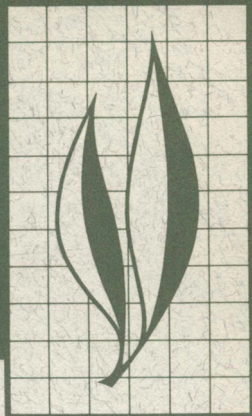


# HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY  
THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

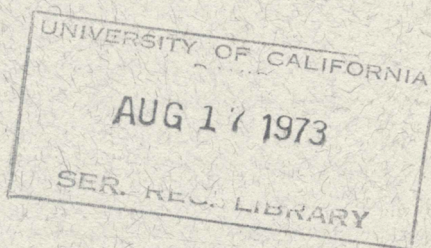


Volume 42, Number 2 • May, 1973

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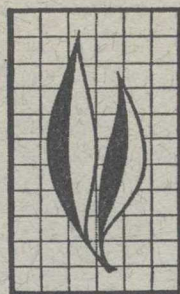
Predation by *Amblyseius potentillae* (Garman)  
on *Panonychus ulmi* (Koch) in Simple Ecosystems  
(Acarina: Phytoseiidae, Tetranychidae)

J. A. McMurtry and M. van de Vrie



HILGA4 42(2) 17-34 (1973)





Interactions between the European red mite, *Panonychus ulmi* (Koch), and the predaceous mite *Amblyseius potentillae* (Garman) were studied under semicontrolled glasshouse conditions in two types of ecosystems: single leaves, isolated by a sticky barrier at the petioles, and eight-leaf seedlings. Three different starting numbers of the prey (one, four, and eight females, respectively) were established in each type of ecosystem, and a single adult female predator was introduced 10 days later. Predator-free controls were also included.

In the single-leaf systems, prey:predator ratios at the beginning averaged 23, 94, and 152 to 1, respectively. Suppression of the *Panonymus ulmi* populations from the peaks occurred within about seven days after predator introductions. In some cases the prey population "escaped" control after the initial suppression, because the predators declined either to extinction or to one or two nonreproductive individuals.

In the eight-leaf ecosystems, the numerical response of the predator population was somewhat more delayed, and the prey population peaks attained before initial suppression averaged higher than those of the single-leaf systems. There was considerably more variation among replicates on these more complex systems. The experiments showed that *Amblyseius potentillae* had the potential for responding to and suppressing a wide range of densities of *Panonychus ulmi*. As much as a 14-fold increase in predator populations in two weeks was observed, and the cases of an inadequate numerical response to overtake an increasing prey population were attributed, not to inadequate reproductive capacity, but to other factors, such as failure to find prey or mates.

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# Predation by *Amblyseius potentillae* (Garman) on *Panonychus ulmi* (Koch) in Simple Ecosystems (Acarina: Phytoseiidae, Tetranychidae)<sup>1,2,3</sup>

## INTRODUCTION

*Amblyseius potentillae* (Garman) is a European species of phytoseiid mite common on apple trees in the Netherlands where it is a potentially valuable predator in the control of the European red mite, *Panonychus ulmi* (Koch) (van de Vrie and Kropczynska, 1965; van de Vrie and Boersma, 1970). It feeds on all stages of *P. ulmi* except the egg, but apparently prefers the immature stages (van de Vrie and Kropczynska, 1965).

To learn more about the dynamics of predation of *Amblyseius potentillae* on *Panonychus ulmi*, we studied predator-prey interactions in an ecosystem sufficiently small that all stages of both species could be frequently assessed on all leaves in the system. In nature, the simplest conceivable ecosystem in which an interaction could occur is on a single leaf; therefore, the initial studies were conducted under those conditions. Sub-

sequently, the study progressed to a more complex system in which the mites could move from leaf to leaf, but which was still small enough that events on each leaf could be closely followed.

We hoped to gain information on the following: (1) potential of the predator species to suppress the prey when starting with a single adult female at different prey levels (the adult female is the overwintering stage of the predator, and thus the starting unit of an interaction in the beginning of the season in temperate climates); (2) effect of predation on age structure and distribution of prey; (3) persistence of the predator in small ecosystems, and reasons predators fail either to persist or respond to a resurging prey population; (4) degree of uniformity of population fluctuations on different leaves of the same plants; (5) possible inhibition of predator response at high prey densities.

## MATERIALS AND METHODS

Small EMII apple rootstocks in pots were used as host-plant material. During the experiments, the plants were

maintained in cabinets in a semi-air-conditioned glasshouse as used by van de Vrie and Kropczynska (1965).

<sup>1</sup> Submitted for publication September 4, 1972.

<sup>2</sup> See "Literature Cited" for citations referred to in text by author and date.

<sup>3</sup> This study was conducted at the Research Station for Fruit Growing, Wilhelminadorp, The Netherlands, during a sabbatical leave of the senior author.

## Experiment I

Twelve seedlings were reduced to four leaves each, and each leaf was isolated by a tanglefoot barrier around the petiole. Four of the plants (16 leaves) were infested with one adult female of the prey, *Panonychus ulmi*, on each leaf, four plants with four female *P. ulmi* on each leaf, and four with eight female *P. ulmi* to a leaf. To insure having mated females of comparable age, males and quiescent deutonymphs were placed on excised apple leaves in the laboratory about four days before the start of the experiment. At the end of that time, adult females from those leaves were then placed on the experimental plants. Ten days after the plants were infested with *P. ulmi*, one adult female of the predator, *Amblyseius potentillae*, was placed on each leaf of two of the four seedlings in each of the three groups. Thus, the experiment began with eight replicates (individual leaves) with one predator at each of the three starting levels of prey, plus eight predator-free replicates at each level of prey.

All stages of prey were counted and recorded separately twice weekly with the aid of a binocular microscope detached from its base and held by hand. Illumination was provided by a slide projector mounted on a tripod and placed slightly above and about 0.5m away from the leaf on which the mites were being counted. At that distance the light field was sufficiently large to illuminate an entire leaf.

## Experiment II

A series of 36 seedlings was prepared by reducing the number of leaves to

eight per plant and placing a tanglefoot barrier around the stem near the base. Thus in this experiment, an eight-leaf plant rather than a single leaf served as the experimental ecosystem. The same three starting levels of prey density—one, four, and eight adult female *Panonychus ulmi*—were used in these systems, with 12 plants at each density. On plants inoculated with one female, a single *P. ulmi* was placed on leaf 4 (leaves numbered from base to top); on plants inoculated with four females, one *P. ulmi* was placed on each of leaves 2, 4, 6, and 8; on plants inoculated with eight females, two *P. ulmi* were placed on each of leaves 2, 4, 6, and 8. The plants were inspected daily for 10 days, and any missing females were replaced. On the tenth day, the predators were introduced to the plants. A single adult female *Amblyseius potentillae* was placed on each of eight plants at each of the three prey densities. Predators were placed on leaf 6 of the plants started with one *P. ulmi* and on leaf 4 of the plants started with four and eight *P. ulmi*. This left four plants at each of the three prey densities to serve as predator-free controls. These were reduced to two plants each, however, as the time involved in making counts on so many plants became prohibitive. Furthermore, it was felt that six plants were sufficient to demonstrate the potential increase of *P. ulmi* in the absence of predation. Counts were made twice weekly on all leaves of the predator-infested plants, but usually only weekly on the predator-free ones. Instead of recording all developmental stages separately, as in Experiment I, each quiescent stage was grouped with its preceding active stage.

## RESULTS

### Experiment I

The populations of *Panonychus ulmi* were still increasing on the predator-

free leaves (fig. 1) when the counting was terminated because of difficulties in counting such high numbers accurately.



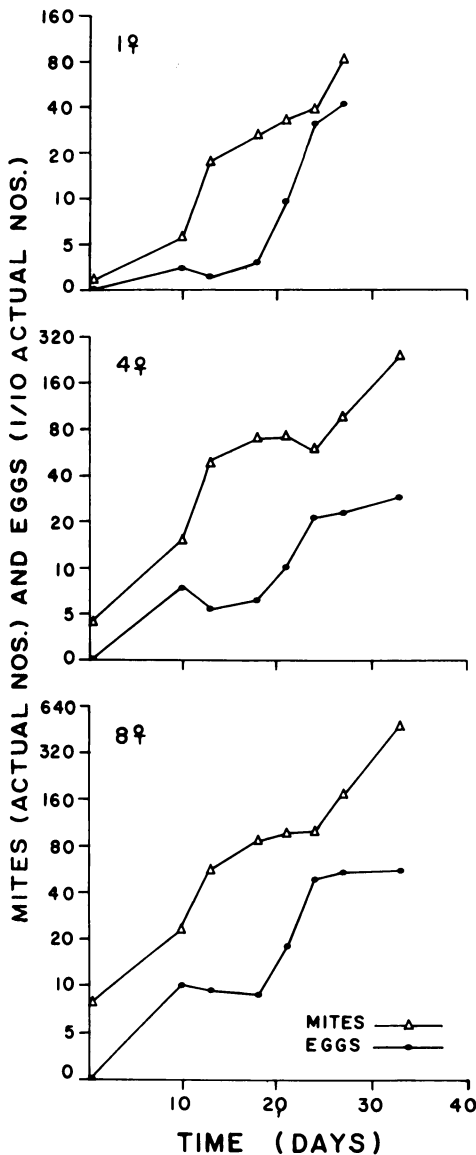


Fig. 1. Population trends of *Panonychus ulmi* in single-leaf ecosystems without predators. Based on averages of eight replicates of each of three different starting numbers of adult females (1, 4, and 8).

Numbers at the final count averaged highest on the leaves started with eight female *P. ulmi* (576 eggs and 464 active stages per leaf). The population growth curves for all three groups showed the same general trends. The

average numbers of eggs declined between 10 and 13 days, then increased sharply from 18 to 24 days, after which there was either a slower increase or a leveling trend. The sharp increase in eggs reflected the maturing of large numbers of progeny of the original females. As the increase in numbers of eggs started to level off, another surge in numbers of active stages was evident.

Population trends on the plants having predators are shown separately for each leaf (fig. 2). Differences in trends among leaves of the same groups varied to the extent that averaging the replicates would have given misleading impressions. On leaves initially infested with one female *Panonychus ulmi* (fig. 2, left column), populations of the latter were all suppressed from an initial peak of fewer than 10 active stages per leaf, and they were essentially eliminated from all replicates except nos. 2 and 4, where the predators died out first. The prey density at the time of the predator introductions averaged 17 eggs and six active stages per leaf. Four days later, when all progeny of the predators were still eggs, the active stages of prey had already declined in five of eight replicates.

On the leaves infested with four female *Panonychus ulmi* (fig. 2, middle column), the prey averaged 79 eggs and 15.5 active stages per leaf when the adult predators were introduced. Leaf 8 became chlorotic and died. On the other replicates, the populations of *P. ulmi* increased to a peak of about 20 to 30 active stages (highest, 38), and then declined. A peak in predator active stages followed. The prey continued to decline with little or no further increase only on replicates 5 and 6, whereas on the others, a resurgence occurred. The predators declined to extinction on replicates 2, 3, and 4, and the prey "escaped" control. The prey populations were considered controlled on replicates 1, 5, 6, and 7.

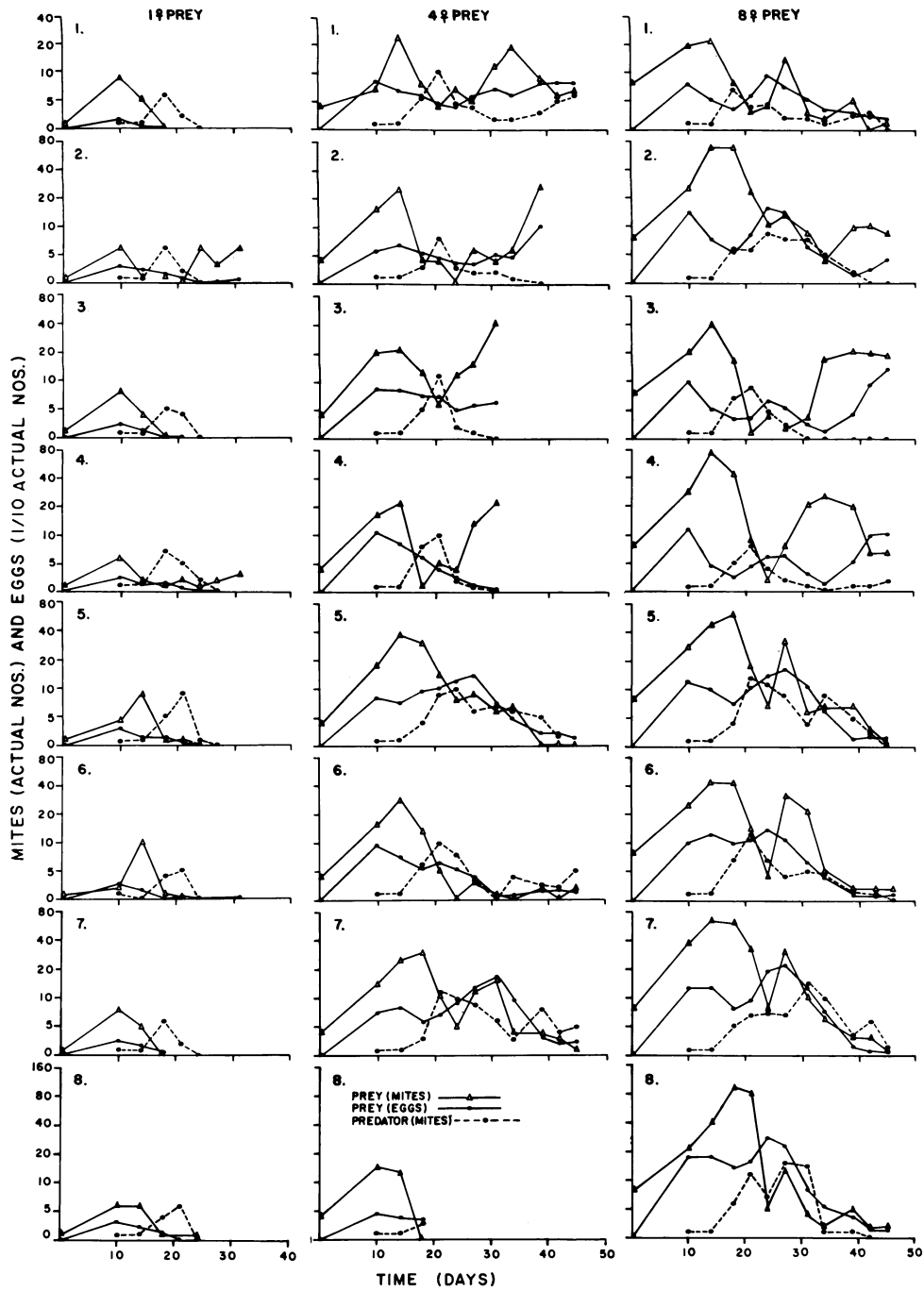


Fig. 2. Population trends of *Panonychus ulmi* (prey) and *Amblyseius potentillae* (predator) on single-leaf ecosystems, eight replicates of each of three different starting numbers of adult female prey.



On the leaves infested with eight female *Panonychus ulmi*, the latter averaged 26.6 active stages and 126 eggs per leaf when the predators were introduced. Four days later (14 days total), still only the original predators were present, plus their eggs, and the prey population averaged 51 active stages and 97 eggs (fig. 2, right-hand column). At the 18-day count, immature predators were present, and either a leveling or declining trend was evident in active stages of prey. Prey numbers reached a peak of at least 40 active stages on all replicates except no. 1, the highest being 106 (no. 8). A decline in active stages of prey had started on all replicates at the 21-day count.

Generally, numbers of prey eggs were still increasing when the active stages were declining (fig. 2, right-hand column). The egg population had bimodal peaks, the second peak coinciding with maturation and reproduction in some of the  $F_1$  generation. With the exception of replicates 3 and 4, the second egg peaks were the highest (at 24 or 27 days), and followed the highest adult female counts by three to six days. There were also bimodal peaks in the active stages of prey, and populations escaped suppression in the second cycle of increase on replicates 2 and 3 as the predators declined to extinction. It could not be determined whether this was a result of mortality or escape of the predators. All other replicates, except for no. 4, had very low numbers of either prey or predators or both at the final count (45 days), and the prey was considered "controlled" by *Amblyseius potentillae* in these cases. Apparently there was no predator reproduction on replicate 4 between 30 and 40 days, but progeny were again evident (2 protonymphs and 3 eggs) at the 45-day count. Another inspection at 53 days revealed three prey and six predators.

The data from this experiment show that *Amblyseius potentillae* had the po-

tential for suppressing populations of *Panonychus ulmi* even though originally greatly outnumbered. The counts on the replicates initiated with eight *P. ulmi* females indicated that each predator produced an average of about nine and 11.6 progeny at eight and 11 days, respectively, following predator introductions. Thus, while prey density was relatively high, *A. potentillae* produced about one progeny per female per day. Because eggs were difficult to see and some could have been missed, this estimate is a conservative one. Although this is not a high fecundity rate for phytoseiids as compared with most laboratory results (McMurtry, Huffaker, and van de Vrie, 1970), the response was sufficient to reverse the upward trend of the prey population. During the first 10 days on these same replicates, *P. ulmi* averaged 14.7 progeny per leaf or 1.8 per female per day.

It is evident (fig. 2) that if only the active stages of prey were considered, a misleading impression could be formed of the overall population trends. For example, when the density of active stages of *Panonychus ulmi* was declining on the leaves started with eight females, the density of eggs was generally increasing, as some  $F_1$  females escaped predation and started reproducing. A curve combining both eggs and active stages would have appeared somewhat similar to the one for the eggs, because eggs comprised the greatest proportion of the total population.

The stage distribution of the prey populations in relation to time is shown in figures 3 and 4 (averages of the eight replicates at each starting prey density). On the predator-free leaves (fig. 3), the proportion of adult females increased to a maximum at the 18-day count on all three groups. The proportion of eggs was generally lowest when that of the adult females was highest. After many  $F_1$  females matured, the percentage of eggs started rising, peak-

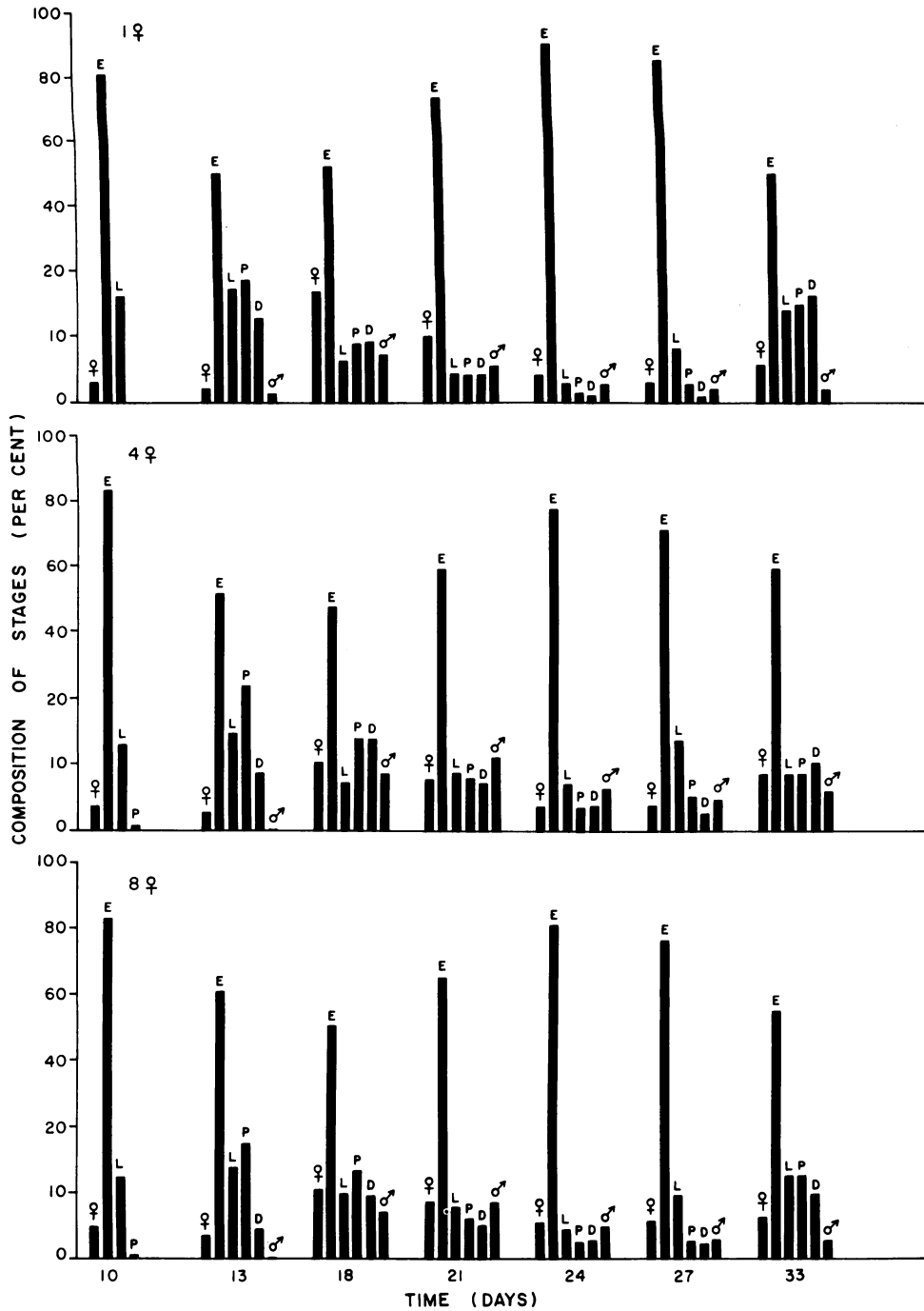


Fig. 3. Stage distribution of prey (*Panonychus ulmi*) populations in the single-leaf ecosystems without predators. Averages of eight replicates of each of three starting levels. ♀ = females, E = eggs, L = larvae, P = protonymphs, D = deutonymphs, ♂ = males.



ing at 24 days and then leveling or declining at the end. There was a relatively even distribution among the various immature stages except in the first count and at 27 days, when the percentage of larvae was distinctly higher than that of other immature stages. The percentage of males showed no definite

trends in relation to time, and always comprised a fairly low percentage of the population.

The stage distribution of *Panonychus ulmi* on the leaves with predators differed from that on the predator-free leaves mainly in the percentages of immature stages and males (fig. 4). Per-

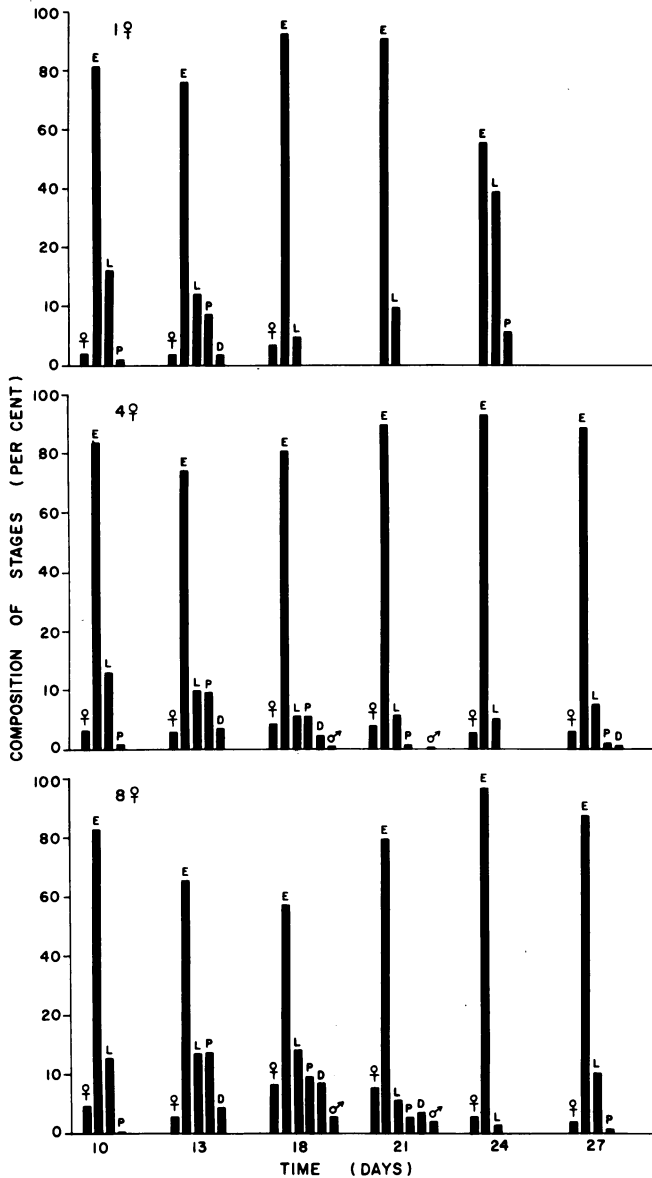


Fig. 4. Stage distribution of prey (*Panonychus ulmi*) populations in single-leaf ecosystems with predators (*Amblyseius potentillae*) present. Averages of eight replicates at each of three starting levels of prey.

centages were generally progressively lower from larvae to protonymphs to deutonymphs to males, suggesting that most progeny were destroyed by predators before they reached the later stages of development. The general trend in percentages of eggs and adult females in relation to time was similar

to that on the predator-free leaves, especially on the replicates started with eight female *P. ulmi*, although the percentage of eggs was higher, as might be expected from the fact that *Amblyseius potentillae* does not prey on the eggs.

The distribution of *Panonychus ulmi* between upper and lower sides of leaves

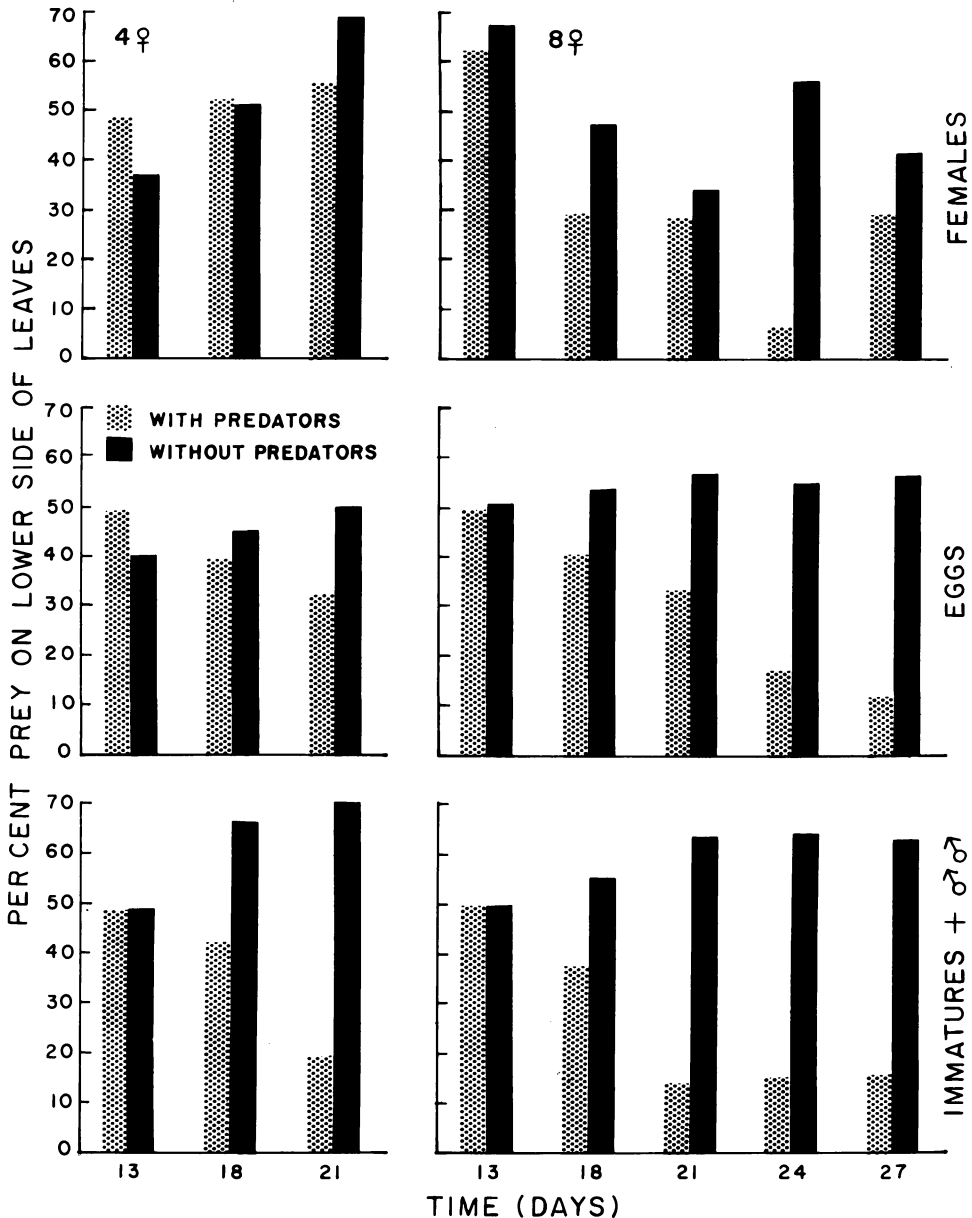


Fig. 5. Distribution of prey (*Panonychus ulmi*) in relation to the side of the leaf (upper or lower) inhabited, on plants with or without predators (*Amblyseius potentillae*), at two different starting prey levels. Values represent averages of eight replicates at each prey level.



is shown for the leaves started with four and eight female *P. ulmi* (fig. 5). At 13 days, or three days after the predators were introduced, there was little difference in prey distribution between the predator-free leaves and those containing predators. Subsequently, however, the percentage of prey on the lower sides of the predator-free leaves was considerably higher than on the lower sides of those containing predators. These data show that predation altered the intraleaf distribution of the prey populations. This presumably resulted because the predators spend more time on the lower surfaces, and deposit almost all eggs there. Thus, prey on the lower side would generally be more exposed to predation. Predators were seldom seen on the upper surface during counting. It is possible, however, that they came to the upper side more frequently at night. The apparent preference for the under surfaces of leaves is common in the Phytoseiidae. Putman (1962) found that several types of responses determined this behavior in *Typhlodromus caudiglans* Schuster.

## Experiment II

The populations of *Panonychus ulmi* on the eight-leaf plants increased rapidly in the absence of predators (fig. 6). The egg populations showed a typical leveling or decline after 10 days, then a sharp increase as the F<sub>1</sub> females started reproducing, and finally a leveling trend at the final count, at which time a rapid increase in active stages was still evident. Because of time limitations for counting, we did not determine how much higher the populations might have increased before starting to decline. However, the potential of *P. ulmi* for reaching high densities quickly in the absence of predation was demonstrated. On the final count, the populations started with eight females averaged over 1,400 each of eggs and active

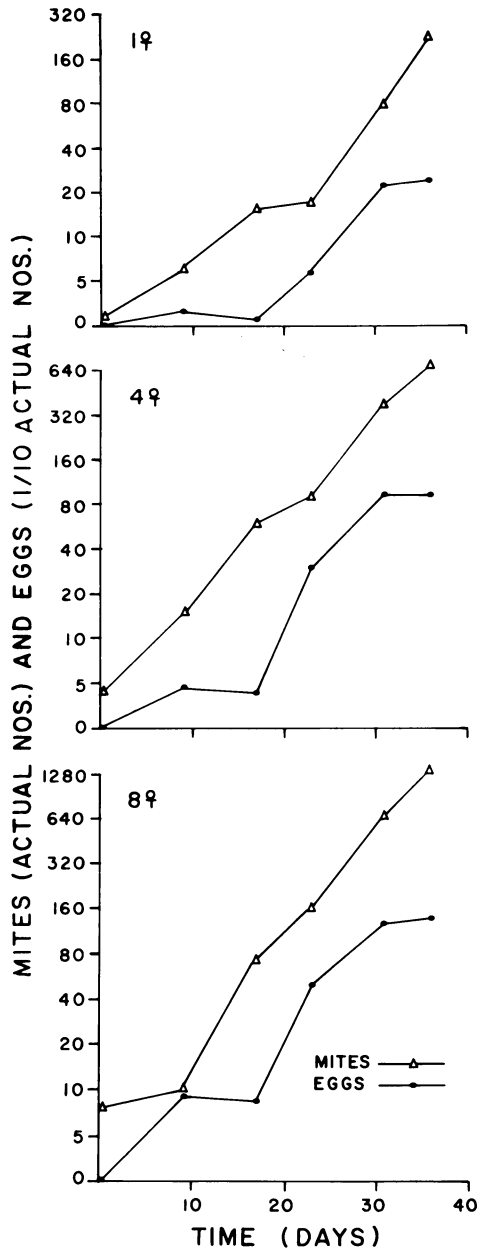


Fig. 6. Population trends of *Panonychus ulmi* in three eight-leaf ecosystems, without predators; based on averages of two replicates of each of three starting levels.

stages per plant, or about 175 per leaf of each.

On the plants started with one female *Panonychus ulmi* and one female *Am-*

*blyseius potentillae*, the prey population was considered controlled by the predators on four of the eight replicates (fig. 7, replicates 4, 5, 6, and 7), whereas they escaped control on the remaining four because the predator populations died out or dwindled to a nonreproductive individual. In daily observations for seven days after the predators were introduced, all but one

of the original predators were seen on the infested leaf (leaf 4) at least once. However, during those first few days, most predator eggs were laid on the noninfested leaves, especially on replicates 1, 2, and 3. Most of these progeny probably starved, and the numerical response was generally not so great as on the single-leaf systems. As compared with the single-leaf ecosystem, the in-

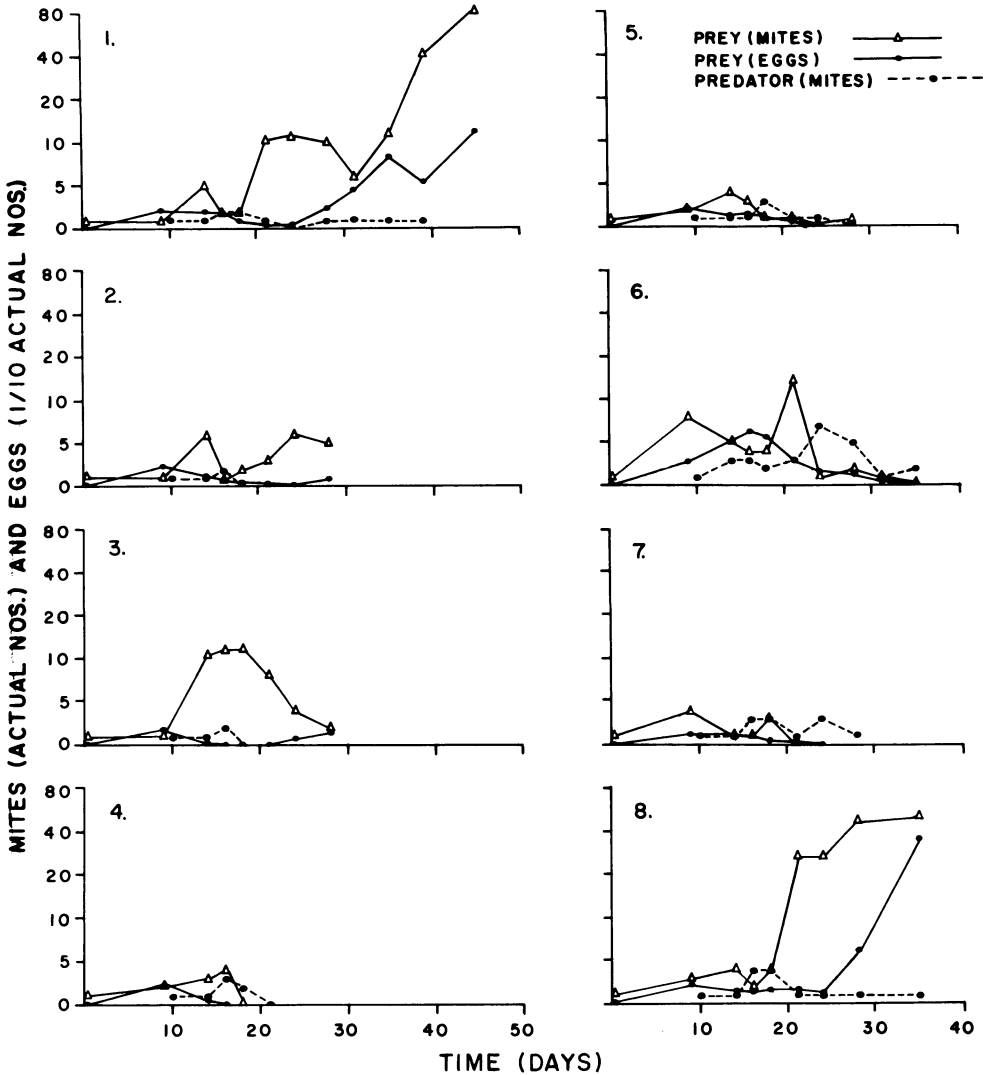


Fig. 7. Population trends at *Panonychus ulmi* (prey) and *Amblyseius potentillae* (predator) shown separately for each of eight replicates on eight-leaf ecosystems started with one adult female *P. ulmi*.



creased complexity of the eight-leaf ecosystem apparently reduced the predators' chances of controlling the prey. The slightly more complex interaction on replicate 6 was probably the result of the greater initial prey density produced by an additional adult female *P. ulmi* accidentally infesting this plant.

Populations of *Panonychus ulmi*

were considered controlled by *Amblyseius potentillae* on four of the eight plants started with four female prey (fig. 8, replicates 3, 6, 7, and 8), although counting was terminated before this was actually shown on replicate 6. On the other four plants (1, 2, 4, and 5), an initial reduction of the prey occurred following the numerical re-

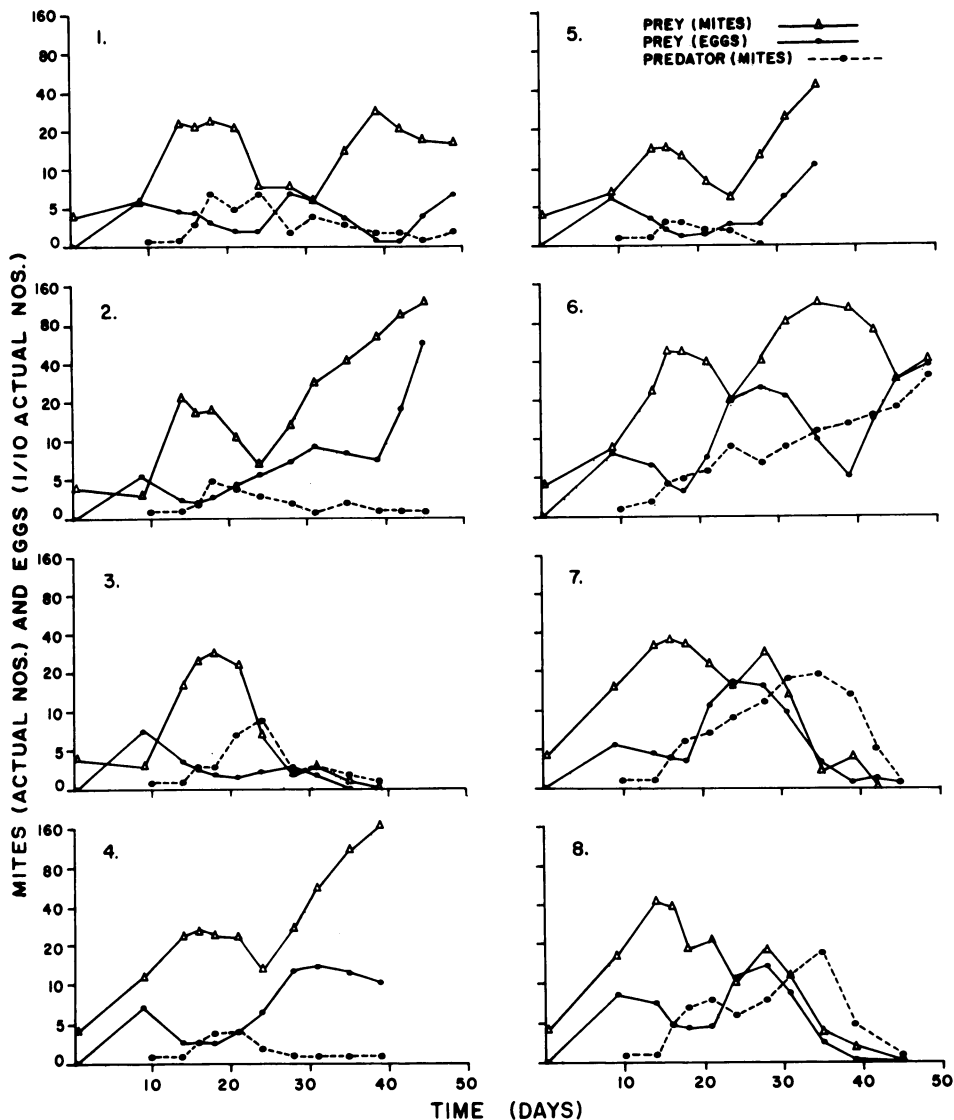


Fig. 8. Population trends of *Panonychus ulmi* (prey) and *Amblyseius potentillae* (predator) shown separately for each of eight replicates on eight-leaf ecosystems started with four adult female *P. ulmi*.

sponse of the predator populations. However, predator numbers then declined to one or two nonreproducing females which probably had failed to mate. As a result, the prey population subsequently increased essentially unchecked.

Replicate 3 had only a single peak of both prey eggs and active stages. At least one reproducing female predator (as evidenced by the presence of eggs) was present on this replicate at each count date up to the final one, so that immature predators were probably always playing a part in preventing any resurgence in the prey population. Continuous predator reproduction, with the offspring searching for food, should result in more complete dispersion on the plant (even if few progeny find sufficient food to enable them to mature), and thereby reduce the possibility of resurgence of the prey population.

Replicates 6, 7, and 8 increased rapidly in prey eggs from about 18 to 28 days (fig. 8), due to relatively large numbers of  $F_1$  progeny reaching the reproductive stage. The start of a second cycle of increase in prey active stages was evident at 28 days. A decline had started by the next count (31 days) on replicates 7 and 8, however, and the prey was essentially eliminated at 45 days.

This second cycle of increase in active stages of prey was not checked as rapidly on replicate 6 as on replicates 7 and 8 (fig. 8). The predator response was insufficient to prevent the maturing of a relatively large number of  $F_2$  females, as indicated by the third cycle of increase in prey eggs from days 40 to 50. From the 21-day count through the next several counts, the number of active stages of predators in relation to the number of eggs seemed low, indicating a relatively low survival rate of the progeny. Between 24 and 28 days, the number of leaves with predators decreased from six to three, whereas rep-

licates 7 and 8 both had five of eight leaves containing predators at the 28-day count. The predator population brought about a decline in the prey population on replicate 6, however, after a peak of 124 active stages (about 15 per leaf). Although the final count indicated another increase in *Panonychus ulmi*, the active stages were primarily larvae hatching from the large number of eggs remaining. At that time, large numbers of predators were present on all leaves, and the prey probably would have declined to low numbers in a short time.

On the plants started with eight female *Panonychus ulmi*, the prey population escaped eventual suppression by the predator on only one of eight replicates (fig. 9, replicate 5). Apparently the predators produced no new progeny on this plant after about 18 days. At the 28-day count, there were six mature females, but none reproduced. If any males were produced, they may have died or escaped from the plant before contacting and mating with any of the females.

Prey populations were held to peaks near or below 80 active stages per plant (10 per leaf) on five of eight replicates (nos. 2, 3, 4, 7, and 8). There was no numerical response by the predator populations on replicates 1 and 6 during a critical period, and suppression was not initiated until after about 40 days. Replicate 1 showed generally moderate bronzing of the foliage at the final count with two leaves heavily bronzed; replicate 6 showed light to medium bronzing. The damage to these plants by *P. ulmi* was still considerably less than on replicate 5, where control by predation failed completely, and on the predator-free plants. Although counting was discontinued on the latter plants before *P. ulmi* populations declined (fig. 6), examination on day 49 revealed partial defoliation and heavy bronzing on remaining leaves.

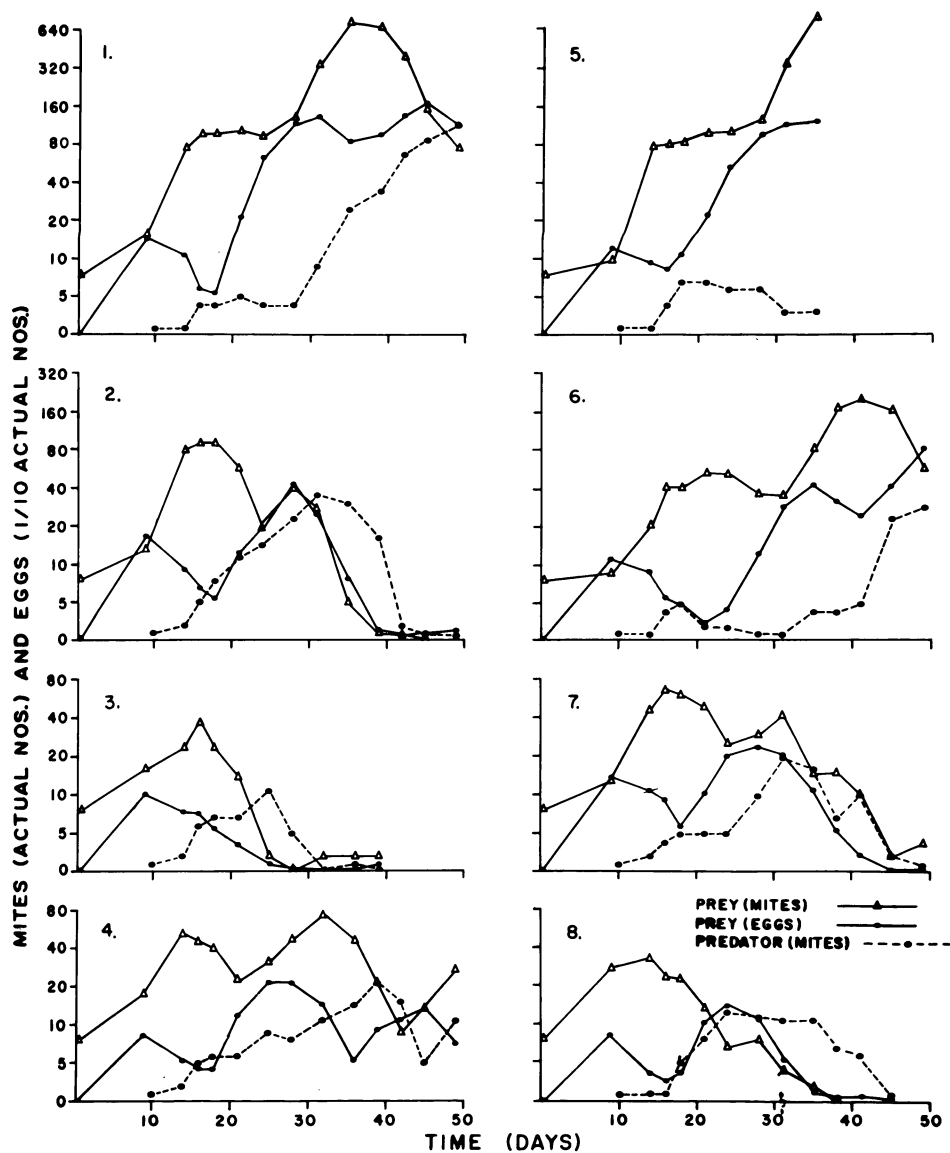


Fig. 9. Population trends of *Panonychus ulmi* (prey) and *Amblyseius potentillae* (predator) shown separately for each of eight replicates on eight-leaf ecosystems started with eight adult female *P. ulmi*.

No adult female predators were present at the 21-day count on replicates 1 and 6, and no new progeny were produced from then until after 24 or 28 days. By the time reproduction resumed, the F<sub>1</sub> female prey had produced many eggs (over 1,000 were counted on plant 1 and over 400 on

plant 6), resulting in a very high prey: predator ratio. No eggs of *Amblyseius potentillae* were found, and apparently little or no predation occurred, on the most heavily infested leaves (nos. 2 and 6 on replicate 1 and no. 2 on replicate 6) before 28 days.

Apparently replicate 6 was less fav-



orable for increase of *Panonychus ulmi* than was replicate 1, because the numerical response of the predators was more delayed on the former, yet numbers of prey did not become as high. The high number of predators and the downward trend in the prey population at the final count on both of these replicates indicated that the prey density would have declined to a low level in a few more days. As *P. ulmi* did reach high densities and leaf bronzing was evident, an unfavorable food supply in addition to predation could have contributed to their decline in numbers.

The two plants (3 and 8) having the

lowest peaks of *Panonychus ulmi* had only a single peak in active stages. Replicate 3 had a single peak in eggs also, apparently because no  $F_1$  female prey matured. Two peaks in both eggs and active stages occurred on replicates 2, 4, and 7. This was the more usual sequence of events—i.e., some  $F_1$  progeny escaped predation to become reproductive females, resulting in an abrupt rise in egg density, followed by another increase in active stages, and then a corresponding increase in predator density. A third cycle of increase started on replicate 4 with predator numbers also increasing.

## DISCUSSION

Although the starting prey:predator ratios were the same in both the single-leaf and eight-leaf ecosystems, some differences in population trends between the two ecosystems were evident on the plants started with four or eight female *Panonychus ulmi*. The initial prey population peaks attained before suppression by predation averaged somewhat lower in the single-leaf ecosystems than in eight-leaf ones. The numerical response of the predators on the single leaves was generally quicker and more consistent, as was the suppression of active stages of prey from the initial peak. These responses were probably the result of the differences in complexity of the two types of ecosystems. The eight-leaf systems contained not only eight times the leaf area, but also the added complexity of the stem and petioles as compared with the one-leaf systems. Thus, with the lower average prey density and the additional aspect of leaf-to-leaf migration, it is not surprising that the numerical response of the predator was generally slower and the predator-prey interactions more variable on the more complex eight-leaf ecosystems.

The single-leaf ecosystems were valu-

able in showing the potential of *Amblyseius potentillae* for exerting control of *Panonychus ulmi* populations in a highly simplified situation, whereas the eight-leaf systems showed some of the complexities involved in a larger but still very simple ecosystem. Even when they were started with the same numbers of prey of the same age on each replicate, no two replicates were closely alike in the eight-leaf systems. In some instances, fluctuations occurred in different phases on individual leaves of the same seedling. Variation also seems to be the rule in field populations, occurring at all levels—e.g., leaf to leaf, limb to limb, tree to tree, and orchard to orchard. Because of this characteristic, it is generally inadvisable to lump or average the data from subunits of the plot or ecosystem, as details of varying interactions among subunits will then be obscured (Huffaker, van de Vrie, and McMurtry, 1970, p. 428).

Probably fewer prey populations would have escaped the effects of predation if larger ecosystems had been used, thereby reducing the possibility that control by predation would fail merely because of some event such as the failure of one or two predators to

mate and produce progeny. The studies of Huffaker (1958), Huffaker, Shea, and Herman (1963), and Laing and Huffaker (1969) have shown that the larger the ecosystem the greater the insurance against extinction of prey and/or predator after one or a small number of oscillations. Also, in these experiments, predator survival was completely dependent on finding prey, whereas in nature, other foods might serve to prolong survival and improve stability.

The replicates in which *Amblyseius potentillae* held *Panonychus ulmi* to low peak numbers demonstrate the control potential of this predator. In these cases the increase was usually less than 10-fold in active stages of prey before initial suppression occurred (figs. 2, 8, and 9). This was considerably lower than the 50-fold increase that occurred with *Oligonychus punicae* being preyed on by *A. limonicus*. (McMurtry and Scriven, 1971), before suppression by the predator.

Even with a greatly delayed numerical response and extremely unfavorable ratio, as on replicates 1 and 6 started with eight female prey (fig. 9), *Amblyseius potentillae* was capable of exerting suppressive action. At the 28-day count on replicate 1, there were only four predators and one egg to 135 prey active stages and 1,270 prey eggs. Fourteen days later the predators had increased to 70 active stages, and 18 days later to 105, with a marked decrease in prey density. Thus predator response was not inhibited at high prey densities, as has been suggested for some species on the basis of laboratory studies (Kuchlein, 1965; Mori and Chant, 1966).

The ability of *Amblyseius potentillae* to respond to and suppress a wide range of densities, as demonstrated in these studies, supports the conclusions of van de Vrie and Boersma (1970) from their experiments with the same species on

host plants with three different levels of nitrogen. The ability to overtake and suppress increasing prey populations, even though greatly outnumbered, requires an extensive numerical increase (numerical response) of the predators and adequate dispersion over the leaves. *A. potentillae* appears to have sufficient reproductive potential for a rapid numerical response to increasing prey density. In these experiments, a critical factor in the numerical response seemed to be whether or not the  $F_1$  progeny reproduced. When the prey density was suppressed to low numbers after the initial peak, only a few individual predators of the  $F_1$  generation reached the adult stage. As mating is necessary for reproduction, the presence of males and their ability to locate the females were critical at this time. Where the numerical response failed, it was usually because the remaining females failed to reproduce, presumably because they had not mated. This was the consequence of such a limited ecosystem.

In this study, the adults of *Amblyseius potentillae* appeared to roam freely over the plant and showed little tendency to remain on an infested leaf in preference to a noninfested one. Eggs were sometimes deposited on noninfested leaves; consequently those progeny could not survive unless they were successful in finding prey on other leaves. This was probably a critical factor in the interaction during periods of low prey density, such as on plants infested with only one adult female *Panonychus ulmi*, or at the low point in the fluctuations on plants infested with four or eight *P. ulmi*. In studies with the same mite species, van de Vrie and Bakels (1968) observed no correlation between the interleaf distribution of the predator or its eggs and that of the prey, *P. ulmi*. Thus, *A. potentillae* does not seem to respond to a given prey distribution. This characteristic may have been responsible

for its failure to respond numerically in some of the replicates in these experiments. Examining the plants only twice weekly, however, was insufficient for elucidating the details of movement and distribution. The numerical response is considered an important factor in effecting suppression of and regulation of a tetranychid mite population. However, the underlying factors which initiate or limit the response (e.g., prey consumption, searching, distribution) are probably more critical than reproductive capacity in the case of *A. potentillae*.

As *Amblyseius potentillae* does not prey on the eggs of *Panonychus ulmi* (van de Vrie and Kropczynska, 1965), that portion of the population is protected from predation. These authors also found that, of the active stages, adult females are preyed upon the least. Thus, as a population is being suppressed by the predator, it will be re-

duced mainly to adult females, eggs, and hatching larvae, and finally, to only eggs and hatching larvae. This phenomenon could be partially seen in the stage distribution data from the single-leaf ecosystems (fig. 4), and is probably the main reason why it was possible to have two or more population cycles in such a simple ecosystem. It was impossible to show consistent trends in stage distribution in the eight-leaf systems, as the phase of individual interactions in relation to time differed considerably among replicates and even between leaves on the same plant. Van de Vrie and Kropczynska (1965) considered the relatively low preference for adult female *P. ulmi* to be an advantage in maintaining an equilibrium because preservation of some adult females would, by their producing offspring, ensure a supply of food for the predatory mites.

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