on acarine predator-prey systems is one of the few examples, in which the significance of physical complexity to the stability or persistence of the interactive systems was examined, whereas LUCKINBILL (1973) could establish a continued interactive system between ciliated predator and prey species without introducing physical barriers into the system.

Many of the theoretical studies or models on stability assume that predators themselves can control their prey populations, or at least predation is the most important stabilizing force, but this is often not the case in real field situations. Another problem in those theoretical works is that they have been so much sophisticated that it is often impossible to test the adequacy of the theories by empirical experimentation.

In this regard, mites may be very suitable for studying the relationship between stability and spatial distributions of predator and prey with an emphasis on their movement among patches: several species of predacious phytoseiid mites can efficiently suppress the populations of tetranychid mites (see HUFFAKER *et al.*, 1970), and in addition, both have small capacities of movement and therefore spatial relationships between the two can be reasonably examined in a relatively small experimental system.

In the present study, the dispersal behaviour of a predacious phytoseiid mite, *Phytoseiulus persimilis* ATHIAS-HENRIOT, was studied among patchily distributed host plants, and the effect of the rate of successful dispersal of the predators among the patches on the persistence of the interactive system between the predators and their prey was experimentally tested.

MATERIALS AND METHODS

Experiments were carried out from October 20 th, 1974 to January 14 th, 1975 in a large greenhouse at the Faculty of Agriculture, Kyoto University, Kyoto. A large fan was set in a corner of the greenhouse, which automatically worked to exhaust the inside air of the house when the indoor temperature exceeded 30°C. From November 21st on, four 400 watt panell heaters were placed to prevent the temperature from falling below 10°C. In this way, the temperature in the greenhouse was controlled between 12°C and 35°C.

The predator species, *P. persimilis* which is native to Chile was obtained from the culture maintained in the Tea Research Institute at Shizuoka, Japan. The prey species was *Tetranychus kanzawai* KISHIDA which injuries various kinds of crops such as tea, beans and strawberries.

Experiment 1. Dispersal behaviour of P. persimilis in response to prey density.

This experiment was designed to elucidate the dispersal behaviour of the predators between two neighboring plants in response to the density of its prey.

A mottled kidney bean plant with two leaves about 12 to 15 cm in height was planted in a flower pot (9.5 cm in diameter and 8 cm in depth) filled with vermiculites. The upper surface of the pot was covered with fine sands to enable the predators to walk smoothly. Two of such flower pots were connected with a "bridge" of plywood (3 cm in width and 20 cm in length), and they were placed in a water-filled tray. Thus, the predators were allowed to move between plants only through this bridge.

Sixteen adult females of *T. kanzawai* were introduced into one of the two plants, and either of 0, 2, 4, or 8 adult females of the prey and two adult females of *P. persimilis* introduced together to the other one. Changes in the numbers of predator and prey were observed over 5 days. The experiment was repeated 10 times for each of the four different prey densities.

Experiment 2. Population interactions between P. persimilis and its prey.

The experiments on the interaction were conducted in two different systems in which the distribution patterns of the host palnts were different with each other. Fig. 1 illustrates the two different distribution patterns of the plants. In both systems, 32 flower pots with single bean plant (the same as used in Experiment 1) were distributed in a large water-filled tray.

In system A, all the flower pots were closely in contact with each other and the plants also touched with each other. Thus, the predators were able to move among plants through leaves and also across the edges of the pots. In system B, the 32 flower pots were equally divided into 8 patches and within each patch 4 flower pots

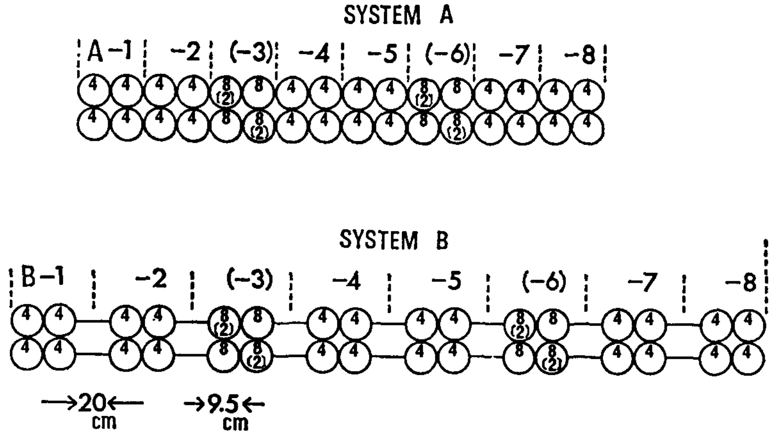

Fig. 1. The distribution patterns of host plants, and the location and the numbers of *P. persimils* and *T. kanzawai* initially introduced into each of the two interactive systems. The numerals in circles and those in brackets show the number of adult females of the prey and that of the predators respectively. The circles and lines indicate the flower pots with single bean plant and 20 cm plywood "bridges" respectively.

were joined together just as in system A. Those 8 patches were connected with each other with two plywood "bridges", the same as used in Experiment 1, and thus the predators were able to disperse between patches only through the bridges. Preliminary observations showed that very few prey move from a plant to another, unless the plant heavily deteriorates.

Fig. 1 shows also the numbers of predator and prey which were initially introduced and their initial distributions on the plants. Predators were introduced into two of the four plants only in the third and sixth patches (A3, A6, and B3, B6 in systems A and B respectively).

The entire populations of predator and prey were counted every 2 to 4 days.

RESULTS

1. *Experiment 1.*

Fig. 2 shows the change in the number of predators on the plants into which they were initially introduced. When there was no prey on the plants, 95% of the predators left the plants after 2 hours, and after 4 hours all the predators dispersed. Thereafter, no individuals returned there. As prey density was increased, proportion of predators remaining became greater. For example, with prey density of 8, 75% of them still remained on the plants even after 48 hours. Although predators did not always leave the plants eliminating all the prey (Table 1), the number of prey which escaped predation, mostly eggs, was very small, only 1 to 3.

Thus, it was clear that predator dispersal occurs mainly in response to a decrease in prey density available per individual predator and therefore with an increase in

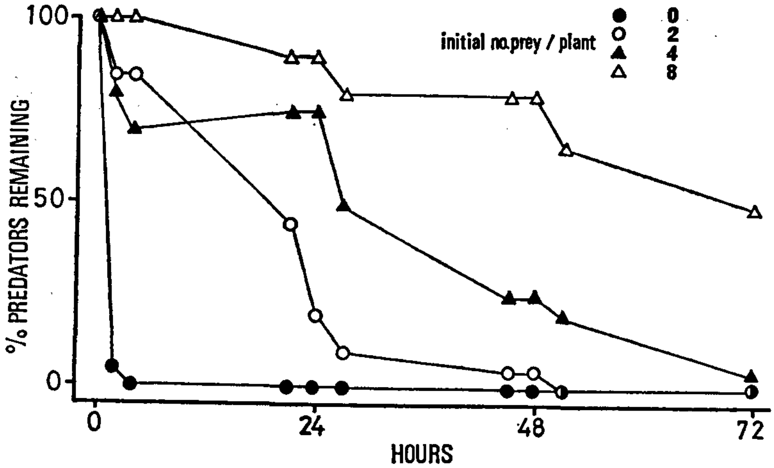

Fig. 2. Dispersal pattern of the adult females of *P. persimilis* between two neighboring plants which were connected with a bridge. I). Change in the number of predators remaining on the plants where either of 0, 2, 4 or 8 adult females of *T. kanzawai* was initially introduced.

Table 1. Percentage of the populations of *T. kanzawai* which had been completely eliminated by *P. persimilis*, when two adult females of the predator dispersed from the plants with either of 2, 4, 8 adult females of the prey.

Initial density of prey	% eliminated	Replicates
2	100	10
4	90	10
8	80	10

hunger level of the predators, although there were some individuals which dispersed quickly after their introduction into the plants with sufficient prey.

The rate of successful dispersal of predators in this system was only 20 to 25% and this rate did not change with the initial prey density on plants where the predators were introduced (Fig. 3), whereas it was 95% if the plants touched with each other. However, the lower was the prey density, the more quickly did predators succeed in dispersing to a neighboring plant. Successful dispersal occurred only during the first two days with prey densities of 0, 2, and 4. Predators which failed to reach the neighboring plants were observed to wander very actively around the flower pots or on the bridges at first, and then they were resting there because of starvation.

2. *Experiment 2.*

Fig. 4 shows the changes in the total populations of predator and prey in each of the two interactive systems. During the first 11 days, the pattern of the increase in the prey population in each system was quite similar to each other. The number of

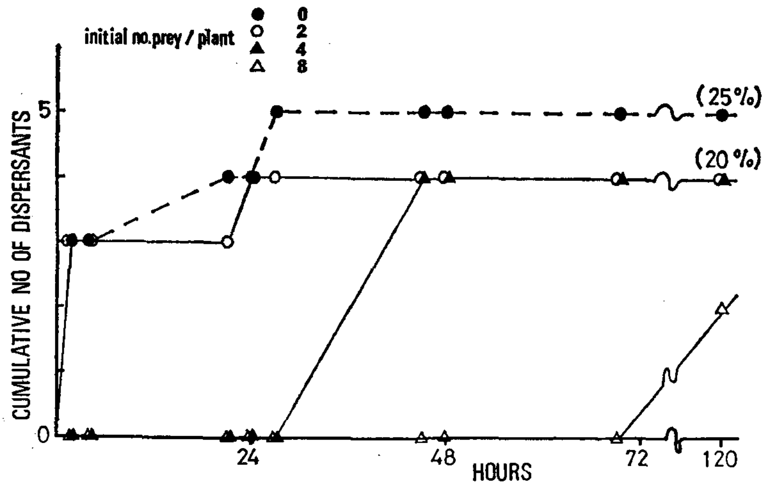

Fig. 3. Dispersal pattern of the adult females of *P. persimilis* between two neighboring plants which were connected with each other with a bridge. II). Change in the number of predators which succeeded in dispersing to the plant with 16 adult females of the prey from the one with either of 0, 2, 4 or 8 adult females of the prey.

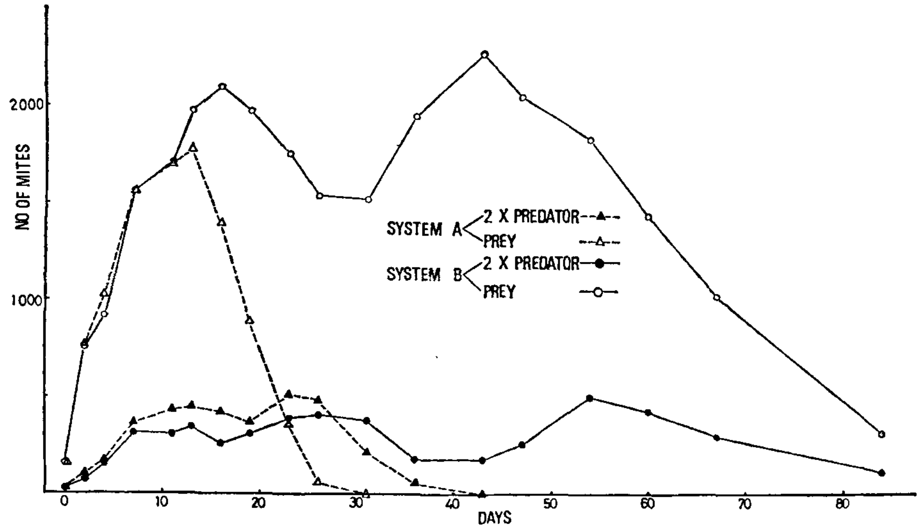

Fig. 4. Changes in the total populations of *P. persimilis* and its prey, *T. kanzawai* in each of the two interactive systems.

the prey population in system A reached a peak on the 13th day and then rapidly began to decrease. By the 31st day, it was completely eliminated. With the prey population of system B, although its number decreased from the 16th to 26th day, it again increased up to about 2500. The population then began to decrease from the 43rd day, but the prey were still maintaining its population on the 92nd day when the experiment was terminated.

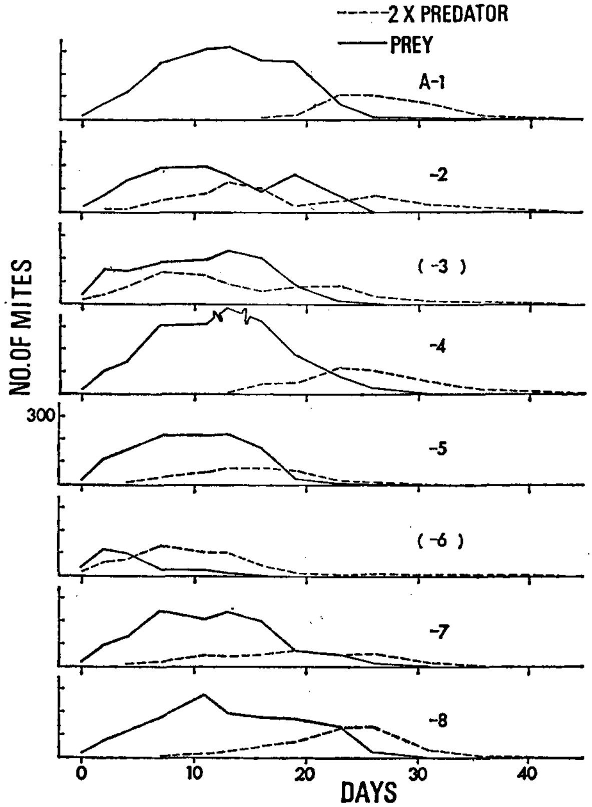

Fig. 5. Changes in the poputations of *P. persimilis* and its prey, *T. kanzawai* in each of the eight patches (a group of four host plants) of system A (see Fig. 1).

Figs. 5 and 6 shows the changes in the predator and prey populations in each of the 8 patches in systems A and B respectively. In both systems, the decrease in the prey populations and increase in the predator populations generally occurred first in the two patches where the predators were initially introduced, and the prey populations which were closer to either of these two patches were decreased more rapidly by the predators that immigrated.

As time elapsed, the differences between the densities of the predator and prey populations in the 8 patches became larger, and thus the distribution patterns of the entire prey populations became more contagious (Fig. 7). This tendency was more obvious in system B.

The increase in the predator population in system A was more rapid than that in system B. This was because predators in system A could move more easily among patches compared to those in system B, and the former could locate the plants with many prey and reproduce more quickly. This is clearly shown in Fig. 7: the degree of aggregation in the distribution of the predator population in system A decreased much more rapidly than in system B, which showed that the dispersal of

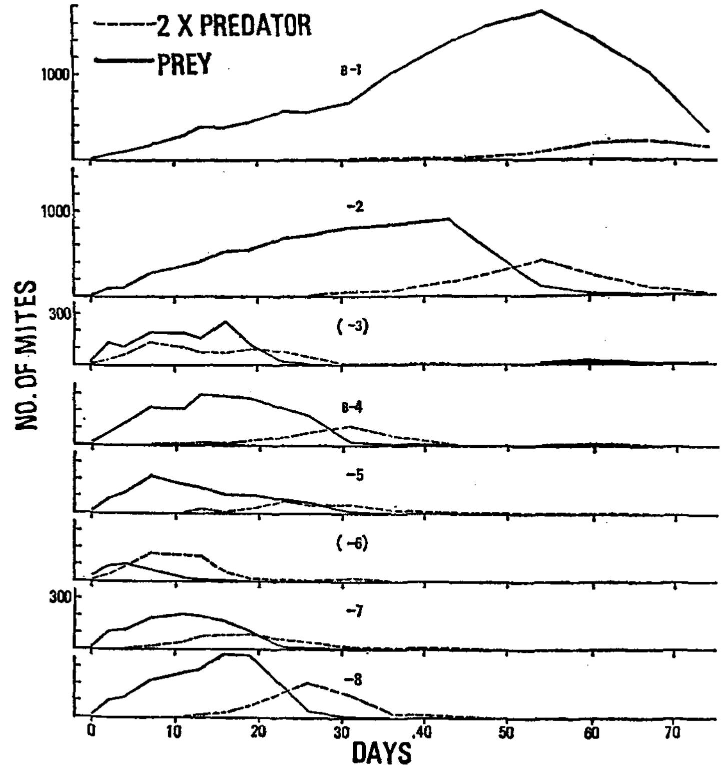

Fig. 6. Changes in the populations of *P. persimilis* and its prey, *T. kanzawai* in each of the eight patches (a group of four host plants) of system B (see Fig. 1).

the predators was more rapid in the former.

The prey populations in the 8 patches of system A were completely eliminated one by one by the predators, and the population in patch A-1 which survived longest was finally eliminated by the 33rd day and the entire population in system A disappeared. Although the predators could survive rather long after the prey had been eliminated, they also disappeared by the 50th day.

As mentioned earlier, the pattern in the change in the prey population of system B was quite different from that of system A. This was simply because the successful dispersal of predators to two of the 8 patches (B-1 & B-2) was greatly delayed in system B; predators could immigrate into B-1 and B-2 for the first time on the 26th and 31st day respectively, whereas in system A, the predators immigrated into all the patches by the 16th day. Because of this, the prey populations in B-1 and B-2 increased up to about 1,700 and 900 respectively, which resulted in the resurgence in the total population of system B. This caused a heavy deterioration of the plants in these patches and there was a heavy webbing of prey over many leaves, which gave a better chance for prey to disperse by air current. In fact, around the 54th day a

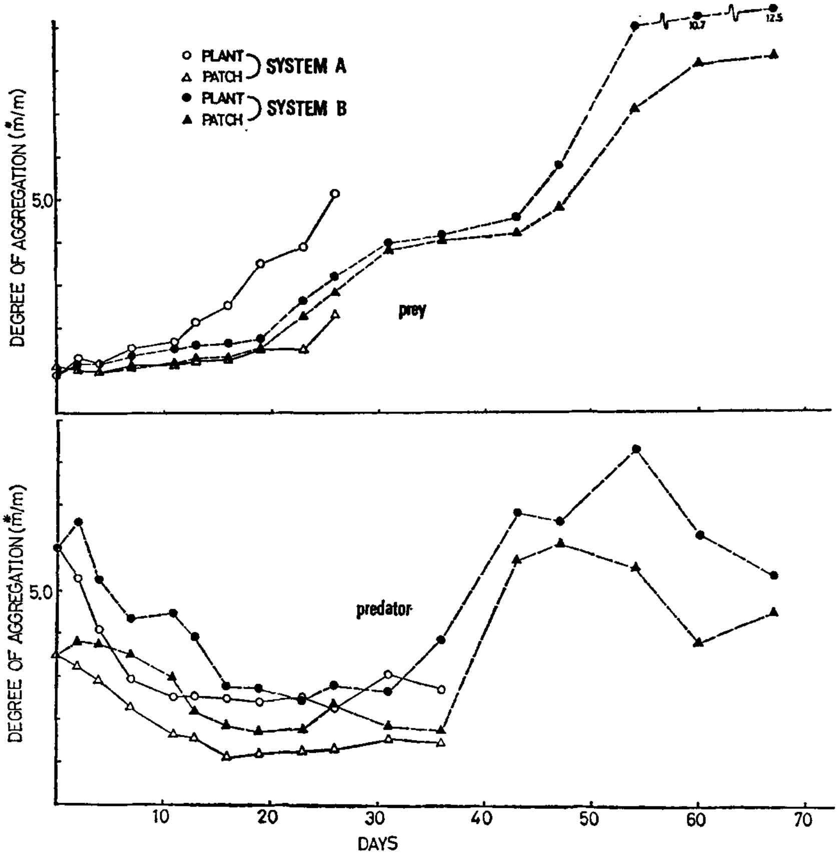

Fig. 7. Changes in the degree of aggregation, $\overset{*}{m}/m$ (see Iwao, 1968) in the distributions of the populations of *P. persimilis* and its prey, *T. kanzawai*. ○ and ● are the values of $\overset{*}{m}/m$ based on the numbers of the mites per individual plant, and △ and ▲ are those for the numbers of the mites per patch (a group of four plants).

few prey moved from B-2 to a neighboring patch, B-3, on which the prey population once had been eliminated. The prey population in B-3 was soon suppressed by predators which were probably the immigrants from B-2, however, and the increased prey populations in B-1 and B-2 also were suppressed with increases in the predator populations. Thus, the prey population in system B could persist about three times longer than that in system A.

DISCUSSION

As shown in the experiment with system A, it is evident that *P. persimilis* can quickly suppress the prey population and often eliminate it completely without food limitation on the prey population, if the dispersal of the predators is free between patches.

Dispersal of the adults of this predator is sharply induced by a heavy decline in prey density available per individual predator. Although they often leave a patch leaving a few prey uneaten, predation by the immatures remaining there, which have much lower capacity and tendency to disperse than adults, leads to complete elimination of the few prey.

The results with system B shows that to lower the rate of successful dispersal of the predators may prolong the period of coexistence of the whole predator and prey populations. This is simply because some patches were free from predators for a period, during which the prey were allowed to increase to high levels, followed by the dispersal of the prey to a neighboring patch in which the prey were once eliminated.

The systems used in this study consist of patches with various densities of predator and prey which change with time. The functional response of predators to prey patchiness and its effect on prey stability has been theoretically examined by HASSELL and MAY (1973) and MURDOCH and OATEN (1975). The former discusses the effects of predator's aggregation to patches of high prey density and the interference among the predators on the stability of prey population. The latter emphasizes the effect of predator's travelling time between patches. However, these factors do not seem to be so important for the stability in the interactive system between predators such as *P. persimilis* that have very high potential rates of population increase and its prey, because once only a few individuals of the predators immigrate into a patch, then the prey population in the patch is inevitably reduced to very low levels or completely eliminated. Rather, the mortality of the predators which may occur in the process of their dispersal between patches when prey density has heavily declined, and therefore the rate of successful dispersal of the predators is likely to be more important for the persistence of the interactive system.

The rate of successful dispersal between patches will in fact form a probabilistic distribution with a mean. Therefore, as occurred in system B, if mean rate is rather low, it is quite possible that predators do not immigrate at all into some patches for a certain period, even though the conditions of all the patches are identical throughout the system. This, then, suggests that the more is the total number of patches, the more is the number of patches where immigration of predators is nill for a period, thereby decreasing more the chance for the entire prey population to be extinct, if there is a frequent dispersal of prey.

A continued coexistence of a predacious mite, *Typhlodromus occidentalis* and its prey mite, *Eoteranychus sexmaculatus* was established by HUFFAKER (1958), by increasing the number of patches (oranges) up to 120, by curtailing the dispersal of the predators, and at the same time by increasing the chance of the dispersal of the prey. Thus, the main factors which contributed to the coexistence seem to be the increased number of patches and the physical structure which is more advantageous for prey than for predators in terms of dispersal success, rather than the environmental heterogeneity in the system. Simulation studies by MAYNARD-SMITH (1974) which were suggested by HUFFAKER's experiments also confirm that such factors are important for a permanent coexistence of predator and prey.

In HUFFAKER's experiments, however, there seems to be another factor which contributed to the persistence of the system: in his system some of the oranges were periodically replaced with new ones, and with this manipulation it is doubtful whether the proportion of the predator population which was removed from the system is similar to that of the prey because it is generally the case that on older host plants there are more predacious mites than prey mites. The replacement should also have changed greatly the spatial distribution patterns of the mites during the course of their interaction.

Such a disturbing factor is excluded from the present experimental system. However, the system did not allow the prey to disperse frequently because air current in the experimental system was small: the dispersal of the prey seem to have occurred only once during the experiment. In addition, the predator species used here has much higher capacities of feeding, reproducing and searching compared with that used by HUFFAKER, which probably are unfavorable features for coexistence, other things being equal. In order to establish a longer coexistence of *P. persimilis* and its prey, it would be necessary to introduce a larger physical barrier which reduces the rate of successful dispersal of the predators, and to give much more chances for the prey to disperse, though by doing so prey populations may fluctuate greatly as there will be more patches where immigration of the predators does not occur for a period. Such a system is not unrealistic at all in the light of the natural habitats of the mites where the host plants are patchily distributed, because predacious phytoseiid mites can usually disperse only by means of walking, whereas tetranychid mites can often migrate to a longer distance by the aid of air current.

The dispersal activity of tetranychid mites is greatly stimulated when food quality heavily deteriorates, and therefore it is closely related with its own density. Thus, when a habitat is continuous so that predators such as *P. persimilis* can easily move within the habitat, predation by itself can suppress prey population, but in a highly discontinuous habitat, food limitation on the prey population can be also the stabilizing force of the prey.

SOME IMPLICATIONS TO BIOLOGICAL CONTROL OF TETRANYCHID MITES USING *P. PERSIMILLS*

It has been observed by a number of authors that *P. persimilis* completely eliminates the populations of tetranychid mites, followed by the extinction of its own population, both in laboratory and outdoor conditions (see, eg. HUFFAKER *et al.*, 1970; MORI, 1975; TAKAFUJI and CHANT, 1976). But it is also the case that the predators themselves first disappear leaving a very few prey uneaten and this then eventually result in a resurgence of the prey populations, freed from predation pressure (TAKAFUJI and CHANT, *l.c.*). The prey mites may also immigrate from outside by wind or men's activity into areas where they have once been eradicated. In such cases, multiple introduction of the predators into the systems is required to prevent the later increase of the prey. The establishment or prolonged maintenance of the predator population, however, seems to be possible by partially preventing the dispersal success of the predators, for example, by changing the distance between host plants. But this may sacrifice some of the plants on which the prey may increase to high levels, freed from predation pressure.

Tolerance against mite inquries vary among crop species. If the crop is highly tolerable, or a permanent one, it will be worth-while making efforts to establish a cultivation system in which predator dispersal is kept low. Otherwise, it will be rather realistic to facilitate the dispersal of the predators, so that they can quickly cover a wider area. This can be easily done, for example, by connecting host plants by strings.

SUMMARY

Dispersal behaviour was studied on a predacious phytoseiid mite, *Phytoseiulus persimilis* ATHIAS-HENRIOT in response to the density of its prey, *Tetranychus kanzawai* KISHIDA. And the effect of the change in the rate of successful dispersal of the predators among patches was tested on the persistence of the predator-prey system. The results of the study are summarized as follows:

1. With a severe decline in prey density available per individual predator, the predators exhibited a marked behavioural change and dispersed to other areas.
2. When two neighboring host plants did not touch with each other and the dispersal of the predators was possible only through a 20cm plywood "bridge" which connected the two plants, the rate of successful dispersal of the predators was only 20 to 25%, whereas it was 95% when the plants touched with each other.
3. In the system where 32 host plants touched with each other, the predators succeeded in immigrating into all the plants by the 16th day, and they completely eliminated all the prey by the 33rd day.
4. In another system, the 32 plants were equally divided into eight "patches" which were connected with each other with two of the bridges and the predators could move between them only through the bridges as mentioned above. In such a system the predators and their prey coexisted about three times longer than in the other one.
5. It is suggested that for a longer continued coexistence of the predators and prey, it would be necessary to introduce more physical barrier against the dispersal of the predators and to provide more chances for the prey to disperse.

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チリカブリダニの分散成功率がハダニとの作用システムの存続におよぼす影響

高藤晃雄

捕食性カブリダニの一種，チリカブリダニ（*Phytoseiulus persimilis* Athias-Henriot）のカンザワハダニ密度に反応した分散行動を調べ，捕食者のパッチ間分散成功率の差がハダニ―カブリダニのシステムの維持にどのように影響するかを実験的に調べた。その結果は次のように要約される。

1) 捕食者1頭あたりのハダニ密度が急激に減少するにつれて捕食者は顕著な行動的変化をおこし，分散をはじめた。

2) 2本の寄主植物が互いに接触せず，捕食者の分散がそれらを連結した20cmのベニヤ板ブリッジをとおしてのみ可能にすると分散成功率は20～25%にすぎなかった。一方，2本の植物を互いに接触させると成功率は95%だった。

3) 32本の植物を互いに接触させたシステムでは，捕食者はすべての植物に16日目までに侵入し，33日目までにはハダニを完全に食いつくした。

4) 32本の植物を4本ずつひとまとめにして8つのパッチをつくり，パッチ間を先述のブリッジで連結して捕食者がそれをとおしてしか分散できないようにすると，その相互作用システムは上記のシステムより3倍ほど長く存続した。

5) このシステムをより長く存続させるには捕食者の分散を妨げるより大きなbarrierが必要であり，また同時にハダニの分散をさらに促進させる必要があろう。