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Dynamics and potential impact of 'generalist' phytoseiids in agroecosystems and possibilities for establishment of exotic species

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ABSTRACT

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'Generalists', i.e. those species which consume a wide variety of foods, including some of plant origin such as pollen, are the dominant members of the phytoseiid mite fauna in some perennial crops. Biological attributes commonly evident in 'generalist' in contrast to 'specialist' phytoseiids include a lower reproductive potential on mite prey, close association with certain plant species, population increases in the absence of mite prey, and intraplant distribution unrelated to that of spider mites. Some studies are reviewed that suggest the ability of certain generalist phytoseiids to maintain tetranychid populations at low densities. Possible biological factors influencing the establishment of exotic generalist phytoseiids are considered. Some of the attributes usually considered important in effective phytoseiid predators may be of minor importance in more stable situations at low population densities.

INTRODUCTION

Most of the notoriety enjoyed by the family Phytoseiidae as biological control agents has come from species that are specialized predators of tetranychid mites, especially those in the genus *Tetranychus*. Probably the most notable of these phytoseiids are *Phytoseiulus persimilis* Athias-Henriot and *Typhlodromus occidentalis* Nesbitt. Much data has been accumulated from field experiments on these species showing their ability to suppress spider mite populations (McMurtry, 1982). Moreover, extensive laboratory studies have contributed to knowledge of the evolutionary biology of the Phytoseiidae (reviewed in Helle and Sabelis, 1985).

However, in many agroecosystems, especially more stable ones, such as certain tree crops receiving minimal pesticide applications, phytoseiid specialists are scarce or absent, and the phytoseiid fauna is dominated by generalist

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species, i.e. those species that feed on a wide range of substances and whose numbers are not necessarily correlated with the presence of tetranychid mites. Many phytoseiids can be considered generalists. This probably applies to all or most members of the genera *Euseius* and *Amblyseius*, some *Typhlodromus* such as the *pyri* group and some *Neoseiulus* such as *cucumeris* (Oudemans) and *barkeri* Hughes. In many genera and species groups, too few species have been studied to generalize on their food habits, but it is possible that the majority of species of Phytoseiidae are generalists (McMurtry and Rodriguez, 1987). In fact, one tends to wonder if the evolution of specialist phytoseiid predators in association with certain genera or ecological groups of tetranychid mites is the exception rather than the rule. Moreover, we might ask the question, are some of the principles formulated from studies on specialist phytoseiids applicable to generalist predators as well?

Our investigations of phytoseiid mites and their interactions with tetranychid mites on citrus and avocado in California have revealed that only generalist phytoseiids are consistently present in these two systems. From this perspective, I will endeavor to consider: some biological and ecological attributes of generalist phytoseiids; the potential impact of generalist phytoseiids on spider mite populations and some methods used to estimate their effects; and, progress and prospects regarding introductions and establishment of exotic generalists in some perennial crops.

SOME BIOLOGICAL AND ECOLOGICAL ATTRIBUTES OF GENERALIST PHYTOSEIIDS

Reproductive potential

Generalist phytoseiids usually have lower rates of increase on mite prey than their specialist counterparts (Sabelis, 1985; McMurtry and Rodriguez, 1987). Thus, specialists might be considered opportunists or 'r-selected' strategists, with the ability to reproduce rapidly when abundant prey is found and to disperse when the prey is scarce. Generalists, on the other hand, are probably more likely to be 'k-selected', characterized by lower reproductive potential and more stable populations less dependent on dispersal to new sites in search of prey because of their ability to utilize many different types of food. Many species of generalists have lower rates of increase on mite prey than on other foods, such as pollen (McMurtry and Rodriguez, 1987; Osakabe, 1988; Abou-Setta and Childers, 1989; James, 1989; Zhao and McMurtry, 1990). In fact, some species may not even complete development on tetranychid mite prey alone (Tanigoshi et al., 1981; James, 1989). On the other hand, other species may have comparable rates of increase on tetranychid mite prey and pollen or other foods (Bounfour and McMurtry, 1987; Ferragut et al., 1987). However, the usual protocol of determining reproductive rates on only one food at a time may lead to erroneous conclusions, as the addition of some supplemental food, such as honeydew, may considerably increase survival and oviposition on mite prey (McMurtry and Scriven, 1964; Ragusa and Swirski, 1977; James, 1989; Zhao and McMurtry, 1990).

Foods utilized

Generalist phytoseiids tend to utilize many different foods and combinations, even those which promote only a low rate of increase. Thus, the strategy of generalists seems to be to use what is at hand rather than to track a certain prey resource. Switching from one food source to a more abundant or even a more favorable one, should not be assumed. For example, *Euseius hibisci* (Chant) fed on both pollen and spider mites, even when the former, which promotes a higher rate of increase, was abundant (McMurtry and Scriven, 1966a). This species more effectively suppressed populations of *Oligonychus punicae* (Hirst) when pollen was present (McMurtry and Scriven, 1966b). *Amblyseius andersoni* (Chant) (=*potentillae* Garman) also fed on both pollen and spider mites when both were available (Sabelis, 1981). Some of the foods shown to be eaten by phytoseiids include tetranychid, tenuipalpid, eriophyid, tarsonemid and tydeid mites, thrips, scale crawlers, whiteflies, pollen, nectar, honeydew and fungi, with pollen frequently being the most favorable in terms of promoting a high rate of increase (McMurtry and Rodriguez, 1987). There is some evidence to support the possibility that even leaf sap may be utilized as food (Chant, 1959; Porres et al., 1975; Ivancich Gambaro, 1986; B.A. Croft, pers. commun., 1991). Tetranychid mites which develop in patchy colonies with copious webbing (e.g. most *Tetranychus* species) may be less favorable as prey than those species which produce less webbing (e.g. *Panonychus* species) because the phytoseiids may either become entangled in the strands or are deterred by the webbing from contacting the prey (Putman, 1962; McMurtry and Scriven, 1964; McMurtry and Johnson, 1966; Ragusa, 1981; Abou-Setta and Childers, 1989).

Response to kairomones

Generalists phytoseiids may or may not respond to kairomones emanating from spider mite infestations. *Typhlodromus pyri* Scheuten and *Euseius finlandicus* (Oudemans) generally do not respond to volatiles emanating from *Tetranychus* species in a Y-tube olfactometer but do respond to *Panonychus ulmi* (Koch) and eriophyid mite infestations, on which they are known to prey (Sabelis and van de Baan, 1983; Dicke, 1988; Nyrop, 1988). *Euseius hibisci* (Chant) showed arrestment responses on filter paper disks treated with extracts of leaves infested with either *Oligonychus punicae* (Hirst), a favorable prey, or *Tetranychus urticae* Koch, a prey that appears unfavorable, as well as to pollen extracts. However, *Amblyseius (Typhlodromalus) limonicus* Garman & McGregor, another generalist on avocado in California, showed no arrestment responses to either prey species or to pollen (McMurtry et al., 1992). Additional studies are needed to investigate whether these two species would react also to volatiles emanating from mite-infested leaves or pollen.

Association with plant species

Some species of generalist phytoseiids appear to have a complex relationship with the plants on which they occur. Porres et al. (1975) found that *E. hibisci* acquired radioactivity when placed on avocado leaves labeled with $H_3^{32}PO_4$ but not when placed on labeled citrus leaves. *Euseius hibisci* is common on both citrus and avocado trees in coastal areas of California, while a similar species, *E. tularensis* Congdon, is common on citrus trees throughout California, but is rarely found on avocado trees. Apparently, the latter species is unable to complete with *E. hibisci* on avocado. In the laboratory, *E. tularensis* had a lower fecundity when confined on avocado or oak leaves and fed pollen of *Malephora crocea* (Jacq.) (Aizoaceae) than when confined on valencia orange (*Citrus sinensis*) leaves with the same food. *Euseius hibisci* showed no differences in fecundity between the two leaf substrates (Congdon, 1985). *Euseius quetzali* McMurtry does not occur on citrus and was collected on avocado only in one area outside the range of *E. hibisci*. However, it is the main or only *Euseius* species on oak (*Quercus* sp.) and *Rubus* spp. (Congdon and McMurtry, 1986). *Euseius quetzali* had a reduced fecundity on avocado leaves compared to either citrus or oak leaves and fed pollen (Congdon, 1985). It is possible that these phytoseiids are affected both by anatomical and physiological differences in their plant substrates.

Intraplant distribution

Unlike most specialist phytoseiids, which usually show tendencies to aggregate in patches of prey or on infested leaves, generalists may show no correlation with the distributions of various mite prey species. On avocado leaves, sites that *E. hibisci* uses for resting, oviposition, etc., are usually on the underside of the leaf, at junctures of the midrib and main veins, rather than in or near the colonies of the most common spider mite, *O. punicae*, which tends to develop in patchy colonies under a canopy of webbing on the upper sides of the leaves. The distribution of *E. hibisci* on avocado leaves is more similar to that of the six-spotted spider mite, *Eotetranychus sexmaculatus* Riley, which prefers the same sites on the leaf. This coincident distribution probably is a factor involved in the ability of *E. hibisci* to maintain *E. sexmaculatus* at low endemic densities (McMurtry, 1985). Although this spider mite may be partially protected from predation by its webbing (Abou-Setta and Childers, 1989), the presence of *E. hibisci* in the preferred colonization sites may deter the establishment of new colonies or the expansion of existing ones. The distribution of *Panonychus citri* (McGregor) on orange trees is much less clumped than that of *O. punicae* on avocado and thus more similar to that of the phytoseiids, *E. hibisci* or *E. tularensis*, which show potential as biological control agents of *P. citri* (McMurtry and Johnson, 1966; McMurtry, 1969).

Amblyseius andersoni shows little or no correlation with the distribution of *P. ulmi*, even though it is a potentially effective predator, capable of a marked numerical response to increase in densities of that species. The predators tend to roam over the leaves without aggregating or laying eggs on infested leaves, even if there is an abundance of prey (Van de Vrie and Backels, unpublished data, 1968; McMurtry and Van de Vrie, 1973). Nyrop (1988) found that *T. pyri* showed little tendency to remain on leaves infested with *P. ulmi*. A species that has not evolved toward exploiting a certain type of prey, might be expected to have a more random distribution on the plant. It seems logical, also, for pollen feeders like the *Euseius* species, to have a vagrant behavior, searching on many leaves of a plant in order to contact airborne pollen grains deposited on the foliage.

Seasonal population trends

Population trends of generalist predators can be expected to differ from those of specialist predators. For example, *E. hibisci* on California avocado typically has two population peaks each year, the highest one often being in the spring, in the virtual absence of any mite prey species. Avocado pollen apparently is the food responsible for this early-season increase (McMurtry and Johnson, 1965). A second peak, occurring in late summer, is correlated with increases of *O. punicae*. However, spider mite populations may continue to increase until checked by the coccinellid beetle *Stethorus picipes* Casey (McMurtry and Johnson, 1966). A similar early-season increase of *Euseius tularensis* occurs on citrus in association with an abundance of airborne pollen (McMurtry, 1969; Kennett et al., 1979). *Typhlodromus pyri* showed less tendency to migrate from apple trees with dwindling prey mite populations than the specialist *T. occidentalis* (Dunley and Croft, 1990). Thus, phytoseiid generalists are more likely to be year-round residents of the microhabitat than specialists which tend to track prey populations.

POTENTIAL IMPACT OF GENERALIST PHYTOSEIIDS ON TETRANYCHIDS: FIELD STUDIES

Do the above mentioned characteristics argue against generalist phytoseiid predators being effective biological control agents? Results of studies in several perennial crop systems suggest that these types of phytoseiids can in fact be valuable predators. Several different experimental methods have yielded evidence of the impact that some generalist phytoseiids have on tetranychid mite populations. Examples of predator-exclusion techniques include those of Collyer (1964) who removed *T. pyri* from experimental trees by placing sack bands around trunks of trees and later removing the bands which overwintering females used for hibernation sites. Higher *P. ulmi* populations developed on the trees from which the overwintering phytoseiids were removed, indicating that *T. pyri* was maintaining the pest mite populations at low densities on control trees from which no phytoseiids were removed. Excluding phytoseiids from branches in cages has been partially successful. Data obtained by Keetch (1972) indicated that *Euseius citri* van der Merwe & Ryke was an effective predator of *Panonychus citri*, provided that the predator:prey ratio was at least 1:3. However, McMurtry and Johnson (1966) were unsuccessful in excluding phytoseiids from caged avocado terminals.

The 'insecticide check' method (i.e. removing predators with a 'selective' insecticide) sometimes has been used, and various studies have been reported suggesting that the species in question was effective because of high pest populations and low predator numbers on the sprayed plots compared to the reverse on unsprayed check plots (e.g. Collyer and Kirby, 1955; Wearing et al., 1978). With such methods it is important to attempt to rule out the possibility that the pesticide was not causing a stimulation in the pest population in addition to the elimination of predators.

Experimental methods to increase predator populations by augmentative releases have produced data indicating effectiveness of generalist phytoseiids. Duso (1988, 1989) showed that releases of low numbers of *Amblyseius aberrans* (Oudemans) on grapevines resulted in maintenance of low levels of *Eotetranychus carpini* (Oudemans) on release plots. He attributed the efficiency of this species to its ability to increase early in the season on other foods and to colonize all parts of the vine. Gruys (1982), by a combination of releasing phytoseiids and withholding toxic sprays, obtained evidence that phytoseiids, initially *Euseius finlandicus* (Oudemans) and a few years later, *T. pyri*, maintained both *P. ulmi* and the apple rust mite, *Aculus schlechtendali* (Nalepa) at low levels during a long-term experiment.

Using a combination of pesticide exclusion (malathion application) and predator release in part of the malathion-sprayed block of citrus trees, McMurtry and J.G. Morse (unpublished data, 1984–86) concluded that the introduced phytoseiid *Euseius stipulatus* Athias-Henriot was able to increase in numbers and spread to other trees, even to those on which the native *E. tularensis* was released, and apparently prevent *P. citri* from increasing. The native *E. tularensis*, when released in sprayed plots, appeared to prevent increases of *P. citri* one season, but not the following one, when the *E. stipulatus* release plots were the only ones in which *P. citri* was maintained at low levels.

Non-experimental methods of frequent sampling of mite populations have given indications of the impact of particular phytoseiid species. James (1990) concluded that *Euseius victoriensis* (Womersley), by increasing in peach orchards on various foods, was present in sufficient numbers to prevent *Tetranychus urticae* (Koch) from establishing a foothold on the trees. James attributed the high mobility of *E. victoriensis* as an important attribute in biological control of this spider mite, which is a less than optimal food source. The lack of aggregation of *T. pyri* and the search strategy of not remaining on single infested leaves seems to result in effective biological control of *P. ulmi*, which also does not have a high degree of aggregation (Nyrop, 1988). Nyrop considered *T. pyri* to have coevolved with *P. ulmi*. If this is a valid assumption, then *T. pyri* might be considered a generalist that has evolved toward specialized predation on mites in the deciduous tree habitat. Dicke and de Jong (1988) found that *T. pyri* in field plots in the Netherlands fed mainly on *P. ulmi*, even though apple rust mite was a more favorable food for reproduction of this phytoseiid (Dicke et al., 1990). Ivancich Gambaro (1986) from several years of field studies concluded that *Amblyseius andersoni* was an effective predator of *P. ulmi* on deciduous fruits.

Population trends showing a peak and subsequent 'crash' in the prey population followed by a peak in the predator population do not necessarily indicate that the phytoseiid species was responsible for the suppression. For example, highly voracious *Stethorus* species may be the predators responsible (McMurtry, 1985).

INTRODUCTION AND ESTABLISHMENT OF GENERALIST PHYTOSEIIDS

My original hypothesis was that if we could establish additional species of phytoseiids in the agroecosystem, especially species with more affinity to prey on spider mites, we could reduce the frequency of *P. citri* and *O. punicae* escaping from low, endemic levels to damaging levels on citrus and avocado respectively. In numerous exploration trips conducted, in Mexico and Central America on avocado, and mainly in the Mediterranean, Middle East and parts of Asia on citrus, considerably fewer specialist than generalist phytoseiids were collected. Of 20 species collected from citrus and introduced to California (McMurtry, 1989) only three could be considered specialists: *Phytoseiulus persimilis*, only associated with *Tetranychus* species, which usually do not occur on citrus in California; *Neoseiulus californicus* (McGregor); and *Typhlodromus rickeri* Chant. Only *T. rickeri* from India, which reproduces readily on various tetranychids as well as eriophyids, is known to be established on citrus in California. Recoveries of this species have been made in orchards several kilometers distant from original colonization sites (1962–64) on both citrus and avocado in association with *P. citri* and *E. sexmaculatus* respectively. However, *T. rickeri* has been found in only a limited number of orchards, and only in low numbers, so that its overall impact probably is minimal. The other 17 introduced species all can be placed in or near the generalist category. The only one of these species established on citrus is *E. stipulatus*, which apparently has displaced the native *E. hibisci* and, in some cases, *E. tularensis* in some coastal areas of southern California (McMurtry, 1982, 1989). Although a generalist, *E. stipulatus* reproduces at a fairly high rate on spider mites (McMurtry, 1977; Ferragut et al., 1987), and appears to be a more effective predator of *P. citri* than the two native species. Of seven species from avocado introduced to California, three species in the *Typhlodromus occidentalis* group (*porresi* (McMurtry), *helveolus* (Chant), and *annectens* DeLeon) could be considered specialists; the others are generalists. None has become established on avocado in California (McMurtry, 1989).

Many factors could influence the establishment of an exotic species in an environment in which indigenous species already thrive, but I would suggest that the following biotic factors should be considered:

(1) The availability of prey at different times of the year could be important in competition between introduced specialists and indigenous generalists. In an environment where a certain prey resource is available only during part of the year, the generalist probably has the advantage, and when the generalist has built up to large numbers on some resource such as pollen, the specialist, unable to utilize this resource, could be at a competitive disadvantage. Augmentative releases of certain specialist phytoseiids when populations of *O. punicae* were increasing on avocado, did not result in an increase in total numbers of phytoseiids. Increases in number of the released species apparently was limited by the native generalist *E. hibisci* (McMurtry et al., 1984).

(2) The availability of alternate or supplemental foods could be important in competition between introduced and indigenous generalists. One species might be able to increase on a food substance that the other could not utilize. For example, Calis et al. (1988) showed that *T. pyri* could reproduce on the tydeid mite *Tydeus caudatus* (Dugés), but a *A. andersoni* could not. *Typhlodromus pyri* was able to persist in apple orchards in the absence of tetranychid and eriophyid mite prey and was the more important predator of *P. ulmi*.

(3) The plant substrate may be involved in favoring one species of phytoseiid over another. The introduced *E. stipulatus* apparently is the superior competitor over *E. hibisci* on citrus, but it has not become established on avocado, even where the trees are adjacent to citrus trees. McMurtry (1989) speculated that *E. stipulatus*, in its native home (Mediterranean region) may have been associated with citrus long enough have evolved a closer association with that plant compared to *E. hibisci*, native to the Americas, where citrus has a relatively short history. The reverse would apply to avocado, native to the Americas, on which *E. stipulatus* apparently cannot compete with *E. hibisci*.

CONCLUSIONS

There is an accumulating amount of information that suggests that generalist phytoseiids sometimes can control populations of tetranychid mites, even if those prey species are a suboptimal food resource. Moreover, laboratory tests showing poor reproduction on the target prey species in the absence of any other food may be misleading, and such results should not necessarily be used as criteria for evaluation of phytoseiid predators.

Relatively high predator:prey ratios may be required for generalist phytoseiids to control a tetranychid mite population at low densities. This ratio may be as high as 1 : 1 or higher for some species. Thus, the major impact of the generalist phytoseiid may be at low prey densities on perennial crops, preventing widespread colonization and limiting population fluctuations to low amplitudes. This phenomenon necessitates the phytoseiids increasing or maintaining their numbers on some other food source. Thus, generalist phytoseiids probably will not be able to 'catch up' from a low predator:prey ratio to suppress a rapidly increasing spider mite population. However some generalists do seem to have the capacity to overcome relatively unfavorable predator:prey ratios and build up to suppress a tetranychid population, e.g. *A. andersoni* as a predator of *P. ulmi* (McMurtry and van de Vrie, 1973; Ivancich Gambaro, 1986).

Exotic phytoseiid generalists can enhance biological control. The establishment of *E. stipulatus* in California and its apparent impact on citrus red mite suggests that generalist species should also be considered for introduction against a target pest species. In fact, such phytoseiids might be greater contributors to stability of tetranychid mite populations at low densities than specialists. I suggest that we cannot exclude any category of phytoseiid, whether it be generalist or specialist or somewhere in between the two, as being of potential value in limiting the numbers of pest mites, especially in more permanent agroecosystems. Some of the attributes considered important in effective phytoseiid predators, such as high reproductive potential and high specificity to spider mite prey (McMurtry, 1982) may not be of major importance in more stable situations at low population densities.

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