



Mite population dynamics on different grape varieties with or without phytoseiids released (Acari: Phytoseiidae)

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Abstract. In a three-year study, mite populations were monitored in two vineyards, each having two grape varieties with different leaf hair density. In both vineyards native phytoseiids were present: *Amblyseius andersoni* in one vineyard, and *Phytoseius finitimus* in the other. The economically important predators *Kampimodromus aberrans* and *Typhlodromus pyri* were released in both vineyards in order to study their efficacy in controlling tetranychids and eriophyids and their persistence during periods of prey scarcity. In both vineyards, relative abundances of the mite species, especially phytoseiids, were found to differ on different varieties in the same vineyard. In the first experiment, *A. andersoni* reached higher densities and was more persistent on the variety with slightly pubescent leaf under-surface (Merlot). *Typhlodromus pyri* and *K. aberrans* releases were successful and the mites became more abundant on the variety with pubescent leaf under-surface (Verduzzo). In the second experiment, *P. finitimus* was more abundant on a variety with pubescent leaf under-surface (Prosecco) than with glabrous leaf under-surface (Riesling). The most interesting results of the present study concerned the interactions between native and released predators. In the first vineyard, different results were obtained when releasing *T. pyri* on the two varieties. On the variety with pubescent leaves, *A. andersoni* was rapidly displaced by *T. pyri*, whereas the former species persisted on the other variety throughout the three-year study, apparently becoming dominant during the last season. In contrast to *T. pyri*, interactions between *K. aberrans* and *A. andersoni* in this vineyard did not depend on variety. The results of the experiments carried out in the second vineyard stressed the importance of interspecific competition for phytoseiid releases. *Typhlodromus pyri* colonization failed on both varieties. *Kampimodromus aberrans* releases appeared to be more successful on Riesling than on Prosecco, where *P. finitimus* was more abundant. At the end of the experiments, *K. aberrans* displaced *P. finitimus* on both varieties.

Key words: biological control, interspecific competition, leaf hairiness, grapevine, Tetranychidae, Eriophyidae, Phytoseiidae, Stigmaeidae

Introduction

Persistence after prey extinction is often related to a predator's capacity to survive on a variety of foods and to compete successfully with other predatory species,

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frequently of closely related taxa. In bio-control programmes, knowledge of the mechanisms involved in the displacement of one predator species by a more competitive species is instrumental. Interspecific competition and predation affect the evolution of predator-prey relationships within arthropod communities. Sometimes the coexistence of two or more predators enhances the control level of a pest, but intraguild predation may disrupt biological control (McMurtry *et al.*, 1970; Croft and McRae, 1993; Rosenheim *et al.*, 1995).

In studies on predatory mites of the family Phytoseiidae, factors have been analysed that affect coexistence in or exclusion from simple systems. These studies were carried out in laboratory experiments on interspecific predation in the absence or presence of prey (Yao and Chant, 1991; Croft and Croft, 1993, 1996; MacRae and Croft, 1993; Zhang and Croft, 1995). A series of studies on the interaction of several phytoseiid species in apple orchards in Oregon (USA) is of particular interest. Climatic conditions, prey composition and abundance, interspecific predation and the co-occurrence of other competitors were the most important factors in regulating relationships between the generalist predator *Typhlodromus pyri* Scheuten and the specialist *Typhlodromus occidentalis* (Nesbitt). The former displaced the latter in several cases, but coexistence between the two species was also found, and could be explained by their different ecological niches (Croft and MacRae, 1992a,b; MacRae and Croft, 1993). The general feeding habits of *T. pyri* were considered a major factor in its successful competition with *T. occidentalis* (Zhang and Croft, 1995).

For a number of years the ecology and behaviour of the generalists *Kampimodromus aberrans* (Oudemans), *Amblyseius andersoni* (Chant) and *T. pyri* were studied in northern Italy (mainly in the Veneto region) in order to obtain successful control in vineyards and orchards. The distributions of species in vineyards in this area are affected by several factors, especially climate and pesticide application. In previous experiments, single or mixed releases of *K. aberrans*, *A. andersoni* and *T. pyri* were carried out in vineyards that were treated with selective pesticides in order to study their effects on spider mite populations. *Kampimodromus aberrans* was the most competitive predator; *T. pyri* dominated over *A. andersoni* in some vineyards, but showed low persistence; and *A. andersoni* releases were unsuccessful as the predator disappeared in several cases (Duso, 1989; Duso *et al.*, 1991; Girolami *et al.*, 1992). In subsequent studies, *K. aberrans* and *T. pyri* were released successfully in distinct plots of two vineyards, but after some years the former species displaced the latter (Duso and Pasqualetto, 1993). In parallel experiments, the release of *K. aberrans* was carried out in vineyards naturally colonized by *T. pyri* and *vice versa*. Results confirmed the higher competitiveness of *K. aberrans*. Moreover, *T. pyri* displaced *A. andersoni* on grape varieties with pubescent leaf under-surface when colonized by large populations of this predator, but *T. pyri* declined when *K. aberrans* was allowed to colonize the same vineyard (C. Duso, unpublished data). Apparently, coexistence between *K. aberrans* and the other two species is not possible in the long term.

The majority of *T. pyri* releases in this area of the Veneto region failed (16 out of 22 cases), because of climatic conditions, grape variety features, interspecific competition and predation by insects. Grape variety was found to be one of the most important factors, as *T. pyri* releases failed especially on varieties with glabrous or slightly pubescent leaf under-surface (12 out of 13 cases), but were more successful on those characterized by a pubescent leaf under-surface (4 out of 9 cases unsuccessful). Competition with native phytoseiids was also not successful, in particular competition with *A. andersoni* on varieties with non-pubescent leaves, and with *Phytoseius finitimus* (Ribaga) on varieties with pubescent leaves. Successful cases were obtained, especially on the latter varieties, regardless of the colonization of *A. andersoni*.

The importance of plant variety for the colonization of phytoseiids was also noted in a vineyard containing varieties with leaf under-surface which had differing degrees of hairiness. *Typhlodromus pyri* was found to be most dominant on two varieties with pubescent leaves and *A. andersoni* on one with non-pubescent leaves. Release of *A. andersoni* was unsuccessful on varieties colonized by *T. pyri*. *Typhlodromus pyri* was able to displace *A. andersoni* only when the latter reached very low densities (Camporese and Duso, 1996). More recently, similar coexistence was found between *A. andersoni* and *P. finitimus* (C. Duso *et al.*, unpubl. data).

Kampimodromus aberrans was also released on the two varieties where *A. andersoni* was displaced, and on the one variety where *T. pyri* was displaced. Apparently, the effect of variety on interspecific competition between *K. aberrans* and the native species was negligible. Experiments carried out in the Veneto region showed that *K. aberrans* releases are unsuccessful in a small number of cases. Failure of *K. aberrans* releases may be explained by competition with native phytoseiid species, in particular *P. finitimus*.

In the present study mite populations were monitored in two vineyards (A and B) with grape varieties with different leaf morphology, and with different naturally occurring phytoseiid species, *A. andersoni* (vineyard A) and *P. finitimus* (vineyard B). In northern Italy, the former species colonizes a large number of vineyards as well as wild and cultivated plants, but is unable to persist on grapevines for long periods. The latter species seems to colonize a small variety of hosts, but can build up large populations on grapevines. Moreover, *A. andersoni* is more common on glabrous leaf under-surface while *P. finitimus* is abundant on plants with pubescent leaf under-surface (Duso and Moretto, 1994; Duso and Ren, 1997). The economically important predators *K. aberrans* and *T. pyri* were released in both vineyards to study their effectiveness and persistence when prey was scarce. Preliminary observations carried out in the two vineyards have been reported previously. In the first contribution (Duso, 1992), the effects of releasing *T. pyri* and *K. aberrans* on different varieties were briefly described, but the occurrence of native phytoseiids (i.e., *A. andersoni*) was not considered relevant. The continuation of experiments for

a longer period indicated the potential role of grape variety in interspecific competition rendering reappraisal necessary of the existing results. In the second contribution, *P. finitimus* was found to be more abundant on varieties with pubescent leaf under-surface (Duso and Moretto, 1994), whereas the effects of releasing *K. aberrans* and *T. pyri* were not reported.

Materials and methods

Experiments were carried out in two vineyards in the Veneto region, with different grape varieties of equal age and trained with the espalier system. The experimental design is summarised in Table 1.

Vineyard A

In a vineyard of approximately 1 ha, two varieties were grown: Merlot (medium maturing, leaf under-surface glabrous to slightly pubescent with domatia at the conjunction of the main veins and low hair density along the veins); and Verduzzo (late maturing, leaf under-surface pubescent with domatia at the conjunction of the main veins and high hair density along the veins). The ratio between the Merlot and Verduzzo areas was approximately 6:1, and the varieties were not interplanted. In samplings carried out one year before the experiments, moderate populations (peaks of 1–3 motile forms per leaf) were recorded of *Panonychus ulmi* (Koch), *Eotetranychus carpini* (Oudemans) and *A. andersoni*. In February 1989, *T. pyri* and *K. aberrans* were released by using two-year old branches collected from experimental vineyards. Approximately 100 *T. pyri* or *K. aberrans* overwintered females were released per plant; this number was estimated using values obtained from samplings previously carried out on the branches. This method proved to be more successful than releasing the predators in spring (Duso, 1989; Duso *et al.*, 1991).

In this experiment, three geographical strains of *T. pyri* and two of *K. aberrans* were released. Since the strains were not found to differ during the first years, only results of *K. aberrans*-Negrar and *T. pyri*-Montagnana are reported here. Populations of mites (mainly Tetranychidae, Eriophyidae, Tydeidae, Phytoseiidae and Stigmaeidae) and predatory insects were monitored in treatment plots characterized

Table 1. Characteristics of experimental design

Released species	Vineyard	Native species	Variety	Leaf under-surface
<i>T. pyri</i>	A	<i>A. andersoni</i>	Verduzzo	pubescent
<i>K. aberrans</i>			Merlot	glabrous
<i>T. pyri</i>	B	<i>P. finitimus</i>	Prosecco	pubescent
<i>K. aberrans</i>			Riesling	glabrous

by phytoseiid releases, and in the controls, where phytoseiids were not released. Each plot consisted of 18 plants (three replications, six plants per replicate).

Samples of 18 leaves per plot (one leaf per plant) were collected every 1–2 weeks from 1989 to 1991. The leaves were taken from the middle of the shoots, usually from the third to the eighth leaf and immediately examined in the laboratory under a binocular microscope to assess the density of different mite species. Phytoseiid mites were mounted on slides, in Hoyer's medium, and examined under a phase contrast microscope. Specific literature (Chant, 1958, 1959) and slides containing juveniles of vineyard-collected phytoseiids, previously identified by taxonomists, were consulted for the identification of the phytoseiid species. As the variation in leaf area among grape varieties could affect phytoseiid densities found, the average leaf surfaces of the two varieties were measured (LI-COR area meter), in total 50 leaves per variety. Since no significant difference was found, the data are expressed as numbers of active forms per leaf. Numbers of *Calepitrimerus vitis* (Nalepa) were difficult to assess over the entire leaf area. As their distribution was observed to be rather homogeneous, 5 sections of approximately 1 cm² on different positions of the leaf blade were explored under a binocular microscope (25×), and data are expressed as numbers of active forms per 5 cm² of leaf.

Only fungicides considered harmless to phytoseiids were used (copper oxychloride and wettable sulphur, 2000 g of a.i./ha and 800 g of a.i./ha, respectively). Neither insecticides nor acaricides were used.

Vineyard B

In a vineyard of approximately 2 ha, three varieties were cultivated: Riesling (medium maturing, leaf under-surface glabrous to slightly pubescent with domatia at the conjunction of the main veins, and low hair density along the veins); Prosecco (late maturing, leaf under-surface pubescent with domatia at the conjunction of the main veins and high hair density along the veins); and Cabernet Sauvignon (medium maturing, leaf under-surface slightly more pubescent than that of Riesling). The vineyard area was approximately equally divided between the three varieties, which were not interplanted. Only Riesling and Prosecco were taken into consideration in the present study because of their different leaf under-surface.

During spring 1989, the vineyard was heavily infested by eriophyids, but phytoseiids were rare. Therefore, in February 1990, *T. pyri* and *K. aberrans* were released by using the same procedures as in vineyard A. Surprisingly, at sprouting the same year, moderate densities of *P. finitimus* occurred on both varieties. Apparently, this predator immigrated to the vineyard in late summer of the previous year. Its occurrence rendered possible a comparison of the results of *K. aberrans* and *T. pyri* releases in a vineyard colonized by a predatory species (*P. finitimus*) previously involved in release failures. Populations of mites (mainly Tetranychidae and Phytoseiidae) and predatory insects were monitored in treatment plots characterized by

phytoseiid releases and in the controls, where phytoseiids were not released. Each plot consisted of 18 plants (two replications, nine plants per replicate). Samplings were carried out from 1990 to 1992, usually every two weeks, by observing 18 leaves per plot (one leaf per plant). The data are expressed as numbers of active forms per leaf.

Only fungicides considered harmless to phytoseiids were used (copper oxychloride, phenylamides and wettable sulphur (2000 g of a.i./ha, 200 g of a.i./ha and 800 g of a.i./ha, respectively). Neither insecticides nor acaricides were used.

Statistical analyses

The data from each experiment were analysed across years using the REPEATED option of Proc GLM of SAS (SAS Institute, 1989) with a two-way analysis of variance (year, treatment) considering the date as a repeated measure. Treatment variance (d.f. = 2) was split into two orthogonal contrasts considering control vs. release treatments (d.f. = 1) and *K. aberrans* release vs. *T. pyri* release (d.f. = 1). Since interactions between years and treatments were always significant, the data were analysed year by year with a one-way analysis of variance. The means were separated by using the option REGWG of SAS, and the level of significance was $\alpha = 0.05$. For a synthetic presentation of the results, the discussion focuses on the analysis of contrasts. Before carrying out an ANOVA, logarithmic transformation, i.e. $\log(y + 1)$, was applied to the dependent variable (mites per leaf).

Results

Population dynamics in vineyard A

On Merlot, both *E. carpini* and *P. ulmi* were recorded, whereas the former species was largely dominant on Verduzzo. Among predatory mites, *A. andersoni* and *Zetzellia mali* (Ewing) occurred naturally on both varieties.

In the first year of experiments, tetranychids were more abundant in Verduzzo control plots than in Merlot control plots, while *A. andersoni* showed an opposite trend in late summer (Figs 1A, 2A). *Zetzellia mali* was recorded at low levels and mainly on Verduzzo. One year later, the levels reached by the tetranychid and phytoseiid populations in Verduzzo and Merlot control plots were similar to those of the previous year (Figs 1A, 2A). In mid-summer, eriophyids and stigmæids were recorded more frequently on Verduzzo than on Merlot. In the third year, spider mites reached only low densities, but phytoseiids persisted probably because of rust mite abundance (Figs 1A, 2A). On Verduzzo, *A. andersoni* was gradually displaced by *K. aberrans* and *T. pyri* migrating from adjacent release plots (Fig. 3). *Zetzellia mali* numbers increased in late summer.

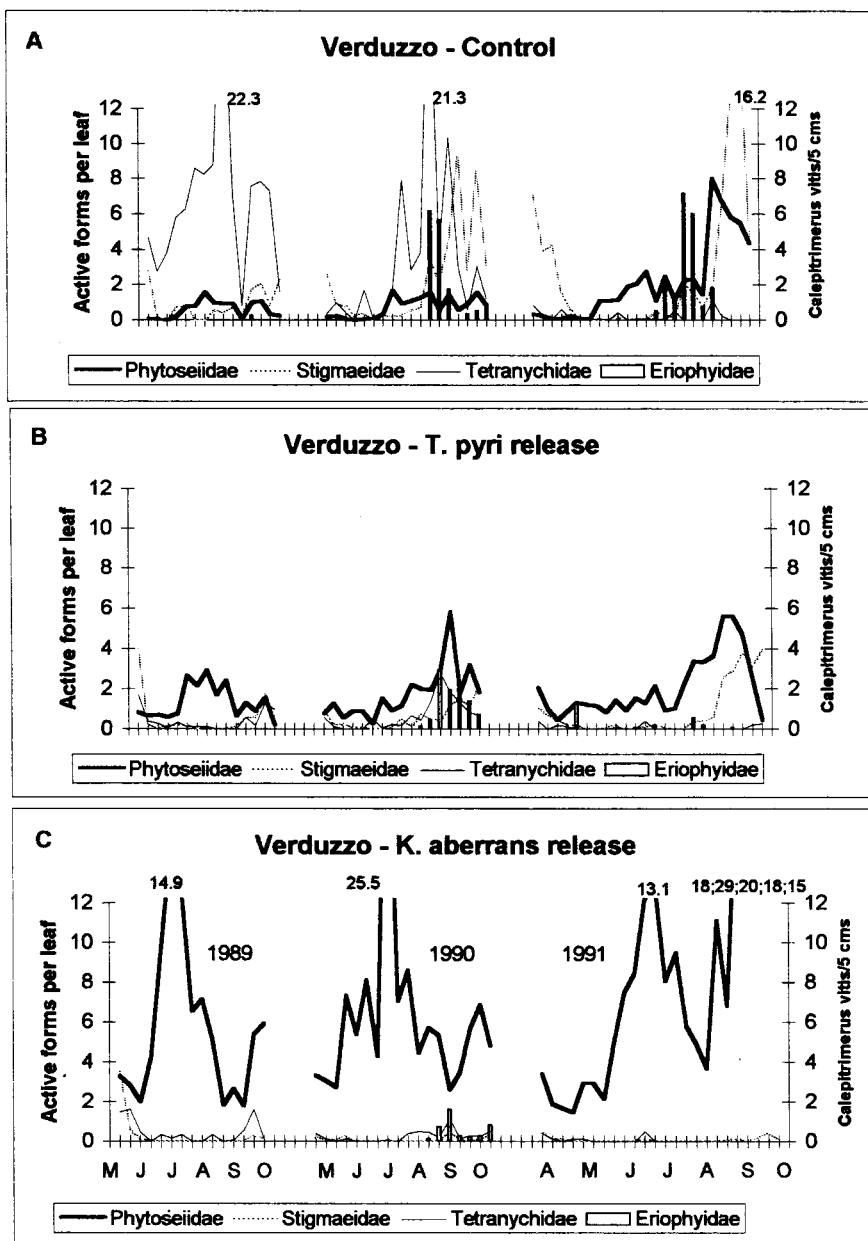


Figure 1. Population dynamics of Phytoseiidae, Stigmaeidae, Tetranychidae and Eriophyidae on different Verduzzo treatments (control, *T. pyri* release, *K. aberrans* release) during 1989–1991.

In the *T. pyri* release plots, spider mites occurred at low to moderate levels on both varieties. Phytoseiids appeared to be more abundant on Verduzzo than on Merlot

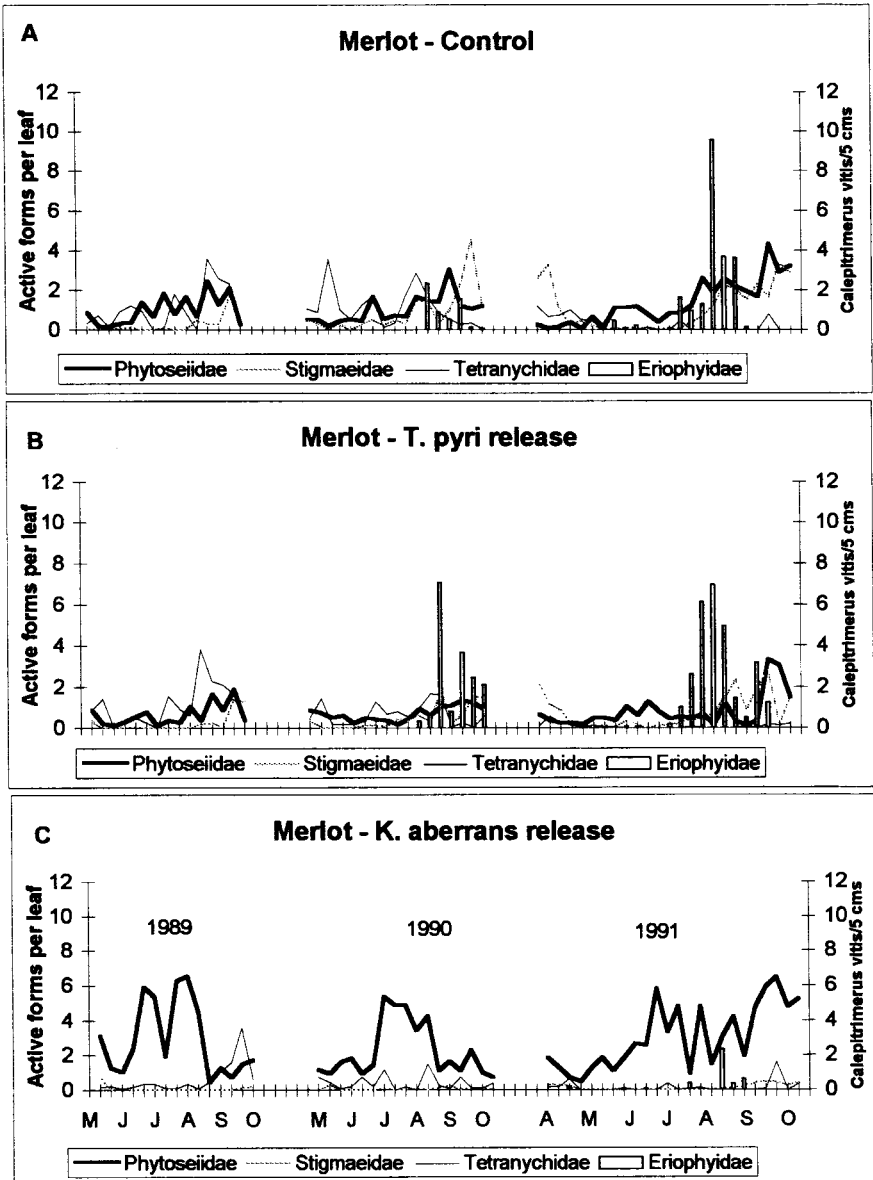


Figure 2. Population dynamics of Phytoseiidae, Stigmaeidae, Tetranychidae and Eriophyidae on different Merlot treatments (control, *T. pyri* release, *K. aberrans* release) during 1989–1991.

while the occurrence of spider mites was similar or occasionally slightly higher on the latter variety (Figs 1B, 2B). Differences in the phytoseiid composition on the two varieties were found constantly throughout the three-year study. In particular, *T.*

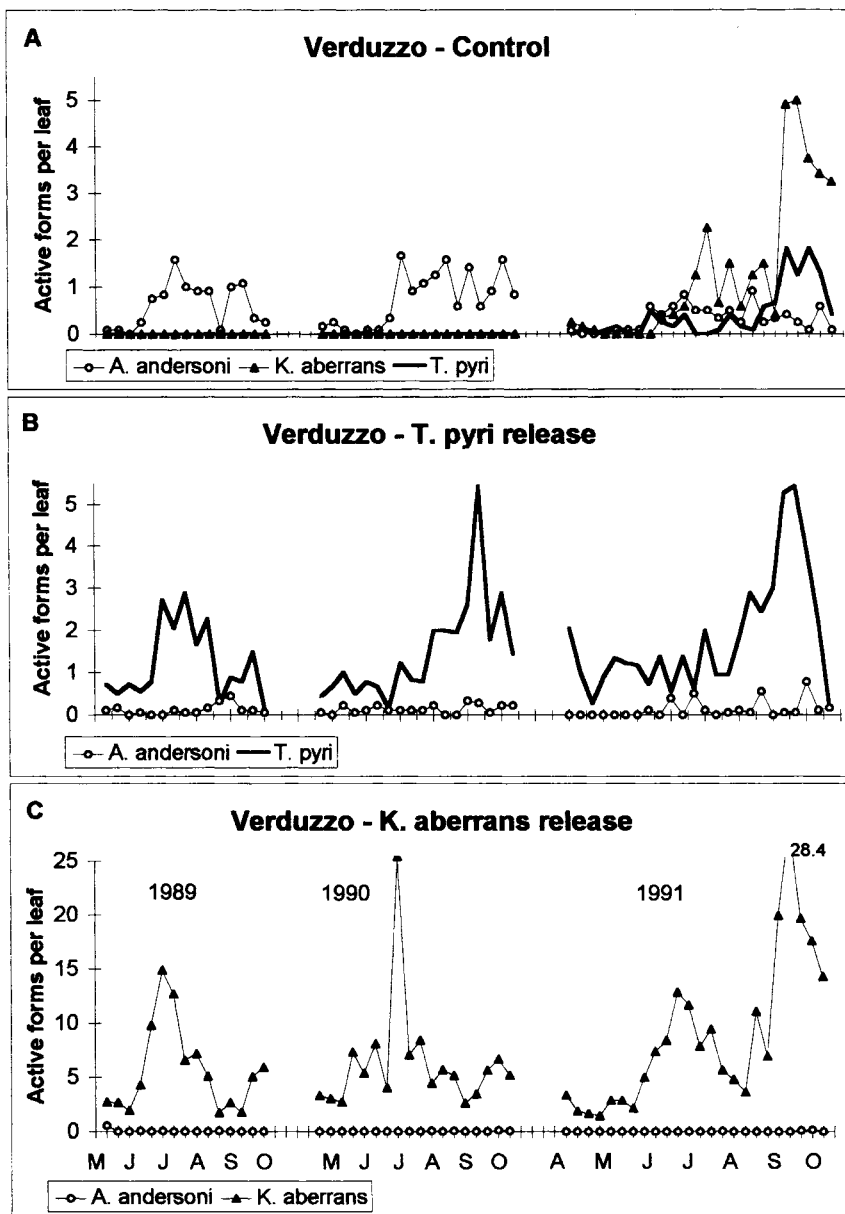


Figure 3. Population dynamics of *A. andersoni*, *K. aberrans* and *T. pyri* on different Verduzzo treatments (control, *T. pyri* release, *K. aberrans* release) during 1989–1991.

pyri largely dominated *A. andersoni* on Verduzzo (Fig. 3), while the two species fluctuated without any evident dominance on Merlot, with the exception of the third year, when *A. andersoni* became more important (Fig. 4). *Calepitrimerus vitis* was

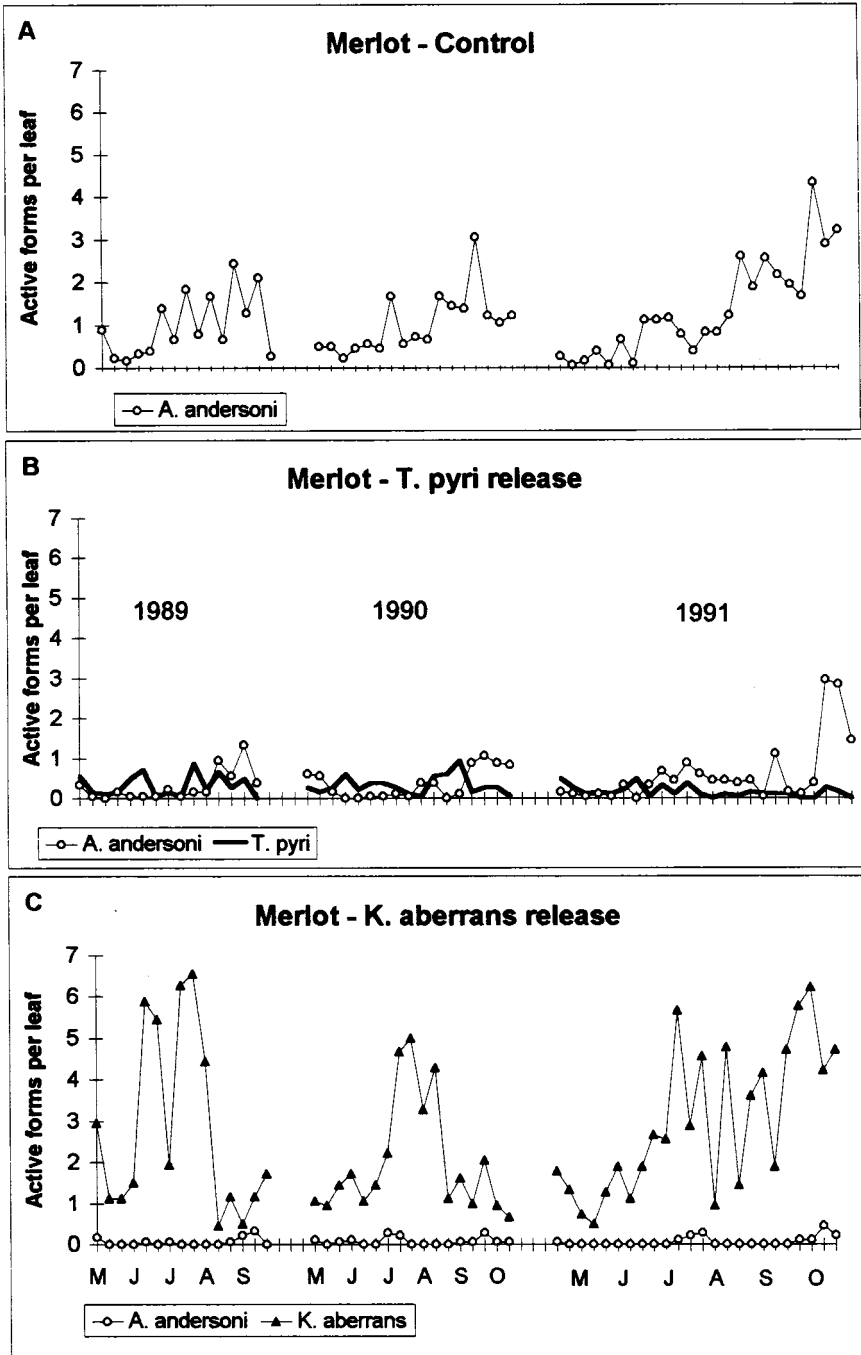


Figure 4. Population dynamics of *A. andersoni*, *K. aberrans* and *T. pyri* on different Merlot treatments (control, *T. pyri* release, *K. aberrans* release) during 1989–1991.

found more frequently and reached higher densities on Merlot than on Verduzzo while *Z. mali* numbers were similar (Figs 1B, 2B).

In the *K. aberrans* release plots, spider mite populations fluctuated at low levels throughout the three-year study, and *K. aberrans* reached higher densities on Verduzzo than on Merlot during the entire period (Figs 1C, 2C). A comparative analysis of phytoseiid composition showed that *K. aberrans* displaced *A. andersoni* completely on both varieties (Figs 3 and 4). *Calepitrimerus vitis* and *Z. mali* were seldom found on the two varieties (Figs 1C, 2C).

The effect of phytoseiid releases on the mite complex in vineyard A (1989–1991)

Data regarding tetranychids (*P. ulmi* and *E. carpini*), eriophyids (*C. vitis*), phytoseiids (*K. aberrans*, *T. pyri*, *A. andersoni*) and stigmatids (*Z. mali*) were analysed separately by comparing three treatments: controls, *T. pyri* release, and *K. aberrans* release.

Tetranychids (*P. ulmi* and *E. carpini*): The analysis across the years, carried out on Merlot, revealed that the effects of year and treatment were highly significant ($F_{2,153} = 48.65$ and $F_{2,153} = 7.20$, respectively, $P < 0.001$), and that their interaction was significant, too ($F_{4,153} = 3.08$, $P = 0.0179$). Spider mite populations were reduced ($F_{1,153} = 6.67$, $P = 0.0107$) by phytoseiid releases and, in particular, the *K. aberrans* release was more effective than the *T. pyri* release ($F_{1,153} = 7.72$, $P = 0.0061$).

In the same variety and during 1989, there were no differences between the control and release plots ($P = 0.7086$), but *K. aberrans* was seen to reduce spider mite densities more effectively than *T. pyri* ($F_{1,51} = 4.62$, $P = 0.0364$). In 1990, differences between the control and release plots were highly significant ($F_{1,51} = 13.80$, $P = 0.0005$), whereas those between *K. aberrans* and *T. pyri* releases were less so ($F_{1,51} = 3.95$, $P = 0.0522$). In 1991, the lack of differences could have been caused by the decrease in spider mite densities.

On Verduzzo, the effects of year, treatment and their interaction were highly significant ($F_{2,153} = 91.82$, $P < 0.0001$; $F_{2,153} = 152.03$, $P < 0.0001$; and $F_{4,153} = 46.37$, $P < 0.0001$, respectively). Spider mites were controlled to a large extent on phytoseiid release vines ($F_{1,153} = 302.45$, $P < 0.0001$), and their numbers were no different in *K. aberrans* or *T. pyri* release plots ($P = 0.2066$). The ability of phytoseiid releases to reduce tetranychid densities was found consistently in the experimental period, 1991 included ($F_{1,51} = 9.10$, $P = 0.0040$), when phytophagous mites were rare.

Calepitrimerus vitis: Concerning Merlot, the effects of year, treatment and their interaction were highly significant ($F_{2,153} = 49.95$, $P < 0.0001$; $F_{2,153} = 41.29$, $P < 0.0001$; and $F_{4,153} = 12.57$, $P < 0.0001$, respectively). Eriophyid densities were not significantly reduced by release treatments ($P = 0.7273$), but the *K. aberrans* release was more effective than the *T. pyri* release ($F_{1,153} = 82.47$, $P < 0.0001$). This

observation was made during 1990 and 1991 ($F_{1,51} = 69.18$ and $F_{1,51} = 27.90$, $P < 0.0001$), as rust mites were rare in the first year.

The effects of year, treatment and their interaction were highly significant, even on Verduzzo ($F_{2,153} = 39.38$, $P < 0.0001$; $F_{2,153} = 23.41$, $P < 0.0001$; and $F_{4,153} = 5.93$, $P < 0.0001$). In contrast to the situation observed on Merlot, phytoseiid releases significantly reduced rust mite numbers ($F_{1,153} = 42.12$, $P < 0.0001$), and the results obtained with the *K. aberrans* and *T. pyri* releases did not differ ($P = 0.1028$).

Amblyseius andersoni: On Merlot, the effects of year, treatment and their interaction were significant ($F_{2,153} = 8.86$, $P < 0.001$; $F_{2,153} = 242.09$, $P < 0.0001$; and $F_{4,153} = 2.08$, $P = 0.0067$). *Amblyseius andersoni* was more abundant in the control than in the release plots ($F_{1,153} = 280.19$, $P < 0.0001$) and, among the latter, more in the *T. pyri* release plots than in *K. aberrans* plots ($F_{1,153} = 204$, $P < 0.0001$). These results were confirmed during all three experimental years.

On Verduzzo, the effects of year, treatment and their interaction were significant ($F_{2,153} = 8.45$, $P < 0.0001$; $F_{2,153} = 270.33$, $P < 0.0001$; and $F_{4,153} = 8.83$, $P < 0.0001$, respectively). *Amblyseius andersoni* was recorded in lower densities on the release plants than on the controls ($F_{1,153} = 222.13$, $P < 0.0001$), and the predator was less abundant in the *K. aberrans* plots than in the *T. pyri* ones ($F_{1,153} = 318.54$, $P < 0.0001$). However, this trend was not constant throughout the experimental period. Differences between the two release treatments were found in 1990 ($F_{1,51} = 6.03$, $P = 0.0175$) and 1991 ($F_{1,51} = 7.76$, $P = 0.0075$), but not in 1989 ($F_{1,51} = 2.82$, $P = 0.0993$).

Zetzellia mali: On Merlot, the effects of year, treatment and their interaction were highly significant ($F_{2,153} = 16.54$, $P < 0.0001$; $F_{2,153} = 52.37$, $P < 0.0001$; and $F_{4,153} = 6.24$, $P < 0.0001$). *Zetzellia mali* was more abundant in the controls than in the release plots ($F_{1,153} = 66.06$, $P < 0.0001$). Concerning the latter, stigmæids reached lower densities in *K. aberrans* plots than in *T. pyri* plots ($F_{1,153} = 38.69$, $P < 0.0001$). When analysis was conducted across the years, the results obtained on Verduzzo were quite similar. The effects of year, treatment and their interaction were also significant ($F_{2,153} = 13.39$, $P < 0.0001$; $F_{2,153} = 253.62$, $P < 0.0001$; and $F_{4,153} = 18.16$, $P < 0.0001$, respectively), and stigmæids were recorded more frequently in the control than in the release plots ($F_{1,153} = 447.59$, $P < 0.0001$). In accordance with the previous situation, *Z. mali* densities were reduced more by *K. aberrans* than by *T. pyri* ($F_{1,153} = 59.64$, $P < 0.0001$).

However, when these effects were analysed year by year, some interesting differences between the varieties were found. On Merlot and during 1989, *Z. mali* numbers recorded in the control plots were not significantly different from those observed in the release plots ($P = 0.1665$), while the effect of predator releases was clear in 1990 and 1991 ($F_{1,51} = 51.41$ and $F_{1,51} = 22.97$, $P < 0.0001$). In *K. aberrans* plots, *Z. mali* densities were significantly lower ($P < 0.001$) than on *T. pyri* plots during the three-year period. Concerning Verduzzo, the effects of predator releases were highly significantly different ($P < 0.0001$) during the three years. The differences

between *K. aberrans* and *T. pyri* release plots were smaller in 1989 ($F_{1,51} = 4.15$, $P = 0.0468$) than in 1990 and 1991 ($F_{1,51} = 20.87$ and $F_{1,51} = 39.56$, $P < 0.0001$).

Kampimodromus aberrans: Concerning Merlot, the effects of year, treatment and their interaction were significant ($F_{2,153} = 3.87$, $P = 0.0277$; $F_{2,153} = 659.42$, $P < 0.0001$; and $F_{4,153} = 3.67$, $P = 0.0069$, respectively). *Kampimodromus aberrans* successfully colonized the release plots, but was never found in the remaining plots.

The situation was different on Verduzzo where *K. aberrans* moved into non-release plots, especially during 1991. In the analysis across the years, the effects of year and treatment were highly significant ($F_{2,153} = 16.36$ and $F_{2,153} = 652.30$, $P < 0.0001$), and their interaction was also significant ($F_{4,153} = 5.80$, $P = 0.0002$). The predator reached higher levels ($F_{1,153} = 1294.51$, $P < 0.0001$) in its respective release plots. The *K. aberrans* numbers recorded in the control were higher than those observed in the *T. pyri* release plots ($F_{1,153} = 10.09$, $P = 0.0018$). Analysis by year showed that the latter result was obtained during 1991 ($F_{1,51} = 21.99$, $P < 0.0001$).

Typhlodromus pyri: On Merlot, the effects of year and treatment were significant ($F_{2,153} = 4.78$, $P = 0.0097$ and $F_{2,153} = 103.89$, $P < 0.0001$), as also their interaction ($F_{4,153} = 4.78$, $P = 0.0012$). The predator was found only in its respective release plots.

The effects of year, treatment and their interaction were highly significant even on Verduzzo ($F_{2,153} = 20.12$, $P < 0.0001$; $F_{2,153} = 466.88$, $P < 0.0001$; and $F_{4,153} = 6.36$, $P < 0.0001$, respectively). In 1991, *T. pyri* was also recorded in the control plots and less frequently in the *K. aberrans* release plots ($F_{1,51} = 19.08$, $P < 0.0001$).

Population dynamics in vineyard B

In the control plots, *P. ulmi* was recorded in low densities (Figs 5A, 6A). Among the phytoseiids, *P. finitimus* was generally dominant while *T. pyri* and *Amblyseius finlandicus* (Oud.) were found in low numbers. Phytoseiids (i.e., *P. finitimus*) appeared to be more abundant on Prosecco than on Riesling, especially in the second and third experimental years (Figs 5A, 6A).

Low levels of *T. pyri* were recorded in the respective release plots, where *P. finitimus* dominated on both varieties. On several dates the latter predator reached higher densities on Prosecco than on Riesling (Figs 5B, 6B).

Kampimodromus aberrans successfully colonized its respective release plots, displacing native predators (Figs 5C, 6C). On Riesling, *K. aberrans* and *P. finitimus* populations coexisted during the first year, but the latter species was displaced one year later (Fig. 6C). In contrast, on Prosecco, *K. aberrans* reached only low densities in the first year, while its importance increased in the second and especially in the third season when the predator became dominant over *P. finitimus* (Fig. 5C). In

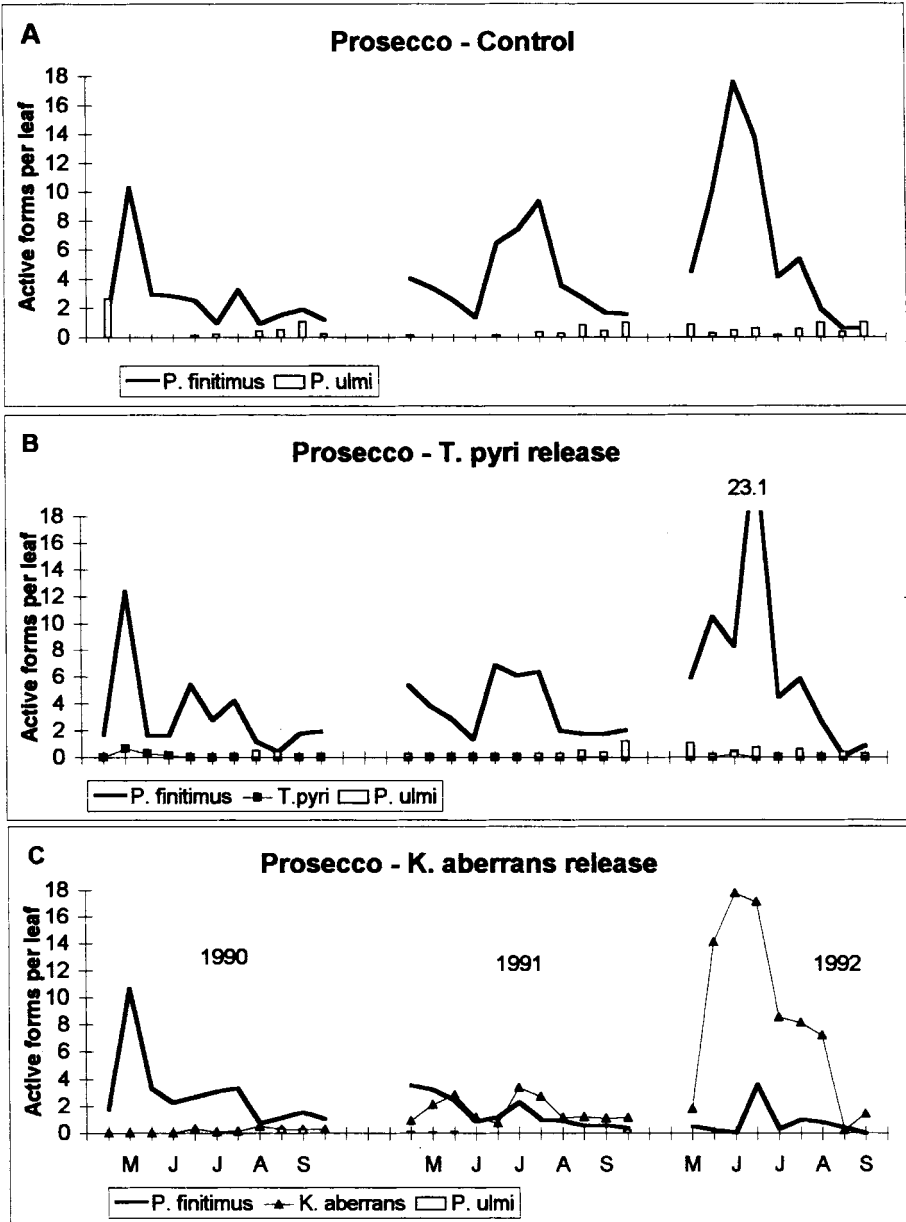


Figure 5. Population dynamics of *K. aberrans*, *P. finitimus*, *T. pyri* and *P. ulmi* on different Prosecco treatments (control, *T. pyri* release, *K. aberrans* release) during 1990–1992.

the last year, *K. aberrans* population dynamics showed a similar trend on both varieties.

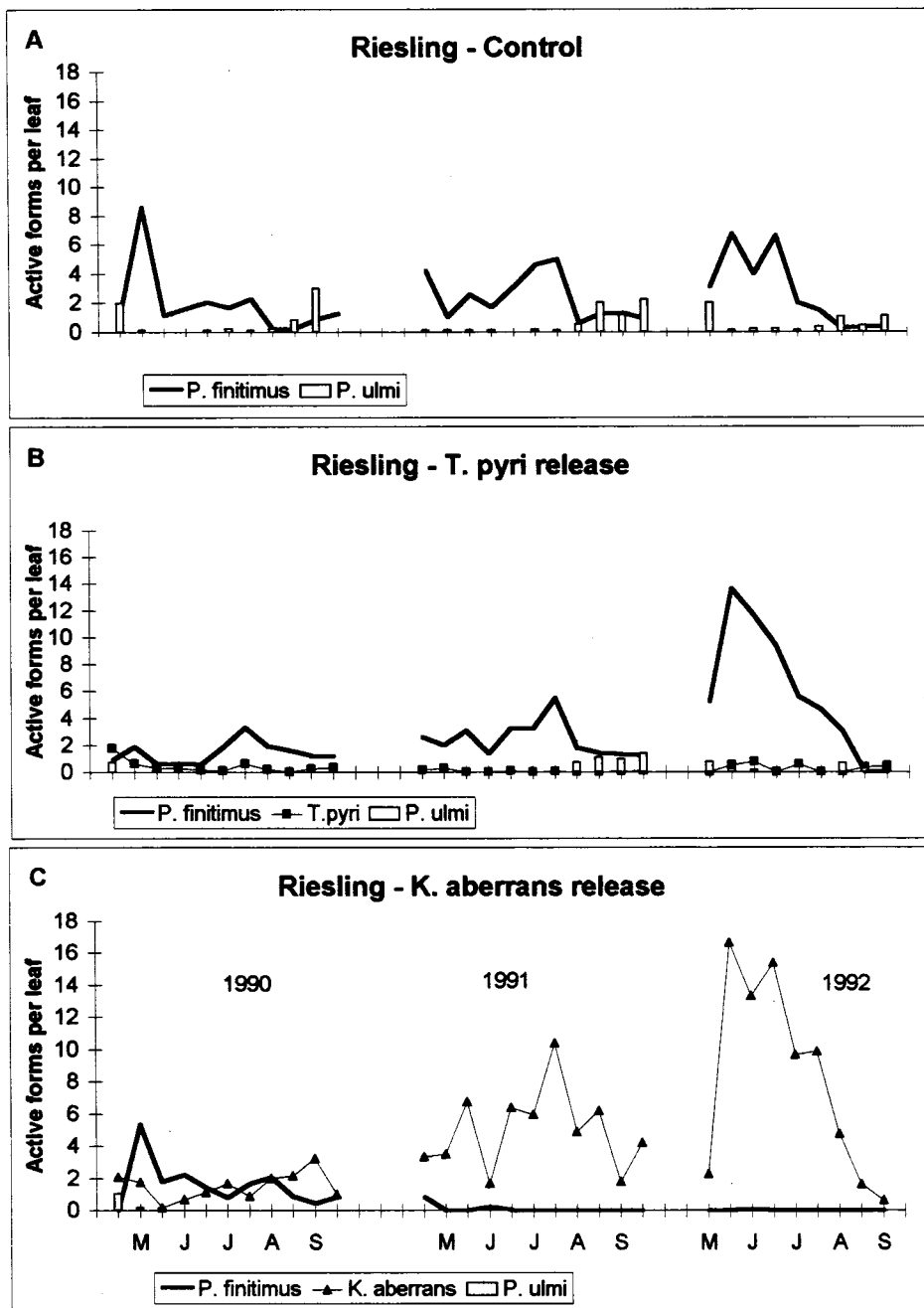


Figure 6. Population dynamics of *K. aberrans*, *P. finitimus*, *T. pyri* and *P. ulmi* on different Riesling treatments (control, *T. pyri* release, *K. aberrans* release) during 1990–1992.

The effect of phytoseiid releases on the mite complex of vineyard B (1990–1992)

Data regarding tetranychids (*P. ulmi*) and phytoseiids (*K. aberrans*, *T. pyri*, *P. finitimus*) were analysed separately by comparing three treatments: controls, *T. pyri* release and *K. aberrans* release.

Panonychus ulmi: The overall analysis carried out on Riesling showed that the effects of year, treatment and their interaction were highly significant ($F_{2,153} = 20.65$, $P < 0.0001$; $F_{2,153} = 148.83$, $P < 0.0001$; and $F_{4,153} = 15.06$, $P < 0.0001$, respectively). Spider mites were significantly reduced by phytoseiid releases ($F_{1,153} = 268.72$, $P < 0.0001$), and the *K. aberrans* release was more effective than the *T. pyri* release ($F_{1,153} = 28.93$, $P < 0.0001$).

In the year-by-year analysis, differences among treatments or between the controls and phytoseiid releases were always significant. During the first experimental year there were no differences between *K. aberrans* and *T. pyri* releases ($P = 0.7224$), while the higher effectiveness of *K. aberrans* was clear in 1991 ($F_{1,51} = 29.84$, $P < 0.0001$) and 1992 ($F_{1,51} = 10.87$, $P = 0.0018$).

On Prosecco, the effects of year and treatment and their interaction were also highly significant ($F_{2,153} = 15.24$, $P < 0.0001$; $F_{2,153} = 37.89$, $P < 0.0001$; and $F_{4,153} = 6.95$, $P < 0.0001$). Spider mites reached lower levels in phytoseiid release plots than in the controls ($F_{1,153} = 47.30$, $P < 0.0001$), and the *K. aberrans* release was seen to be more effective than the *T. pyri* release ($F_{1,153} = 28.48$, $P < 0.0001$). However, also in this case, the year-by-year analysis revealed no differences between the predator releases in the first year, but statistically significant effects in the remaining two years ($F_{1,51} = 9.39$, $P = 0.0035$ and $F_{1,51} = 21.79$, $P < 0.0001$). This is probably due to the low numbers of *T. pyri* on this variety in 1991 and 1992.

Phytoseius finitimus: The effects of year, treatment and their interaction were highly significant on Riesling ($F_{2,153} = 17.33$, $P < 0.0001$; $F_{2,153} = 301.88$, $P < 0.0001$; and $F_{4,153} = 102.36$, $P < 0.0001$). At the same time, *P. finitimus* was more abundant in the control than in the release plots ($F_{1,153} = 60.15$, $P < 0.0001$) and, among the latter, more abundant in the *T. pyri* release plots than in the *K. aberrans* plots ($F_{1,153} = 543.62$, $P < 0.0001$).

The year-by-year analysis showed that differences between the control and release treatments were not significant ($P = 0.7223$) in 1990 because of the moderate impact of released predators, but significant in 1991 and 1992 ($F_{1,51} = 65.66$ and $F_{1,51} = 44.59$, $P < 0.0001$) when *K. aberrans* displaced *P. finitimus*.

The effects of year, treatment and their interaction were highly significant even on Prosecco ($F_{2,153} = 5.16$, $P < 0.001$; $F_{2,153} = 210.21$, $P < 0.0001$; and $F_{4,153} = 67.33$, $P < 0.0001$). *Phytoseius finitimus* reached higher densities in the control than in the release plots ($F_{1,153} = 89.44$, $P < 0.0001$) and in the *T. pyri* release plots than in the *K. aberrans* plots ($F_{1,153} = 330.99$, $P < 0.0001$). Native predatory mites were not significantly affected in the release plots in the first experimental year ($P = 0.1804$).

while a significant reduction in their numbers was recorded in 1991 and 1992 ($F_{1,51} = 43.32$, and $F_{1,51} = 135.22$, $P < 0.0001$).

In 1990, the occurrence of *P. finitimus* in the release plots showed no differences on either variety. Later, *P. finitimus* densities were reduced more in *K. aberrans* than in *T. pyri* plots both on Riesling ($F_{1,51} = 171.03$, $P < 0.001$ in 1991, and $F_{1,51} = 448.90$, $P < 0.001$ in 1992) and Prosecco ($F_{1,51} = 45.25$, $P < 0.001$ in 1991, and $F_{1,51} = 201.67$, $P < 0.001$ in 1992).

Kampimodromus aberrans. The effects of year, treatment and their interaction were highly significant on Riesling ($F_{2,153} = 203.48$, $P < 0.0001$; $F_{2,153} = 1907.80$, $P < 0.0001$; and $F_{4,153} = 131.10$, $P < 0.0001$) and on Prosecco ($F_{2,153} = 494.77$, $P < 0.0001$; $F_{2,153} = 1525.14$, $P < 0.0001$; and $F_{4,153} = 461.58$, $P < 0.0001$). During the three-year study, the predator reached significantly higher levels in its respective release plots ($F_{1,153} = 3804.8$ and $F_{1,153} = 3050.28$, $P < 0.0001$, on Riesling and Prosecco, respectively). Concerning the occurrence of *K. aberrans* in the remaining treatments, there were no differences on Prosecco ($P = 0.9636$), while they were found on Riesling ($F_{1,153} = 11.43$, $P = 0.0009$), especially during 1992, when *K. aberrans* was recorded more frequently in the *T. pyri* release plots than in the controls ($F_{1,51} = 27.15$, $P < 0.0001$).

Typhlodromus pyri: On Riesling, the effects of year, treatment and their interaction were highly significant ($F_{2,153} = 6.11$, $P = 0.0028$; $F_{2,153} = 37.54$, $P < 0.0001$; and $F_{4,153} = 5.42$, $P = 0.0004$, respectively). The predator occurred in higher densities ($F_{1,153} = 74.95$, $P < 0.0001$) in its respective release plots, while there were no differences regarding its occurrence between the remaining treatments ($P = 0.7101$). This trend was confirmed during the three seasons.

In contrast, on Prosecco, the effects of year and treatment were not significant ($P = 0.0611$ and $P = 0.1589$) and *T. pyri* numbers in the respective release plots were not higher ($P = 0.1857$) than those observed in the remaining treatments. During 1990, *T. pyri* occurred in higher densities ($F_{1,51} = 9.09$, $P = 0.0040$) in its respective release plots, but no differences were found in subsequent years. At the same time, in the three-year analysis, there were no differences between *T. pyri* populations recorded in the controls or in the *K. aberrans* plots owing to their low levels. Slight differences ($P = 0.0573$) were recorded in 1992 when *T. pyri* was observed more frequently in the controls.

Discussion

Mite population dynamics on different grape varieties

In the control plots of vineyard A, spider mites reached high densities on the variety with pubescent leaf under-surface, i.e. Verduzzo. Eriophyid populations were also larger on Verduzzo during 1990, and reached a comparable size in the subsequent

year. Among the phytoseiids, *A. andersoni* appeared to be most abundant and persistent on the variety with a slightly pubescent leaf under-surface, i.e. Merlot. In contrast, stigmatheids were most abundant on Verduzzo.

In the *T. pyri* release plots, spider mites were reduced to low levels and *C. vitis* populations persisted longer on Merlot than on Verduzzo. The latter variety was colonized by relatively large numbers of *T. pyri*, and *Z. mali* reached comparable densities.

Coinciding with the introduction of *K. aberrans*, all other mite species declined in numbers, while larger populations of the released predator were found on Verduzzo.

The three-year study showed that *T. pyri* and *K. aberrans* populations reached larger numbers on the variety characterized by pubescent leaves, i.e. Verduzzo, than on other varieties. This trend, which was observed independently of prey abundance, is consistent with previous observations (Duso, 1992; Camporese and Duso, 1996). At the same time, *A. andersoni* was recorded more frequently in Merlot plots (especially in the first season) confirming preliminary observations on the preference of this predator for varieties with glabrous or slightly pubescent leaf under-surface (Camporese and Duso, 1996; Duso and Ren, 1997).

In the second vineyard, the original mite complex was restricted to *P. ulmi* and *P. fnitimus*. *P. ulmi* reached low levels on both varieties, whereas *Phytoseius fnitimus* appeared to be more abundant on the variety with pubescent leaf under-surface, i.e. Prosecco, as also observed in previous investigations (Rasmy and El-Banhawy, 1974; Castagnoli and Liguori, 1985; Duso and Moretto, 1994).

The results of both experiments showed significant differences in the relative abundance of mite species and of phytoseiids in particular, on different varieties within the same vineyards. The varieties were not interplanted so the cause of this effect cannot be definitely ascertained. However, some trends were repeated over the years, suggesting a potential effect of variety, and presumably of leaf morphology, on mite population dynamics and species interactions. Moreover, recent studies, based on a randomized treatment design, have confirmed that leaf hairiness has a positive effect on the colonization ability of *K. aberrans* and *T. pyri* (C. Duso, unpubl. data).

Does grape variety affect interspecific competition?

The year-by-year analysis performed on data from vineyard A revealed that the effect of phytoseiid releases on phytophagous mite abundance varied among varieties. On Verduzzo, tetranychid densities were significantly reduced in the release treatments in the three experimental years while, on Merlot, this was only observed in 1990. The release of *K. aberrans* and *T. pyri* produced similar results for controlling spider mites on Verduzzo, while the *T. pyri* releases on Merlot were sometimes less effective than those of *K. aberrans*. The latter was observed especially during 1989,

when native predator populations (i.e. *A. andersoni* and *Z. mali*) persisted at higher densities in *T. pyri* plots than in those with *K. aberrans*. In contrast, on Verduzzo, the occurrence of *A. andersoni* and *Z. mali* was almost the same in *K. aberrans* and *T. pyri* release plots. In 1989, *T. pyri* population densities reached maximum values of almost three motile forms per leaf on Verduzzo and one motile form per leaf on Merlot.

In the second experimental year, eriophyid importance increased, and the impact of phytoseiid releases on their populations was different among varieties. On Merlot, eriophyid densities were not significantly reduced in the release plots considered together, but this result was due to the poor performance of the *T. pyri* release. In contrast, rust mite populations were effectively controlled in the Verduzzo release plots where *K. aberrans* and *T. pyri* obtained similar results. Native predator (*A. andersoni* and *Z. mali*) densities were reduced in the release plots of both varieties, and *K. aberrans* was confirmed to be more competitive than *T. pyri*. Population levels reached by *T. pyri* on Verduzzo exceeded five motile forms per leaf compared with one on Merlot.

Data from 1991 confirmed that the abilities of *K. aberrans* and *T. pyri* to reduce *C. vitis* populations were similar on Verduzzo, but different on Merlot. At the same time, native predators reached lower densities in *K. aberrans* plots than in *T. pyri* plots. Densities of the latter predator reached values of approximately five motile forms per leaf on Verduzzo and less than one on Merlot.

In terms of predation and interspecific competition, the results obtained by releasing *T. pyri* clearly differed for the two varieties. We suggest that their different leaf morphologies constitute a major factor causing this phenomenon. The relative hairlessness of Merlot leaves is known to be disadvantageous to *T. pyri* when prey is scarce (Duso, 1992), but, at the same time, this leaf feature seems to enhance colonization of its competitor, *A. andersoni* (Camporese and Duso, 1996; Duso and Ren, 1997).

In some situations, the results of interspecific competition between native predators (*A. andersoni* and *Z. mali*) and *T. pyri* differed among varieties, which thus represent a potential factor affecting the ability of *T. pyri* to control phytophagous mites. Data regarding *A. andersoni*-*T. pyri* interactions were particularly interesting as *T. pyri* displaced *A. andersoni* on Verduzzo, while the native predatory mite persisted at higher levels on Merlot where it became dominant in the last season. When *A. andersoni* was abundant, especially in spring and late summer, *T. pyri* densities declined. Recent laboratory studies have shown that interspecific competition between *A. andersoni* and *T. pyri* favours the former species: in the competition between these generalist predators, body size is considered to be of major importance, but other factors, such as prey and climate, could also be involved (Zhang and Croft, 1995; Croft and Croft, 1996; Croft *et al.*, 1996). Our results indicate that the physical surrounding of the predators is also important, since the outcome of

competition was apparently determined by leaf morphology. Interspecific competition with native predators mediated by leaf structures may represent one of the most important mechanisms affecting *T. pyri* success in vineyards and could explain the contrasting results obtained when releasing this predator. In contrast to *T. pyri*, interactions between *K. aberrans* and *A. andersoni* in vineyard A appeared not to be affected by variety. In conclusion, direct and indirect effects of leaf structure can be involved in *T. pyri* performance, but their relative importance is difficult to assess.

The different tetranychid levels observed in the two varieties, especially in the first experimental season, may constitute another factor improving the colonization of *T. pyri* on Verduzzo rather than on Merlot and could lead to its successful competition against *A. andersoni* and *Z. mali*. The influence of prey on mediating interspecific competition between predatory mites requires more study (Walde *et al.*, 1997).

In vineyard B, phytoseiid releases significantly reduced tetranychid densities on both varieties. The *K. aberrans* releases yielded more success than the *T. pyri* releases in 1991 and 1992 because *T. pyri* colonization failed. *Phytoseius fnitimus* populations were affected by phytoseiid releases on both varieties, but only *K. aberrans* was involved in a clear decline of the native predator.

Implications for the management of phytophagous and predatory mites in vineyards

In several cases phytophagous mites reached the highest levels in the control plots, thus demonstrating the positive role of phytoseiid releases. In vineyard A, a lack of numerical response by *A. andersoni* to high densities of *E. carpini* on Verduzzo was observed during two subsequent years. Tetranychids were less abundant in the Merlot control plots, suggesting a lower susceptibility of this variety to spider mites and/or a better performance by *A. andersoni* on slightly pubescent leaves. It should be mentioned that this predator responds to kairomones emitted by *E. carpini* and *P. ulmi* and, in the laboratory, both are optimal prey for *A. andersoni* (Duso and Camporese, 1991; C. Duso, unpublished data). The results confirm the low efficacy of *A. andersoni* on grape spider mites compared with that of other phytoseiids (Duso, 1989; Girolami *et al.*, 1992; Camporese and Duso, 1996), but they also point out that host plant characteristics should be considered more carefully when tetranychid–phytoseiid interactions are studied. The presence of eriophyids improved the persistence of *A. andersoni* on Merlot, confirming observations carried out in apple orchards (Strapazzon and Dalla Montà, 1988). Ad hoc studies may determine whether the presence of rust mites can enhance the potential of *A. andersoni* to control tetranychids in vineyards.

Stigmaeids reached higher densities when prey was abundant and in the presence of *A. andersoni*, but their numbers declined in *T. pyri* plots and especially in *K. aberrans* plots. The ability of the native predators (*Z. mali* and *A. andersoni*) to

reduce pest populations was lower in the Verduzzo control plots than in *K. aberrans* and *T. pyri* plots.

The results of experiments carried out in vineyard B confirmed the positive role of phytoseiid releases in controlling *P. ulmi*, but also stress the importance of inter-specific competition affecting the colonization of released predators. *Typhlodromus pyri* releases failed on varieties with unsuitable leaf morphology and when *P. finitimus* was present.

Kampimodromus aberrans was able to displace native phytoseiids, i.e. *A. andersoni* and *P. finitimus*, on grape varieties where the two species were relatively abundant. With respect to *K. aberrans*–*A. andersoni* interactions, previous data are confirmed (Duso, 1989; Duso and Pasqualetto, 1993; Camporese and Duso, 1996): namely that body size alone does not explain the outcome of interspecific competition, as *K. aberrans* is smaller than *A. andersoni* and *T. pyri*. Interactions between *K. aberrans* and *P. finitimus* have been studied only to a limited extent, as have the ecology and behaviour of *P. finitimus*. This species is becoming more widespread in some viticultural areas in Northern Italy, and its phenology is somewhat similar to that of *K. aberrans* as suggested in the present and in other studies. In previous experiments, *K. aberrans* was released in two vineyards where *E. carpini* constantly occurred at high densities despite the presence of *P. finitimus*. In the first year, releases appeared to be unsuccessful as *K. aberrans* populations were low and *P. finitimus* continued to persist (C. Duso, unpublished data). Therefore, observations were discontinued in these vineyards. It should be mentioned that the varieties in the two vineyards were characterized by pubescent leaf under-surface (Verduzzo and Raboso). In the present experiment, *K. aberrans* displaced *P. finitimus* two years after release on glabrous leaves and one year later on pubescent leaves. However, one year after this study samplings showed very low densities of *P. finitimus* in this vineyard whereas *K. aberrans* persisted. The predator decline, already observed in the third year, was not associated with any obvious factors. The recent experiments, in which *K. aberrans* was released in vineyards naturally colonized by *P. finitimus*, show that none of the predators became completely dominant in the short term. Therefore, long-term observations are needed before conclusions can be drawn concerning the results of interspecific competition between the two species.

Results of both experiments and of previous investigations (Duso and Pasqualetto, 1993) show that two to three years after its introduction, *K. aberrans* populations can colonize non-release plots. Factors that affect the successful colonization and dispersal of *K. aberrans* require specific studies (Duso *et al.*, 1997; Tixier *et al.*, 1998) in order to improve the use of this species in IPM.

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