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Developmental times and oviposition rates of predatory mites *Typhlodromus pyri* and *Amblyseius andersoni* (Acari: Phytoseiidae) reared on different foods[1]

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ABSTRACT

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The developmental times and the reproduction of two resistant Italian strains of *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) were studied in the laboratory by rearing them on the spider mites *Panonychus ulmi* (Koch) and *Eotetranychus carpini* (Oud.), on the eriophyid *Colomerus vitis* (Pgst.) and on pollen of *Mesembryanthemum criniflorum*. The response of *T. pyri* and *A. andersoni* females to a spider mite supply (*P. ulmi* or *E. carpini*) of 4, 8 and 16 adult female prey per female predator per day was also studied.

Development of *T. pyri* on *E. carpini* and *C. vitis* required a shorter period than on *M. criniflorum* pollen, while intermediate values were recorded for *P. ulmi*. When the highest number of prey was offered, the influence of different foods on oviposition rates of *T. pyri* was not significant. An increase in spider mite supply favoured a shorter pre-oviposition period and higher oviposition rates.

Development of *A. andersoni* was faster on pollen than on spider mites, while intermediate values were found concerning *C. vitis*. Differences statistically significant were recorded for development on *P. ulmi* and *C. vitis*. *Colomerus vitis* proved to be the more suitable food in terms of oviposition. The oviposition rate decreased when feeding upon *P. ulmi*, but reached intermediate values on *E. carpini* and *M. criniflorum*. Increasing spider mite densities caused shorter pre-oviposition times and higher oviposition rates. Using a given number of *E. carpini* females, rather than those of *P. ulmi*, resulted in higher oviposition rates and shorter pre-oviposition times.

For both predators, the results suggest a higher intrinsic rate of population increase on *E. carpini* or *C. vitis* than on *P. ulmi*.

INTRODUCTION

Results of laboratory studies performed on the development and oviposition of several species of phytoseiid mites (Acari: Phytoseiidae) have been

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widely reported (McMurtry et al., 1970; Tanigoshi, 1982; Helle and Sabelis, 1985). *Typhlodromus pyri* Scheuten is one of the most important bio-control agents of spider mites in orchards and vineyards and its feeding habits have been discussed (Dicke, 1988). Another phytoseiid mite which may be of importance in biological control programmes is *Amblyseius andersoni* (Chant). The most important laboratory studies on the biology of *A. andersoni* have been carried out by Amano and Chant (1977, 1978). However, data concerning *Amblyseius potentillae* (Garman) should be considered, since the latter species has been found to be a junior synonym of *A. andersoni* (Chant and Yoshida-Shaul, 1990; Messing and Croft, 1991). The biology of *A. potentillae* in the laboratory has been studied by Van de Vrie (1973), Rabbinge (1976), Sabelis (1981) and Dicke (1988).

Typhlodromus pyri and *A. andersoni* are widespread in European vineyards and they have been employed in biological control programmes against some phytophagous mites of grapes. However, the relationships between these predators and the mites, living on grapes, have been studied in a few cases only (Mathys, 1958; Baillod et al., 1982; Duso, 1989) and little is known about their feeding habits and the demographic parameters relating to phytophagous mites. In fact, the life-history components of *T. pyri* and *A. andersoni* have been studied mainly in relation to Tetranychidae or Eriophyidae living in apple orchards i.e. *Panonychus ulmi* (Koch), *Tetranychus urticae* Koch and *Aculus schlechtendali* (Nal.). Partially, data relating to *P. ulmi* and *T. urticae* can be considered in studying the predator–prey interactions in vineyards. Laboratory studies on *T. pyri* and *A. andersoni* reared on other phytophagous mites occurring in European vineyards, such as the spider mite *Eotetranychus carpini* (Oud.) and the eriophyid *Colomerus vitis* (Pgst.), are needed. In particular, large populations of *E. carpini* have been recorded in several Italian viticultural areas in which the species is a serious pest and can displace *P. ulmi* (Duso, 1989; Duso et al., 1991). The biology of *E. carpini* regarding its demographic parameters (Bonato et al., 1989) and the relationships with a phytoseiid mite (Castagnoli et al., 1989) have only recently been studied. The eriophyid *Colomerus vitis* is not considered of importance in European vineyards but the 'Bud strain' of the mite can cause severe damage in other viticultural areas (Smith and Stafford, 1948). However, the interest in *C. vitis* is due to its possible function as an alternative prey for phytoseiid mites in vineyards.

Several laboratory studies on the biology of phytoseiids have been performed on strains originating either from non-cultivated plants or those which have been reared for many years in the laboratory. Insecticide-resistant strains of *T. pyri* and especially of *A. andersoni* have received little attention on this subject.

The developmental times and the reproduction of two resistant Italian

strains of *T. pyri* and *A. andersoni* have been studied in the laboratory by rearing the predators on different grape mites. The pollen of *Mesembryanthemum criniflorum* was also selected in the experiment due to its suitability for predatory mites (Overmeer and van Zon, 1983). The response of *T. pyri* and *A. andersoni* to a supply of 4, 8 or 16 spider mites per day (*P. ulmi* or *E. carpini* females) was also studied.

MATERIALS AND METHODS

Developmental times

The strain of *T. pyri* originated from a vineyard situated near Verona and it is organophosphate (OP) resistant. The strain of *A. andersoni* was collected in a vineyard situated near Treviso and it is also OP-resistant. When the experiments were performed, the vineyards were not infested by phytophagous mites.

To determine developmental times, ovipositing phytoseiid females were collected from leaves in the vineyards and reared in 'arenas' similar to those described by Overmeer (1981). The arenas consisted of a 10×15-cm black plastic plate which served as substrate surrounded by wet paper tissue. The plastic plate was placed on a piece of foam rubber contained in a small tray with water. The paper tissue covered about 1 cm of the upper-surface of the plate along the four edges and the rest was dipped in water. A barrier of glue was made on the paper tissue along the edges of the tile. Small 2-cm^2 roof-shaped pieces of transparent plastic were placed as a shelter in order to allow mite oviposition. Pollen of *Mesembryanthemum criniflorum* was provided as food. After the commencement of oviposition, new arenas were made. This plastic plate was divided into four parts (units) of approximately 20 cm^2. One predator egg was transferred to each unit from the cultures. Four diets (*P. ulmi, E. carpini, C. vitis* and *M. criniflorum* pollen) were compared. A treatment in which only water was provided was also included as a control. For each treatment, 60–80 eggs were employed. Larvae and protonymphs (varying from 5 to 20 per day) of spider mites as well as active stages (30–60 per day) of *C. vitis* were provided for every unit. The phytophagous mites were transferred from infested leaves, collected in vineyards treated with selective pesticides (copper oxychloride and low doses of wettable sulphur), using a fine brush. The prey were offered ad libitum and their number increased according to the stage of the predator. The daily supply per unit for the fourth treatment consisted of 0.1–0.2 mg of the pollen of *M. criniflorum*.

Observations were performed every 8 h. A moult was recorded only if the exuvium was found. When a female deutonymph was 24 h old, one adult male

was placed in the unit to allow for mating. All the experiments were performed at 26–27°C and 70–90% RH.

Oviposition

Female deutonymphs and males of phytoseiids, reared on *P. ulmi, E. carpini, C. vitis* or *M. criniflorum* pollen, were placed in rearing units to oviposit on these foods. Each unit received one female and one male. The presence of males was necessary during the oviposition period because multiple matings are indispensable in *T. pyri* and *A. andersoni* to obtain maximum egg production (Amano and Chant, 1978; Overmeer et al., 1982). The experiments were carried out using 10 females and 10 males per treatment. For the spider mites, the pre-oviposition period and the oviposition of predators were considered, offering each female 4, 8 or 16 adult females of *P. ulmi* or *E. carpini* daily. In other treatments, 60 females of *C. vitis* or 0.1–0.2 mg of *M. criniflorum* pollen were provided daily. When counts were made, a number of living eriophyids was constantly found in the units. For this reason, the number provided to each predator female can be considered an ad libitum supply.

Oviposition was recorded daily for a 20-day period since the highest oviposition rates of phytoseiids were generally reached within this period when there was a high food supply. Phytoseiid eggs and dead prey were removed daily in order to estimate the prey consumption.

RESULTS

Typhlodromus pyri

Developmental times

The developmental times of *T. pyri* females and males reared on *P. ulmi, E. carpini, C. vitis* and *M. criniflorum* pollen are reported in Table 1. The deutonymphal stage of females was reached on *C. vitis* in a significantly shorter time than on pollen, while intermediate values were found for spider mites. Considering the period from egg to female, the predators developed significantly more rapidly on *E. carpini* (152.0 h) and *C. vitis* (154.0 h) than on pollen (170.0 h) while intermediate times were recorded for *P. ulmi* (158.8 h). There was no difference in pre-oviposition times, which varied from 55.2 to 59 h. When the period of egg to egg development was examined, significant differences were found between *E. carpini* (207.2 h) and pollen (225.2 h) treatments only. These results appear to be due to the similar pre-oviposition times among treatments. Finally, the larva to egg period was considered as egg-hatching is not influenced by a particular diet. A shorter period was observed using *C. vitis* and *E. carpini* as food but no significant differences were found. The lack of significance may be related to similar pre-oviposition times,

TABLE 1

Developmental times (h) of females and males of *Typhlodromus pyri* reared on different foods (*P. ulmi, E. carpini, C. vitis, M. criniflorum* pollen)

Stage	*P. ulmi*	*E. carpini*	*C. vitis*	*M. criniflorum*
Female				
Egg	44.4	45.6	47.6	50.8
Larva	13.6	12.0	12.6	13.6
Protonymph	50.4	46.4	49.2	48.0
Deutonymph	50.4 ab	47.2 ab	43.2 a	57.6 b
Egg–adult	158.8 AB	152.0 A	154.0 A	170.0 B
Pre-oviposition	56.8	55.2	59.0	55.2
Egg–egg	215.6 AB	207.2 A	213.2 AB	225.2 B
Larva–egg	171.2	161.6	165.4	174.4
Male				
Egg	47.2	46.8	48.0	48.4
Larva	12.8	13.2	12.8	12.6
Protonymph	49.3	42.6	43.7	45.3
Deutonymph	44.0	42.6	39.5	46.6
Egg–adult	153.8	143.6	144.6	152.6

Data followed by the same letter are not significantly different using Duncan's test (capital letters indicate $P<0.05$, small letters indicate $P<0.01$).

found in different treatments and to a greater variance among data in the treatments. Development was more rapid for males than for females and was not influenced by different diet. Mortality during development did not exceed 5% in any of the treatments. In the treatment receiving no food, nine predatory mites (three females and six males) surprisingly reached the adult stage. The developmental times (in h) of females were: 48.1 for eggs, 14.8 for larvae, 131.4 for protonymphs, 186.2 for deutonymphs. These results were not obtained in successive experiments, in which mortality was generally reached at the protonymphal stage.

Oviposition on various foods

The oviposition of *T. pyri* ranged from 0.35 to 1.24 eggs per adult per day. The highest oviposition rate (1.24 eggs per day) was recorded from females reared on *C. vitis*. Significant differences were found using *M. criniflorum* pollen (1.01 eggs per day) or providing 16 adults of *P. ulmi* per day (1.02 eggs per day) while the maximum supply of *E. carpini* gave intermediate values (1.18 eggs per day). Oviposition rates increased with the spider mite density offered (Table 2). Pre-oviposition times ranged from 2.3 to 4.2 days. No differences were found between *C. vitis, M. criniflorum*, the higher supply of *P. ulmi* and all the supplies of *E. carpini*. Pre-oviposition times decreased with the prey supply, in particular from 4.2 to 2.7 days on *P. ulmi* and from 3.4 to 2.5 on *E. carpini*. For a particular prey supply (eight females per day),

TABLE 2

Pre-oviposition (days) and oviposition rates of *Typhlodromus pyri* (average number of eggs female^{-1} day^{-1} for a 20-day period) reared on different foods

Treatments		Pre-oviposition	No. eggs female^{-1} day^{-1}
P. ulmi	4	4.2 C, b	0.35 A, a
	8	4.0 C, b	0.60 BC, bc
	16	2.7 AB, a	1.02 D, e
E. carpini	4	3.4 BC, ab	0.52 B, ab
	8	2.7 AB, a	0.78 C, cd
	16	2.5 A, a	1.18 DE, e
C. vitis		2.5 A, a	1.24 E, e
M. criniflorum		2.3 A, a	1.01 D, de

Data followed by the same letter are not significantly different using Duncan's test (capital letters indicate $P<0.05$, small letters indicate $P<0.01$).

TABLE 3

Prey consumption of *T. pyri* and *A. andersoni* reared on females of *P. ulmi* or *E. carpini* (average number of prey destroyed per day)

Treatments		No. prey consumed per day	
		T. pyri	*A. andersoni*
E. carpini	4	2.30 a	2.78 a
	8	4.28 b	4.81 b
	16	7.78 c	8.22 c
P. ulmi	4	2.20 a	2.50 a
	8	4.22 b	4.29 b
	16	6.86 c	7.75 c

Data followed by the same letter are not significantly different using Duncan's test (capital letters indicate $P<0.05$, small letters indicate $P<0.01$).

the pre-oviposition times obtained for *E. carpini* were significantly shorter than on *P. ulmi*.

The consumption of *E. carpini* females appeared to be slightly higher than that of *P. ulmi* females but no significant differences were found (Table 3). The number of prey daily available for predators was lower than 4, 8 or 16 due to the spider mites escaping over the wet tissues in the arena. These prey were rarely killed by predators. Only in the maximum prey supply, a constant availability of prey was found.

Amblyseius andersoni

Developmental times

Females of *A. andersoni* developed more rapidly on *M. criniflorum* (110.4 h) than on *P. ulmi* (132.8 h) and *E. carpini* (127.0 h), due to the shorter

TABLE 4

Developmental times (h) of females and males of *Amblyseius andersoni* reared on different foods (*P. ulmi, E. carpini, C. vitis, M. criniflorum* pollen)

Stage	*P. ulmi*	*E. carpini*	*C. vitis*	*M. criniflorum*
Female				
Egg	37.6	36.0	37.2	38.8
Larva	16.0	18.4	16.4	14.4
Protonymph	42.4 b	37.6 ab	34.8 ab	30.4 a
Deutonymph	36.0 B	34.4 B	31.6 AB	28.0 A
Egg–adult	132.8 c	127.0 bc	117.4 ab	110.4 a
Pre-oviposition	48.0	45.6	40.0	48.0
Egg–egg	168.9 c	163.0 bc	157.4 ab	148.6 a
Larva–egg	130.9 b	127.0 b	120.2 ab	109.6 a
Male				
Egg	37.0	36.2	37.8	38.0
Larva	15.5 AB	16.0 B	15.2 AB	13.2 A
Protonymph	30.2 b	25.5 ab	26.2 ab	23.7 a
Deutonymph	26.0	27.7	27.7	24.7
Egg–adult	109.0 b	105.2 ab	107.2 ab	99.7 a

Data followed by the same letter are not significantly different using Duncan's test (capital letters indicate $P<0.05$, small letters indicate $P<0.01$).

period required to reach the protonymphal and the deutonymphal stages (Table 4). Development of females reared on *C. vitis* (117.4 h) was not statistically different to that of females reared on pollen or on *E. carpini*. Pre-oviposition times varied from 40 to 48 h and did not appear to be influenced by different foods. The larva to egg period was shorter for females reared on pollen than those on spider mites. When the eriophyids were provided intermediate values were found. Males developed more rapidly than females. Males reared on pollen developed faster than on *P. ulmi* due to the duration of the protonymphal stage. Mortality was less than 5% in all the experiments excluding the treatment in which no food was provided. In the latter mortality was reached at the protonymphal stage.

Oviposition on various foods

The oviposition rates ranged from 0.38 to 1.64 eggs per adult per day. The highest oviposition rates was found when *C. vitis* (1.64 eggs per day) and the maximum supply of *E. carpini* females (1.48 eggs per day) were offered (Table 5). Highly significant differences were found between the two treatments and the maximum supply of *P. ulmi* females (1.17 eggs per day). Intermediate values were found when pollen was provided (1.38 eggs per day). Oviposition rates increased with the density offered, in particular from 0.38 to 1.17 eggs on *P. ulmi* and from 0.75 to 1.48 eggs on *E. carpini*. Increasing prey supply resulted in a decrease of the pre-oviposition times, in particular from 5.3

TABLE 5

Pre-oviposition (days) and oviposition rates of *Amblyseius andersoni* (average number of eggs female^{-1} day^{-1} for a 20-day period) reared on different foods

Treatments		Pre-oviposition	No. eggs female^{-1} day^{-1}
P. ulmi	4	5.3 C, c	0.38 A, a
	8	3.5 B, b	0.65 B, b
	16	3.4 B, b	1.17 C, de
E. carpini	4	2.3 A, ab	0.75 B, bc
	8	2.2 A, ab	1.00 C, cd
	16	2.0 A, a	1.48 DE, f
C. vitis		1.7 A, a	1.64 E, f
M. criniflorum		2.0 A, a	1.38 D, ef

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to 3.4 on *P. ulmi* and from 2.3 to 2.0 on *E. carpini*. When a given number of prey was offered, higher oviposition rates were found using *E. carpini* rather than *P. ulmi*. Pre-oviposition times were also significantly shorter using *E. carpini*.

Consumption of *E. carpini* females was higher than *P. ulmi* females but no significant differences were found (Table 3). The number of *C. vitis* provided for each female was adequate, since living individuals were constantly found in rearing units. The voracity of *A. andersoni* appeared to be higher than that of *T. pyri*. Only when 16 females were provided per day, the prey were constantly available for predators.

DISCUSSION

Influence of diets on development

The development of *T. pyri* on *E. carpini* and *C. vitis* was reached in significantly shorter times than on *M. criniflorum* pollen. There were no differences between *E. carpini, C. vitis* and *P. ulmi*. The developmental times of *T. pyri* females on *P. ulmi* were very close to those recently reported by Dicke et al. (1988) using a Munger-cell as a rearing unit and the same temperature. The better response of *T. pyri* to spider mites, rather than to pollen, confirms the reports of Dosse (1961). Considering the egg to egg periods, significant differences were found between *E. carpini* and *M. criniflorum*. When the larva to egg period was considered, differences among treatments were not significant, suggesting that the influence of diet on development was relatively unimportant. Concerning development of *T. pyri*, the nutritional value of *E. carpini* and *C. vitis* appeared to be similar to that of *P. ulmi* which is often

considered to be the most important prey for the predator on apple trees (Dicke, 1988). The development of predators in absence of food requires further investigation.

In contrast with *T. pyri*, the development of *A. andersoni* was significantly more rapid on pollen than on spider mites while the use of *C. vitis* gave intermediate results. The feeding capacity of *A. andersoni* larvae on pollen might accelerate its developmental times. However, the protonymphal stage of the predators appeared the most influenced by different diets.

Influence of diets on oviposition

The influence of different foods on the *T. pyri* oviposition was not evident when the highest number of spider mites was provided for predators. As in these treatments, the prey was available ad libitum, the influence of diet did not appear to be important. Different results were obtained with the lower prey supplies. For example, providing eight prey, the use of *E. carpini* instead of *P. ulmi* resulted in shorter pre-oviposition times. Moreover, when four prey were provided, there was a significantly higher oviposition rate on *E. carpini* than on *P. ulmi*. As the prey consumption of *E. carpini* was only slightly higher than that of the larger *P. ulmi* females, it may be assumed that a comparable biomass was consumed by the predators. In the two cases considered, consuming *E. carpini* favoured higher performances of *T. pyri*. For each spider mite species (*P. ulmi* or *E. carpini*) there was a positive relation between oviposition rates and number of prey supplied.

Considering *A. andersoni*, the influence of diet on oviposition appeared to be more important than for *T. pyri*. Higher oviposition rates were reached on *C. vitis* and *E. carpini* (maximum prey supply), followed by *M. criniflorum* and *P. ulmi* (maximum prey supply). In all these treatments the prey was provided ad libitum. When a given spider mite supply was considered, oviposition rates were higher on *E. carpini* than on *P. ulmi*. Moreover, pre-oviposition times were shorter when the former prey was employed. Prey consumption of *E. carpini* females appeared to be slightly higher than on *P. ulmi* but, even in this case, a comparable amount of food was destroyed by predators. The *E. carpini* females were easily preyed upon by phytoseiids, but feeding on *P. ulmi* females appeared less severe. A higher conversion into egg biomass, of *E. carpini* females than *P. ulmi* females, by predators might explain these results. This is confirmed by the similar pre-oviposition times when preying upon juvenile stages (during developmental studies) or females of *E. carpini*. Moreover, the oviposition rates on *E. carpini*, at the maximum prey supply, were comparable with the best food (*C. vitis*). In contrast, pre-oviposition times of females of *A. andersoni*, reared on *P. ulmi* juveniles were not different from those recorded using *C. vitis* but significantly shorter than those obtained on the females. Different results, in terms of oviposition, should be obtained when using juvenile stages of *P. ulmi* instead of females.

Oviposition rates on *C. vitis* were highest for both phytoseiid species. The

supply of eriophyids was 60 females per day, a biomass comparable with one female of *P. ulmi*. Eriophyids were easily consumed, probably favouring a high food conversion into egg biomass.

The results confirm, that phytoseiid pre-oviposition and oviposition are influenced, not only be the features of prey utilized but even by the size or the stage of the prey. The consumption of more suitable prey (i.e. eggs or larvae vs. nymphs or adults), favouring a high conversion of food into egg biomass, determined higher intrinsic rates of increase (Croft, 1972; Croft and McMurtry, 1972; Sabelis, 1985; Bruce-Olivier and Hoy, 1990).

Implications for pest management

Developmental times, oviposition rates and low mortality of *T. pyri* and, especially *A. andersoni*, on *E. carpini* and *C. vitis* suggest a higher intrinsic rate of increase on these mites rather than on *P. ulmi*. However, the response of phytoseiids on juvenile stages of *P. ulmi* could be reasonably better than that obtained on adult females. The above-mentioned performances of *T. pyri* and *A. andersoni* on *E. carpini* and their prey capacity suggest a successful biological control of the mite in vineyards. Field studies on this subject confirm the efficiency of *T. pyri*, but further data are needed concerning *A. andersoni*. The reports obtained for *C. vitis* suggest that this mite plays an important role as the prey for phytoseiid mites. Eriophyids are probably used as an alternative prey by phytoseiids when spider mites are scarce. This aspect appear particularly interesting for *A. andersoni*, since it disappears from vineyards when tetranychid densities decrease. Moreover, the response of phytoseiids to spider mite infestations may be positively influenced by the occurrence of eriophyids.

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REFERENCES

Amano, H. and Chant, D.A., 1977. Life history and reproduction of two species of predacious mites, *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius andersoni* (Chant) (Acarina: Phytoseiidae). Can. J. Zool., 55: 1978–1983.

Amano, H. and Chant, D.A., 1978. Some factors affecting reproduction and sex ratios in two species of predacious mites, *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius andersoni* (Chant) (Acarina: Phytoseiidae). Can. J. Zool., 56: 1593–1607.

Baillod, M., Schmid, A., Guignard, E., Antonin, Ph. and Caccia, R., 1982. Lutte biologique contre l'acarien rouge en viticulture. II. Equilibres naturels, dynamiques de population et expériences de lâchers de typhlodromes. Rev. Suisse Vitic. Arboric. Hortic., 14: 345–352.

Bonato, O., Cotton, D., Kreiter, S. and Gutierrez, J., 1989. Les principaux paramètres démo-

graphiques d'une population de l'acarien jaune de la vigne *Eotetranychus carpini* (Acari: Tetranychidae). In: Colloque sur les Acariens des Cultures, Montpellier, 24–26 October 1989. Annales A.N.P.P. No. 2, Vol. 1/1: 541–551.

Bruce-Olivier, S.J. and Hoy, M.A., 1990. Effect of prey stage on life-table attributes of a genetically manipulated strain of *Metaseiulus occidentalis* (Acari: Phytoseiidae). Exp. Appl. Acarol., 9: 201–217.

Castagnoli, M., Amato, F. and Monagheddu, M., 1989. Osservazioni biologiche e parametri demografici di *Eotetranychus carpini* (Oud.) (Acarina: Tetranychidae) e del suo predatore *Typhlodromus exhilaratus* Ragusa (Acarina: Phytoseiidae) in condizioni di laboratorio. Redia, 72: 545–557.

Chant, D.A. and Yoshida-Shaul, E., 1990. The identities of *Amblyseius andersoni* (Chant) and *A. potentillae* (Garman) in the family Phytoseiidae (Acari: Gamasina). Int. J. Acarol., 16: 5–12.

Croft, B.A., 1972. Prey stage distribution, a factor affecting the numerical response of *Typhlodromus occidentalis* to *Tetranychus mcdanieli* and *Tetranychus pacificus*. Great Basin Nat., 32: 61–75.

Croft, B.A. and McMurtry, J.A., 1972. Comparative studies on four strains of *Typhlodromus occidentalis* Nesbitt (Acarina: Phytoseiidae). IV. Life history studies. Acarologia, XIII (3): 460–470.

Dicke, M., 1988. Infochemicals in tritrophic interactions, Ph.D. Thesis, Agricultural University, Wageningen, Netherlands, 235 pp.

Dicke, M., Sabelis, M.W. and de Jong, M., 1988. Analysis of prey preference in phytoseiid mites by using an olfactometer, predation models and electrophoresis. Exp. Appl. Acarol., 5: 225–241.

Dosse, G., 1961. Über die Bedeutung der Pollennahrung für *Typhlodromus pyri* Scheuten (= *tiliae* Oud.) (Acari: Phytoseiidae). Entomol. Exp. Appl., 4: 191–195.

Duso, C., 1989. Role of the predatory mites *Amblyseius aberrans* (Oud.), *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) (Acari, Phytoseiidae) in vineyards. I. The effects of single or mixed phytoseiid population releases on spider mite densities (Acari, Tetranychidae). J. Appl. Entomol., 107: 474–492.

Duso, C., Pasqualetto, C. and Camporese, P., 1991. Role of the predatory mites *Amblyseius aberrans* (Oud.), *Typhlodromus pyri* Scheuten and *Amblyseius andersoni* (Chant) (Acari, Phytoseiidae) in vineyards. II. Minimum releases of *A. aberrans* and *T. pyri* to control spider mite populations (Acari, Tetranychidae). J. Appl. Entomol. (in press).

Helle, W. and Sabelis, M.W., 1985. Spider Mites, their Biology, Natural Enemies and Control. World Crop Pests Vol. 1B. Elsevier, Amsterdam, 458 pp.

Mathys, G., 1958. The control of phytophagous mites in Swiss vineyards by *Typhlodromus* species. 10th Int. Congr. Entomol., 4: 607–610.

McMurtry, J.A., Huffaker, C.B. and van de Vrie, M., 1970. Tetranychid enemies: their biological characters and the impact of spray practices. Hilgardia, 40: 331–390.

Messing, R. and Croft, B.A., 1991. Biosystematics in *Amblyseius andersoni* Chant and *Amblyseius potentillae* Garman. Exp. Appl. Acarol., 10: 267–278.

Overmeer, W.P.J., 1981. Notes on breeding phytoseiid mites from orchards (Acarina: Phytoseiidae) in the laboratory. Meded. Fac. Landbouwwet. Rijksuniv. Gent, 46: 503–509.

Overmeer, W.P.J. and van Zon, A.Q., 1983. The effect of different kinds of food on the induction of diapause in the predacious mite *Amblyseius potentillae*. Entomol. Exp. Appl., 33: 27–30.

Overmeer, W.P.J., Doodeman, M. and Zon, A.Q., 1982. Copulation and egg production in *Amblyseius potentillae* and *Typhlodromus pyri* (Acari, Phytoseiidae). Z. Angew. Entomol., 93: 1–11.

Rabbinge, R., 1976. Biological control of fruit tree red spider mites. Simulation Monograph, Pudoc, Wageningen, Netherlands, 228 pp.

Sabelis, M.W., 1981. Biological control of two-spotted spider mites using phytoseiid predators. Part I. Modelling the predator–prey interaction at the individual level. Pudoc, Wageningen, Netherlands, Agric. Res. Rep. 910, 242 pp.

Sabelis, M.W., 1985. Capacity for population increase. In: W. Helle and M.W. Sabelis (Editors), Spider Mites, their Biology, Natural Enemies and Control. World Crop Pests Vol. IB. Elsevier, Amsterdam, pp. 35–41.

Smith, L.M. and Stafford, E.M., 1948. The bud mite and the erineum mite of grapes. Hilgardia, 18: 317–334.

Tanigoshi, L.K., 1982. Advances in the knowledge of the biology of the Phytoseiidae. In: M.A. Hoy (Editor), Recent Advances in Knowledge of Phytoseiidae. Univ. Calif. Berkeley, Publ. No. 3284, pp. 1–22.

Van de Vrie, M., 1973. Studies on prey–predator interactions between *Panonychus ulmi* and *Typhlodromus (A.) potentillae* (Acarina: Tetranychidae, Phytoseiidae) on apple in the Netherlands. In: FAO Conference on Ecology in Relation to Pest Control, Rome, 1973. FAO, Rome, pp. 145–160.