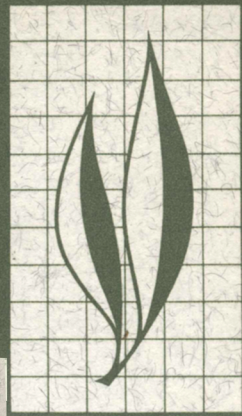


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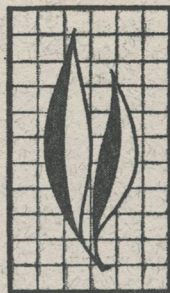
The Dynamics of Predation of  
*Stethorus picipes*  
(Coleoptera: Coccinellidae) and  
*Typhlodromus floridanus* on the Prey  
*Oligonychus punicae*  
(Acarina: Phytoseiidae, Tetranychidae)

Part I. Comparative Life History  
and Life Table Studies

Part II. Effects of Initial Prey-Predator Ratios  
and Prey Distribution

L. K. Tanigoshi and J. A. McMurtry





## Part I. Comparative Life History and Life Table Studies

Life history studies first were conducted for the prey, the avocado brown mite *Oligonychus punicae* (Hirst), and the predators, the phytoseiid mite *Typhlodromus floridanus* (Muma) and coccinellid *Stethorus picipes* Casey, in an insectary chamber on excised *Persea indica* Spreng leaves. Both mite species developed at a faster mean rate than did *S. picipes*. A life table was constructed for each species from the life history data. Despite a shorter oviposition period than that of either predator, *O. punicae* not only laid more eggs/female per day, but also had a higher mean-age specific fecundity rate. The intrinsic rate of increase,  $r_m$ , was highest for *O. punicae* (0.222), followed by *T. floridanus* (0.159) and *S. picipes* (0.121).

In feeding tests, *T. floridanus* females indicated a significant preference for the egg stage of *O. punicae*. In contrast, females of *S. picipes* did not show a significant preference for a particular life stage of *O. punicae*. Assuming no problem whatever in finding prey (an inapplicable assumption for field situations), an arithmetic model was generated from the  $r_m$  values, fecundity, and the prey consumption rate of *T. floridanus*. At an initial ratio of 10 prey to 1 predator, this model indicated that *T. floridanus* preying on *O. punicae* eggs could annihilate such a population of *O. punicae* within 13 days.

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# The Dynamics of Predation of *Stethorus picipes* (Coleoptera: Coccinellidae) and *Typhlodromus floridanus* on the Prey *Oligonychus punicae* (Acarina: Phytoseiidae, Tetranychidae)

## Part II. Effects of Initial Prey-Predator Ratios and Prey Distribution

### INTRODUCTION

SINCE the commercial introduction of avocado into California in about 1910, numerous native and introduced arthropod pests have become established on it. Fortunately, most of these pests are maintained below economic levels by native natural enemies (Ebeling, 1959).

Field studies by Fleschner (1953, 1958) and Fleschner *et al.* (1955) on the natural balance of the avocado brown mite, *Oligonychus punicae* (Hirst) on avocado in southern California disclosed that the most effective predators were several species of phytoseiid mites and the coccinellid beetle *Stethorus picipes* Casey. These studies indicated that phytoseiid mites were the most efficient predators in maintaining *O. punicae* populations at low levels and that *S. picipes* was the most effective predator in suppressing high spider mite populations. McMurtry and Johnson (1966) indicated that the most important natural enemies of the avocado brown mite in southern California were two phytoseiid mites, *Amblyseius hibisci* (Chant), *A. limonicus* Garman and McGregor, and *S. picipes*. However, although *A. hibisci* was much more abundant in spring and early summer than was *O. punicae*, it did not

prevent rapid increases of this pest species in late summer. Factors which may limit the effectiveness of *A. hibisci* in responding numerically to an increasing *O. punicae* population are: 1) a relatively low reproductive rate when feeding on spider mite prey alone, 2) a different interleaf distribution (less clumped) than that of *O. punicae*, and 3) inability of *A. hibisci* to prey upon *O. punicae* that are protected beneath a complex of silken webbing (McMurtry and Johnson, 1966). Greenhouse studies by McMurtry and Scriven (1971) revealed that *A. limonicus*, in contrast, congregated on leaves heavily infested with *O. punicae*. This phytoseiid predator also possesses a sufficient response (functional and numerical) to changes in *O. punicae* density to overtake and suppress high and increasing *O. punicae* populations. McMurtry and Scriven (1971) reported, however, that for this predator also a relatively high *O. punicae* density was required to evoke a marked numerical response by *A. limonicus*.

McMurtry and Johnson (1966, 1967) concluded that *S. picipes* was the most important spider mite predator regulating *O. punicae* populations at tolerable levels in unsprayed avocado or-



chards. This voracious and mobile insectan predator requires even higher prey densities in order to reproduce effectively. McMurtry and Johnson (1966) indicated that the lowest density of prey sufficient to evoke a marked numerical response by this beetle was an average of 10 adult female *O. punicae* per leaf.

Although *Typhlodromus floridanus* (Muma) does not occur in California, it is a highly specialized spider mite predator that will feed and reproduce on *O. punicae* (Muma, 1970, 1971; Sandness, 1969). Because of these characteristics and its potential for field use, laboratory studies were conducted to measure the ability of this predator to initially suppress thriving populations of *O. punicae* and to maintain them subsequently at low population levels.

## MATERIALS AND METHODS

Three basic experiments were conducted to study population interactions of the following: 1) *Typhlodromus floridanus* and *Oligonychus punicae*, 2) *Stethorus picipes* and *O. punicae*, and 3) both *T. floridanus* and *S. picipes* and *O. punicae*. These are described below.

### Experiment I

*Typhlodromus floridanus*—*Oligonychus punicae* interactions. This experiment was conducted in the insectary under the artificial conditions described for the life history studies of *Oligonychus punicae*, *Typhlodromus floridanus* and *Stethorus picipes* (Part I). The experimental ecosystems were 2- to 3-year-old avocado seedlings (McMurtry, 1970; McMurtry and Scriven, 1966, 1971) planted in a 3.8-liter plastic pots containing vermiculite. Each plant received 1 quart of modified Hoagland and Arnon's (1950) nutrient solution once a week and was watered with tap water when indicated. Each seedling had 15 mature leaves of nearly equal

To better understand the properties and dynamic effects of these two distinct types of predators in relation to their prey, a study was conducted on the potential and actual ability of *T. floridanus* and *S. picipes* to suppress or regulate *O. punicae* populations under simplified, controlled conditions. The major objectives of the study were: 1) to compare the potential ability of the two predators to overtake and suppress increasing populations of *O. punicae*, 2) to determine the minimum prey density necessary for populations of each predator to persist, 3) to determine the effects of each species of predator on the dispersal and distributional patterns of the prey, and 4) to determine the degree of competition that may exist between the two predator species.

size and uniform surface. Subsequent new growth was removed.

To minimize cross-contamination due to the dispersal of adult female *O. punicae* by "ballooning" on strands of silk, Mylar® cylinders were placed around each plant (Fleschner *et al.*, 1956; McMurtry, 1970; McMurtry and Scriven, 1966, 1968, 1971). These cylinders were 46 cm in diameter and 91 cm high. A Mylar® floor, coated with Emcol 5100® (diluted 1:1 with water) and placed on the bottom of each cylinder, served as an effective trap for both the prey and predator species. To estimate the number of mites dispersing or perishing since the previous count, the trapped mites were washed with water from the Mylar® floor. The solution was poured into a Buchner funnel lined with filter paper on which the mites were collected. The filter paper and the filtrate were then stored in petri dishes and placed in the refrigerator for future evaluation.

A ring of Tanglefoot® was placed



around both the top and bottom of the stem of each seedling. Two days before *O. punicae* was introduced, all the seedlings were fumigated with 115 g of methyl bromide per 4.9 m<sup>3</sup> for 2 h. Their leaves were then carefully washed with distilled water.

The method by which the predator-prey interaction was initiated was similar to that utilized by McMurtry and Scriven (1971). Because incipient orchard outbreaks of *O. punicae* usually occur in aggregated foci of infestation on individual trees, these experiments were initiated by inoculating only one central leaf (Leaf 7) with prey. Cellulose cotton bands were placed around the petiole of this leaf to impede dispersal of the prey. These bands were removed after 1 week (McMurtry and Scriven, 1971). Each of the 12 *P. indica* seedlings used in this study was infested in this way with 30 adult female *O. punicae*. Four days later, Leaf 7 of each plant was carefully examined and all missing females were replaced. Females found on other leaves were removed. Three of these plants were used as predator-free controls. The other nine were divided into three groups of three plants designated as Series T<sub>1</sub>, T<sub>2</sub>, and T<sub>3</sub>. At 1-, 2- and 3-week intervals after the initial prey inoculation, plants of the three series each received two adult *T. floridanus* per leaf (total of 30). Thus, the experiment consisted of a control (predator-free) and three different groups with predators, in which three different initial prey:predator ratios were obtained by the differences in times of predator introduction.

The population densities of both predator and prey were determined by examining both leaf surfaces with a 10× binocular microscope mounted on a shoulder harness. All active stages of the predator and prey were counted at first. Each immature stage, the subsequent quiescent stage, and adult males and females were recorded separately. When prey population became over-

whelmingly dense, however, and appeared more or less evenly distributed, as indicated by damage to the upper and lower leaf surfaces, only a quarter of each surface of a leaf was censused. The quadrat to be censused for a given week was determined from a random numbers table.

## Experiment II

*Stethorus picipes*—*Oligonychus punicae* interactions. The physical conditions and *P. indica* ecosystems used were similar to those utilized in Experiment I. Because the effects of predation by adult as well as by larval stages of *S. picipes* on the avocado brown mite were to be measured, a modification of the experimental universe was necessary. In addition to minimizing cross-contamination as was accomplished in Experiment I with Mylar®-covered cylinders, a cage was designed to prevent dispersal by adult beetles and also to trap "ballooning" female *O. punicae*. The cage designed to house individual *P. indica* seedlings was a wooden rectangular-shaped frame 122 cm high and 46 cm square. One side consisted of a full length door sealed with weather stripping. All sides were covered and sealed with clear Mylar® (4 mils thick), and the top was covered with iced organandy. Lumite® plastic screen (32 × 32 mesh) was stretched across three wooden crossmembers of the floor. The unit rested firmly upon a box 46 × 46 × 4 cm in size. A closely fitting sheet of Mylar® covered with Emcol 5100® (diluted 1:1 by volume with water) was placed on the floor of the box. This provided an effective trap for use in evaluating the relative rates of dispersal by the avocado brown mite females between censusing dates. The Lumite® screen prevented accidental mortality of the adult stages of *Stethorus*, which tend to drop from the foliage when physically disturbed. It was assumed that most falling mites passed through the screen to the trap and that reinfestation by fall-

ing mites was negligible. A Mylar® disc, slightly larger than the opening of the 3.8-liter plastic pot, was fitted around the base of the stem of the plant to minimize loss of "ballooning" females into the vermiculite substrate. Prior to the removal of the Mylar® trap, this disc and the plastic screen floor were carefully brushed to collect recently dispersed females or dead ones which had not fallen through the screen barrier. The aluminum pans on which the plants rested were washed, as were their respective Mylar® traps.

Leaf 7 on each of 12 different seedlings was inoculated with 30 female *O. punicae*. The experimental set-up consisted of a predator-free control and test Series T<sub>1</sub>, T<sub>2</sub> and T<sub>3</sub>, as with Experiment I. In this case, the subscripts designate the number of weeks allowed to elapse before first instar *Stethorus* larvae were introduced. Each test consisted of three replicates, except for the control series in which Replicate 3 was removed after the fourth week because of contamination by *T. floridanus*. In the Series T<sub>1</sub>, seven newly hatched first instar *S. picipes* were introduced on Leaf 7 one week after the introduction of prey; and eight more first instar larvae were introduced 5 days later, also on Leaf 7. These introductions were staggered because of the relatively long, inactive pre-pupal and pupal stages of this predator, during which time the prey would be free from predation, in order to assure continuous predation. By Week 3, however, it became evident that the rapid increase exhibited by the initial *O. punicae* population of 30 females would result in their control, mainly by intraspecific competition for food, rather than by predation, if the procedure utilized for Series T<sub>1</sub> were applied to Series T<sub>2</sub> and T<sub>3</sub>. Therefore, each leaf was infested with a first instar larva in the T<sub>2</sub> and T<sub>3</sub> series in Weeks 2 and 3, respectively.

The procedures utilized to assess the predator and prey population trends

and age distributions were as outlined for Experiment I.

### Experiment III

*Typhlodromus floridanus*—*S. picipes*—*O. punicae* interactions. The experimental procedures were similar to those used in Experiment II.

This experiment also consisted of a predator-free control and a Series T<sub>1</sub>, T<sub>2</sub>, and T<sub>3</sub>. Each series included three *Persea* seedling replicates. Thirty *O. punicae* females were placed on Leaf 7 of each replicate of the predator-free control and also on T<sub>1</sub> and T<sub>2</sub> seedlings; 45 were placed on the T<sub>3</sub> series. Two weeks later, one first instar larva of *S. picipes* and two adult females of *T. floridanus* were placed on all leaves in Series T<sub>1</sub> and T<sub>3</sub>. The T<sub>2</sub> series of seedlings received the same infestation of *T. floridanus* at the second week, but first instar larvae of *S. picipes* were introduced on only the even numbered leaves (2, 4 . . . 14), a total of seven larvae per seedling. All life stages of each species, except for the eggs of *O. punicae*, were counted on each leaf at weekly intervals after the first week. In addition, those individuals having dropped or dispersed to the trap substrate were counted.

The methods used to assess the predator and prey population trends, age distributions and spatial aggregations were as outlined earlier.

### Spatial distribution

Two statistical parameters useful in describing the spatial distribution of living organisms are their variance (*V*) and mean (*m*). By assuming each leaf to be a sampling site, and the seedling a discrete habitable unit, it is statistically possible to measure aggregation patterns of the predator, the prey and the predator-prey coaction. Pielou (1969) described the mathematical proofs for two methods of measuring aggregation or clumping between different populations, independent of density,



whether their means differ or not. The indices derived by the method of Lloyd (1967) Index of Mean Crowding,  $\bar{m}^*$ , and David and Moore's (1954) Index of Clumping,  $I$ , are proportional to density only when clumping is assumed to be reduced through random predation, intraspecific competition, or both.

In this study, Lloyd's index of mean crowding was used as a measure of the changes in spatial distribution which occurred during both the predator-free and the predator-present interactions. Lloyd (1967) defined mean crowding as the mean number per individual of other individuals in the same quadrat. Other individual(s) co-occupying the unit with the first individual may be referred to as neighbors. The index of mean crowding is calculated by the formula:

$$\bar{m}^* = \frac{m + V}{m} - 1, \text{ or } m + I.$$

A rapid decrease of  $\bar{m}^*$  indicates that clumping has exceeded a favorable survival threshold and that a significant mortality or dispersal rate, or both, has been evoked. Conversely, if living in dense clumps favors survival, the index will decrease less rapidly (Pielou, 1969). Thus, the index provides a mathematical method for comparing the intensity of density-dependent factors operating within and between different populations (here predator-prey interactions).

Lloyd's (1967) index of patchiness

$\bar{m}^*/m$  is a measure of aggregation that is not affected by random mortality. He defined patchiness as a property of a spatial pattern considered by itself, without regard to density. Thus, two populations may have the same index of patchiness even though their respective densities are different (Lloyd, 1967; Pielou, 1969). Therefore, this index allows one to compare and describe the spatial aggregations of different populations whose mean densities may have been altered, as by predation, which leaves the survivors at their original sites. An important aspect of this ratio of mean crowding to mean density is that random deaths leave patchiness unaltered, whereas density-dependent (non-random) deaths will alter the patchiness. It also indicates how much more crowded each individual is, as compared to what it would be if the population were randomly distributed. Lloyd (1967) also demonstrated that density-dependent mortality factors (i.e., intraspecific competition and predation) operate continually to decrease the quantity  $\bar{m}^*/m$ . This will inevitably result in a decrease in the index of patchiness, unless there is a long-term population increase of considerable magnitude. Iwao (1968) and Iwao and Kuno (1971) showed that the patchiness index is equal to unity when the distribution is random and larger or smaller than unity in clumped and uniform populations.

## RESULTS AND DISCUSSION

### Experiment I—Predation by *Typhlodromus floricornis* on populations of *Oligonychus punicae*

This experiment is presented in terms of the general population trends, stage distribution and spatial distributions exhibited. Following this will be a synthesis of these results.

**Population trends.** In the predator-free ecosystems, adult females of *Oligonychus punicae* dispersing by "ballooning" were trapped after Week 1 (Fig. 1). The peak population density of *O. punicae* occurred on Week 4, with high densities persisting for the following 2 weeks. High mean trap counts for Week 5 indicated that the highest numbers may actually have occurred on the

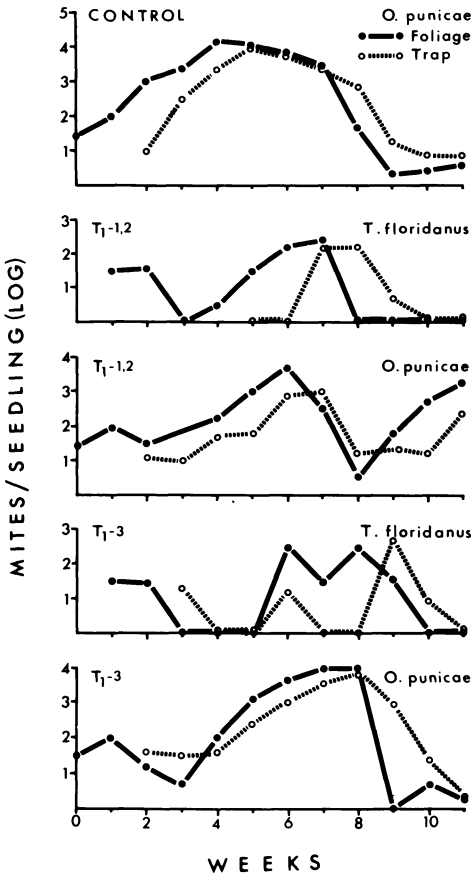


Fig. 1. Experiment I. Population trends of *Oligonychus punicae* in the predator-free controls (three replicates) and the *O. punicae*—*Typhlodromus floridanus* (predator) interactions (Series T<sub>1</sub>-1,2 and T<sub>1</sub>-3) on seedlings of *Persea indica*.

foliage sometime between Weeks 4 and 5. This high dispersal rate was evidence of an increasingly unfavorable food supply. The marked decrease in the numbers trapped on Week 7 (about 3,000), as compared to a decrease of 4,495 on the foliage (Fig. 1) indicated high mortality of immature stages and males on the foliage. The observed progressive "bronzing" of the foliage, coupled with the increasing proportion of dispersing females collected in the Emcol® traps, indicated the impact of intraspecific competition in reducing the *O. punicae* populations.

**Series T<sub>1</sub>.** Population trends on the

plants exhibiting a 1-week lag between prey and predator introductions indicated that by Week 3, *T. floridanus* reduced the *O. punicae* population to the extent that annihilation of the predator nearly occurred (Fig. 1) on all three replicates. Apparently a few predators were overlooked during these counts, because in Replicates 1 and 2 the predators eventually suppressed the increasing population of prey after Week 6 and then died out. Prey suppression on Replicate 3 occurred after the eighth week. Unimpeded then by predators and in the presence of still favorable nutrition, the remaining *O. punicae* populations on Replicates 1 and 2 underwent subsequent weekly numerical increases of 11-, 6- and 5-fold on Weeks 4, 5, and 6, respectively. Even with a delayed numerical response and an extreme prey: predator ratio of 53:1 on Week 4, *T. floridanus* was able to suppress the prey population by the seventh week. The resurgence of the prey population after Week 8 in Replicates 1 and 2, after the apparent "self-annihilation" by overexploitation of the *T. floridanus* populations, resulted in a third cycle of increase of *O. punicae* which approached the same magnitude as the second cycle. The combined action of predation and intraspecific competition resulted in the subsequent crash of the active stages of *O. punicae* between Weeks 8 and 9 in Replicate 3. A conservative measure of the ability of *T. floridanus* to suppress *O. punicae* populations (prey eggs not included) can be derived by comparing the mean of the means for the predator-free controls with that for Replicates 1 and 2 during the first 8 weeks of the experiment. Their respective weekly means were 5,289 and 769; i.e., the *O. punicae* populations were 85 percent lower in the presence of the predators (85% controlled).

**Series T<sub>2</sub>.** During the 2-week interval before *T. floridanus* females were introduced, population trends on the T<sub>2</sub> series of plants approximated those observed for the predator-free control



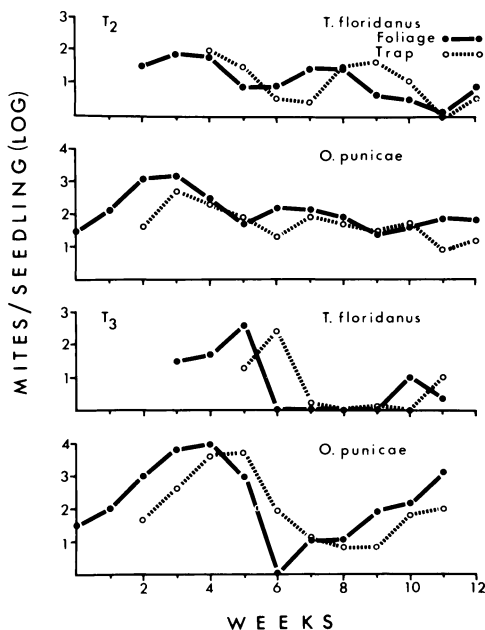


Fig. 2. Experiment I. Population trends for the *Oligonychus punicae* (prey)—*Typhlodromus floridanus* (predator) Series T<sub>2</sub> and T<sub>3</sub> interactions on seedlings of *Persea indica*, each replicated three times.

(Fig. 2). The decrease in predator density after Week 3 and the large numbers of predators which perished during that week resulted from both the marked reduction of the prey and dispersal of the predators. From Week 5 on, interactions between the prey and predator for all three replicates were relatively stable and, in some cases, there were predator phase lags, contrasting the two oscillating populations. These data indicate that *T. floridanus* possesses the ability to regulate *O. punicae* at low densities. The weekly mean prey densities for the predator-free control and the T<sub>2</sub> series results were 4,223 and 329 per seedling, respectively, for a 9-week period. Thus, in the presence of *T. floridanus*, the prey populations on the T<sub>2</sub> series plants averaged about 92 percent lower than those on the predator-free controls.

**Series T<sub>3</sub>.** By Week 3, when *T. floridanus* was introduced on the T<sub>3</sub> plants,

the average *O. punicae* density per seedling was slightly more than twice that attained on the predator-free control after a comparable period (Fig. 2). By Week 5, the predator population had increased more than seven-fold over that of the previous week, whereas the prey population already had about a 90 percent reduction. Predator numbers then declined abruptly by Week 6 to near extinction due to scarcity of prey. As a result of the near absence of predators between Weeks 6 and 10, a resurgence in the prey population was evident by Week 7. Besides predation, the other major factor suppressing the prey density, which had become very high, was the concurrent severity of intraspecific competition for food by *O. punicae*, which was evidenced as acute bronzing of the foliage. About 5,100 adult female *O. punicae* per seedling were estimated to have emigrated ("ballooned") from the foliage during Week 4. The suppressive effects of predation apparently occurred too late, although there was a more rapid crash from the respective peak, compared with that of the predator-free plants. The average weekly population densities were 4,594 and 1,767 *O. punicae* on the predator-free control and T<sub>3</sub> series plants, respectively.

**Stage distribution.** The dominance of the larval stage (37 percent) of *O. punicae* on the predator-free plants at Week 3 (Fig. 3) represented the contribution of offspring to the increasing population by maturing F<sub>1</sub> females. Unlike McMurtry's (1970) observations that immature stages comprise the largest proportion of the population well into the declining population phase, the dominance of immature stages ceased after the peak in population density. The presence of a preponderance of males and larvae after Week 8 is indicative of, or a prelude to, an abruptly declining *O. punicae* population.

**Series T<sub>1</sub>.** In Replicates 1 and 2 of Series T<sub>1</sub> (Fig. 3), the census for Week

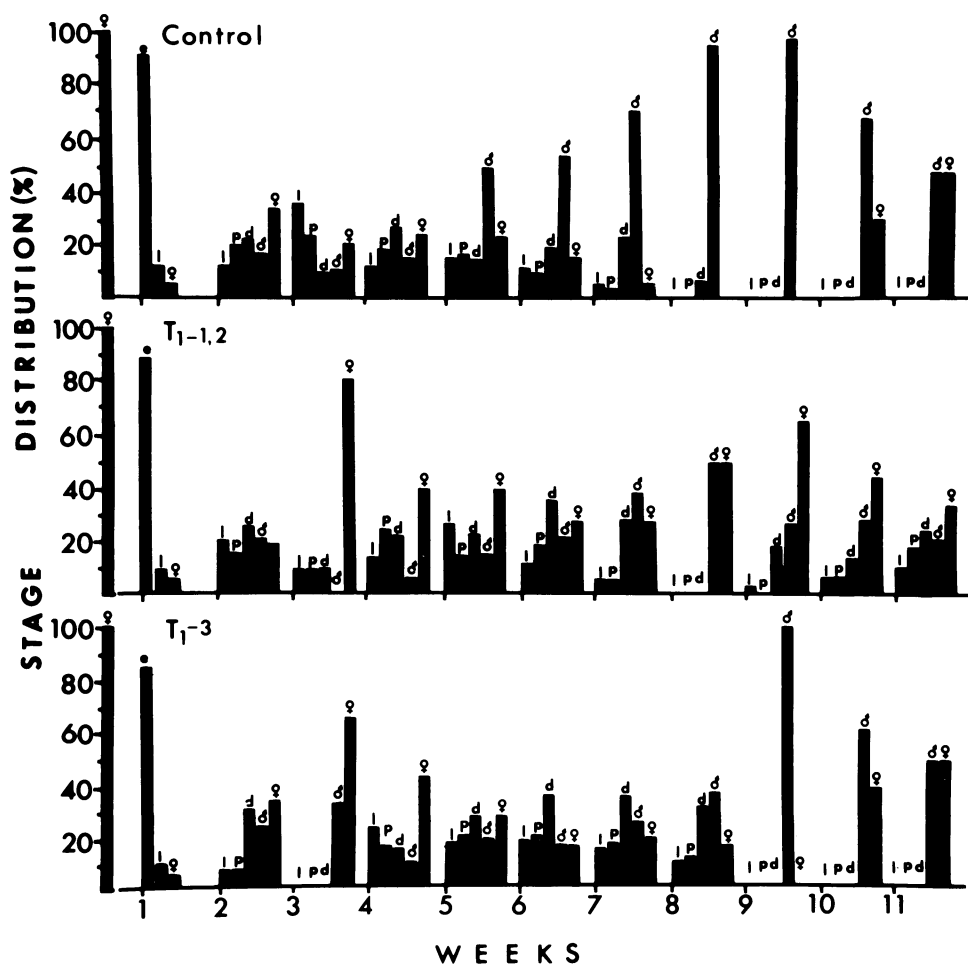


Fig. 3. Experiment I. Stage distribution of *Oligonychus punicae* (prey) populations in the predator-free controls (three replicates) and the *O. punicae*-*Typhlodromus floridanus* (predator) interactions (Series T<sub>1-1,2</sub> and T<sub>1-3</sub>). e = eggs, l = larvae, p = protonymphs, d = deutonymphs, ♂ = males, and ♀ = females.

4 revealed a distribution of 57 percent immature stages and a surprisingly large proportion of adult females (40 percent). As expected from a population in an ascending growth phase for this species, adult females outnumbered the males. This was true from Weeks 3 through 7. A decreasing trend in proportion of females was noticed, however, during this period. This fact, along with the increasing proportion of deutonymphs, implied a decreasing rate of egg production. Perhaps mainly as a

result of heavier predation on larvae and protonymphs, a 94 percent decrease in the *O. punicae* population occurred by Week 7. The females were the dominant stage during the following 2 weeks, as was observed for the stage distribution trends during the second oscillation (Weeks 4 to 6). Though differing in absolute numbers, the stage distributions at the peaks of the second (Week 6) and third (Week 11) oscillations were markedly similar.

**Series T<sub>2</sub>.** After the introduction



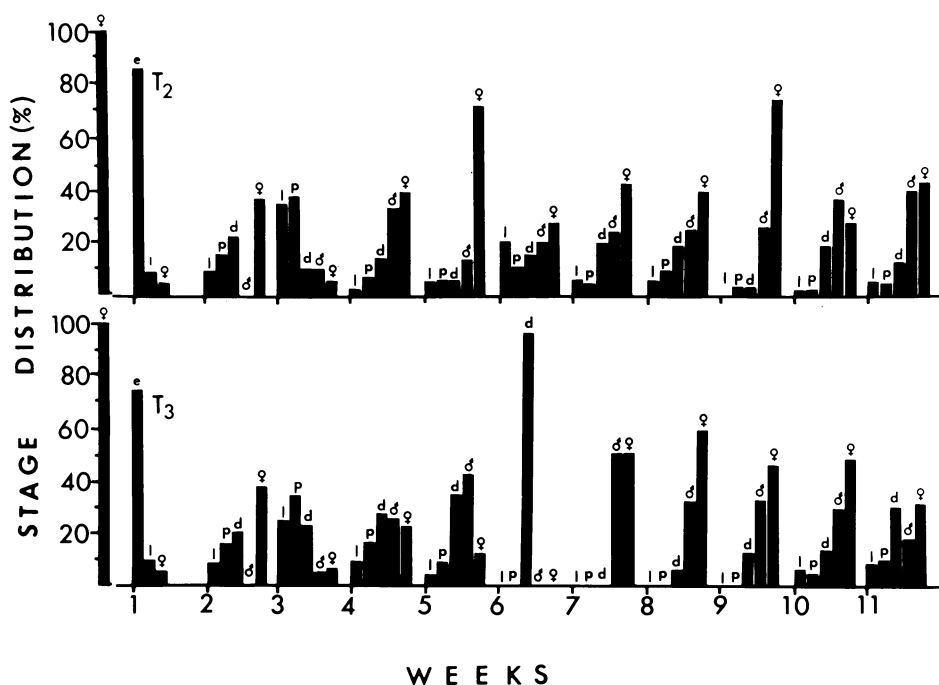


Fig. 4. Experiment I. Stage distribution of *Oligonychus punicae* (prey) populations in the *O. punicae*-*Typhlodromus floridanus* (predator) Series T<sub>2</sub> and T<sub>3</sub> interactions, each replicated three times. e = eggs, l = larvae, p = protonymphs, d = deutonymphs, ♂ = males, and ♀ = females.

of *T. floridanus*, the distribution of the prey consisted of 84 percent immature stages and 16 percent adults on the T<sub>2</sub> series plants by Week 3 (Fig. 4). The subsequent stage distribution from Weeks 5 to 8 were indicative of a *T. floridanus*-*O. punicae* oscillation, characterized by: 1) a large proportion of female adults which survived predation during the initial phase of the cycle; 2) subsequent increases in proportions of immature stages, this resulting from maturation of the F<sub>1</sub> progeny; and 3) progressive reduction of immature progeny as predator pressure intensified and subsequent increases in the proportions of adult females. After Week 9, the scarcity of immature stages, especially the larval and protonymphal stages, was characteristic of a population under intense suppression by such predation.

**Series T<sub>3</sub>.** The stage distribution of

*O. punicae* on the T<sub>3</sub> series of plants at Week 5, consisted mostly of males (43 percent) and deutonymphs (35 percent) during the decreasing phase of the first cycle (Fig. 4). The low prey population at Week 7 consisted of an even proportion of only males and females. On Weeks 8 and 9, the stage distributions were proportionately stable, although the larvae and protonymphs were again absent. In the absence of *T. floridanus*, the prey had undergone a seven-fold increase by Week 9, and the population comprised about 13 percent deutonymphs, 37 percent males, and 49 percent females. As a result of being released from the predator pressure, the stage distribution shifted, showing a weekly increase in the ratio of immature to mature individuals.

**Spatial distribution.** In the predator-free ecosystems, the density-dependent effect of intraspecific competition

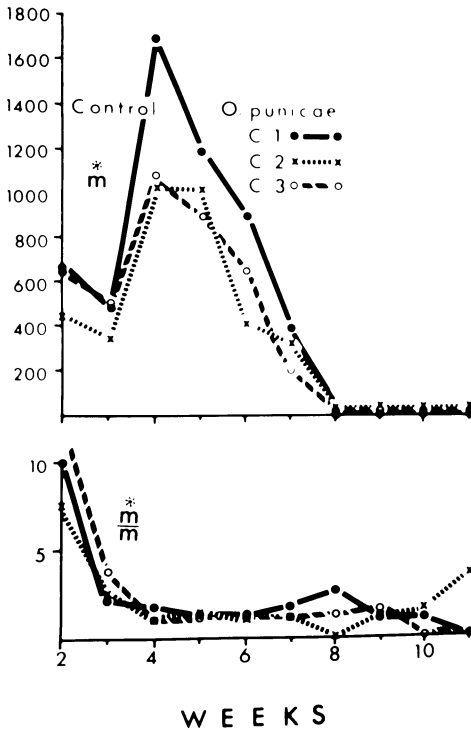


Fig. 5. Experiment I. Indices of mean crowding ( $\bar{m}$ ) and patchiness ( $\bar{m}/m$ ) of *Oligonychus punicae* in the predator-free controls, replicated three times.

on Leaf 7 resulted in increased *O. punicae* dispersal by Week 2 (Fig. 5). An approximate 73 percent decrease in the patchiness indices indicated that the *Oligonychus* populations were becoming more randomly distributed in response to their increasing density. The decline of the index of mean crowding on Week 3 indicated that, even though the populations were increasing in numbers, crowding had decreased because of dispersal from Leaf 7. On Week 4, crowding and average density per leaf reached maximums. The low indices of patchiness from Weeks 4 through 7 implied that the population had become nearly randomly distributed on the seedlings, an indication that considerable inter-leaf movement may have occurred.

**Series T<sub>1</sub>.** From Weeks 4 to 6, the

mean indices of crowding for *O. punicae* indicated a marked numerical increase, whereas their indices of patchiness implied a propensity to randomly disperse through the T<sub>1</sub> series of seedlings (Fig. 6). Thus, dispersal was already occurring when the average prey density was still below that where intraspecific competition would seem to be very operative. Even though *T. floridanus* decreased numerically on Replicates 1 and 2 during Week 7, and after Week 8 on Replicate 3, the rapidly decreasing  $\bar{m}$  for the prey can be attributed mainly to predation.

**Series T<sub>2</sub>.** By Week 5, the indices of patchiness indicated that the *O. punicae* populations for all T<sub>2</sub> replicates had assumed an essentially random distri-

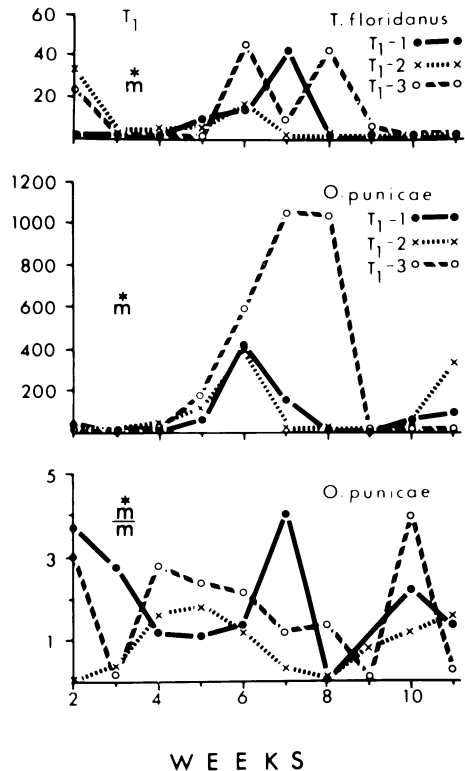


Fig. 6. Experiment I. Indices of mean crowding ( $\bar{m}$ ) for both *Typhlodromus floridanus* (predator) and *Oligonychus punicae* (prey), and index of patchiness ( $\bar{m}/m$ ) of *O. punicae* in the Series T<sub>1</sub> interaction, replicated three times.



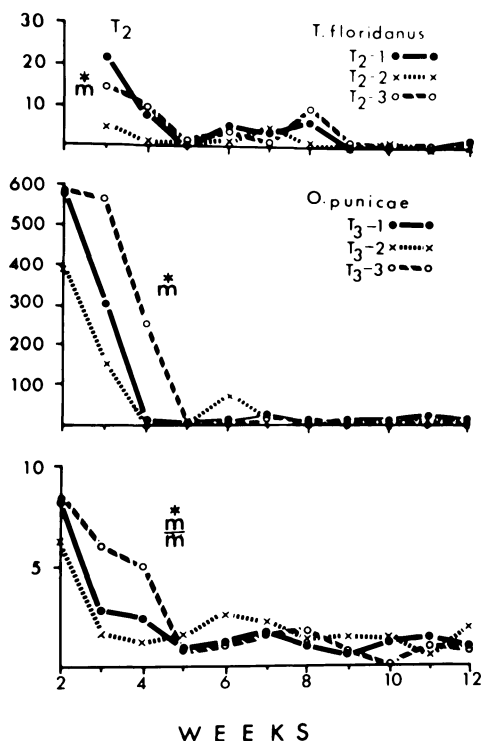


Fig. 7. Experiment I. Indices of mean crowding ( $\bar{m}$ ) for both *Typhlodromus floridanus* (predator) and *Oligonychus punicae* (prey) and index of patchiness ( $\bar{m}/m$ ) of *O. punicae* in the Series T<sub>2</sub> interaction, replicated three times.

bution (Fig. 7). A slight clumping trend after Weeks 5 through 7 resulted from the temporary cessation of predatory pressure during Week 5. With some variation in their patchiness indices, the prey again assumed a uniform distribution throughout the remaining weeks of this experiment.

**Series T<sub>3</sub>.** The prey population was essentially randomly distributed on each of the T<sub>3</sub> series replicates during a 3-week period of rapid exponential increase and subsequent decline to low levels (Weeks 3 through 6, Fig. 8). Both indices indicated that these recovering prey populations were phasing toward both a denser and a more moderately aggregated spatial distribution.

**Synthesis.** The T<sub>2</sub> ecosystems, in

which predators were introduced 2 weeks after the initial prey infestation, were the most favorable for the predators to suppress the prey population and stabilize it at subsequent low densities. With an initial prey:predator ratio averaging about 35:1, the 15-leaf *P. indica* universes apparently possessed perhaps just enough spatial heterogeneity to allow or generate three successive predator-prey oscillations, these being ones of decreasing amplitude. This combination of delay in introducing the predator, the initial prey:predator ratio used, and the pattern of initial distribution (placement) on the seedlings, was subsequently used, therefore, to study the competition between *T. floridanus* and *S. picipes* in the same system. Apparently, the decreasing amplitude of the successive oscillations resulted

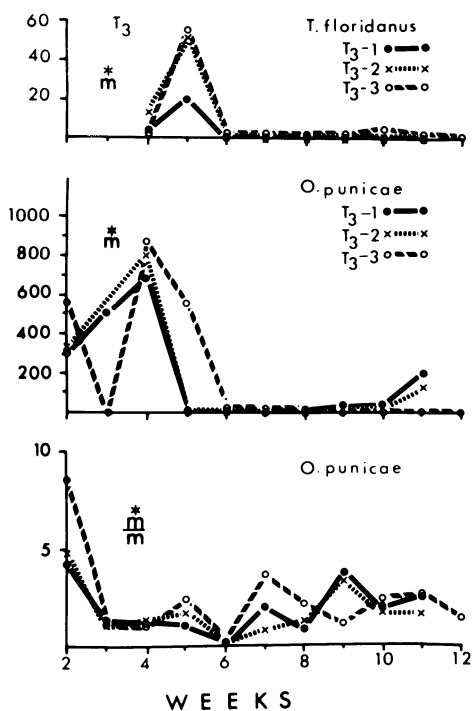


Fig. 8. Experiment I. Indices of mean crowding ( $\bar{m}$ ) for both *Typhlodromus floridanus* (predator) and *Oligonychus punicae* (prey), and index of patchiness ( $\bar{m}/m$ ) of *O. punicae* in the Series T<sub>3</sub> interaction, replicated three times.

primarily from the stabilizing effects of predation, but partly from the progressive depletion of its food by *O. punicae* and, thus, of food for the predator as well. Based upon the cyclic trends exhibited by both interactants in the  $T_2$  ecosystems, predation by *T. floridanus* was considered the major factor synchronizing events at both high and low prey densities. Huffaker *et al.* (1963) showed predation to be a synchronizer of cycle phases. At no time was it apparent that the prey had escaped control by the predator.

The establishment of a rough equilibrium between *T. floridanus* and *O. punicae* was highly influenced by the original starting ratios. Under the conditions of this study, the predator had a relatively rapid numerical response to increasing prey density and sometimes overexploited ("over responded") and then died out from lack of food. The data also indicate that the higher the predator density, the greater was the possibility of such "self-annihilation." Huffaker (1958) showed that systems that could generate higher densities of prey, and thus predators, would be more likely to be overexploited. A striking example of the ability of *T. floridanus* to respond to and suppress the prey at various densities over a wide range was demonstrated between Weeks 5 and 7 on Replicates 1 and 2 of Series  $T_1$  (Fig. 1). By Weeks 5 and 6, the prey:predator ratios were 32:1 and 30:1, respectively, with the prey having increased numerically by five-fold. Within the following 7 days, however, this ratio was reduced to 1:1 and was soon followed by near annihilation. The starting ratios for Series  $T_1$ ,  $T_2$ , and  $T_3$  were 3:1, 35:1 and 176:1, respectively.

McMurtry and Scriven's (1971) data on predation by *Amblyseius limonicus* and *O. punicae* indicated that a prey:predator ratio of over 50:1 developed before suppression occurred in similar ecosystems. Four to five weeks later,

however, the ratio also approached 1:1 and was followed by annihilation of the predators. On the basis of prey:predator ratios derived from the various experimental conditions of these studies, a ratio of a least two prey to one predator for the whole system was necessary to assure a high probability that enough prey would be missed somewhere in the system to sustain a minimum number of predators before they starve and the interaction ended. The progressive conditioning of the host plant by about Week 12, however, acted as a damping mechanism to both predator and prey increase. Huffaker (1958) and Huffaker *et al.* (1963) obtained three to four successive predator-prey oscillations of nearly equal amplitudes, between *Eotetranychus sexmaculatus* (Riley) and *Typhlodromus occidentalis* (Nesbitt), before the predators perished through starvation.

These interactions provide additional evidence to that of Huffaker (1958) and Huffaker *et al.* (1963) which contradicts the arguments of many population ecologists, initially Gause (1934), that the predator-prey interaction inherently results in self-annihilation, because the predator ultimately overexploits its prey. In Gause's view, immigration of the prey from other foci, or the existence of protective refuges excluding predators, has been held as the principal mechanism preserving such a coaction in nature. The  $T_2$  series revealed that migrant prey and protective refuges are not necessary in a closed and spatially complex system. An ecologically diverse ecosystem will also increase the probability of the participants surviving the low-density phase.

An arithmetical model generated after Laing and Huffaker (1969), at a theoretical prey:predator ratio of 10:1 indicated that *T. floridanus* could suppress an increasing *O. punicae* population in 13 days (Part I herein). The results of the actual population inter-



action experiments here reported are consistent with the general conclusions derived from the model.

The effectiveness of *T. floridanus* in reducing *O. punicae* populations from high densities and/or regulating it at low densities can be attributed, in part, to the predator's ability to search effectively for prey within the moderately dense webbing produced by *O. punicae*. Not only does this predator have a strong tendency to aggregate on leaves heavily infested with *O. punicae*, but it also lays its eggs in clumps on strands of *O. punicae* webbing or under debris on the upper leaf surface, which surface is also highly preferred by *O. punicae* for both feeding and oviposition. Another favored site for the deposition of eggs by the predator is under the curled margins of the leaves of *P. indica*. The tendency of the predator to place its eggs in close proximity to its prey increases the chances for the predator progeny to contact prey, and thus survive.

The data of McMurtry and Scriven (1971) indicated that *A. limonicus* was more effective in suppressing an initially aggregated or clumped *O. punicae* population concentrated on one leaf than a dispersed population of the same average density. Values obtained in this study for two statistical parameters (index of mean crowding and index of patchiness) support McMurtry and Scriven's (1971) observations that incipient *O. punicae* infestations have a propensity toward a clumped distribution. Census data for *T. floridanus*, introduced in a uniformly dispersed distribution, indicated that these predators quickly responded (*i.e.*, numerically and functionally) to foci of higher *O. punicae* densities. The effects of hypothesized random mortality factor (*i.e.*, unrealistically hypothesizing *T. floridanus* to be a random factor) responding to changes in prey density can be measured by the index of patchiness. The hypothesis of random action itself

can be tested. Weekly trends for indices of mean crowding and patchiness indicated that predation by *T. floridanus* both reduced prey density and the tendency of the prey to exhibit a contagious spatial distribution. The predator thus acted as a density-dependent factor.

Another characteristic of the  $T_2$  interaction was the high proportion of female prey and low proportion of immature stages present in the  $T_2$  ecosystems after Week 4. Feeding tests conducted previously (Part I) also indicated that *T. floridanus* will not consume as many adult female *O. punicae* if immature stages are present in abundance. Laboratory feeding studies by van de Vrie and Kropczynska (1965) and van de Vrie and Boersma (1970) for *Typhlodromus pyri* (Scheuten) and *Amblyseius potentillae* (Garman) indicated that these predatory mites prefer the immature stages over the adult stage of *P. ulmi*. This preference for young stages rather than adult females was suggested by them as a mechanism by which these predators can control their prey at low densities under natural conditions. This may be the reason their interaction was sustained for over 12 weeks. Thus, sufficient female prey were conserved to produce a continuous source of immature prey to sustain more predators.

In conclusion, this experiment indicated that *T. floridanus* possesses both an adequate total response (numerical and functional) to increasing prey density and adequate searching and consumption capacities to suppress rapidly increasing populations of *O. punicae* on avocado and subsequently to regulate them at low densities.

### Experiment II—Predation by *S. picipes* on populations of *O. punicae*

This experiment is presented in terms of general population trends, stage dis-

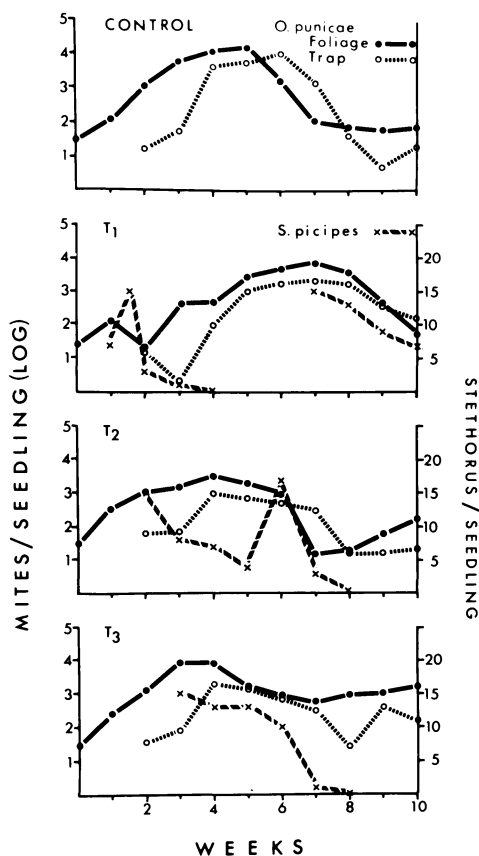


Fig. 9. Experiment II. Population trends of *Oligonychus punicae* on seedlings of *Persea indica* in the predator-free controls, and *O. punicae*-*Stethorus picipes* (predator) Series T<sub>1</sub>, T<sub>2</sub>, and T<sub>3</sub> interactions, each replicated three times.

tributions, spatial distributions and synthesis of results.

**Population trends.** The peak population density of 14,611 *O. punicae* per seedling in the predator-free ecosystems occurred in Week 5. At this time the foliage was heavily bronzed, especially on the upper leaf surfaces (Fig. 9). A rapid decline followed, with an 89 percent reduction in population density by Week 6. Trap counts indicated that a rapid rate of dispersal also occurred in response to the depletion of food.

**Series T<sub>1</sub>.** On Series T<sub>1</sub> seedlings there was an average of 125 active

stages of *O. punicae* per tree, and there were 806 eggs on Leaf 7 by the end of Week 1 (Fig. 9). The potential for increase of *O. punicae* was thus evident. In Week 2, one week after the introduction of the first seven *Stethorus picipes* larvae and 2 days after the introduction of an additional eight predators, the average population densities per replicate declined to 22 active prey stages and three third instar larval predators. The impact of predation on Leaf 7 resulted in overexploitation of the initially aggregated prey; and because of the limited powers of dispersal of the early instar *S. picipes* larvae to other leaves, none of them survived. After Week 2, prey numbers increased to a peak in Week 7. The subsequent decline in numbers of trapped prey by Week 3 was apparently associated with their movement from Leaf 7 onto undamaged leaves. Trap data from Weeks 3 to 7 were characteristic of a prey population increasing to high numbers in the absence of predation.

In Week 7, one first instar *S. picipes* per leaf was again introduced onto all replicates of T<sub>1</sub> series (Fig. 9). By Week 8, an average of 13 second instar larvae were found, mostly singly on a leaf. It appears that the second introduction should have been made around Week 5, as the foliage on the three replicates had sustained medium to heavy damage by Week 7. The juvenile predators accounted for about a 43 percent prey reduction after the first week. This estimate represents the difference between the number of trapped *O. punicae* females which dispersed during the week and their density on the foliage on Week 8. Because prey eggs and the number of prey larvae hatching between counts were not determined, however, the impact of predation may be underestimated. The mean prey density declined to 431 active stages by Week 9, a decrease of 2,867 per seedling. A trap count of 325 females accounted for only 11 percent of this decline, despite fur-

ther foliage bronzing. The remaining loss of 2,542 active stages was attributed to predation, at least an 89 percent decrease in numbers of prey. After Week 9 there was an average of nine adult predators per seedling, but the prey density was then insufficient to sustain them, and they starved. By Week 10 predator mortality averaged about 79 percent of those present during the preceding week. By this time, the number of active stages of prey had been reduced to an average of 43 per seedling.

**Series T<sub>2</sub>.** Seedlings of Series T<sub>2</sub> were inoculated with first instar *S. picipes* larvae 2 weeks after introduction of the prey, when the level of *O. punicae* averaged about 1,038 active individuals per seedling (Fig. 9). This prey density was similar to that of the predator-free controls. On Week 3, the developing *Stethorus* larvae averaged about eight per seedling, for a decline of 49 percent from the initial stocking density of 15. The prey population averaged 1,611, however, which was an increase of only about 573 per seedling. In addition, the trap data for Week 3 indicated that intraspecific competition within the prey population was minimal. These data, when compared to the average density of 5,281 *O. punicae* per seedling on the predator-free controls after 3 weeks, indicate that predation by *S. picipes* reduced the potential for increase of *O. punicae* by about 70 percent. Counts for Week 4 revealed a post-larval *S. picipes* mortality of about 12 percent. The prey then increased to a peak density of 3,433 individuals per seedling. A factor probably accounting for this increase of more than two-fold from the previous week was the nearly simultaneous entry, earlier in the week, of all the predators into the non-feeding pupal stage. Trap counts also indicated a significant increase in dispersal rate of adult female *O. punicae* in response to their increased crowding. The census for Week 5 showed the *S. picipes* popu-

lation had declined to an average of only four active stages per seedling, but at Week 6 there were 14 which indicates a numerical response. Life history studies had indicated that *S. picipes* females can lay up to 12 eggs per day, though not consistently from day to day (Part I). By this time, the prey population had declined to a mean of 603 individuals per seedling. Of the total decline which averaged about 1,559 *O. punicae* per seedling (not including eggs and the progeny hatching during the week), about 567 (36 percent) were recovered from the traps. The remaining 64 percent decline was attributed to predation. None of the F<sub>1</sub> predators attained adulthood. Overexploitation of prey apparently resulted in starvation of nearly all the immature predators by Week 7, and all predators died by Week 8. After Week 7, the prey population was freed from predation, and a resurgence of the population occurred through Week 10.

**Series T<sub>3</sub>.** In the 3-week period before the predators were introduced to the Series T<sub>3</sub> plants the initial population of 30 *O. punicae* females increased over 35-fold to an average of 8,295 per seedling, compared to only 5,281 for the predator-free control (Fig. 9). This was simply a biological variation in performance. Feeding by this high population had produced moderate to heavy bronzing of the upper foliage surfaces by Week 4, at which time the population density of *O. punicae* averaged 7,709 active stages per seedling, representing a slight decline from the previous week. In only 9 days after being introduced as eggs, *S. picipes* numbered 10 pupae on Replicate 1, 14 on Replicate 2, and one pre-pupa and 13 pupae on Replicate 3. The marked decrease in population density of *O. punicae* after Week 4 from about 7,709 to 1,512 per seedling was attributed to the combined impact of intraspecific competition and predation from the approximately 10 newly matured adult *S. picipes* per

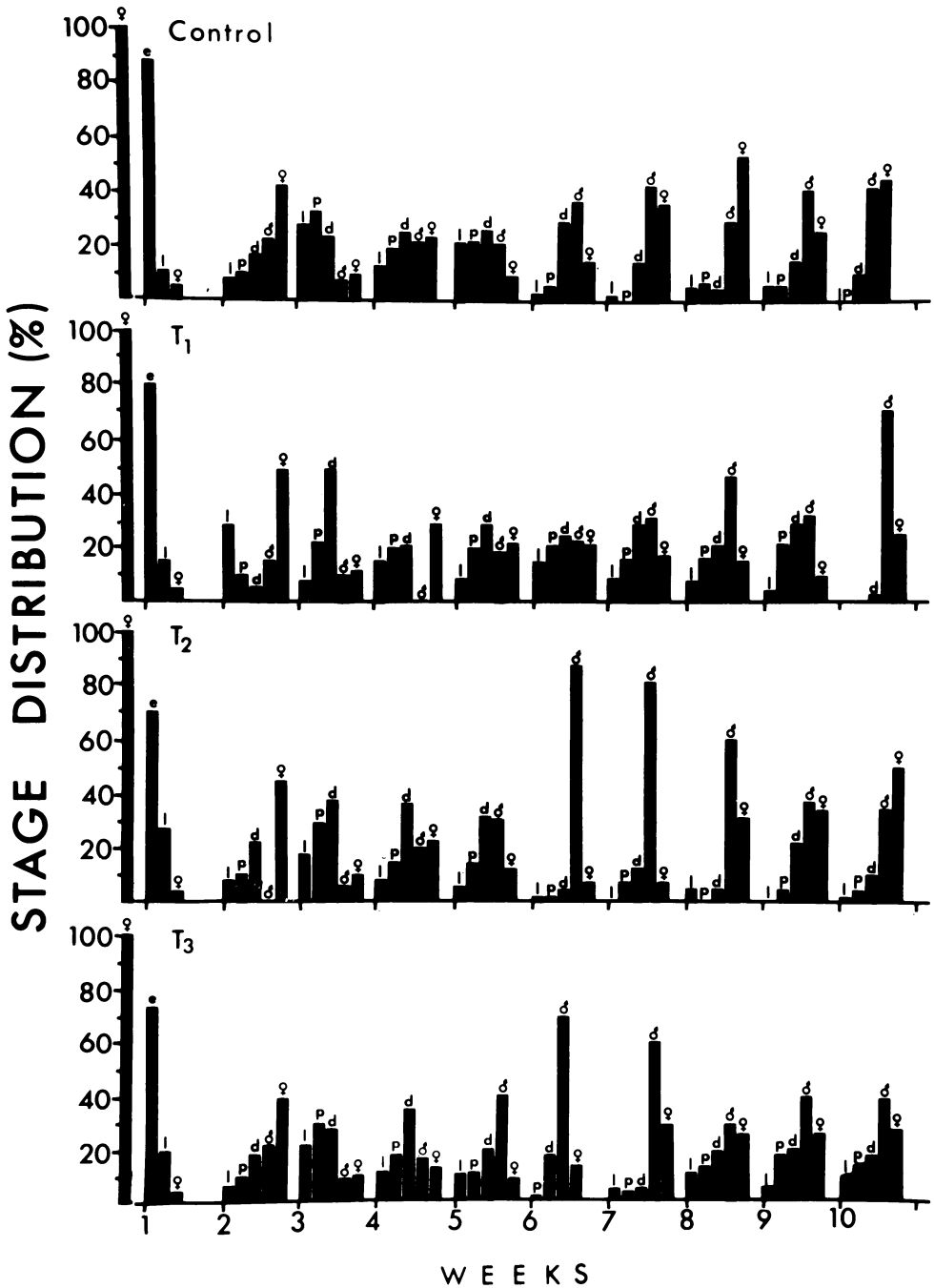


Fig. 10. Experiment II. Stage distribution of *Oligonychus punicae* (prey populations in the predator-free controls, and the *O. punicae*-*Stethorus picipes* (predator) Series T<sub>1</sub>, T<sub>2</sub>, and T<sub>3</sub> interactions, each replicated three times. e = eggs, l = larvae, p = protonymphs, d = deutonymphs, ♂ = males, and ♀ = females.



seedling. Between Weeks 5 and 6 the adult predators further suppressed the prey population by an average of 600 individuals per seedling to a density of 150 per seedling. Despite the abundance of food still available to the adult predators, they did not reproduce. Possibly mating did not occur. Despite the excessive bronzing of foliage by Week 7, the prey population increased steadily through the following 3 weeks.

**Stage distribution.** The stage distribution of *O. punicae* on the predator-free controls was relatively stable during Weeks 4 and 5, except that a decrease of over 57 percent occurred with adult females (Fig. 10). This indicated the increasing propensity for females to migrate as the nutritional condition of the foliage declined. Furthermore, the marked changes in the proportion of immature stages after Week 5, combined with a decrease in percentages of the larvae to zero on Week 10, strongly indicated a virtual cessation in egg production.

**Series T<sub>1</sub>.** The low proportions of F<sub>1</sub> *O. punicae* protonymphs and deutonymphs (Fig. 10) and numerical decreases of both larvae and adult females by Week 2 of the T<sub>1</sub> series is additional evidence of a suppressive effect of *S. picipes* predation at high prey densities. The stage distribution for the prey population was relatively stable from Weeks 4 through 6. Reintroduction of predators in Week 7, and the subsequent rapid decline of the prey population, resulted in a decreasing proportion of adult female prey in weeks 8 and 9. This was accompanied by a progressive reduction in percentage of prey larvae to 0 in Week 10.

**Series T<sub>2</sub>.** At the time of the introduction of 15 first instar *S. picipes* larvae per T<sub>2</sub> seedling on Week 2, the distribution of active stages of the prey population was similar to that of the predator-free control (Fig. 10). Immature stages comprised the largest proportion for the next 3 weeks. A de-

crease in proportions of both larvae and deutonymphs, and an increase in adults, was observed from Weeks 3 to 5. This stage distribution may reflect the feeding of late-stage larval predators on immature *O. punicae* during the early part of Week 3.

**Series T<sub>3</sub>.** Upon introducing first instar *S. picipes* larvae at the beginning of Week 3, the population of *O. punicae* on Series T<sub>3</sub> seedlings consisted of about 82 percent immature stages (Fig. 10). All the immature stages of *S. picipes* were either pre-pupae or pupae by Week 4, thus the prey population was released from predation pressure long enough to recover somewhat before the adult predators emerged. The stage distribution of the *O. punicae* population from Weeks 7 through 10 was relatively stable. Even though the population density of *O. punicae* was increasing through Week 10, the fact that the proportion of females held relatively constant and lower than the proportion of males, coupled with the increasing rate of female dispersal, was indicative of their food source having been depleted.

**Spatial distribution.** On the predator-free controls, *O. punicae* populations had a moderately aggregated and similar spatial distribution (Fig. 11) by Week 2. Despite their rapid numerical increase to a plateau by Week 5 and subsequent decrease attributable primarily to overexploitation of food, the *O. punicae* population after Week 3 maintained rather constant indices of patchiness throughout the experiment, except for Week 8 for Replicate 1.

**Series T<sub>1</sub>.** Indices of mean crowding ( $\bar{m}$ ) indicated that individual crowding of *O. punicae* was minimal to Week 4 in the T<sub>1</sub> ecosystems (Fig. 11). From Weeks 2 through 5 the disproportionately larger crowding indices on Replicates 2 and 3 for Weeks 3 and 5, respectively, were the result of different degrees of aggregation on certain leaves, which consequently resulted in larger variances. Also, the prey populations

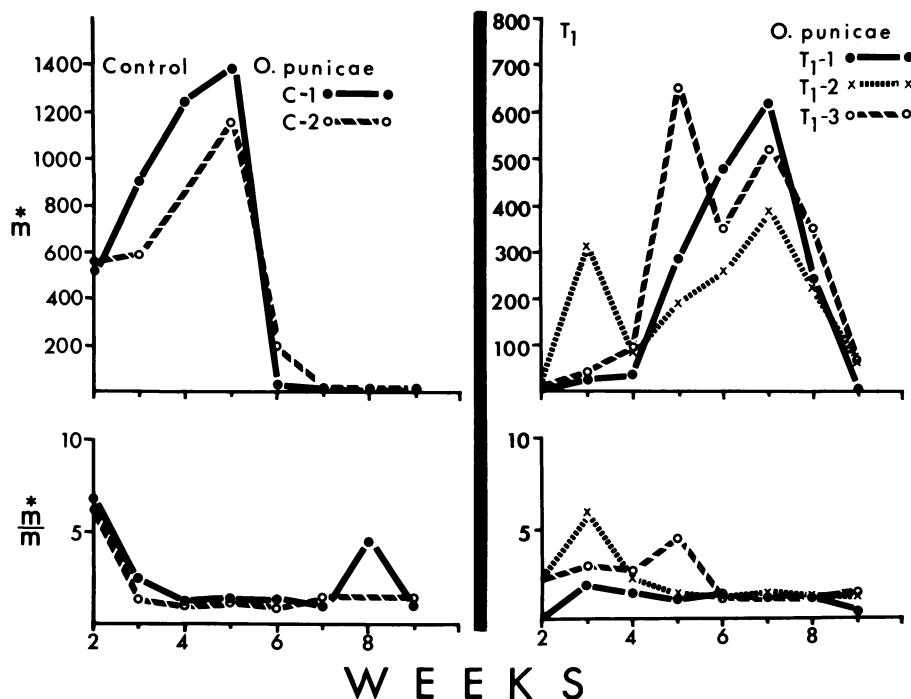


Fig. 11. Experiment II. Indices of mean crowding ( $\bar{m}^*$ ) and patchiness ( $\bar{m}^*/\bar{m}$ ) of *Oligonychus punicae* in the predator-free controls, replicated twice, and for the Series T<sub>1</sub> interactions with *S. picipes*, replicated three times.

at this time were tending toward more randomly distributed patterns as a result of their numerical increase and mounting pressure from intraspecific competition. The effects of *S. picipes* larvae on the initially aggregated *O. punicae* populations of the Series T<sub>1</sub> ecosystems can be seen from the weekly indices of patchiness ( $\bar{m}^*/\bar{m}$ ) for the prey.

**Series T<sub>2</sub> and T<sub>3</sub>.** In spite of the numerical fluctuation of the prey populations and despite the effects of predation, the indices of patchiness for *O. punicae* in the T<sub>2</sub> ecosystems to Week 9 also indicated a nearly random distribution (Fig. 12). Predation apparently did not alter the mean distribution (although a little greater variability was exhibited in contrast to the control), even though the predators greatly affected the prey population numerically. This indicated that searching by the

*Stethorus* population was random. Individual crowding and spatial patterns for the T<sub>3</sub> series were also similar to those of the control and T<sub>2</sub> series (Fig. 12). By the time *S. picipes* larvae were introduced, prey density had nearly leveled off.

**Synthesis.** The T<sub>2</sub> series, in which newly emerged larvae of *S. picipes* were introduced 2 weeks after the initial prey infestation, was the most favorable for sustaining successive prey-predator oscillations. At the time the immature predators were introduced, the prey: predator ratio for active stages was 69:1, and 60 percent of the prey population was composed of adults. These predators were able to mature and produce offspring, and they suppressed the *Oligonychus* population by about 75 percent (as compared to predator-free populations) during a 6-week period. Data from the T<sub>3</sub> experiment indicated

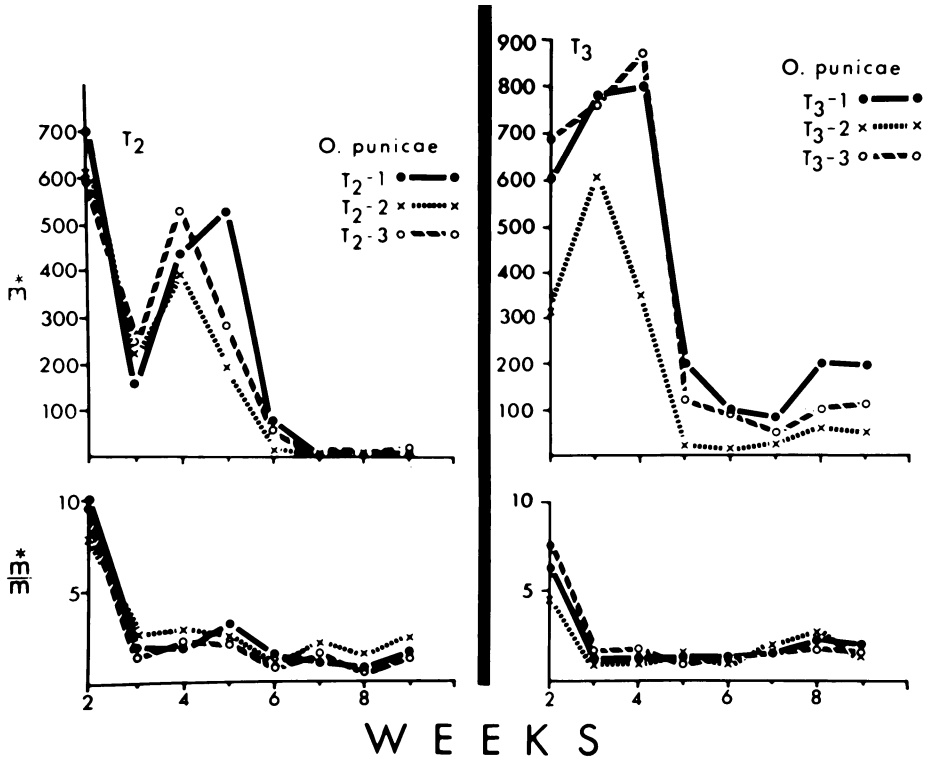


Fig. 12. Experiment II. Indices of mean crowding ( $\bar{m}^*$ ) and patchiness ( $\bar{m}^*/\bar{m}$ ) of *Oligonychus punicae* for the Series  $T_2$  and  $T_3$  interactions with *S. picipes*, each replicated three times.

that delaying the introduction for 3 weeks before introducing the immature predators resulted in the suppression of the prey by only 41 percent. Thus, by Week 3, the immature prey:predator ratio was 533:1. Apparently these 15-leaf ecosystems supported sufficient prey densities to insure the development, maturation and production of immature predator offspring. The census data and life history studies indicated that failure of the predators to maintain their prey at low densities, after Week 7, was the result of overexploitation of their prey and subsequent starvation.

Another significant difference in prey populations, between the predator-free control and seedlings with predators, was the apparent effect this predator had in progressively reducing the proportions of immature stages and adult

female prey, although previous feeding studies have shown that both the larvae and adults of *S. picipes* will prey upon all stages of *O. punicae*. If we assume a *P. indica* leaf possesses relatively uniform surfaces, then the data for the searching patterns of these larvae presented by Fleschner (1950), coupled with their effects on *O. punicae* distribution patterns as analyzed in this study, indicate that searching by *S. picipes* is random. As bronzing became more intense, a few quiescent deutonymphs and adult female *O. punicae* were observed on the undersurfaces of leaves. The majority of the female prey, however, emigrate or escape by "ballooning." Thus, this shift in stage distribution is apparently a combination of the following: predation, followed by emigration of females; agility and es-

cape by the fast-moving "non-balloon-ing" males; or a change in actual sex ratio (McMurtry, 1970). The increasing paucity, especially of adult female prey and the difficulty in finding or capturing males, resulted, therefore, in a further scarcity of food (i.e., eggs and maturing offspring) for the larvae and adult predators. Fleschner (1950) calculated that a larva of *S. picipes* can complete development on a population as low as one adult *Panonychus citri* (McGregor) per 37.8 square centimeters when evenly distributed over a uniform surface. Between Weeks 6 and 8 census data for  $T_2-2$  ecosystems indicated that the prey were very scarce ( $\bar{x} = 16.3$  prey/seedling) and randomly distributed over both surfaces of certain *P. indica* leaves. This low density of prey was undoubtedly an important factor in the high mortality of  $F_1$  progeny of *S. picipes*. Even a density of about 40 prey/leaf, which occurred between Weeks 5 and 6 of experiment  $T_3$ , resulted in high predator mortality. Similarly, the newly emerged adults experienced a high mortality during Weeks 9 and 10 of experiment  $T_1$ . McMurtry and Johnson (1967) concluded that the most effective time for making field releases of *S. picipes* was when the *O. punicae* population averaged about 10 active stages per leaf. Subsequent studies by McMurtry *et al.* (1969) further supported this conclusion. Because *Stethorus* requires large numbers of mites for effective reproduction, the timing of releases was considered to be critical by these researchers. Putman (1955) estimated that a density of about 10 *Panonychus ulmi* (Koch) per peach leaf was necessary to sustain and induce multiplication of adult *Stethorus punctillum* Weise in Ontario, Canada. Very few *S. punctillum* larvae reached maturity at this density, however, unless, before they died or dispersed, they could locate the eggs produced by the overwintering adults.

In conclusion, this experiment further indicates that *S. picipes* is a high-density spider mite predator. It can respond both numerically and functionally to suppress high and increasing populations of spider mites. At generally low densities, however, unless they locate pockets of prey at higher local densities, many of the immature stages will starve. Thus, the residual population of spider mites released from predation will then increase unless checked by immigrant predators from other sources.

### Experiment III—Predation by *T. floridanus* and *S. picipes* on populations of *O. punicae*

This experiment is presented in terms of detailed discussions on general population trends and synthesis of competition between two predator species for a common prey.

**Population trends.** The peak density for *O. punicae* populations on the predator-free control ecosystems averaged 13,250 individuals per seedling by Week 5 (Fig. 13). As was observed for preceding studies, female *O. punicae* were already dispersing from the control seedlings by Week 2. After Week 7 the *O. punicae* populations stabilized at a mean density of 135 and 133 individuals per seedling at Weeks 8 and 9, respectively.

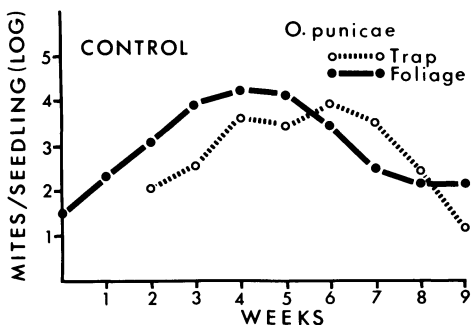


Fig. 13. Experiment III. Population trends of *Oligonychus punicae* on seedlings of *Persea indica* in the predator-free controls (averages of three replicates).



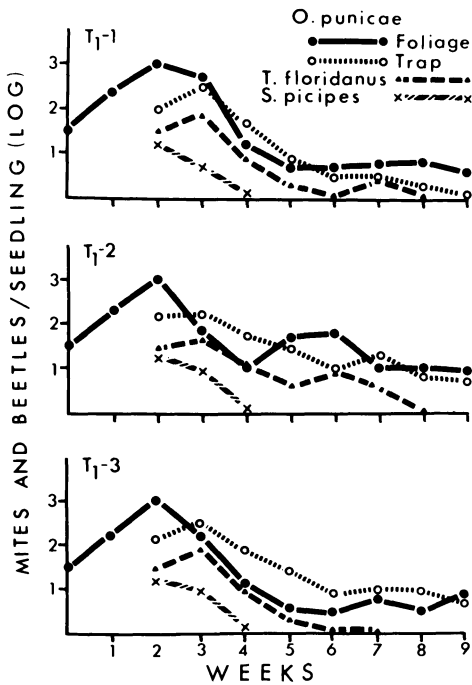


Fig. 14. Experiment III. Population trends of *Typhlodromus floridanus* and *Stethorus picipes* (predators) and *Oligonychus punicae* (prey) on seedlings of *Persea indica* in the Series T<sub>1</sub> interaction, replicated three times.

After a lag time of 2 weeks, when the two predator species were introduced onto the *P. indica* seedlings of Series T<sub>1</sub>, the *O. punicae* population averaged about 1,042 individuals per seedling (Fig. 14). The starting prey:predator ratios for *T. floridanus* and *S. picipes* approximated 35:1 and 69:1, respectively, or 23:1 for both predators combined. This ratio was more favorable to the less voracious *T. floridanus*. After only 1 week, there was a reduction in prey density by over 77 percent. In the previously reported studies on the dynamics of predation by *S. picipes* and *T. floridanus* on *O. punicae*, such a rapid reduction of *O. punicae* did not occur with either predator alone. These earlier experiments indicated that following initiation there was a lag period with each of these predator-prey interactions before a marked prey decrease

occurred. In this case, the combined impact of both predator species resulted in a reduction by more than 98 percent in prey density within only 2 weeks, as contrasted to the populations in the predator-free ecosystems. During this 2-week interval, *Stethorus* did not respond numerically and died out on all three replicates by Week 5 (Fig. 14). *Typhlodromus floridanus* did increase numerically, however, by about 1.9-fold by Week 3, despite the rapid decline of the prey population, but this species also died out in all replicates after Week 8.

A conservative measure of the combined ability of *S. picipes* and *T. floridanus* to suppress a high and increasing *O. punicae* population can be derived by comparing the mean weekly prey densities on the predator-free controls with those on the Series T<sub>1</sub> plants. These densities averaged 275, 169, and 174 per plant on Replicates 1, 2 and 3, respectively, from Weeks 2 to 8, contrasted to 6,063 and 5,216 for Replicates 1 and 2 of the predator-free controls during the same period of time. The combined effects of both predators thus resulted in approximately 95 percent (T<sub>1</sub>-1), 97 percent (T<sub>1</sub>-2) and 97 percent (T<sub>1</sub>-3) reductions in prey numbers as contrasted to the predator-free controls. After starvation of the predators, however, by Week 8, *O. punicae* was freed of predation pressure in all three replicates.

Experiment T<sub>2</sub> was originally designed to measure the effect of introducing first instar larvae of *S. picipes* in groups of seven and eight at weekly intervals. By staggering the introduction, there would have been continuous predation by *Stethorus*, despite an average of 4 days of inactivity during its combined nonfeeding pre-pupal and pupal stages. Daily observations and the census data for Week 3 revealed that the original infestation of 30 *T. floridanus* females and 7 first instar *S. picipes* larvae were responding simi-

larly, however, to the predator complex used on the  $T_1$  series plants in which 15 *S. picipes* larvae were introduced. The *O. punicae* density at Week 3 had been reduced to an average of about 310 individuals per seedling (Fig. 14). It was decided, therefore, not to introduce the additional eight *Stethorus* larvae but rather to compare the effects of seven instead of 15 *S. picipes*, plus the 30 *T. floridanus*, in an ecosystem having nearly identical initial prey populations as in the  $T_1$  experiment. The individual initiating prey:predator ratios for *T. floridanus* and *S. picipes* were approximately 32:1 and 136:1, respectively, at Week 2. The ratio with both predators combined was approximately 26:1. Counts during Week 3 indicated that over half of the immature *S. picipes* population had perished. Of the 10 remaining late instar larvae, only two (Replicate 2) matured to adulthood. Unfortunately, both were females and, not having mated, were thus incapable of responding numerically.

*Typhlodromus floridanus*, on the other hand, had a numerical response by Week 3, increasing by about three-fold in all three replicates (Fig. 15). At this time, the average *O. punicae*:*T. floridanus* ratio was about 10:1. After Week 3, however, the predator density declined by over 92 percent, coinciding with near elimination of the prey population. This was followed by the starvation of both predator species in Replicates 1 and 2. An estimate of the depressive impact on *O. punicae* of both predators combined between Weeks 2 and 4 was made by comparing the weekly mean densities of *O. punicae* populations on the predator-free controls with those on the Series  $T_2$  plants. This comparison indicated that the combination of both predators resulted in at least a 94 percent reduction in prey abundance. Thus, the theoretical advantage of introducing over twice as many *S. picipes* larvae in the  $T_1$  experiment,

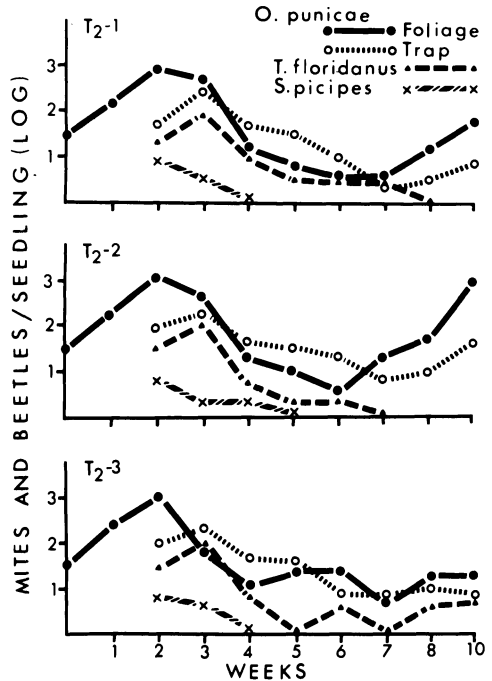


Fig. 15. Experiment III. Population trends of *Typhlodromus floridanus* and *Stethorus picipes* (predators), and *Oligonychus punicae* (prey) on seedlings of *Persea indica* in the Series  $T_2$  interaction, replicated three times.

contrasted to this experiment ( $T_2$ ), did not result in more effective suppression of the prey population. *Typhlodromus floridanus* probably compensated for the lower numbers of introduced *Stethorus* by its increased numerical response.

The prey populations eventually resurged to high densities on Replicates 1 and 2, as all the predators died out (Fig. 15). On Replicate 3, however, nearly three predator-prey oscillations occurred between *O. punicae* and *T. floridanus* (Fig. 15), the last two after *S. picipes* had died out. Although the counts were terminated at Week 9, the minimum bronzing of the foliage and the existing prey-predator ratios strongly indicated that the *T. floridanus*-*O. punicae* interaction on Replicate 3 could have continued at low densities in the absence of *S. picipes*.

Experiment  $T_3$  differed from that of

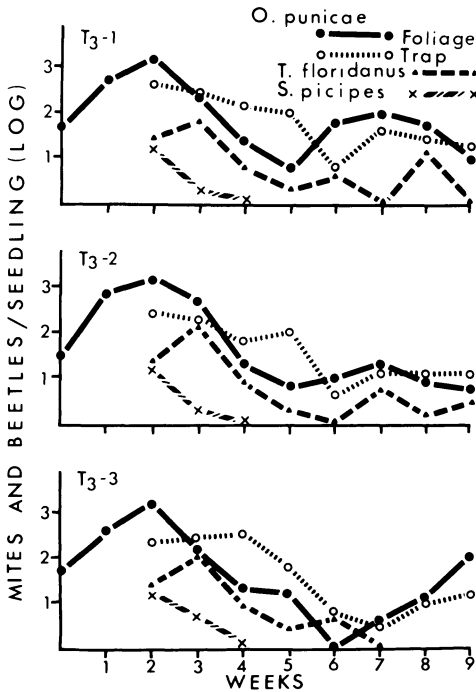


Fig. 16. Experiment III. Population trends of *Typhlodromus floridanus* and *Stethorus picipes* (predators), and *Oligonychus punicae* (prey) on seedlings of *Persea indica* in the Series T<sub>3</sub> interaction, replicated three times.

the T<sub>1</sub> series in that 45 adult female *O. punicae*, rather than 30, were initially introduced as a clumped population on leaf number 7. By Week 2, the prey densities on each replicate were remarkably similar, increasing by an average of 30-fold (Fig. 16). The approximate prey:predator ratios of *T. floridanus* and *S. picipes* were 47:1 and 95:1, respectively, and for both predators combined, about 32:1. Despite these moderately high initial ratios, the *O. punicae* populations were suppressed by the action of the two predator populations by Week 3, and a second cycle of prey increase was brought under control by *T. floridanus* on Replicates 1 and 2 by Week 9 after all *S. picipes* had been eliminated. The single *O. punicae* female remaining on Replicate 3 apparently was not found by the remaining four *T. floridanus* predators

(3 adults + 1 larva observed from individual leaf counts), after Week 6. From this single female and eggs not eaten by the predators, the *O. punicae* population subsequently increased to about 110 individuals by Week 9.

As observed from experiments T<sub>1</sub> and T<sub>2</sub>, the first and second instar *S. picipes* larvae were unable to compete with *T. floridanus* during the second and third weeks of these experiments. By Week 4, each seedling contained a single *S. picipes* adult. The scarcity of prey (averaging only 23 per seedling), probably evoked dispersal of these remaining beetles, and they died during Week 4. The downward trend for the populations of both *O. punicae* and *T. floridanus* continued to Week 5 (Fig. 16). Trap counts for Replicates 1 and 2 indicated that a relatively high proportion of adult female prey had dispersed during Week 4, and *T. floridanus* decreased by 71.5 percent on both replicates. The data for two of the three replicates of this experiment indicate that *T. floridanus* possess the potential to respond numerically to *O. punicae* population densities in a density-dependent manner.

**Synthesis.** The results of these experiments indicates that combining *S. picipes* and *T. floridanus* in the same experiment gave more effective results than using either one by itself in suppressing a high and rapidly increasing prey population. For example, the overall mean population densities of *O. punicae* from Weeks 2 to 9, in T<sub>2</sub> ecosystems with *T. floridanus* alone (Experiment I) and *S. picipes* alone (Experiment II), were 906 and 2,027 mites/seedling per week, respectively. At identical individual starting ratios for the T<sub>1</sub> series with both predators together, the average *O. punicae* density was 301/seedling per week during the same interval. The impact of the two predators together resulted, therefore, in a numerical suppression of the prey which was 3.0 and 6.7 times greater

than that for *T. floridanus* and *S. picipes*, respectively, acting alone.

In all instances, *T. floridanus* persisted longer in the interactions than did *S. picipes*, indicating that this phytoseiid was able to survive at lower prey densities than was the coccinellid. The high prey requirement of *S. picipes* larvae was not satisfied by the conditions produced in these experiments. This predator died of starvation in every replicate of this study, following the rapid decreases of the *O. punicae* populations to low densities. The presence of an increasing *T. floridanus* population apparently adversely affected the immature *S. picipes* population, as almost none of the larvae matured when *T. floridanus* was present. *Stethorus picipes* did not adversely affect the growth and development of *T. floridanus*, however. The numerical response by *T. floridanus* was about 1.3 times greater in the  $T_2$  ecosystems where there were fewer *Stethorus* than in the  $T_1$  ecosystems. During Week 2, *T. floridanus* gave a greater numerical response to higher prey densities in the  $T_3$  experiments, as compared to the lower densities on the  $T_1$  experiment, which were also initiated with the same densities of both predators. In contrast to this response, *S. picipes* had a higher mortality rate in the  $T_3$  experiment. These studies indicate that the survival of *S. picipes* was no better when only seven larvae were introduced per repli-

cate than when 15 were introduced. Apparently intraspecific competition was not a factor in the poor survival rate. The effects on survival at low prey densities by either cannibalism or by *S. picipes* feeding on active *T. floridanus* or their eggs were not determined.

Feeding experiments which indicated that maturing *S. picipes* larvae possess a much higher prey consumption capacity than do *T. floridanus* larvae support the supposition that *S. picipes* contributed markedly to the rapid declines in prey population which occurred less than one week after both predators were introduced.

Thus, *T. floridanus* became the sole predator in the respective systems after the dying out of all *S. picipes*. *Typhlodromus floridanus* apparently possesses all the principal attributes of an effective predator as suggested by DeBach and Schlinger (1964), McMurtry *et al.* (1970) and Huffaker *et al.* (1970). These are: 1) high searching capacity (ability to find the prey when the prey is scarce); 2) short development time; 3) host specificity; 4) adequate fecundity or power of increase; 5) low prey consumption capacity (consequently, it possesses a lower minimum food requirement for development, reproduction, dispersal, and population maintenance; 6) seasonal synchrony with its prey; and 7) distribution patterns similar to those of its prey.

## SUMMARY AND CONCLUSIONS

The most effective predation on initially clumped *O. punicae* populations occurred when *T. floridanus* and *S. picipes* were introduced 2 weeks after the plants were infested with the prey. The resulting prey:predator ratios for *O. punicae*:*T. floridanus* and *O. punicae*:*S. picipes* averaged 35:1 and 69:1, respectively.

Under these conditions, a "balance" was established between *T. floridanus*

and *O. punicae* which was manifested as three oscillations of decreasing amplitude. This interaction was sustained for 10 weeks and included the maturation of several generations of both prey and predator species. During this time, comparative data for the predator-free controls indicated that the presence of *T. floridanus* resulted in at least 92 percent population suppression of *O. punicae*.



Dispersal and distribution patterns of both *T. floridanus* and *O. punicae* were measured by the indices of crowding and patchiness. The weekly trends for these indices indicate that even in monocultures of *O. punicae*, the incipient *O. punicae* populations, initially in clumped patterns, disperse randomly by "ballooning" and crawling and eventually become randomly distributed throughout their universe as crowding is intensified. From these trends, it was surmised that the effects of predation by randomly searching *T. floridanus* populations were to reduce both the prey density and the propensity of the prey toward developing a random spatial distribution. If the prey population escaped the effects of predation as a result of either overexploitation of prey by the predators or excessive lag in numerical response of the predators, a decreasing index of mean crowding of the prey resulted.

The first instar larvae of *S. picipes* (one/leaf), which were introduced in an initially aggregated *O. punicae* population, overcame a 69:1 numerical difference to suppress the prey population. Some of the predators reached maturity and produced progeny during a 6-week period. This predator was unable, however, to persist at low *O. punicae* densities. This resulted in a subsequent annihilation of *S. picipes* and a resurgence of the remaining *O. punicae* to higher densities.

Spatial distribution and feeding studies indicated that searching by *S. picipes* was primarily random and that their prey were perceived by contact. This predator also demonstrated little preference for any particular life stage of *O. punicae*. Predation by *S. picipes* apparently reduced the tendency of *O. punicae* to become randomly distributed but probably mainly by preventing the increase to high densities which then caused more random distributions. This may have been due to the capability of *S. picipes* larvae to rapidly reduce

pockets of the numerically increasing prey population before extensive dispersal occurred.

Comparative data concerning competition between populations of *T. floridanus* and *S. picipes* on *O. punicae* indicated that: 1) the initial prey:predator ratios of 35:1 (*O. punicae*:*T. floridanus*) and 69:1 (*O. punicae*:*S. picipes*) (averaged about 23:1 when combined) of the  $T_1$  experiments favored better survival of the prey; 2) the initial combined prey:predator ratio of 26:1 for the  $T_2$  experiments with both *T. floridanus* and *S. picipes* (32:1 and 136:1 for *O. punicae*:*T. floridanus* and *O. punicae*:*S. picipes*, respectively) favored temporary escape of the prey population in two of the three replicates, although the prey populations were eventually suppressed; 3) the suppression and early death (survivorship) of *S. picipes* was comparable whether they were introduced at an initial density of seven ( $T_2$  experiments) or 15 ( $T_1$ ,  $T_3$  experiments) first instar larvae per seedling; 4) the initial prey:predator ratio of 32:1 for the  $T_3$  series (47:1 and 95:1 for *O. punicae*:*T. floridanus* and *O. punicae*:*S. picipes*, respectively) favored quicker control of *O. punicae* in two of three replicates, with two successive predator-prey oscillations of decreasing amplitude occurring; and 5) the combined action of both predators, after 3 weeks, reduced the prey to such a low density that *S. picipes* did not survive, but *T. floridanus* did.

The data from these studies indicated that: 1) *T. floridanus* and *S. picipes* together were more effective under these simple, short-term experiments than either predator acting by itself; 2) both *T. floridanus* and *S. picipes* possess the ability to respond to and suppress an increasing *O. punicae* population; 3) *T. floridanus* was a more effective predator than *S. picipes* in maintaining low prey densities after the initial suppression of high prey densities; and 4) *S. picipes* is a high density spider mite predator.

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