Final Report

Special project

Investigation of the importance of *Neoseiulus idaeus* and *Typhlodromalus limonicus* as natural enemies of the cassava green mite

Institute for Plant Pathology and Plant Protection
University Gottingen DE
Department of Entomology
Germany

Cassava Program
International Center for Tropical Agriculture (CIAT)
Cali
Colombia

Project number 89 7860 3-01 110
Reporting period September 1991- August 1994

Prof Dr Hans-Michael Poehling
Dipl Ing Agr Andreas Gaigl

1995

FINAL REPORT

1 Cover page of project proposal

SPECIAL PROJECT PROPOSAL TO THE BUNDESMINISTERIUM FUR WIRTSCHAFTLICHE ZUSAMMENARBEIT (BMZ)

1 Name and address of joint applicants

Institut für Pflanzenpathologie
und Pflanzenschutz
der Georg-August-Universita t Gottingen
Entomologische Abteilung
Gottingen
Federal Republic of Germany

Cassava Program
Centro Internacional de Agricultura Tropical (CIAT)
Apartado Aereo 6713
Cali
Colombia

2 Title of research proposal

Investigation of the importance of *Neoseiulus idaeus* and *Typhlodromalus limonicus* as natural enemies of cassava green mite

2 Reporting period

September 1991 - August 1994

3 Duration of project

01 09 1991 - 31 08 1994

3 1 Location of project implementation

Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia

4 Objective-orientated summary of the project

In the 1970's the cassava green mite (CGM) *Mononychellus tanajoa* Bondar was accidentally introduced to Africa where it spread rapidly over the cassava belt from Mozambique through Zaire and the Central African Republic to the coast of West Africa The damages caused by this pest were devastating Yield losses reached 80% in dry years Controlling CGM with acaracides is economically and ecologically impractical under African conditions and a biological control strategy is more appropriate For this reason, the International Institute of Agriculture (IITA) and the International Center of Tropical Agriculture (CIAT), initiated in 1984 a biological control effort to search for efficient natural enemies in South America, where cassava and CGM are originated In Latin America ca 50 potential natural enemies of CGM were identified Since was, is not feasible to introduce all of them selection procedures were necessary

For the selection of natural enemies of CGM it is important to know their food preferences under field conditions In the present work we used two forms of analysis to study predation behaviour Polyacrylamide Gel Electrophoresis (PAGE) to analyze the gut contents of predators collected in the field and preference tests conducted in the laboratory and in the field

For the electrophoretical analyses we tested 10 enzymes to select the most promising staining method for mite enzymes Of these enzymes esterase yielded the clearest band patterns for the predators, their gut content and the prey species With this enzyme we identified 93% of field

collected tetranychid samples Because of poor esterase staining of the phytoseiids we could not identify more than 23% Despite of this limitation the high esterase activity of the prey species permitted the identification of gut contents of 50% of the analyzed samples We assume that the difficulties of the gut analysis were caused by the unknown time of the last food intake and the prey developmental stage, two factors that are unknown for samples collected in the field Another important limitation of this technique was the wide range of esterase activity of the various species This factor might have been responsible for the high fraction of unidentified phytoseiid samples However, electrophoresis of esterase isoenzymes provided an excellent means for discriminating species of the cassava acarine complex

The limitations of the electrophoretic analyses caused us to focus on host preference analyses with three selected phytoseiids *Typhlodromalus manihoti* Moraes[1](strains from Venezuela, Brazil and Colombia), *T limonicus* Garman & McGregor[1] and *Neoseiulus idaeus* Denmark & Muma We studied two strains of the latter species, one from Fonseca (Colombia) and the other from Petrolina (Brazil) Both have been shipped to Africa for release as natural enemies of CGM We offered CGM combined with other acarine prey, such as *M caribbeanae* McGregor, *Tetranychus urticae* Koch and *Oligonychus gossypii* Zacher, or non-acarine food items such as nymphs of *Frankliniella williamsi* Hood (thrips), honeydew-secreting puparia of *Aleurotrachelus socialis* Bondar (whitefly) and conidia of the cassava fungus *Oidium manihotis* Henn, to the predators under free-choice conditions

[1] The species *T manihoti* is synonymous with *T limonicus sensu lato* and *T limonicus* with *T limonicus sensu stricto* according to the new taxonomic classification of Moraes *et al* (1994)

Preliminary experiments showed the importance of feeding history on predation behaviour The predation behaviour of satiated predators was more variable than that of starved Furthermore, satiated phytoseiids killed more immature prey than starved predators All strains fed on all prey stages, however, the consumption of adults by *N idaeus* was extremely low The highest killing rate in all strains was observed when larvae were offered In these preliminary experiments, *T limonicus* was the most voracious species

The preference tests showed that all phytoseiid species fed on all offered mite species CGM and *M caribbeanae* were the preference of favourite prey for all predators On this prey type *T limonicus* showed outstanding predation efficiency and the highest fecundity The association of CGM with *T urticae* or *O gossypii* decreased the predation rate of all phytoseiid species *N idaeus* and *T manihoti* showed the highest oviposition rate on *T urticae*, whereas *T limonicus* reproduced best on pure *Mononychellus* spp combinations

Thrips was of outstanding importance among the alternative food items in the diet of *T manihoti* This species thrived on this prey even better than on the combination CGM - *M caribbeanae* In contrast, *N idaeus* showed poor consumption of thrips when CGM was abundant However, when CGM density decreased this phytoseiid species increased its consumption of thrips nymphs In the presence of honeydew secretion from whitefly puparia, *T limonicus* killed fewer protonymphs of CGM than in the other treatments The predation behaviour of the other phytoseiids was not significantly altered by the presence of honeydew The presence of the conidia of *O manihotis* had no influence on the consumption of CGM, however, *T*

limonicus maintained a low level of oviposition of one egg per day on this diet

An unknown virus disease caused a complete breakdown of the CGM greenhouse colony and made it necessary to replace this mite species with *M caribbeanae* in order to execute field experiments The results were characterized by significant differences between the replicates suggesting a variable dispersal activity of the predators *M caribbeanae* increased the density of all phytoseiid species and lowered variation among replicates The presence of *N idaeus* from Brazil was highly correlated with that of *T urticae* It is suggested that non-acarine food like honeydew or *O manihotis* had some benefits for some species, however, this hypothesis could not be supported In presence of honeydew, *T manihoti* maintained a relatively high density level When whitefly was combined with mite prey *N idaeus*, from Fonseca could recover to release density by the fourth evaluation date On cassava ash fungus, both *Typhlodromalus* species maintained a higher population density than *N idaeus*, indicating that the fungus was supplemental food item for these two species The treatments with thrips confirmed the results from the laboratory that this insect was an adequate prey item for *T manihoti*

5 Description of results

5 1 Electrophoretic analysis of gut content[2]

5 1 1 Experiments to improve electrophoretical gut analysis system

Biochemical gut analysis is a promising tool for the qualitative and quantitative determination of predator diet components Relative simple techniques can separate the proteins of the gut content in polyacrylamide gels (PAGE) Sensitive staining methods of the specific enzymes esterase are considered as a reliable method for their detection (Murray and Solomon, 1978, v d Geest and Overmeer, 1985) However, preliminary gut analyses showed that the esterase of some phytoseiid species (e g *N idaeus)* did not correspond to this method

Taxonomic studies on phytoseiids with electrophoretic methods performed at CIAT, indicated enzymes other than esterase can be used for identification of species (Cuellar, 1992) For this reason nine further enzymes were tested for their suitability as indicator of gut contents of mite predators, focussing on *N idaeus* (one of the phytoseiids with the lowest esterase activity), *T limonicus* and *T manihoti*

A short summary of about the characteristics of each enzyme is listed in Table 1 Species could be distinguished with various enzymes, such as esterase (EST), malate dehydrogenase (MDH),

[2] The major part of the description of the results of the electrophoretic studies was taken from Gaigl *et al* (submitted)

acid phosphatase (ACP), and malic enzyme (ME) ME and ACP also provided some information about gut contents

In the following part we show some examples of different staining procedures as tools for identification of species and gut contents Figs 1 show that the enzyme esterase permitted identification of prey in gut contents Discrimination of predator (*T manihoti*) and prey species (*M tanajoa* and *M caribbeanae*) was possible in this case The arrows indicate the marker band of each prey species The schematic illustration (Fig 1b) shows that band 18 is the marker band of *M tanajoa* and band 28 for *M caribbeanae*

The location of bands yielded with the MDH enzyme allowed discrimination between prey (*M caribbeanae*) and predator (*N idaeus*) when they were processed separately, however, the gut content could not be identified consistently even by using a sample concentration of five adult females of *N idaeus* (Figs 2) No clear band patterns could be obtained with the species *T tenuiscutus* (for this reason gel is not presented)

PGI showed a different band location for *N idaeus* and *M caribbeanae*, but the latter species was not to be detected as consumed prey in spite of processing 13 predator females macerated in one sample (Figs 3) In the experiment with *T limonicus* proteins of *M caribbeanae*--nor as single adult female nor as gut content--could not be identified (Figs 4)

Staining of proteins extracted from *N idaeus* and *M caribbeanae* samples for ACP resulted

in two different band patterns, however, this method failed to detect the gut content (Figs 5) The proteins of *T limonicus* remained stainless (for this reason, gel is not presented)

Protein extracts from *N idaeus* females having fed on *M caribbeanae,* and stained for ME showed the same (single) band as the extract from females of the prey species in the control sample (Figs 6) indicating that only prey proteins were visible *T limonicus* extracts remained stainless

5 1 2 Preparation of standards

Since staining of mite extracts for esterase was the most sensitive method, consequently this staining method was applied in all following experiments Standards were set up for the most frequently encountered cassava-inhabiting phytoseiids and tetranychids We found distinct band patterns for each species of tetranychid and phytoseiid Comparison of the lanes 2 to 6 with the lanes 7 to 9 in Figs 7 showed that esterase isoenzymes from tetranychid samples were concentrated in the upper part of the lane, whereas phytoseiid enzymes migrated faster The phytoseiids had relatively low esterase activities, whereas well-defined bands with high enzyme activity were obtained in most cases from tetranychid samples The prey could be detected and identified in gels with samples from laboratory experiments Figures 8 and 9 reveal that *T manihoti* from Cordoba (Colombia) fed on all offered prey species because the marker bands of *T urticae* (14), M caribbeanae (16), M tanajoa (10), and *M mcgregori* (8, 11) could be identified Note that this gel was run with Tris/Borat as tank buffer For this reason the patterns

of *M tanajoa* and *T urticae* differ from those of previous figures, where Tris/HCl was the buffer Figures 10a and 10b show the electrophoretic standards of *Amblyseius aerialis* Muma The marker bands (see Fig 10c) of *T urticae* (21), *M tanajoa* (20) and *M caribbeanae* (22) are visible, however, the marker band of *O gossypii* (16) cannot be consistently identified as the gut content It is possible that band 16 in lane 2 and 3 respond to the esterase pattern of the phytoseiid

Staining intensity of the phytoseiids and their gut content depended on the strain *T manihoti* from CIAT (Palmira) showed greater esterase activity than the strain from Guajira (Fig 11) Furthermore, the three fast migrating bands 54, 56, and 58 were characteristic for the Palmira strain

5 1 3 Assays to evaluate influence of host plant on band pattern of pest

In order to know if cassava has an impact on the electrophoretic pattern of tetranychids we conducted an experiment, where females of *T urticae* and *M caribbeanae* raised on cassava plants were confined on bean (*Phaseolus vulgaris* L) or cassava After three days they were processed for electrophoresis as previously described We ran extracts from macerated bean and cassava leaves for comparison with the patterns given by the phytophagous mites Many individuals of *Mononychellus* confined on beans were lost because they tried to escape or died suggesting that these species does not feed on this host *M tanajoa* and *M caribbeanae* fed on cassava (clone CMC 40) showed a thick band (34) in the first third of the lane which had

the same migration speed as the extremely thick esterase band of an electrophoresed cassava leaf of the clone CMC 40 (Figs 12) This band appeared in every case, whether or not the individuals of the two *Mononychellus* species were taken from cassava or bean plants However, electrophoresed females of *T urticae* kept on beans did not show the "cassava" band The cassava band in phytoseiid samples was an important indicator for consumption of a cassava pest The presence of the position of a thick band of esterase isoenzymes from cassava leaves with a similar esterase band at the same position in samples of all mites which had fed on cassava suggests that this band is due to ingestion of cassava proteins

5 1 4 Assays to estimate influence of digestion time on detectibility of prey proteins

Since the velocity of degradation of proteins as gut content is of crucial importance for the electrophoretic detectability of proteins we tried to find a relation between digestion time and staining intensity

No decrease in staining intensity was observed for starvation periods of zero and one hour with *T limonicus* (Jaguariuna) (Figs 13) The typical marker band of *M caribbeanae* was clearly detectable (arrow b, band 28) After three hours only the thick cassava band associated with prey mites could be identified (arrow a, band 34) Identification of the prey item was impossible due to the absence of marker bands of *M caribbeanae* After 12 hours no prey proteins were detectable We also observed variation in band intensity among individuals, which were treated similarly The females starved for three or six hours, respectively, showed

a notable variation of the esterase activity (lanes 10-13, 14-17) This observation was made frequently (see also Fig 1, compare lane 5 to lanes 6 and 7)

5 1 5 Electrophoretic evaluation of field samples

More than 1000 mites were collected in 30 cassava fields in Ecuador and brought to CIAT station for electrophoretical identification Initially 263 samples were tested Identification of field-collected phytoseiid mites was limited The predominant part of the phytoseiids collected in Ecuadorian fields did not have sufficient esterase activity for their identification (Fig 14) *T tenuiscutus* was the most frequently identified phytoseiid This species was more often identified than *Galendromus helveolus* Chant The portion of samples with an unknown esterase pattern was low, as well Each of the species *T galendromus* and *P macropilis* were identified once G. annectens

Identification rate of tetranychids samples was high in contrast to phytoseiids (Fig 15) 41% were identified as *M caribbeanae*, 20% as *T urticae*, 18% as *M mcgregori* Thirteen percent of the samples gave a clear but unknown electrophoretic pattern

Figure 16 shows the fractions of the prey species detected by the gut analyses 37%--the major fraction of the phytoseiid samples--did not yield sufficient esterase activity to allow identification of predator gut contents *M caribbeanae* was the most frequently identified prey species of the samples with identifiable gut contents

Fig 17 relates the gut content to the analyzed phytoseiids Phytoseiids which could not identified due to insufficient esterase activity generally had poor staining intensity of the gut contents *M caribbeanae* was the most frequently identified prey The unidentifiable phytoseiid species had a relatively high percentage of gut content which yielded legible, but unknown staining patterns The gut contents of *T tenuiscutus*--the most frequently collected phytoseiid species--had a similar portion of insufficient staining intensity to *M caribbeanae* as identified consumed prey

5 1 6 Assays to quantify gut content of phytoseiid predators

Hypothesizing that the age of the prey may influence the staining intensity of the gut content, we offered separately 50 eggs, 50 larvae, 50 proto- and 50 deutonymphs, and 10 female adults to starved females of *T manihoti* (Guajira) After five hours of association with the prey, the females were macerated for electrophoresis, and the remaining prey were counted To improve staining quality two predator mites were used per sample Assuming that the weight of the prey and the quantity of killed individuals may give some information about the actual intake, we weighed the stages of *M caribbeanae* with a CAHN microbalance after anesthetisizing the mites with diethylether, using three groups of 50 individuals of each motile stage and 100 for eggs All measurements were repeated three times

The weights of different prey stages are listed in Table 2 Prey age classes influenced the staining intensity of the gut content (Figs 18) The gut contents of two females which

consumed 22 eggs (15 µg) in five hours did not yield the typical prey band 28, and the staining intensity was not greater than that of starved females Higher enzyme activity of the "cassava" band occurred when 21 larvae (38 9 µg), 24 protonymphs (50 9 µg) or 11 deutonymphs (40 2 µg), respectively were consumed, but only deutonymphs showed the marker band of *M caribbeanae* in the control sample The two phytoseiid females exposed to adult prey killed three individuals (29 4 µg total weight) Their esterase activity was lower compared to the predators which fed on mobile immature prey

The gel in Figure 19 was chosen as representative example for eight gels to show that an increase in consumed biomass did not necessarily increase staining intensity Here, females of *T tenuiscutus* were macerated immediately after they had consumed the desired quantity No notable difference was found between consumption of two and three larvae, however, staining intensity increased abruptly, when four to eight larvae were consumed When 14 or 17 larvae were killed the gut content had less esterase activity

No correlation between prey density and esterase activity was found, when field-collected predators were tested Multiple box-and-whisker-plot analysis indicated that poor staining intensity was sometimes associated with high prey density and vice versa (Fig 20) Fig 21 shows that predator density had no effect on the esterase activity of the analyzed samples

5 2 Preference tests

This experiment was divided into three phases During the first phase preliminary studies were conducted on the influence of feeding history on the predation behaviour of *N idaeus* from Fonseca, Colombia The consumption capacity of the three species *N idaeus, T limonicus* and *T manihoti* was analyzed first Preference tests with three different prey densities and different diet combinations characterized the second phase of the lab experiments Field experiments with two prey densities should verify the results of the anterior experiments

5 2 1 Impact of the feeding history on the consumption

In a preliminary experiment we assessed the impact of predator satiation (feeding history) on the predation rate with fed and starved females of *N idaeus* (Fonseca strain) The eggs, larvae, nymphs and adults of *M caribbeanae* were offered separately at high and low densities Recently moulted females were mated Half of them were starved for 24 hours while the others were fed on abundant prey before starting the experiment

The females of *N idaeus* (Fonseca) fed on all prey stages (Tables 3, Fig 22) Generally, there was a large variation in the consumption rate, especially at high prey density Hunger increased variability of the killing rate

Prey age and predator feeding history affected the number of consumed individuals Satiated

and starved females consumed more immature stages than adult prey at high and at low density ($P < 0.0001$)[3] Starved and satiated females consumed similar numbers of immature ages, whereas starved females consumed significantly more larvae than nymphs ($P < 0.0001$)

When prey density was high and eggs or larvae were offered, starved and fed females showed a similar feeding rate However, fed predators killed significantly more nymphs than starved ones (t-test, $P < 0.001$), whereas starved predators killed significantly more adult prey (t-test, $P < 0.0001$) At high density, the killing rate of starved predators was more heterogenous on all prey stages than that of satiated predators (test of variance)

5.2.2 Consumption of *N. idaeus*, *T. limonicus* and *T. manihoti* on different developmental stages of *M. caribbeanae*

As the previous experiment, behaviour of predators varied considerably within the same treatments The four phytoseiid strains accepted all offered immature stages (Tables 4, Fig. 23) Overall, *T. limonicus* was the most efficient of the three predator species ($P < 0.0001$) Then followed the Fonseca strain of *N. idaeus*, which was more efficient than *T. manihoti* and the Brazilian strain of *N. idaeus* ($P < 0.0001$) On a diet of larvae this species behaved similarly to *N. idaeus* from Petrolina ($P < 0.05$) *T. limonicus* had by far the highest killing rate of eggs and nymphs Both *Typhlodromalus* species killed significantly more adult prey than *N. idaeus*,

[3] Three-way ANOVA were performed on the predation and oviposition data Means were tested with the Ryan Einot Gabriel Welsch F test for significance (SAS 1990) Variances of predation and field experiment data were stabilized by transformation of natural logarithm those of oviposition data by square roots

which hardly fed on this prey stage ($P < 0.0001$) *Typhlodromalus* were also more efficient on eggs than *N. idaeus* ($P < 0.0001$)

N. idaeus consumed more larvae than nymphs or eggs ($P < 0.0001$) The consumption by *T. limonicus* differed for each prey stage This species killed more larvae than eggs and more eggs than nymphs The females of *T. manihoti* killed a similar number of larvae and eggs, but they consumed significantly fewer nymphs and adults ($P < 0.0001$) All predators exhibited the lowest killing rate on adult prey ($P < 0.0001$)

5.2.3 Preference test with six diet combinations, offered at high density

Table 5 gives an overview of the six prey combinations (= treatments) which were offered to the phytoseiids Although larvae were the preferred prey in the preliminary experiments we found that it was more practical to use protonymphs due to the delicacy of larvae Each combination contained 50 protonymphs of *M. tanajoa* Three of these combinations were associated with acarine prey 50 protonymphs of either *M. caribbeanae*, *O. gossypii* or *T. urticae* the third Mycelium of the mildew *Oidium manihotis* Henn, honeydew-producing nymphs of the whitefly *Aleurotrachelus socialis* Bondar or 10 individuals of the first or second instar of thrips (*Frankliniella williamsi* Hood) were used as complementary non-acarine diet

Since some prey individuals died of causes other than predation both dead and surviving prey were counted A dead individual was considered consumed when the body was deformed due

to the loss of hemolymph that was sucked out by the predator In many cases discrimination of species of the prey remnants was impossible Therefore, all killed individuals were counted in order to obtain information about the effect of prey combination on the total consumption of one predatory female

All four strains preyed on every prey combination Comparison of all 24 treatments suggested that *T limonicus* was the most voracious species and *T manihoti* had the lowest mean of consumption (Table 6), however, due to high variability in consumption rate, no differences were significant (Tables 7, Fig 24)

Prey combination significantly affected predator consumption ($P < 0.0048$) The presence of *O gossypii* and *T urticae* tended to lower the consumption rate, however, only *N idaeus* from Fonseca and *T manihoti* presented significantly different consumptions on the three prey species

In the presence of nonacarine food items, the predators consumed equal numbers of CGM (Tables 8) However, females of *T limonicus* killed fewer CGM when they were combined with honeydew-producing nymphs of the whitefly, but differences were not significant

The means of live prey (protonymphs and deutochrysalis) are presented in Tables 9 in order to permit an evaluation of the impact of acarine prey combinations on the acceptance of CGM by the phytoseiids To simplify presentation the values of CGM and of the three other

tetranychids were presented in two different tables, which can be directly compared with each other ANOVA showed that the means of survived CGM did not significantly differ *N idaeus* (Petrolina) tended to kill less *M caribbeanae* than *T limonicus* (Table 9a) Both *Typhlodromalus* species presented a higher predation rate on the combination *T urticae* - CGM than the *N idaeus* strains (t-test, $P < 0.0001$) In association with *O gossypii* or *T urticae* fewer individuals of CGM survived than in the combination with *M caribbeanae*

The t-test in Table 10 showed that no strain preferred CGM to *M caribbeanae* However, all the predators except *N idaeus* from Petrolina preferred CGM to *O gossypii* or *T urticae* Both *N idaeus* strains killed significantly fewer *T urticae* than *O gossypii* ($P < 0.0001$) The two species of *Typhlodromalus* consumed the same number of *T urticae* and *O gossypii* All three predatory species preyed similarly on *O gossypii* Both *Typhlodromalus* species tended to kill more *T urticae* than *N idaeus*, however, only the difference between *T limonicus* and *N idaeus* from Petrolina was significant ($P < 0.01$)

Both species of *Typhlodromalus* consumed significantly more nymphs of thrips than *N idaeus* (Tables 11, $P < 0.0001$) The latter species showed an average consumption rate of less than 0 5 killed larvae

5 2 4 Preference tests with diet combinations, excluding or including *M tanajoa* low density

These experiments should provide information on how predators perform on alternate diets when CGM is scarce or absent The low density treatments were set up by confining 10 protonymphs of CGM together with other food items in each experimental unit Alternate acarine prey (*M caribbeanae* and *T urticae*) and non-acarine food were offered at the same densities as described before *O gossypii* was not included in these experiments, because *P persimilis* invaded and eliminated the small colony of this tetranychid which was established for these experiments only Absence of this mite from fields in the North Coast of Colombia impeded the restoration of the colony

All species except *T manihoti* exhibited a higher predation activity on pure acarine prey when *M caribbeanae* and *M tanajoa* were offered in combination (Table 12, $P < 0.05$) *T limonicus* was the most voracious species on *M caribbeanae*, whereas the consumption of this prey by the other species did not differ significantly ($P < 0.0001$) On *T urticae* both *Typhlodromalus* species killed the same number of protonymphs Both strains of *N idaeus* were less efficient on this prey combination then the other species ($P < 0.05$) Every strain, except *N idaeus* from Petrolina on *T urticae*, killed significantly less protonymphs when *M tanajoa* was absent

The most efficient predator on thrips in presence of CGM was *T manihoti* followed by *T limonicus* Both *N idaeus* strains hardly fed on this prey (Tables 13, $P < 0.0001$) When CGM

was absent predator females tended to feed more thrips nymphs, however, differences were only significant for *N idaeus* from Petrolina

Comparison of the predation behaviour of the three species towards CGM in presence of nonacarine diets shows that the killing rate of *T limonicus* was lowest when nymphs of the whitefly were present (Tables 14) This species and *T manihoti* had the highest consumption of CGM protonymphs when thrips were present ($P < 0.01$) The three alternative diets had no significant effect on the predation behaviour of the Colombian strain of *N idaeus* towards CGM

Tables 15 indicate the mean number of live CGM nymphs of each treatment When whitefly or mildew were present predators did not differ much in attacking CGM ($P < 0.01$) In the presence of *T urticae* and *M caribbeanae*, *T limonicus* left the lowest number of CGM live The data of alive nymphs confirmed the result that in presence of thrips, *T limonicus* and *T manihoti* left less nymphs alive than *N idaeus* On *O manihotis* the mean of alive nymphs did not differ much from predator to predator

5 2 5 Comparison of consumption at all three densities

Figure 25 shows that with decreasing CGM density the number of survived *M caribbeanae* increased When prey was associated with *T limonicus* then the smallest number of *M caribbeanae* nymphs survived when CGM density was low When *N idaeus* from Petrolina

was the predator a decreasing number of survived nymphs of *T urticae* was accompanied by decreasing CGM density With *N idaeus* from Fonseca, *T limonicus* and *T manihoti* left the smallest number of surviving *T urticae* nymphs when they were associated with CGM offered at low density By pooling the number of killed prey in each experiment unit we observed that feeding activity tended to increase with CGM density On thrips all phytoseiid species increased their feeding activity when CGM density decreased (Fig 26)

5 2 6 Oviposition

The three phytoseiid species have different reproductive potentials (Tables 16) The species with the generally highest oviposition rate was *T limonicus*, followed by *T manihoti* The two strains of *N idaeus* had the same average oviposition Differences between the three species were significant ($P < 0\ 0001$) On *T urticae*, reproduction of the three species was similar, however, on *M caribbeanae T limonicus* had an outstandingly higher fecundity than the other two species ($P < 0\ 0001$) On thrips *T manihoti* laid more eggs than *T limonicus* ($P < 0\ 001$) *N idaeus* did not oviposit on this diet On *O manihotis T limonicus* laid nearly one egg per day, significantly more than the oviposition of the other species ($P < 0\ 001$) *T limonicus* associated with *O manihotis* and CGM maintained an average oviposition of more than one egg per day during five days (Fig 27) All species had their lowest oviposition on whitefly *N idaeus* of Petrolina did not oviposit at all on this prey Both *N idaeus* and *T manihoti* reached their highest potential reproduction on *T urticae* ($P < 0\ 0001$), whereas *T limonicus* oviposited on this tetranychid not more than on *M caribbeanae T manihoti* reproduced on thrips as well

as on *T urticae*

In most of cases, t-tests did not reveal any significant differences between treatments where CGM was present at low density or completely absent Exceptions were *N idaeus* from Fonseca feeding on *M caribbeanae* (t-test, $P < 0.05$), *T limonicus* feeding on *O manihotis* (t-test, $P < 0.05$) and *T manihoti* associated with whitefly (t-test, $P < 0.05$)

5.2.7 Predator - prey relation under field conditions

The adaptability of predators to alternative food items is of crucial importance for their ability to overcome periods of low prey density For this reason field experiments were designed in order to study the influence of alternative prey and food items on the population density of the four phytoseiid predators In one part of the experiment they were released on plants which were only infested with alternative prey In the other part they could choose between CGM and alternative food These treatments should be compared to the treatment where only *M tanajoa* was present

A short time before the scheduled day of predator release a previously unknown virus disease caused the death of thousands of mites during a few days The devastating colony breakdown made the release of *M tanajoa* impossible But in order not to loose all the time and effort invested in the preparation of the experiment, CGM was replaced by its closely related species *M caribbeanae* Since the predators did not show any preference for CGM or *M caribbeanae*

during the lab experiments this replacement seemed to be a reasonable solution

Six-week old cassava plants were set in the field Each plant was covered with a gauze tent which was removed after six weeks According to the treatment, the plants were infested with *M caribbeanae T urticae* and with adults of thrips The insects were collected in the fields of CIAT The design of the experiment also included whitefly and the mildew *O manihotis* The adults of the whitefly were collected in the greenhouse The plants for the fungus treatment were exposed to natural infection for approximately four weeks in a greenhouse situated in a microclimate of high relative humidity near a lake When the plants were set in the field the mycelium covered at least a third, but not more than the half of the leaves The presence of *M caribbeanae* at medium density (approximately 20 females per leaf in the upper part of the plant) characterized the first treatment, its absence the second The medium density was considered as the most common field situation, whereas the absence of *M caribbeanae* was included in order to study the adaptability of the phytoseiids to alternative prey or food

The experiment was designed to evaluate the influence of alternative prey on the population dynamics of the three predatory species Therefore, these treatments were compared to the control treatments, where only *M caribbeanae* was present According to previous experiments conducted at CIAT 50 predator females were released on each plant to start the experiment

Generally, the number of predator individuals per plant were characterized by high standard deviations in all treatments The presence of *M caribbeanae* lowered the heterogeneity of

phytoseiid densities slightly In the absence of tetranychids the coefficient of variation was 83 7, in its presence, 66 4

Populations of all phytoseiid species decreased dramatically after release (Fig 28) Except *N idaeus* (Fonseca) on whitefly and in presence of *M caribbeanae* (Fig 31) none of the species recovered the initial density *M caribbeanae* had a stimulating effect on the recovery of the three phytoseiid species Then, after the first evaluation, all of them increased when *M caribbeanae* was present After the fifth evaluation all phytoseiid populations began to decrease and disappeared completely until the 10th and last evaluation day In the absence of this prey species population densities of all four predator types were low and did not exceed an average of 15 individuals per plant The absence of *M caribbeanae* caused the lowest level and the lowest recovery rate of all predatory populations Differences between the density of the species were negligible when *M caribbeanae* was absent The density of both *N idaeus* strains did not increase significantly when *T urticae* was the alternative prey, whereas the population of both species of *Typhlodromalus* increased remarkably *M caribbeanae* did not increase the density of *T manihoti* when it was combined with whitefly or mildew fungus, whereas the density of T limonicus was similar when *O manihotis* and thrips were part of the diet Table 17 gives an overview of all comparisons

Populations of *Typhlodromalus* recovered better than those of *N idaeus* (Fig 28, $P < 0.01$) The population curves of all phytoseiid species show that density of both species of *Typhlodromalus* increased until the fourth evaluation, whereas *T limonicus* recovered a slightly

higher density Population density of *N idaeus* from Petrolina raised from eight to only twelve individuals per plant between the first and the second evaluation to maintain this level until the sixth week The establishment of the Fonseca strain was slightly higher than that of Petrolina, however, differences were not significant The control treatment did not show significant differences in spite of the big differences at the second, third and fourth evaluation

The population development of *N idaeus* (Petrolina) showed a low correlation with *M caribbeanae* in association with the whitefly (r=0 4, P<0 04, Fig 29) and *O manihotis* (r=0 6, P<0 0004, Fig 29) No correlation was observed when *M caribbeanae* was associated with thrips This phytoseiid strain showed a slight positive correlation with *O manihotis* in association with *M caribbeanae* (r=0 54, P<0 0022, Fig 30), however, in the absence of the tetranychid the correlation between the phytoseiid density and fungus infestation was moderately negative (r=-0 43, P<0 02) The populations of thrips and this *N idaeus* strain were not correlated, however, those of *T urticae* and the predator were significantly correlated in the absence of *M caribbeanae* (r=0 5, P<0 0017, Fig 30) When *T urticae* was present together with *M caribbeanae*, the correlation between predator and first prey species was highly significant (r=0 6, P<0 0005, Fig 30)

As for the Brazilian strain, the populations of *N idaeus* from Fonseca and *M caribbeanae* were correlated when whitefly was present (r=0 5, P<0 0002, Fig 31) In contrast, the infestation of whitefly in presence of the tetranychid was negatively correlated with the density of this phytoseiid (r=-0 4, P<0 044) Population dynamics of *M caribbeanae* and *N idaeus*

were highly correlated in plants infested with *O manihotis* (r=0 7, P<0 0001) In the presence of thrips this predator presented a low correlation with *M caribbeanae* (r=0 4, P<0 016, Fig 32) Population density of this insect was never correlated with that of *N idaeus* On a pure *M caribbeanae* diet, prey and predator were significantly correlated (r=0 5, P<0 002, Fig 37), as well as on pure diet of *T urticae* (r=0 4, P<0 02, Fig 32)

Population densities of *T limonicus* and *M caribbeanae* were correlated in all treatments (see Figs 33 and 34, whitefly r=0 55, P<0 0017, *O manihotis* r=0 74, P<0 0056, thrips r=0 6, P<0 0005, *T urticae* r=0 4, P<0 03) Density of this predator was negatively correlated with that of whitefly (r=-0 45, P<0 0192) Development of thrips was correlated with that of the predator with r=0 4, P<0 03) In the absence of *M caribbeanae* no correlation with alternative prey or food items could be documented

Density of *T manihoti* was only correlated with the population of *M caribbeanae* when only this prey was present (Fig 37) or when whitefly was present (r=0 5, P<0 0061, Fig 35) When the predator population decreased the whitefly density tended to increase This tendency was observed in both treatments, however, this trend was clearer in absence of the acarine prey In presence of *M caribbeanae* a negative correlation between thrips and the predator was observed (r=-0 4, P<0 05, Fig 36) Population dynamics of *T urticae* and of this predator were correlated in the presence of *M caribbeanae* (r=0 5, P<0 007, Fig 36)

6 Discussion of results

6.1 Electrophoretic analysis

Experiments to improve electrophoretic gut analysis Five of the 10 tested enzymes (MDH, PGI, ACP, ME and EST) were suitable for taxonomic discrimination of cassava-inhabiting phytoseiids and four of them (ME, PGI, ACP and EST) could be used for identification of gut contents. The clearest band patterns were obtained with esterase. Gordon (1977, in Giller, 1984) underlined that esterases are more diverse than other enzymes, thus facilitating discrimination of prey and predator proteins. This hypothesis was corroborated by authors who have used this enzyme for taxonomic identification of phytoseiids and their gut content (e.g. Murray and Solomon, 1978; Sula and Weyda, 1982; Solomon *et al.*, 1985; Fitzgerald *et al.*, 1986; Bakker and Klein, 1993).

Preparation of standards The rather different migration pattern of the esterase enzymes of tetranychids and phytoseiids facilitated the discrimination. Phytophagous and predatory mites could be identified by electrophoresis of esterase isoenzymes, corroborating results from a series of publications reporting the applicability of this method for taxonomic analysis with mites and other arthropods (e.g. Wagner and Selander, 1974; Avise, 1974; Ayala, 1978; Buth, 1984), however, the experiment with *A. aerialis* feeding on *O. gossypii* showed that the assignment of bands to predator or prey was not always possible. The bands of the predator can mask those of the gut content or vice versa, confirming similar observations by van der

Geest and Overmeer (1985) As in previous experiments where phytoseiid gut contents were analyzed (Murray and Solomon, 1978), phytoseiids had lower esterase activity than tetranychids Many gels with samples of *N idaeus* yielded no bands even in controlled studies where consumption of known prey types by individual *N idaeus* was documented before electrophoresis We hypothesized that the absence of bands was due to proteolytic enzymes in the gut of this phytoseiid However, we rejected this explanation after failing to observe reduction in staining intensity when *N idaeus* was macerated and electrophoresed together with other phytoseiid or tetranychid mites

Another possible explanation may be seen in the strong preference for young prey stages as Table 4 suggests These stages are characterized by low esterase activity (as the example of *M tanajoa* shows in Fig 38) However, the number of killed larvae in Table 4 indicates an protein intake which should have permitted esterase detection This open question may be the object of further studies

Influence of the host plant The presence of the position of a thick band of esterase isoenzymes from cassava leaves with a similar esterase band at the same position in samples of all mites which had fed on cassava suggests that this band is due to ingestion of cassava proteins Individuals of *M tanajoa* and *M caribbeanae* yielded this cassava marker band even when transferred on beans on which they developed poorly No bands occurred in the esterase pattern of individuals of the cosmopolitan species *T urticae* after feeding on beans The cassava host marker band in *M tanajoa* and *M caribbeanae* may be explained by the specializa-

tion of *Mononychellus spp* for its cassava host (Braun *et al*, 1993)

Influence of digestion time In our experiment esterase (Figs 13) enzyme activity of consumed prey was dramatically reduced after a digestion time of three hours This observation contrasts with Murray & Solomon (1978), who detected esterase activity of the gut content of *Typhlodromus pyri* Scheuten fed on *Panonychus ulmi* Koch after even 31 hours Bakker and Klein (1993) detected esterase enzymes of CGM in *T manihoti* after 24 hours In some sporadic occasions we also found prey proteins as gut content after the same starvation period These observations and those of the other authors (who did not indicate the frequency of the observations) indicate, that the lapse between last food intake and detectibility of enzymes can vary

A possible explanation for this contrast may be that in our experiment phytoseiids were not satiated when the starvation period was initiated Assuming that the predators associated with abundant prey maintain a certain level of gut fullness, we took the samples from colonies in order to deprive them of food for a determined lapse of time Comparing our results with those of the authors mentioned before, we conclude that it is crucial to know the exact feeding history in order to perform this experiment All these experiments indicate the importance of digestion time for the detectibility of prey proteins or enzymes, especially when the predator samples were collected in the field

Analysis of field samples The high proportion of identified tetranychid mites corroborates

electrophoresis as a valuable tool for taxonomic identification when enzyme activity of the sample is high However, this technique is not an adequate method for identification of field-collected mite predators It is worth while to reflect why it was easier to identify phytoseiids from laboratory colonies than from the field It is difficult to find convincing explanations, however, differences between field and laboratory conditions may give a clue (a) in the lab the predator and prey species are known, (b) high prey density is guaranteed, and (c) field temperature may be considerably higher than in the lab where ca 25°C was the average temperature

(a) In order to know the range of possible species in a field sample some individuals were collected for identification However, it was possible that some not identified phytoseiid specimens were processed electrophoretically which belonged to species with low esterase activity

(b) It is possible that the grade of gut fullness may affect the physiology of a mite However, the effect of little gut satiation on mite physiology is not clear Very little is known about how and when the enzymes are produced Norton (1988) (cited in Evans, 1992, p 240) speculated that enzymes acting on structural polysaccharides may be of microbial and not of endogenous origin In the case of esterases, House (1974) mentioned their functions in the digestion of fats and in the nervous system Florkin and Jeuniaux (1974) described the esterases as a permanent part of the hemolymph Considering these works, it seems possible that lack of nutrition reduces metabolism which may have again a decreasing effect on esterase activity Waterhouse (1957) cited various studies on different orders of insects concluding that starvation generally

diminishes enzyme activity He reports that enzyme activity falls temporarily below the starvation level when food is again taken It is likely that this situation occurs under field conditions the predator has to search for a prolonged time to find a prey individual

(c) We collected mites during dry days when temperature was mostly over 30 °C Giller (1984) and Dicke and de Jong (1988) mentioned the importance of temperature on the length of digestion time of the waterbug *Notonecta glauca* and of phytoseiids collected in Dutch orchards, respectively

Considering these three factors the poor staining of field collected phytoseiids and their gut content seem understandable

The high portion of non-detectable gut content of field collected predatory mites was previously reported in other publications In experiments conducted at CIAT with *T manihoti* and *T aripo*, Bakker and Klein (1993) found that most gut content samples had insufficient esterase activity Since many of the predators were associated with *O manihotis*, they hypothesized that the predators were feeding on this diet We also observed frequently in the field the association of phytoseiids and fungus However, since they (and we) failed to characterize this fungus electrophoretically, no consumption could be demonstrated by means of gut analysis

Quantification of gut content Our initial hypothesis of a positive correlation between predator consumption rate and prey density required quantification of predator consumption rate

However, comparison of the staining intensity with the number of consumed prey indicated that a correlation between staining intensity and the quantity of prey consumed did not necessarily exist A similar conclusion was reached by Fitzgerald *et al* (1986), who also failed to find a linear correlation between gut content of *T pyri* and staining intensity with scanning of gels Various reasons may give an explanation for this limitation

1 The determination of the time of consumption is of crucial importance for the quantification of the gut content Furthermore, variation in the time of food intake may influence the quantity of gut proteins as well

2 In spite of the exact determination of the quantity of consumed prey in the laboratory experiments it was possible that the actual consumption of each predator individual was different since the quantity of liquid which predators sucked out of each prey individual was unknown Therefore, relation between weight of prey and staining intensity must not necessarily exist This hypothesis is underlined by the fact that starved predators had to be used for this experiment However, our assays and those of other authors (Sabelis, 1985a, Mori and Chant, 1966) on the influence of the nutritional history on the feeding behaviour of predators showed that satiated predators fed more continuously on captured prey than starved ones Latter ones frequently attacked and abandoned prey within a short lapse leaving the prey alive Probably they are more susceptible to disturbance caused by other prey than satiated predators (Mori and Chant, 1966)

3 Prey age seemed to be a very important factor for the intensity of the

protein bands Table 2 shows that the predator had to kill nearly 15 eggs to ingest the same quantity as an adult female prey can provide When prey density was not abundant (as in our experiments in order to facilitate observation) and only young stages were present, then it was obviously more difficult for the predator to fill its gut

4 Differences between the staining intensity of different phytoseiid individuals of the same species may have a negative effect on relation between staining intensity and protein quantity The slight differences in staining intensity of the samples in the lanes 11-18 (Fig 13) are mentioned as an example They may reflect the variation of enzyme activity between individuals The low staining intensity in lane 12 may be due to only partial filling of the stomach This problem was discussed before in paragraph 2 of this section

6 2 Predation experiments

6 2 1 Impact of the feeding history on consumption

The starvation period of 24 hours strongly affected the behaviour of the predators We observed that starved females frequently attacked and abandoned the prey in order to continue their searching activity This observation was corroborated by the observation that starved females showed a wider range of killing rate than satiated females Mori and Chant (1966) mentioned the importance of the feeding history, a statement, which was later confirmed by

Eveleigh & Chant (1981) For this reason Sabelis (1985a) suggested adapting of the predator to the new conditions for a period of six hours before initializing the predation experiments

The elevated killing rate on immature stages compared to that on adult prey is easy to understand for two reasons Firstly, the latter prey stage contains much more biomass, a few individuals are sufficient to satiate a predator Secondly, it is suggested that the capture rate of the predator is higher on immature stages which are easier to handle However, it is still an open question why starved predators killed more adult prey than satiated predators Interpretation becomes even more difficult when the significantly higher consumption of fed females on nymphs is considered

6 2 2 Consumption of *N idaeus, T limonicus* and *T manihoti* on different prey stages of *M caribbeanae*

It was expected that the predator's consumption depends to a major extent on the prey age supplied (Sabelis, 1985a) For this reason it was surprising that all species preyed more on larvae than on eggs except both strains of *N idaeus* which killed the same number of eggs and nymphs This suggests two explanations One is that all species preferred immature motile stages or that eggs are more nutritive and satiate the predator with less biomass Takafuji and Chant (1976) observed that *Iphiseius degenerans* Berlese on *Tetranychus pacificus* McGregor showed a slight preference for larvae and protonymphs to eggs, which is similar to our own observation They explained this preference by the stimulating effect of the prey movements

on the attacking activity Another explanation for higher killing rate on larvae might be seen in the hypothesis that the egg is of higher nutritive value than the other stages This assumption justifies the conduct of an experiment in order to measure the reproductive capacity of the phytoseiids on various prey stages

The predation tests demonstrated superior voracity of *T limonicus* suggesting that this species was one of the most promising candidates for the control of *Mononychellus* sp It also has the capability to catch and kill adult prey, which is for the population a much more significant loss than any immature stage (Ohnesorge, 1981) In contrast, *T manihoti* seemed to be a predator of inferior efficiency This species killed fewer individuals than the others and hardly attacked adult prey The total consumption of *T manihoti* was less than that of *N idaeus* from Fonseca, however, the superior voracity on adults stage may compensate for the relatively low predation rate on the immature stages To get an estimate of the potential intake we assumed that the predators sucked out all available liquid from their victims and weighed eggs and motile prey stages Under this assumption the intake of *T manihoti* did not depend significantly on the prey stages (Table 18) Accepting the same assumption the results suggested *T limonicus* sucked out the same quantity of liquid from eggs and from adults but strongly preferred larvae and nymphs In accordance with this assumption, *N idaeus* maintained the lowest feeding level on adults

6 2 3 Preference test with six diet combinations, offered at high density

The high standard errors and the significant differences between variances indicated that on some prey types individual predator females differed in their feeding activity This impeded obtaining significant differences between considerably different means It is possible that the design of this experiment needed to include more replicates than our preliminary experiments where we studied the influence of the feeding history During our anterior experiments we offered only one prey species In this experiment we offered CGM in combination with several kinds of food types It is suggested that these combinations altered considerably the predacious activity of the phytoseiids

In spite of the heterogeneity of variances the results of these experiments confirmed the outstanding voracity which *T limonicus* showed in the anterior experiment, especially when pure acarine prey items were offered (except on *O gossypii* at high prey density)

The highest consumption by all predator strains of the acarine prey combination *M tanajoa* - *M caribbeanae* (except for *T manihoti* which exhibited a similar predation rate on CGM - *M caribbeanae* and on CGM - *O gossypii*) suggested that an affinity exists between the cassava-inhabiting predators and these prey species *T urticae* is an cosmopolitan pest and *O gossypii* has been reported on cotton, beans and papaya (Pritchard and Baker, 1955), whereas *Mononychellus* sp is strongly associated with cassava (Braun *et al* , 1993) Another reason for this behaviour can be seen in the smaller body size of *Mononychellus* sp facilitated the attack of phytoseiid predators

Analysis of the means of killed prey in the experiment conducted at high prey density indicated that *T manihoti* was the only species which exhibited a similar predation rate on *O gossypii* and on *M caribbeanae* Former studies at CIAT (1990) showed that this species could not complete the development to adult on the webbing prey type However, the daily change of the leaf discs did not permit intense webbing Unfortunately, the number of replicates of the treatments with *O gossypii* was too small, to allow statistically secure comparisons between the means of the other treatments

The reduced consumption of CGM in presence of alternative food by all species (except *N idaeus* from Petrolina) indicated that the predators included alternative food items in their diet The number of killed thrips nymphs indicated without any doubt that this insect played a role in the diet of both *Typhlodromalus* species Furthermore, observations in the stereomicroscope revealed that the same two phytoseiid species feed on honeydew secretions of whitefly nymphs And in the case of *T limonicus* this diet decisively lowered the killing activity on CGM

We found no evidence that any of the three phytoseiid species fed on the mycelium and conidia of the mildew fungus Former studies showed that 44% of *T manihoti* completed their development from egg to adult on this diet (CIAT, 1990) This observation suggested that the fungus may have some importance as a food supply, but we still do not know exactly in what magnitude and which fungal organs are consumed Poor consumption of thrips and similar killing rates of CGM in presence of the three non-acarine food types indicated that they did not play an important role in the nourishment of *N idaeus* This species exhibited the typical characteristics of a specialized predator behaviour (McMurtry, 1992)

6 2 4 Preference tests with diet combinations, excluding or including *M tanajoa* at low density

This experiment confirmed some results discussed in the section above the variation of phytoseiids' predation behaviour did not permit the detection of significant differences in spite of big differences between the mean values, predators' affinity to *Mononychellus* spp , the outstanding voracity of *T limonicus* and the suitability of thrips as food item for *Typhlodromalus* spp

It was interesting that at low density of CGM *T limonicus* killed more CGM in presence of alternative prey, such as *M caribbeanae, T urticae* or thrips than in presence of whitefly or *O manihotis* This observation raised the conclusion that the fungus or the honeydew secretion were an attractive food resource for *T limonicus* reducing the necessity to attack CGM In contrast, the ability of *N idaeus* to move and oviposit in the webbings of *T urticae* (CIAT, 1990) suggests that this species is able to handle well these obstacles (in our experiments *T urticae* webbing was not dense since the leaf discs were renewed daily) This hypotheses seems to be contradicted by the observation that at high prey density no alternative food type affected the predation of any predator strain on CGM We think that at this density enough CGM individuals were available to secure a minimal consumption of at least 20 protonymphs

The explanation that predators' consumption was reduced by hampered movement may fit *T manihoti* However, in the lab *T limonicus* is able to reproduce on mixed prey colonies consisting of *M caribbeanae* and *T urticae* For this reason another possible explanation theory should be discussed It is possible that the accompanying food may have altered the

feeding activity on CGM Collyer (1964) and Putman and Herne (1964, both cited in Huffaker *et al*, 1970) observed that *T pyri* controlled *P ulmi* better when *Aculus fockeui* or *T glaudicans*, respectively, were also present than when only *P ulmi* was present It may be of interest for further studies to examine in more detail the influence of alternative food like thrips on the feeding behaviour of selected phytoseiid species

6 2 5 Comparison consumption at all three densities

It was expected that the killing rate of all predators would increase when density of offered prey individuals increased Although differences were not significant the tendency was visible These results corroborate observations of Akpokodje *et al* (1990) They observed that the consumption rate of *N idaeus* and *I degenerans* increased on CGM monotonously until reaching a plateau forming the typical type Holling II functional response curve (Holling, 1965) Takafuji and Chant (1976) and Eveleigh and Chant (1982) reported the same tendency for *P persimilis* and *Iphiseius degenerans*, both feeding on *T pacificus*

Comparison of consumption on thrips at three CGM densities indicated that decreasing CGM density increased the readiness of all phytoseiid species to accept thrips as complementary prey Even *N idaeus* was able to kill some thrips nymphs, indicating that this species, which almost did not feed on the insect when CGM was abundant, was able to act as a generalist predator when the main prey is scarce The low consumption rate suggested that the consumption of thrips secured the maintenance of minimal physiological processes It is still not known if this predator can reproduce on this diet, a question which generates interest for further studies Experiments conducted at CIAT showed that *T manihoti* showed a similar oviposition rate on

thrips and on CGM (CIAT, 1990) The importance of thrips was already reported by Swirski and Dorzia (1968), Shipp and Whitfield (1991), Hoy and Glenister (1991), and Gloutier and Johnson (1993)

6 2 6 Oviposition

Five days oviposition on all acarine food items indicate that they were a suitable food source for reproduction of all three phytoseiid species *T limonicus* was not only the most voracious but also the most fecund species on acarine prey The highest oviposition and feeding rate on *M caribbeanae* indicated that this species was the most efficient predator on this prey This superiority did not occur on *T urticae*, where no significant differences within the three predacious species could be found The high oviposition rate of *T manihoti* on thrips was confirmed by experiments conducted at CIAT where *T manihoti* showed a similar oviposition rate on thrips and on CGM (CIAT, 1990) This suggested that this species is not only a potential control agent of mites but also of thrips which can cause damage of considerable economic importance (Bellotti and van Schoonhoven, 1978)

The incapacity of all the three phytoseiid species to reproduce on whitefly honeydew made it obvious that this food item does not have the essential nutrients such as protein to permit oviposition The same explanation might be stated for the cassava mildew fungus Many authors report the consumption by phytoseiids of alternative food which did not allow oviposition Huffaker and Kennett (1956) found that *Amblyseius aurescens* Athias-Henriot did not reproduce in absence of prey mites but utilized honeydew or plant exudates for mere survival Bakker and Klein (1990) mentioned that this food item did not allow reproduction

of *T manihoti* on cassava, however, they discussed the importance of exudate for plants to maintain their "bodyguards" Toko *et al* (1994) observed that females of *T manihoti* (from NE of Brazil) did not reproduce, but increased survival rate and longevity on this non prey food

It was surprising that the females of *T limonicus* were able to maintain oviposition on mildew in presence of only ten protonymphs of CGM They were sufficient to permit an oviposition of more than one egg per day Former experiments showed that *O manihotis* is a potential food item for this phytoseiid species 44% of *T manihoti* (from Palmira) survived from egg to adult on this diet (CIAT, 1990) In this experiment, a pure mildew diet permitted the females to oviposit 2 6 eggs during the oviposition period (compared to 25 4 when CGM was the prey) This suggests that mildew permits *T limonicus* to maintain its population when density of *Mononychellus spp* is low and supports irregular oviposition

6 2 7 Prey preference under field conditions

Large differences between the replicates indicated that factors other than the treatments affected predator behaviour and that three replicates were not sufficient One of the important impacts on field experiments is generally the rainfall However, in our experiment rainfall was obviously not a determinant factor since--in spite of increasing precipitation--the tetranychid and phytoseiid density increased until the second evaluation (Fig 39) The gauze cages probably diminished considerably the impact of the rain drops For this reason it seems more convincing to attribute the heterogeneous behaviour to the predator dispersal activity The abrupt decrease after release was also observed for *T manihoti* (CIAT, 1993) during a field experiment conducted in 1992 at CIAT However, in that experiment, *N idaeus* established

immediately after release The higher release density (100 individuals/plant) combined with a period of less rainfall (less than five mm per week) might have facilitated the establishment The fact that the natural distribution of *N idaeus* and *Typhlodromalus spp* are restricted to seasonally dry or seasonally humid zones, respectively, (CIAT, 1990) suggests that the better establishment of latter genus can be explained by the rainy period after release

The increasing effect of the presence of *M caribbeanae* on the density of all predator strains confirmed their preference for *Mononychellus* spp in the lab experiment indicating the importance of this prey species as part of their diet Assuming that the predators perform similarly on *M tanajoa* suggests that they may be suitable agents in the classical biological control of CGM

The positive correlations between *N idaeus* and *M caribbeanae* in presence of the alternative food items honeydew and *O manihotis* suggested that these items complemented the acarine diet This conclusion agrees with Tanigoshi *et al* (1993) who observed a prolonged survival of this species on exudate and various types of pollen McMurtry (1992) assumed that supplemental food like honeydew or fungus considerably increases survival and oviposition on mite prey, suggesting to include these food items in studies on determining reproductive rates The importance of alternative food for the establishment of exotic predators was stressed by McMurtry and Scriven (1966) They observed that *Euseius hibisci* Chant suppressed more effectively *Oligonychus punicae* Hirst when pollen was present The real existing or negative correlation between *N idaeus* with supplementary food items in absence of *M caribbeanae* suggested, that these food items had not sufficient nutritive values to maintain a population Bakker and Klein (1990) observed that *T manihoti* survived but did not reproduce on exudate

of cassava plants The result that the presence of thrips had no influence on the density of both strains of *N idaeus* corroborates the lab experiment where this predator fed poorly on thrips The observation that the population of both *N idaeus* strains was strongly correlated with that of *T urticae* confirmed its good adaptation to this web-producing species (Mesa *et al* 1990)

The behaviour of *T limonicus* and *T manihoti* on whitefly was probably determined by the same factors as discussed before for *N idaeus* Nethertheless, it was curious that the density of *T manihoti* increased when that of whitefly decreased, and vice versa This indicated that this phytoseiid did not only feed on honeydew but also on the insect Since in the lab experiment this phytoseiid could not reproduce on this diet this conclusion was surprising Furthermore we observed, that the wax protection hampers the movement of this mite However, the population dynamics of the insect and of this phytoseiid suggested that *T manihoti* controlled the whitefly It was possible that the lack of acarine prey obliged this predator to feed on immature whitefly stages that were probably still lacking a dense wax protection This conclusion coroborates various authors who found that phytoseiids are able to control this insect (Wysoki and Cohen, 1983, Maisonneuve *et al*, 1985, Rao *et al* 1989) It would be interesting to evaluate this hypothesis in further experiments The reasons for the negative correlation between *T limonicus* and whitefly can be seen in the dramatic increase of the whitefly infestation in this treatment It is possible that the extremely high density of whitefly hampered the movement of these predators The increase of the density of *T limonicus* on a pure mildew diet until the fourth week, maintaining a level between 10 and 20 mites per plant also suggested that the *T limonicus* accepted temporarily this food The high population densities on the combination *T urticae - M caribbeanae* and thrips - *M caribbeanae* indicated that this species found good nutritional conditions Comparison of these

population dynamics with that on pure thrips diet suggested that *T limonicus* temporarily accepted the insect, however, the combination with acarine prey seemed to improve the conditions for the establishment of this phytoseiid The extremely low density of *T manihoti* on plants infested with mildew in presence or in absence of M caribbeanae suggested that the fungus had no attraction for this species It was surprising that *T urticae* alone was positively correlated with *T manihoti* Earlier experiments with this predator-prey combination showed an extremely low survival rate of the phytoseiid (CIAT, 1990), what makes it impossible to rear this phytoseiid on this prey The phytoseiid is known for its limited ability to move in the dense webbing of the tetranychid However, in our field experiment the rapid decrease of *T urticae* population did not permit formation of intense webbing, indicating that the predator still was able to attack acarine prey

6 3 General conclusions of all predation experiments

In the lab experiments *M tanajoa* and *M caribbeanae* were the most preferred prey species Assuming that the phytoseiid species had no preference for CGM or *M caribbeanae* it can be concluded that CGM would have been also an essential part of the diet of all tested phytoseiid species in the field experiment

T limonicus was the most efficient predator species In all lab experiments this species was the most predacious phytoseiid and performed also the highest oviposition rate In the field experiment this species showed the highest density as well, but without significant differences to *T manihoti*

Thrips was an important prey species of *T manihoti* in all experiments *T limonicus* feeds and reproduces on this insect but this prey type had less importance in its diet than in that of *T manihoti* Thrips was not accepted by *N idaeus* in any experiment Only when no other food was available this species killed a minimal number of individuals of this insect

The honeydew secretion of whiteflies had an increasing effect on the density of all phytoseiid strains in the field experiment This result corroborated the semi-field experiments of Bakker and Klein (1992) They observed that in presence of cassava exudate *T manihoti* was able to reach a higher population density than in the absence of this food item They concluded that the presence of carbohydrates leads to enhanced juvenile survival and to improved mass conversion (lower prey intake leads to equal egg production)

7 Relevance of the results for farmers' practice

CIAT identified about 50 potential natural enemies of CGM in beginning the Classical Biological Control Project Since the shipment costs of all these candidates to Africa are high and in order to minimize or avoid introduction of species that have unknown ecological effects, a selection process for the most promising candidates was needed The present project was initiated as part of the selection efforts with the objective to provide data on the three as promising considered phytoseiid species *T manihoti T limonicus*, and *N idaeus*

Preliminary investigations at CIAT yielded a great deal of data supporting introduction and release of *T manihoti* in Africa, based on its preference for CGM However, efforts to establish this candidate in the exotic site failed The present work showed that its consumption of thrips and the lack of consumption of adult mites may be limited compared to *T limonicus* The high voracity, fecundity and relative ease of establishment in the field of *T limonicus* highly recommended the release of this phytoseiid for the control of CGM in Africa Furthermore, the results of this project showed possible limitations of *N idaeus* as a successful predator in Africa Limited voracity and poor reproduction on alternative food such as fungi, thrips or honeydew secretion of whitefly were considered as possible reasons However, its adaptation to prolonged dry seasons indicates its importance as a potential control agent of CGM The specific advantages of each species suggest that a multiple species release, as has been practiced, is a good pragmatic approach to the problem in Africa

An additional, secondary output of this project was that *T manihoti* seems to be a promising control agent of thrips Our experiments show that presence of alternative food sources, like honeydew, secretion or fungus, may aid in the establishment of these phytoseiids on cassava plants

8 Major problems/constraints

One of the most important limitations of the use of electrophoresis as tool for the diet analysis of field collected predators was their low esterase activity The majority of the collected phytoseiid specimen could not be identified Furthermore, the fraction of unstained gut contents was considerable We failed to detect proteins of the mildew *O manihoti* as gut content of

phytoseiids Bakker and Klein (1993) experienced similar difficulties with this fungus They concluded that the phytoseiid gut capacity of 3-5 µg is too small to permit its identification Their, our and studies at CIAT (1989) suggested that this fungus is part of the diet of phytoseiids as *Typhlodromalus*, however, this hypothesis remained unsupported by electrophoretic data

Another goal of the electrophoretic assays was to quantify predator consumption First of all, it was not possible to establish a calibration curve of consumed prey individuals and staining intensity Even if this difficulty were be overcome, other unknown factors like digestion time and consumed prey stage impede reliable electrophoretic analysis

Two experimental problems hampered the realization of the experiments considerably The break downs of the colonies of *O gossypii* and *M tanajoa*

During the lab experiments it was very difficult to maintain the colony of *O gossypii* Phytoseiids (especially *P persimilis*) reduced the colony considerably Absence of this mite in the fields at the North Coast of Colombia did not allow the reestablishment of the colony For the second part of these experiments we were obliged to eliminate this part of the experiment

The major constraint consisted in the sudden collapse of CGM colony due to an unknown virus disease Since all the preparations like plant growing, rearing of pests and mildew were scheduled for the 1st of November 1993--the day of the release of the phytoseiids--we could not postpone the experiment Furthermore, for the release we needed to increase the phytoseiid

colonies The large quantity of plant material required for their maintenance, and the fact that the cassava variety CMC 40 was running short presented another pressure to release the phytoseiids on the planned date For these reasons there was no other alternative but to substitute CGM with its relative, *M caribbeanae*

One of the major constraints for the analysis of the results of field experiment was the heterogeneity of the data This indicated that on one side that the number of replicates was too small If evaluation personnel (as in our case) or space are limited then the number of treatments should be reduced in favour of more replicates On the other side the results showed that control treatments were missing, where *M caribbeanae* or only predators were present The design of the experiment was characterized by the thought to study the population dynamics of the four predators on four different alternative food types testing against the behaviour on pure *M caribbeanae* population For this reason and for the size of the experiment these control treatments were not included Finally, the heterogeneity of the results showed that more effects than only the food items influenced the phytoseiids However, without these control treatments it is difficult to identify these influences

9 Documentation of results

Table 1 Applicability of enzymes for staining of prey proteins and discrimination of *N idaeus* *T limonicus* and *T manihoti*

Enzyme	Identification of phytoseiid species	Identification of gut content
Malate dehydrogenase (MDH)	++	+
Phospho-gluco-isomerase (PGI)	++	+
Esterase (EST)	+++	+++
Acid phosphatase (ACP)	++	o
Diaphorase (DIAP)	o	o
Glucose-6-phosphate dehydrogenase (G6DPH)	+	+
Glutamate oxalatacetate transaminase (GOT)	+	o
Malic enzyme (ME)	++	++
Alcohol dehydrogenase (ADH)	o	o
Shikimic dehydrogenase (SKDH)	+	+

o = no staining
\+ = staining, however, bands of all samples were uniform
++ = identification possible
+++ = identification with very good results

Table 2 Live weight of stages of *M caribbeanae*

Stage (number of individuals per group)	mean weight of group (µg) ± SE	mean weight of individual (µg)	range of weighing errors (µg)	n
egg (100)	68 0 ± 0 01	0 7	± 0 001	3 x 100
larva (50)	92 5 ± 0 07	1 9	± 0 002	3 x 50
protonymph (50)	105 0 ± 0 16	2 1	± 0 001	3 x 50
deutonymph (50)	182 5 ± 0 16	3 7	± 0 001	3 x 50
adult ♀ (50)	490 0 ± 0 50	9 8	± 0 040	3 x 50

Table 3a Influence of feeding history and prey density on predation rate of *N idaeus* (Fonseca) (prey individuals killed)

	low density								high density							
Prey age	starved females				fed females				starved females				fed females			
	n	D_i[1]	means ± SE		n	D	means ± SE		n	D_i	means ± SE		n	D	means ± SE	
eggs	32	12 5	10 9±0 5	D	38	10 9	9 6±0 5	D	37	59 9	25 2±1 8	BC	36	62 1	31 2±1 6	AB
larvae	19	10 0	9 5±0 4	D	18	10 0	8 2±0 7	D	11	40 0	35 2±1 4	AB	19	40 0	37 7±0 6	A
nymphs	16	10 0	8 5±0 4	D	20	10 0	8 6±0 4	D	11	40 0	20 4±2 7	C	20	40 0	30 8±1 1	AB
adult	12	10 0	1 8±0 5	F	16	10 0	1 1±0 2	F	13	30 0	4 5±0 6	E	16	40 0	1 6±0 3	F
TOTAL	79	11 0	8 7±0 4		92	10 2	7 6±0 4		72	48 2	22 6±1 5		91	48 6	26 8±1 4	

Means which are followed by the same letter are not significantly different (REGW multipler F-test)

Table 3b Analysis of variance for data on influence of feeding history and prey density on predation rate of *N idaeus* (Fonseca) (prey individuals killed)

Source of variation	*df*	Mean squares	*F*-Value	*P*
Prey age	3	54 6	390 2	<0 0001
Feeding history	1	0 3	2 4	>0 05
Density	1	59 4	424 9	<0 0001
Prey age*Feeding history	3	1 8	12 6	<0 0001
Prey age*density	3	2 0	14 2	<0 0001
Feeding history*density	1	0 4	2 8	>0 05
Feeding history*prey age*density	3	0 7	4 8	<0 003
Error	322	0 1		

[1] D_i = initial density

Table 3c Coeffecients of variance of data grouped in prey density and feeding history

	High density	Low density
Fed predators	11 1	18 8
Starved Predators	16 6	14 2

Table 4a Mean consumption by the phytoseiids *N idaeus*, *T limonicus* and *T manihoti* of various prey stages of the tetranychid *M caribbeanae*

Prey age	N idaeus (Petrolina)				N idaeus (Fonseca)				T limonicus				T manihoti			
	n	[2]D1	means±SE		n	D	means±SE		n	D	means±SE		n	D	means±SE	
eggs	13	61 3	27 8±4 2	E	36	61 1	29 9±1 6	DE	19	71 4	59 6±3 2	AB	14	71 7	46 9±6 2	BCD
larvae	7	100	58 1±4 9	AB	10	100	76 3±3 1	A	6	100	73 0±6 0	AB	7	100	55 6±6 4	AB
nymphs	18	40	28 3±1 4	DE	20	40	30 8±1 1	CDE	21	50	45 6±1 1	BC	12	50	22 9±2 0	E
adults	14	15	1 3±0 4	G	8	15	0 6±0 3	G	10	15	3 5±0 4	F	14	15	6 1±0 8	F
TOTAL	52	46 8	24 9±2 8		74	56 1	33 3±2 4		56	56 4	45 8±3 2		47	63 8	29 9±3 4	

Means followed by the same letter are not significantly different (REGW multiple F-test)

Table 4b Analysis of variance table for data on mean consumption by the phytoseiids *N idaeus* *T limonicus* and *T manihoti* of various prey stages of the tetranychid *M caribbeanae*

Source of variation	*df*	Means of square	*F*-Value	*P*
Strain	3	3 6	24 4	<0 0001
Prey age	3	78 3	537 4	<0 0001
Specie*Prey age	9	1 6	10 9	<0 0001
Error	213	0 2		

[2]D_1 = Initial density

Table 5 List of six treatments of the phytoseiid species *N idaeus* (strains of Petrolina and Fonseca) *T limonicus* and *T manihoti*

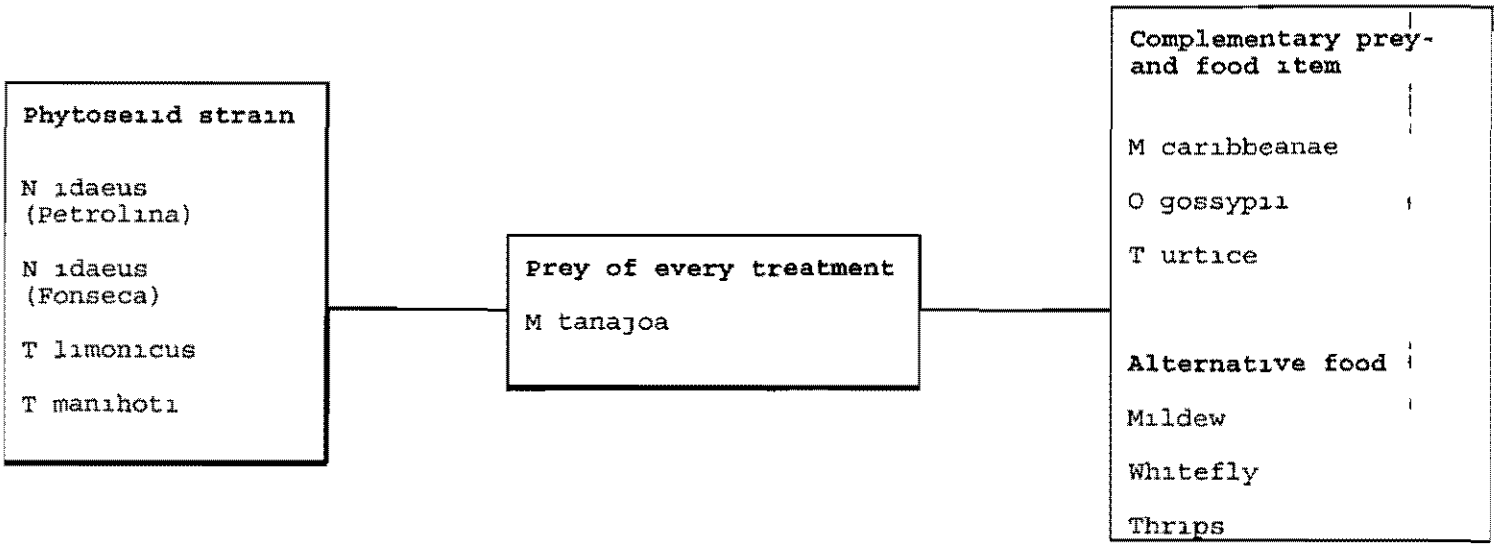


Table 6 Means of consumption of phytoseiids on acarine prey (all treatments, prey density 50 nymphs when alternative food was included 100 nymphs when two tetranychid species were offered) during 24 hours

Phytoseiid species	n	means ± SE
T limonicus	73	33 0 ± 2 2
N idaeus (Petrolina)	74	28 2 ± 1 8
N idaeus (Fonseca)	76	28 9 ± 1 7
T manihoti	80	26 9 ± 1 8
TOTAL	303	29 3 ± 0 9

Means were not significantly different

Table 7a Mean consumption of *N idaeus* *T limonicus* and *T manihoti* on prey combinations of *M tanajoa* with *M caribbeanae* *O gossypii* and *T urticae* (each prey species was offered with 50 protonymphs = high density)

	M tanajoa +									
	M caribbeanae			*O gossypii*			*T urticae*			
Phytoseiid species	n	x ± SE		n	x ± SE		n	x ± SE		
N idaeus (Petrolina)	11	34 5 ± 7 0		5	24 4 ± 3 3		11	24 5 ± 3 9		ns
N idaeus (Fonseca)	11	41 8 ± 3 3	A	5	30 0 ± 3 3	B	12	24 8 ± 4 0	B	*
T limonicus	10	50 5 ± 7 1		5	37 8 ± 7 8		11	37 5 ± 5 2		ns
T manihoti	11	40 9 ± 3 6	A	6	42 3 ± 3 7	A	12	24 0 ± 5 2	B	****
TOTAL	43	41 7 ± 2 9	A[1]	21	34 0 ± 3 2	AB	46	27 5 ± 2 9	B	**

[1] Means in each row followed by the same letter are not significantly different (REGW multiple F-test)

ns = not significant
* = P < 0 05
** = P < 0 01
*** = P < 0 001
**** = P < 0 0001

Table 7b Analysis of variance for data on consumption of *N idaeus*, *T limonicus* and *T manihoti* on prey combinations of *M tanajoa* with *M caribbeanae* *O gossypii* and *T urticae* (each prey species was offered with 50 protonymphs = high density)

Source of variation	*df*	Mean squares	*F*-Value	*P*
Phytoseiid strain (1)	3	1 0	1 8	>0 05
Prey species (2)	2	3 3	5 9	<0 01
(1) * (2)	6	2 7	0 8	>0 05
Error	97	0 6		

Table 8a Consumption by *N idaeus*, *T limonicus* and *T manihoti* of prey combinations consisting of *M tanajoa* and the alternative food items *O manihotis* *A socialis* und *F williamsi*

	M tanajoa +					
	O manihotis		*A socialis*		*F williamsi*	
Phytoseiid species	n	x ± SE	n	x ± SE[1]	n	x ± SE
N idaeus(Petrolina)	16	31 6 ± 3 6	16	26 5 ± 3 6	15	25 6 ± 3 4
N idaeus (Fonseca)	16	27 7 ± 3 5	17	27 0 ± 3 6	16	27 8 ± 3 0
T limonicus	15	31 3 ± 4 5	17	21 0 ± 4 3	15	32 6 ± 3 4
T manihoti	19	23 7 ± 4 4	15	21 5 ± 3 2	16	22 7 ± 3 7
TOTAL	66	28 3 ± 0 1	65	23 9 ± 1 8	62	27 1 ± 1 7

Table 8b Analysis of variance for data on consumption by *N idaeus*, *T limonicus* and *T manihoti* of prey combinations consisting of *M tanajoa* and the alternative food items *O manihotis* *A socialis* und *F williamsi*

Sources of variation	*df*	Mean squares	*P*-Value	*P*
Phytoseiid strain (1)	3	1 5	1 7	>0 05
Alternative food item (2)	2	1 2	1 4	>0 05
(1) * (2)	6	0 4	0 5	>0 05
Error	181			

Table 9a Mean values of surviving individuals of the prey species *M caribbeanae*, *O gossypii* and *T urticae* during an observation period of 24 hours (50 individuals of each species as initial density)

	M caribbeanae			*O gossypii*			*T urticae*			TOTAL		
Phytoseiid species	n	means ± SE		n	means ± SE		n	means ± SE		n	means ± SE	
N idaeus (Petrolina)	19	15 8 ± 1 6		11	24 9 ± 4 1		18	35 1 ± 2 3		48	25 1 ± 1 9	A[1]
N idaeus (Fonseca)	17	13 3 ± 1 2		10	24 4 ± 3 9		19	34 1 ± 2 4		46	24 2 ± 2 0	A
T limonicus	17	8 4 ± 1 2		11	19 4 ± 3 0		20	25 9 ± 2 6		48	18 2 ± 1 7	B
T manihoti	19	11 7 ± 1 5		12	25 8 ± 3 0		20	24 5 ± 3 2		51	20 0 ± 1 8	B
TOTAL	72	12 3 ± 1 5	C	44	23 6 ± 1 7	B	77	29 9 ± 1 4	A			

[1] Means followed by the same letter are not significantly different (REGWF multiple F-test)

Table 9b Mean values of surviving individuals of the prey species *M tanajoa* in combination with the tetranychid species *M caribbeanae*, *O gossypii* and *T urticae* during an observation period of 24 hours (50 individuals of each species as initial density)

	M caribbeanae			*O gossypii*			*T urticae*			TOTAL		
Phytoseiid species	n	x ± SE		n	x ± SE		n	x ± SE		n	x ± SE	
N idaeus (Petrolina)	19	18 1 ± 1 9		11	16 3 ± 2 7		18	12 7 ± 1 8		48	15 6 ± 1 2	A[1]
N idaeus (Fonseca)	17	13 5 ± 1 9		10	11 4 ± 3 1		19	13 2 ± 2 0		46	12 9 ± 1 3	A
T limonicus	17	10 6 ± 2 0		11	7 6 ± 2 5		20	6 3 ± 1 4		48	8 1 ± 1 0	B
T manihoti	19	12 5 ± 1 5		12	13 3 ± 3 7		20	12 8 ± 2 7		51	12 8 ± 1 4	A
TOTAL	72	11 1 ± 1 8	B	44	12 2 ± 1 6	A	77	11 3 ± 2 0	A			

[1] Means followed by the same letter are not significantly different (REGWF multiple F-test)

Table 9c Analysis of variance of data on surviving individuals of the prey species *M caribbeanae, O gossypii* and *T urticae* during an observation period of 24 hours (50 individuals of each species as initial density) (refers to Table (9a)

Source of variation	*df*	Mean squares	*P*-Value	*P*
Phytoseiid strain (1)	3	1 5	5 0	<0 01
alternative tetranychid prey (2)	2	14 4	47 0	<0 0001
(1) * (2)	6	0 5	1 6	>0 05
Error	180			

Table 9d Analysis of variance for data on surviving individuals of the prey species *M tanajoa* in combination with the tetranychid species *M caribbeanae O gossypii* and *T urticae* during an observation period 24 hours (50 individuals of each species as initial density) (refers to Table 9b)

Source of variation	*df*	Mean square	*F*-Value	*P*
Phytoseiid strain (1)	3	6 1	10 1	<0 0001
alternative tetranychid prey (2)	2	2 0	3 3	<0 05
(1) * (2)	6	0 3	0 4	>0 05
Error	180			

Table 10 T-test comparisons between means of alive CGM and alternative prey species (comparing Tables 9a and 9b)

Phytoseiid species	*M caribbeanae*	*O gossypii*	*T urticae*
N idaeus (Petrolina)	ns	ns	****
N idaeus (Fonseca)	ns	**	****
T limonicus	ns	**	****
T manihoti	ns	**	*

ns = not significant
* = P<0 05
** = P<0 01
**** = P<0 0001

Table 11a Consumption of *N idaeus T limonicus* and *T manihoti* on *Frankliniella williamsi* (thrips) in combination with *M tanajoa* at high density

Phytoseiid species	N	consumed thrips means ± SE	
N idaeus (Petrolina)	15	0 4 ± 0 2	A[1]
N idaeus (Fonseca)	16	0 2 ± 0 1	A
T limonicus	11	1 5 ± 0 4	B
T manihoti	17	1 7 ± 0 9	B

[1] Means followed by the same letter are not significantly different

Table 11b Analysis of variance on data for consumption of *N idaeus, T limonicus* and *T manihoti* on *Frankliniella williamsi* (thrips) in combination with *M tanajoa* at high density

Source of variation	*df*	Mean square	*F*-Value	*P*
Phytoseiid strain	3	2 2	11 0	<0 0001
Error	64	0 2		

Table 12 Influence of the presence of CGM on the feeding rate of phytoseiids on tetranychids (t-tests)

	M caribbeanae					*T urticae*				
	with *M tanajoa*		without *M tanajoa*			with *M tanajoa*		without *M tanajoa*		
	n	means ± SE	n	means ± SE	t-test	n	means ± SE	n	means ± SE	t test
N idaeus (Petrolina)	47	25 5±1 9	38	19 4±1 9	*	43	15 0±1 3	47	14 7±0 9	ns
N idaeus (Fonseca)	44	30 0±2 2	41	22 6±1 8	**	46	24 1±1 6	44	12 6±1 2	***
T limonicus	50	47 0±1 3	49	35 7±2 0	***	45	33 1±2 3	48	21 5±1 8	**
T manihoti	40	32 3±2 9	44	24 0±2 4	*	42	31 5±2 0	45	24 2±1 5	*
TOTAL	181	34 0±1 2	172	25 2±1 1	***	176	26 0±1 1	184	18 3±0 8	***

ns = not significant
* = P < 0 05
** = P < 0 001
*** = P < 0 0001

Table 13a Means of phytoseiid consumption of thrips (killed larvae)

	with M. tanajoa		only thrips	
Phytoseiid species	n	means ± SE	n	means ± SE
N. idaeus (Brazil)	39	0.4 ± 0.1 C	34	1.1 ± 0.3 B
N. idaeus (Fonseca)	27	0.6 ± 0.4 C	32	0.7 ± 0.2 B
T. limonicus	42	1.9 ± 0.3 B	46	2.3 ± 0.3 A
T. manihoti	45	3.1 ± 0.3 A	41	3.4 ± 0.3 A
TOTAL	153	1.6 ± 0.2	153	2.0 ± 0.2

[1] Means in every column which are followed by the same letter are not significantly different (P<0.0001, REGW multiple F-test)

Table 13b Analysis of variance for data on consumption of thrips (killed larvae)

Source of variance	*df*	Mean square	*F*-Value	*P*
Phytoseiid strain	3	16.6	46.1	<0.0001
Error	302	0.4		

Table 13c Influence of presence of CGM on phytoseiid feeding rate on thrips larvae (t-test, means are shown in Table 14b)

Phytoseiid strain	*P*
N. idaeus (Petrolina)	*
N. idaeus (Fonseca)	ns
T. limonicus	ns
T. manihoti	ns
TOTAL	ns

ns = not significant
* = P < 0.05

Table 14a Means of killing rate of phytoseiids on CGM in presence of non-acarine food

	Whitefly			Oidium			Thrips		
Phytoseiid species	n	means ± SE		n	means ± SE		n	means ± SE	
N idaeus (Brazil)	39	4 4 ± 0 5	BCD[1]	33	3 9 ± 0 5	CD	42	5 6 ± 0 4	ABC
N idaeus (Fonseca)	45	4 3 ± 0 4	BCD	41	5 4 ± 0 5	ABCD	37	5 2 ± 0 6	BCD
T limonicus	27	2 9 ± 0 5	D	38	5 1 ± 0 6	BCD	45	7 2 ± 0 5	AB
T manihoti	39	4 6 ± 0 4	BCD	32	4 8 ± 0 4	ABCD	45	7 6 ± 0 4	A

[1] Means which are followed by the same letter are not significantly different

Table 14b Analysis of variance for data on feeding rate of phytoseiids on CGM in presence of non-acarine food

Source of variation	*df*	Mean square	*F*-value	*P*
Phytoseiid strain (1)	3	1 5	3 0	<0 03
Alternative non-acarine food items (2)	2	6 9	13 9	<0 0001
(1) * (2)	6	1 3	2 6	<0 02
Error	451	0 5		

Table 15a Mean survival of CGM after exposure to phytoseiids during 24 hours CGM was offered at low density (= 10 protonymphs)

	whitefly			oidium			thrips			M caribb			T urticae		
Specie	n	means ± SE		n	means ± SE		n	means ± SE		n	means ± SE		n	means ± SE	
N idaeus (Brazil)	39	4 5±0 5	AB[1]	41	5 3±0 5	AB	44	3 4±0 5	ABC	47	3 8±0 5	ABC	45	3 9±0 4	AB
N idaeus (Fonseca)	45	4 1±0 4	AB	40	4 2±0 6	AB	38	3 5±0 6	BC	45	3 9±0 5	AB	47	3 1±0 5	BC
T limonicus	30	5 4±0 5	A	39	4 4±0 6	AB	45	2 0±0 4	BCD	50	0 6±0 2	E	46	1 5±0 3	DE
T manihoti	42	3 6±0 2	A	33	4 2±0 4	AB	42	1 7±0 4	DE	40	3 7±0 6	ABC	42	2 7±0 4	BCD

[1] Means which are followed by the same letter are not significantly different (REGW multiple F test)

Table 15b Analysis of variance for data on mean survival of CGM associated with alternative food or prey items after exposure to phytoseiids during 24 hours

Source of variation	*df*	Mean square	*F*-Value	*P*
Phytoseiid strains (1)	3	7 6	13 0	<0 0001
Alternative food or prey item (2)	4	10 0	17 1	<0 0001
(1) * (2)	12	2 6	4 4	<0 0001
Error	820	0 6		

Table 16a Daily mean oviposition of phytoseiids on five different food items

	Whitefly			Oidium			Thrips			M caribbeanae			T urticae		
Phytoseiid species	n	means±SE		n	means±SE		n	means±SE		n	means±SE		n	means±SE	
N idaeus (Brazil)	64	0 0±0 0	G[1]	54	0 3±1 0	FG	60	0 1±0 1	FG	65	1 0±0 1	E	72	1 9±0 2	BC
N idaeus (Fonseca)	59	0 3±0 1	FG	58	0 2±0 1	FG	50	0 0±0 0	G	67	1 1±0 2	E	71	1 8±0 2	BC
T limonicus	45	0 3±0 1	FG	52	0 8±0 2	EF	71	1 4±0 2	CD	79	3 0±0 1	A	74	2 5±0 2	AB
T manihoti	61	0 2±0 1	FG	53	0 3±0 1	FG	67	2 0±0 2	BC	67	1 1±0 2	DE	70	2 3±0 2	A

[1] Means followed by the same letter are not significantly different (REGW multiple F-test)

Table 16b Analysis of variance for data on daily mean oviposition of phytoseiids on five different food items

Source of variation	*df*	Mean square	*P*-Value	*P*
Phytoseiid strain (1)	3	8 3	46 1	<0 0001
Alimentation (2)	4	23 0	127 4	<0 0001
(1) * (2)	12	2 3	12 6	<0 0001
Error	1240	0 2		

Table 17 Increasing effect of presence of *M caribbeanae* in prey combinations on density of phytoseiids in field experiment (t-test)

	N idaeus (Petrolina)	*N idaeus* (Fonseca)	*T limonicus*	*T manihoti*
whitefly	*	***	***	ns
mildew	*	*	ns	ns
thrips	ns	***	ns	**
T urticae	ns	ns	***	****

* P < 0 05
** P < 0 01
*** P < 0 001
**** P < 0 0001

Table 18 Hypothized biomass ingestion of phytoseiids consuming on various prey stages Values of consumption (Tab 4) were multiplied by weights (see Table 2) (Analysis of variance see Table 4a)

Prey age	N idaeus (Petrolina)				N idaeus (Fonseca)				T limonicus				T manihoti				
	n	means ± SE	V[1]	H[2]	n	means ± SE	V	H	n	means ± SE	V	H	n	means ± SE	V	H	
eggs	13	18 9±10 2	B	B	36	20 4±6 6	C	B	19	40 2±9 5	B	A	14	31 9±13 7	B	A	****
larvae	7	108±24 1	A	AB	10	141±18	A	A	6	135±27	A	A	7	103±31	A	B	*
nymphs	18	88 9±14 5	A	B	20	88 9±14 5	B	B	21	132±15	A	A	12	66 2±20 2	BA	C	****
adults	14	6 1±7 3	C	B	8	6 1±7 3	D	B	10	34 3±11 5	D	A	14	60 2±27 7	B	A	****
TOTAL	52	53 7±48 0	****	C	74	53 7±48 0	****	B	56	83 7±49 6	****	A	47	59 7±32 0	**	C	****

[1] V = Means in every column followed by the same letter are not significantly different (REGW multiple F-test)
[2] H = Means in every row followed by the same letter are not significantly different
* = P < 0 05
** = P < 0 001
**** = P < 0 0001

Initial prey densities
eggs (mean values) N idaeus (P) 61 3, N idaeus (F) 61 1 T limonicus 71 4 T manihoti 71 7
larvae 100
nymphs 40
adult ♀♀ 15

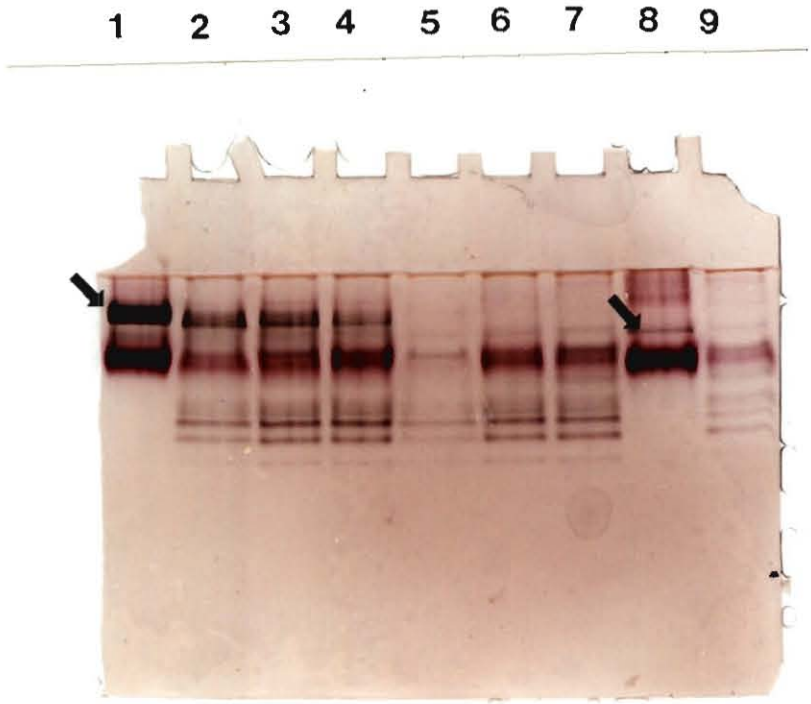


Figure 1a. Staining for esterase-isoenzymes (EST). PAGE of proteins extracted from *T. manihoti* (Cruz das Almas, Brazil) fed on *M. tanajoa* and *M. caribbeanae*. Arrows indicate marker bands of *M. tanajoa* and *M. caribbeanae* (15% homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 120 V, 120 minutes running time).

1 : *M. tanajoa*
2-4 : 3 ♀♀ of *T. manihoti* fed on *M. tanajoa*
5-7 : 3 ♀♀ fed on *M. caribbeanae*
8 : 1 ♀ of *M. caribbeanae*
9 : 3 ♀♀ of *T. manihoti* starved for 48 hours

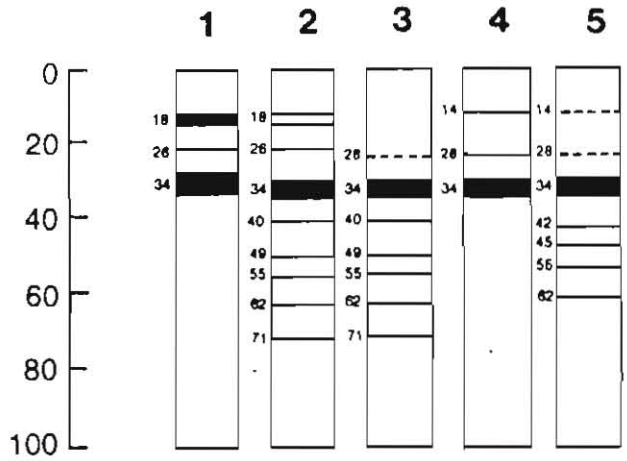


Figure 1b. Schematic illustration of Figure 1a

1 : *M. tanajoa*
2 : *T. manihoti* fed on *M. tanajoa*
3 : *M. caribbeanae*
4 : *T. manihoti* fed on *M. caribbeanae*
5 : *T. manihoti* starved for 48 hours

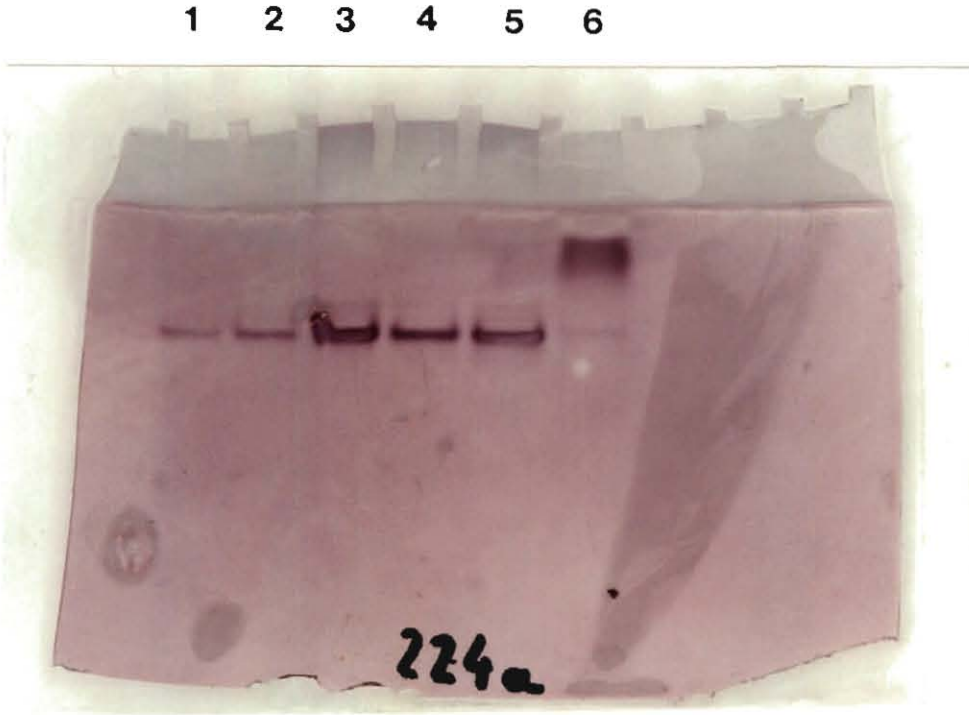


Figure 2a. Staining for malate dehydrogenase (MDH). PAGE of proteins extracted from *N. idaeus*, starved or fed with *M. caribbeanae* (12.5 % homogenous gel, 0.15 M boric acid (pH 8.2) as tank puffer, 100 V, 300 minutes running time).

1: 1 ♀ *N. idaeus* (starved for 24 hours)
2: 2 ♀♀ *N. idaeus* (starved for 24 hours)
3: 10 ♀♀ *N. idaeus* (starved for 24 hours)
4: 4 ♀♀ *N. idaeus* (starved for 24 hours)
5: 5 ♀♀ *N. idaeus* fed on *M. caribbeanae*
6: 2 ♀♀ *M. caribbeanae*

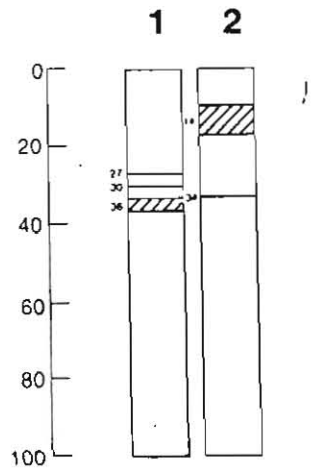


Figure 2b. Schematic illustration of Figure 2a

1: *N. idaeus* (starved or fed with *M. caribbeanae*)
2: *M. caribbeanae*

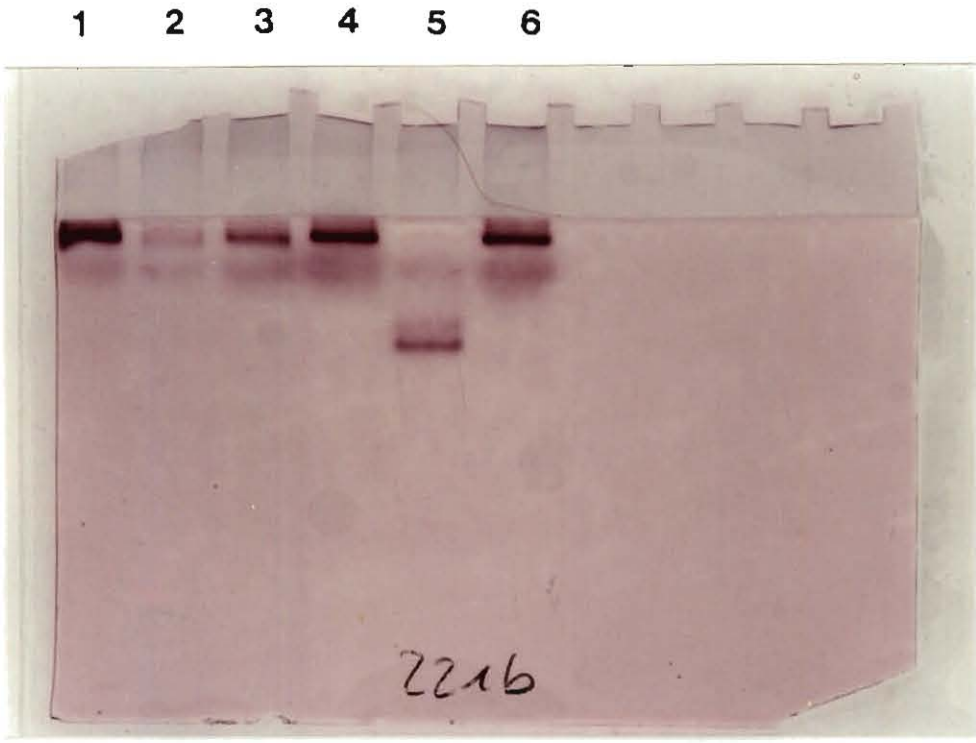


Figure 3a. Staining for phospho-gluco-isomerase (PGI). Page from proteins extracted from *N. idaeus* fed *M. caribbeanae*. 15% homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 100 V, 270 minutes running time).

1: 7 ♀♀ *N. idaeus* (starved for 24 hours)
2: 1 ♀ *N. idaeus* (starved for 24 hours)
3: 2 ♀♀ *N. idaeus* (starved for 24 hours)
4: 5 ♀♀ *N. idaeus* (starved for 24 hours)
5: 2 ♀♀ *M. caribbeanae*
6: 13 ♀♀ *N. idaeus* fed on *M. caribbeanae*

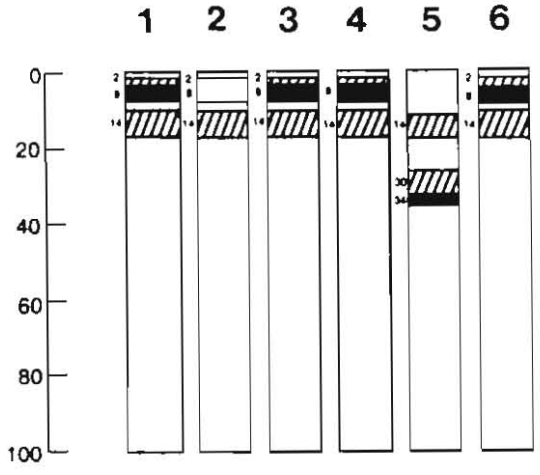


Figure 3b. Schematic illustration of Figure 3a.

1: 7 ♀♀ *N. idaeus* (starved for 24 hours)
2: 1 ♀ *N. idaeus* (starved for 24 hours)
3: 2 ♀♀ *N. idaeus* (starved for 24 hours)
4: 5 ♀♀ *N. idaeus* (starved for 24 hours)
5: 2 ♀♀ *M. caribbeanae* (starved for 24 hours)
6: 13 ♀♀ *N. idaeus* fed on *M. caribbeanae*

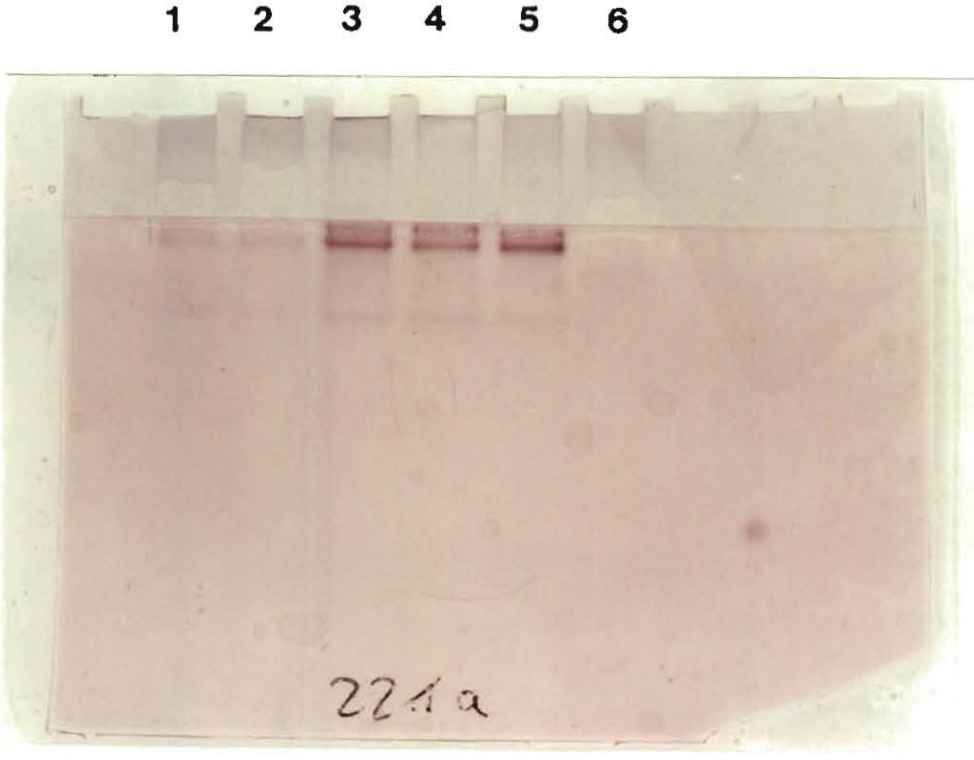


Figure 4a. Staining for phospho-gluco-isomerase (PGI). (15% homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 100 V, 270 minutes running time).
1: 1 ♀ *T. limonicus* (starved for 24 hours)
2: 2 ♀♀ *T. limonicus* (starved for 24 hours)
3: 5 ♀♀ *T. limonicus* (starved for 24 hours)
4: 5 ♀♀ *T. limonicus* (starved for 24 hours)
5: 2 ♀♀ *T. limonicus* fed on *M. caribbeanae* (gut content did not yield any visible staining)
6: 1 ♀ *M. caribbeanae*

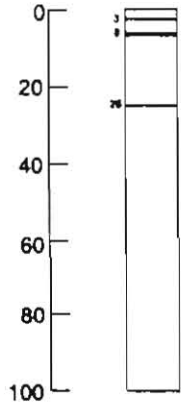


Figure 4b. Schematic illustration of Figure 4a. Represents the three treatments *T. limonicus* (starved), *M. caribbeanae*, and *T. limonicus* fed on *M. caribbeanae*

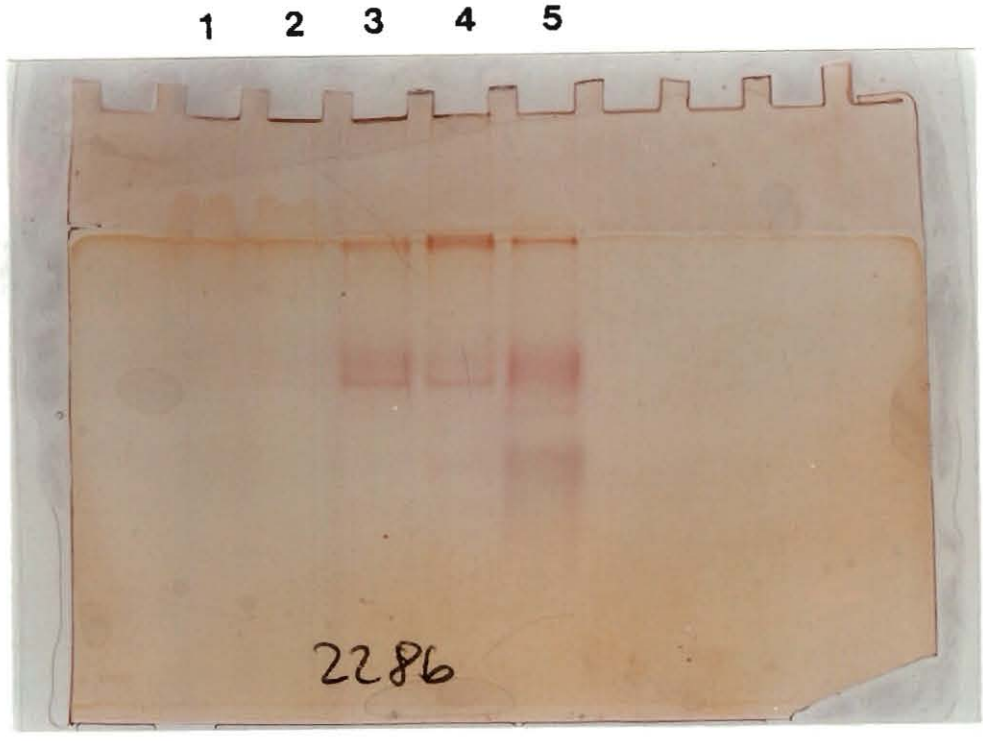


Figure 5a. Staining for acid phophatase (ACP). (15% homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 100 V, 210 minutes running time).

1: 1 ♀ *N. idaeus* (starved for 24 hours)
2: 2 ♀♀ *N. idaeus* (starved for 24 hours)
3: 7 ♀♀ *N. idaeus* (starved for 24 hours)
4: 4 ♀♀ *N. idaeus* fed on *M. caribbeanae* (gut content remained unstained)
5: 2 ♀♀ *M. caribbeanae*

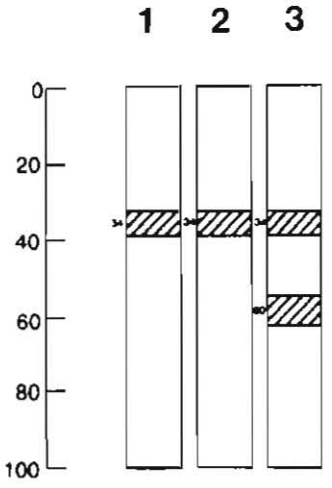


Figure 5b. Schematic illustration of Figure 5a.

1: 7 ♀♀ *N. idaeus* (starved for 24 hours)
2: 4 ♀♀ *N. idaeus* fed on *M. caribbeanae* (gut content remained unstained)
3: 2 ♀♀ *M. caribbeanae*

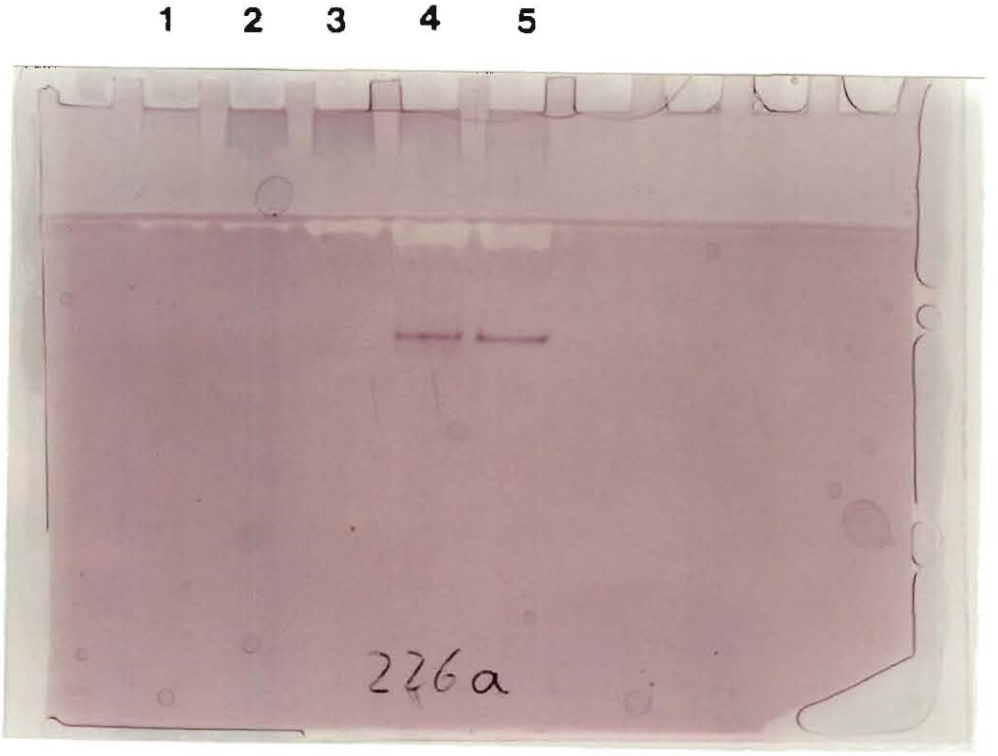


Figure 6a. Staining for malic enzyme (ME). PAGE of proteins extracted from females of *N. idaeus* fed with *M. caribbeanae* (12.5 % homogenous gel, 0.15 M boric acid (pH 8.2) as tank puffer, 100 V, 225 minutes running time).

1: 1 ♀ *N. idaeus* (starved for 24 hours)
2: 2 ♀♀ *N. idaeus* (starved for 24 hours)
3: 10 ♀♀ *N. idaeus* (starved for 24 hours)
4: 2 ♀♀ *N. idaeus* vs *M. caribbeanae*
5: 4 ♀♀ *M. caribbeanae*

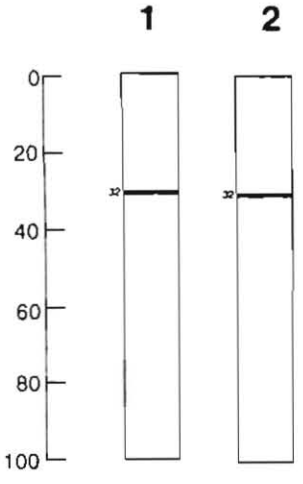


Figure 6b. Schematic illustration of Figure 6a

1: *N. idaeus* fed on *M. caribbeanae*
2: *M. caribbeanae*

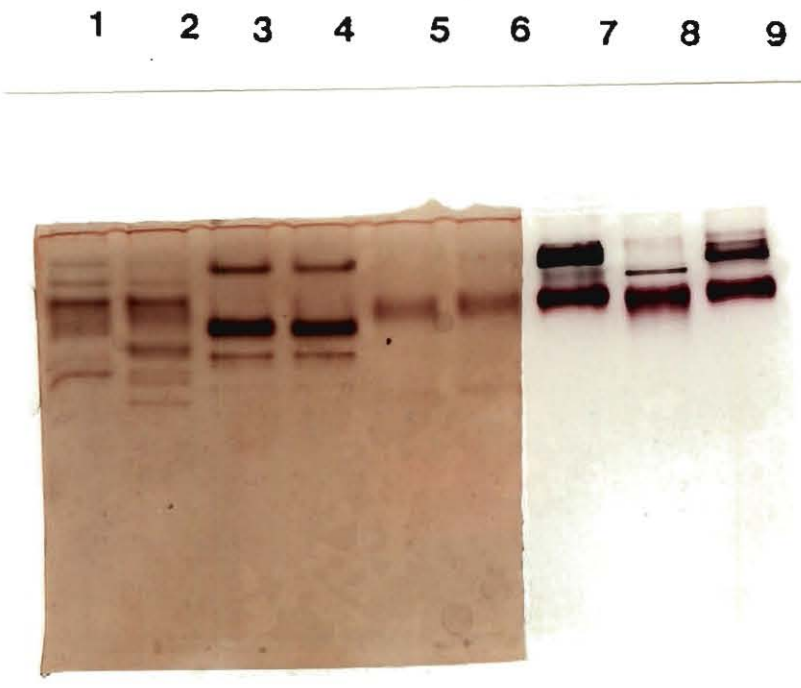


Figure 7a. Fingerprints of starved phytoseiids and tetranychids. Phytoseiids were starved for 24 hours. The phytoseiids were stained for esterase overnight, the tetranychids were stained only for three hours to avoid excessive staining (15% homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 120 V, 120 minutes running time).

1-2 : 2 ♀♀ of *T. manihoti* (Sta. Isabel)
3-4 : 2 ♀♀ of *T. limonicus* (Jaguariuna)
5-6 : 2 ♀♀ of *N. idaeus* (Fonseca)
7 : 1 ♀ of *M. tanajoa*
8 : 1 ♀ of *M. caribbeanae*
9 : 1 ♀ of *T. urticae*

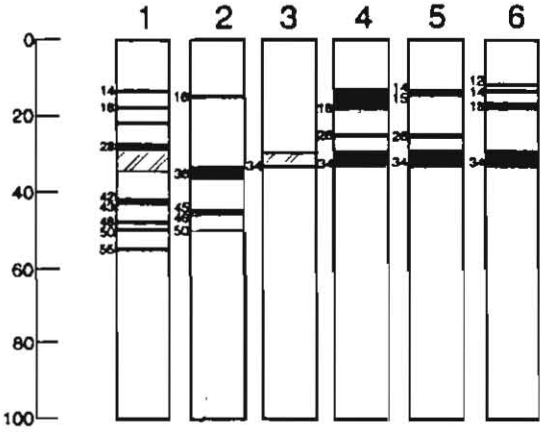


Figure 7b. Schematic illustration of Figure 7a

1: *T. manihoti* (Sta. Isabel)
2: *T. limonicus* (Jaguariuna)
3: *N. idaeus* (Fonseca)
4: *M. tanajoa*
5: *M. caribbeanae*
6: *T. urticae*

Figure 8a. Standard of *T. manihoti* (Córdoba) on different prey types I. Staining for esterase-isoenzymes (EST). 15% homogenous gel, 0.15 M Tris/Borat (pH 8.2) as tank puffer, 100 V, 240 minutes running time).

1-3 : *T. manihoti* vs *T. urticae*
4 : *T. urticae*
5-7 : *T. manihoti* vs *M. caribbeanae*
8 : *M. caribbeanae*
9-10 : *T. manihoti*, starving

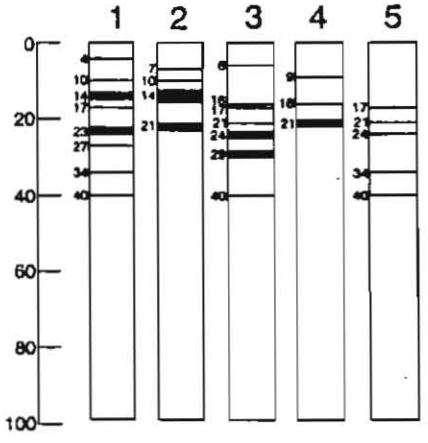


Figure 8b. Schematic illustration of Figure 8a

1: *T. manihoti* vs *T. urticae*
2: *T. urticae*
3: *T. manihoti* vs *M. caribbeanae*
4: *M. caribbeanae*
5: *T. manihoti*, starved

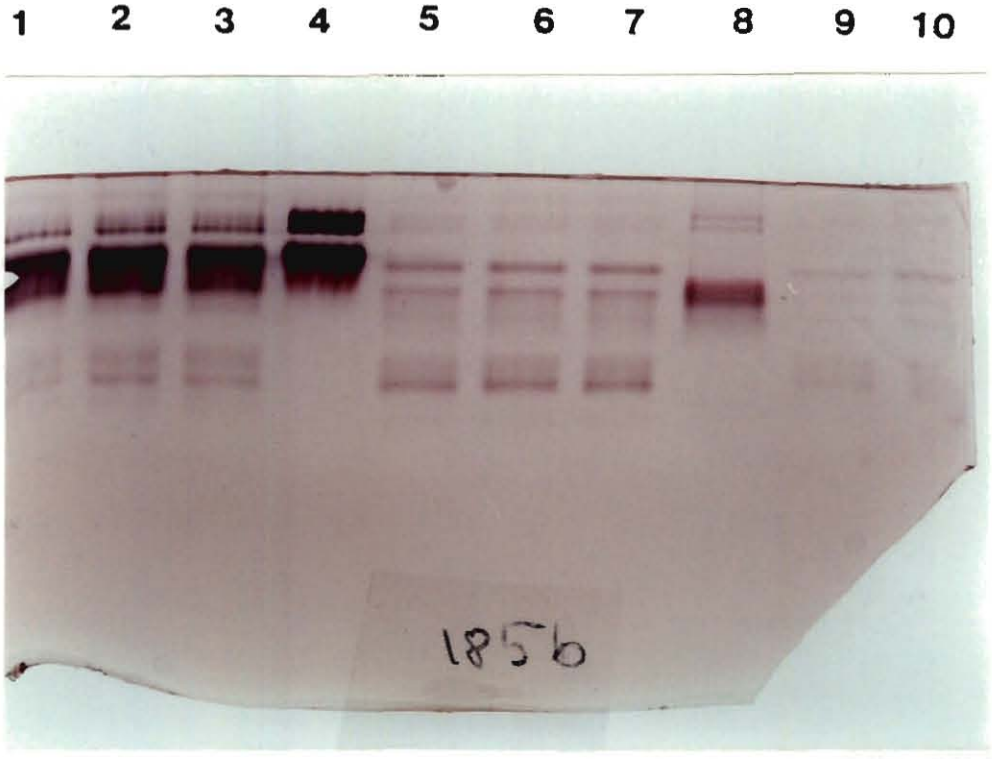


Figure 9a. Standard of *T. manihoti* (Córdoba) on different prey types II. Staining for esterase-isoenzymes (EST). 15% homogenous gel, 0.15 M Tris/Borat (pH 8.2) as tank puffer, 100 V, 240 minutes running time).

1-3 : *T. manihoti* vs *M. tanajoa*
4 : *M. tanajoa*
5-7 : *T. manihoti* vs *M. mcgregori*
8 : *M. mcgregori*
9-10 : *T. manihoti*, starving

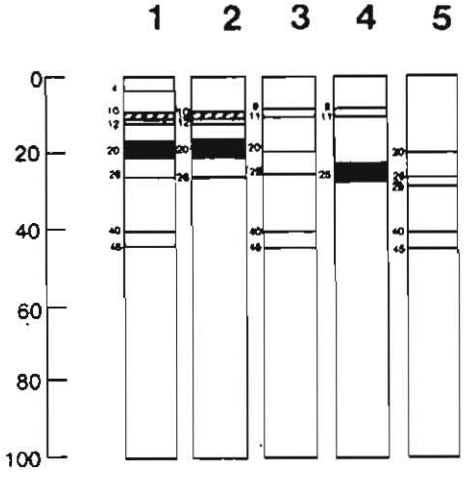


Figure 9b. Schematic illustration of Figure 9a. Note, that Tris/Borate was used as tank buffer, causing different patterns compared to the use of Tris/HCl.

1: *T. manihoti* vs *M. tanajoa*
2: *M. tanajoa*
3: *T. manihoti* vs *M. mcgregori*
4: *M. mcgregori*
5: *T. manihoti*, starved

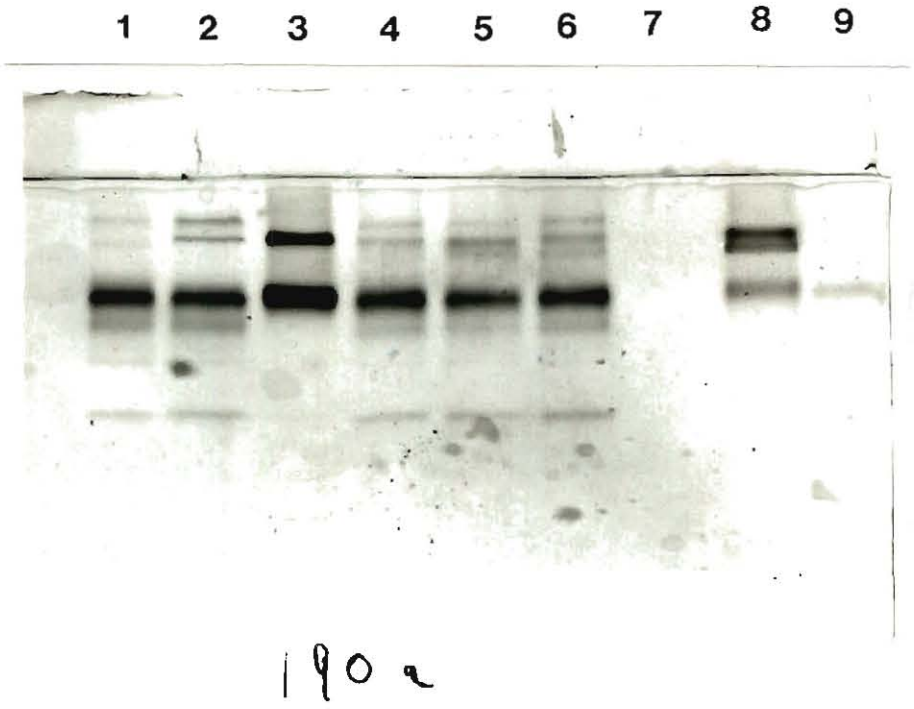


Figure 10a. Standard of *A. aerialis* on different prey types I. Staining for esterase-isoenzymes (EST). 15% homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 120 V, 120 minutes running time).

1-2 : *A. aerialis* vs *O. gossypii*
3 : *O. gossypii*
4-7 : *A. aerialis* vs *T. urticae*
7 : void
8 : *T. urticae*
9 : *A. arialis*, starving

Figure 10b. Standard of *A. aerialis* on different prey types II. Staining for esterase-isoenzymes (EST). 15% homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 120 V, 120 minutes running time).

1-3 : *A. aerialis* vs *M. tanajoa*
4 : *M. tanajoa*
5-7 : *A. aerialis* vs *M. caribbeanae*
8 : *M. caribbeanae*
9 : void
10 : *A. arialis*, starving

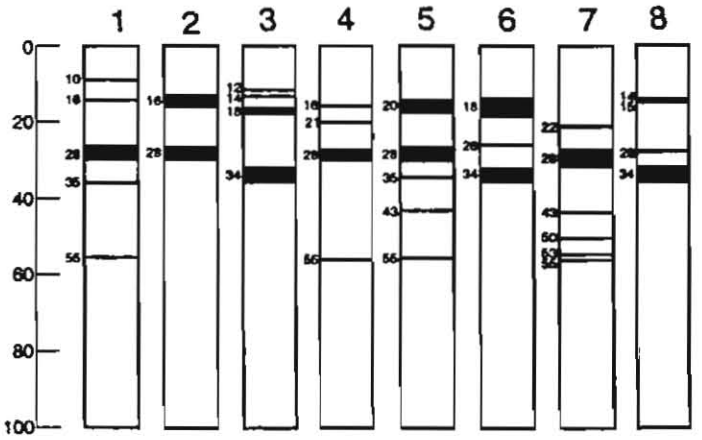


Figure 10c. Schematic illustration of Figures 10a and 10b
1: *A. aerialis* vs *O. gossypii*
2: *O. gossypii*
3: *T. urticae*
4: *A. aerialis* vs *T. urticae*
5: *A. aerialis* vs *M. tanajoa*
6: *M. tanajoa*
7: *A. aerialis* vs *M. caribbeanae*
8: *M. caribbeanae*

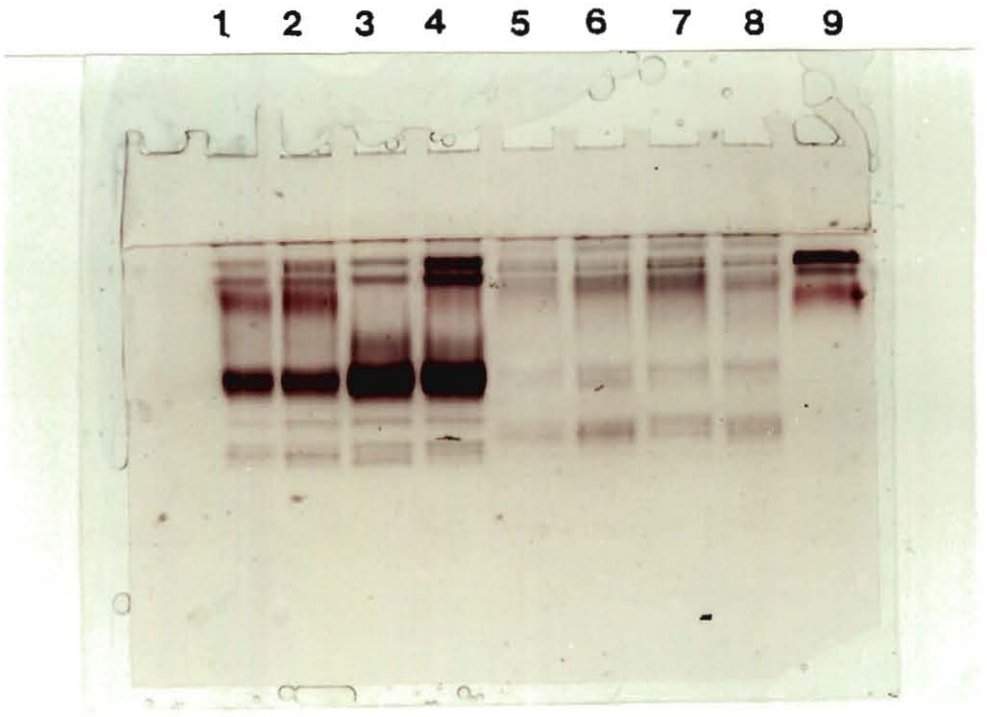


Figure 11a. Effect of strain on esterase activity of *T. manihoti* (12.5 % homogenous gel, 0.15 M boric acid (pH 8.2) as tank puffer, 100 V, 240 minutes running time).

1-4 : 2 ♀♀ *T. manihoti* (Palmira strain) fed on *M. tanajoa*
5-8 : 2 ♀♀ *T. manihoti* (Guajira strain) fed on *M. tanajoa*
9 : 1 ♀ *M. tanajoa*

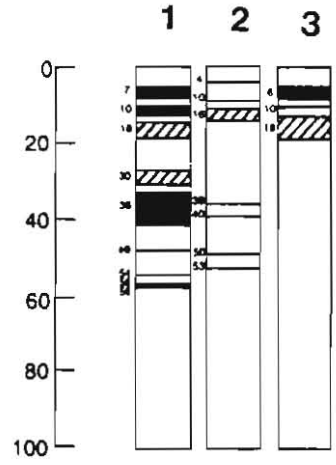


Figure 11b. Schematic illustration of Figure 12a

1: *T. manihoti* (Palmira strain) fed on *M. tanajoa*
2: *T. manihoti* (Guajira strain) fed on *M. tanajoa*
3: *M. tanajoa*

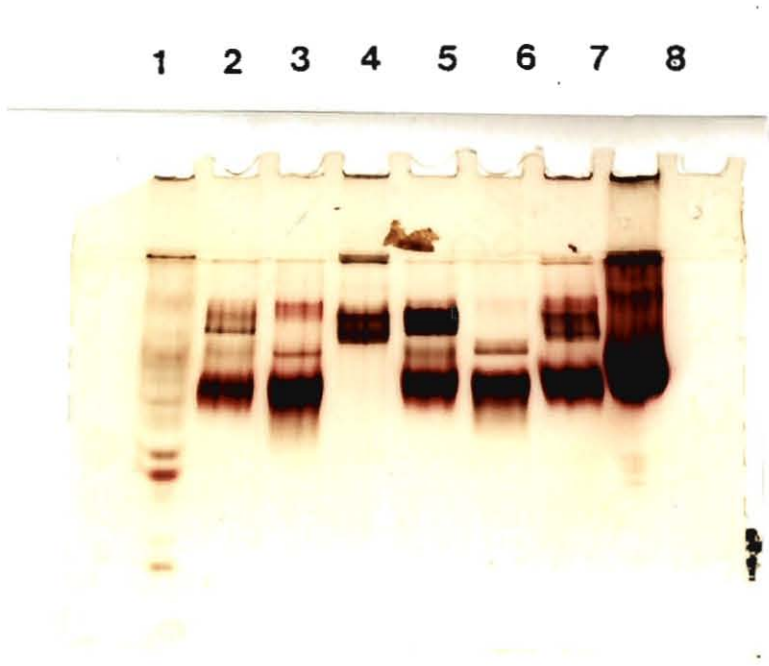


Figure 12a. Effect of the host plant on the electrophoretic esterase pattern of *M. tanajoa*, *M. caribbeanae* and *T. urticae* (clone CMC 40) (15 % homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 120 V, 120 minutes running time).

1: Bean leaf
2: *M. tanajoa* on bean
3: *M. caribbeanae* on bean
4: *T. urticae* on bean
5: *M. tanajoa* on cassava
6: *M. caribbeanae* on cassava
7: *T. urticae* on cassava
8: Cassava leaf

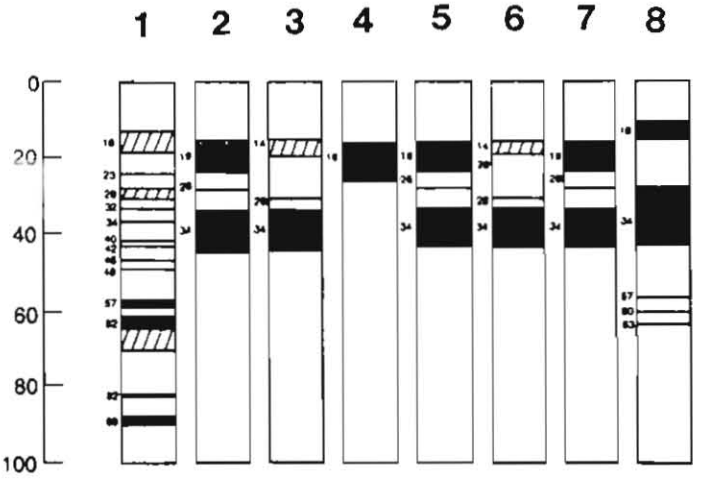


Figure 12b. Schematic illustration of Figure 13a.

1: Bean leaf
2: *M. tanajoa* on bean
3: *M. caribbeanae* on bean
4: *T. urticae* on bean
5: *M. tanajoa* on cassava
6: *M. caribbeanae* on cassava
7: *T. urticae* on cassava
8: Cassava leaf

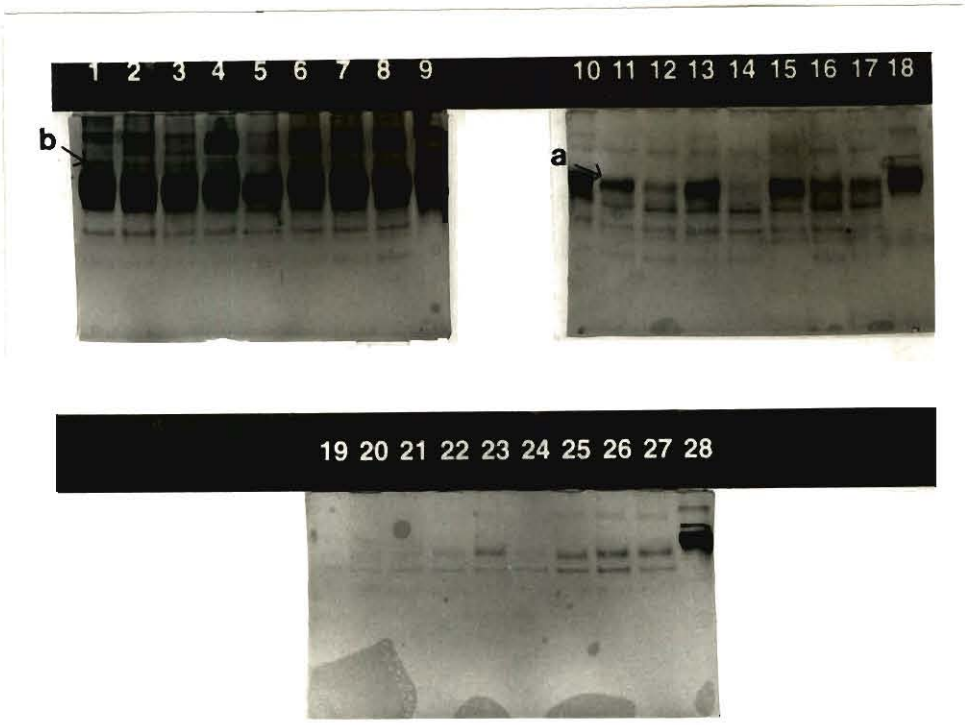


Figure 13a. Effect of starvation period on esterase activity of gut content of *T. limonicus* fed on *M. caribbeanae*. One female was processed per sample. Arrow a indicate the cassava band, arrow b the marker band of *M. caribbeanae* (15 % homogenous gel, 0.5 M Tris/HCl (pH 8.8) as tank puffer, 120 V, 120 minutes running time).

1-4 : 0 hours
5-8 : 1 hour
9 : *M. caribbeanae*
10-13 : 3 hours
14-17 : 6 hours
18 : *M. caribbeanae*
19-21 : 12 hours
22-24 : 24 hours
25-27 : 48 hours
28 : *M. caribbeanae*

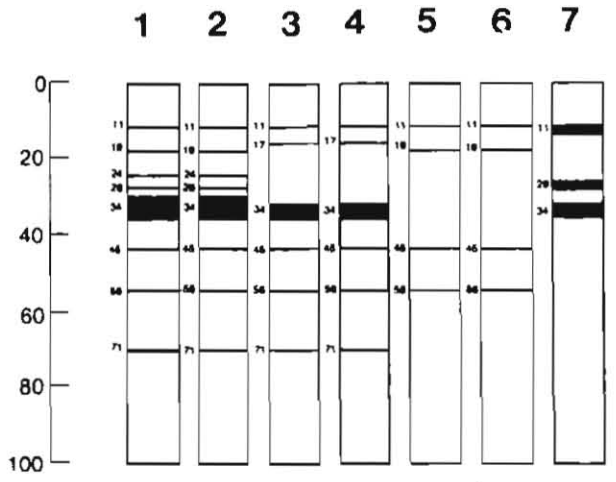
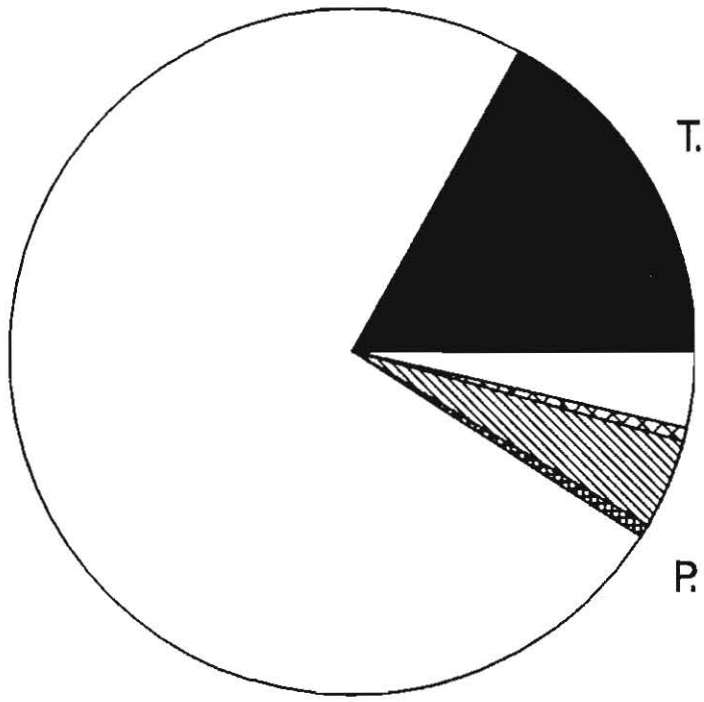


Figure 13b. Schematic illustration of Figure 14a.

1: 0 hours
2: 1 hours
3: 3 hours
4: 6 hours
5: 12 hours
6: 24 and 48 hours
7: *M. caribbeanae*



est. no.
28
6.5
1
6.5
1
123 =

Figure 14. Identification of in Ecuador collected phytoseiids using electrophoresis.

n = 166
isi = insufficient staining intensity
ni = unknown esterase pattern

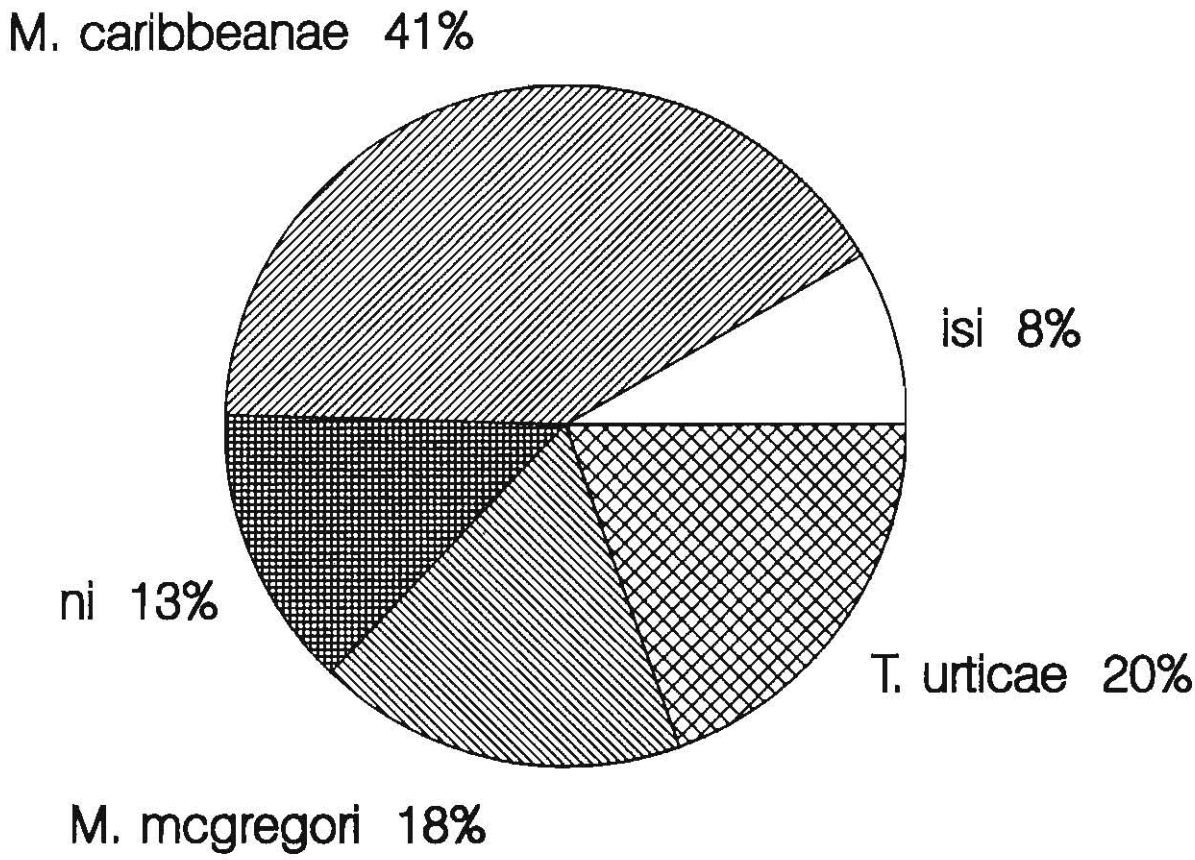


Figure 15. Identified phytophagous mites collected in Ecuador

n = 97
isi = insufficient staining intensity
ni = unknown esterase pattern

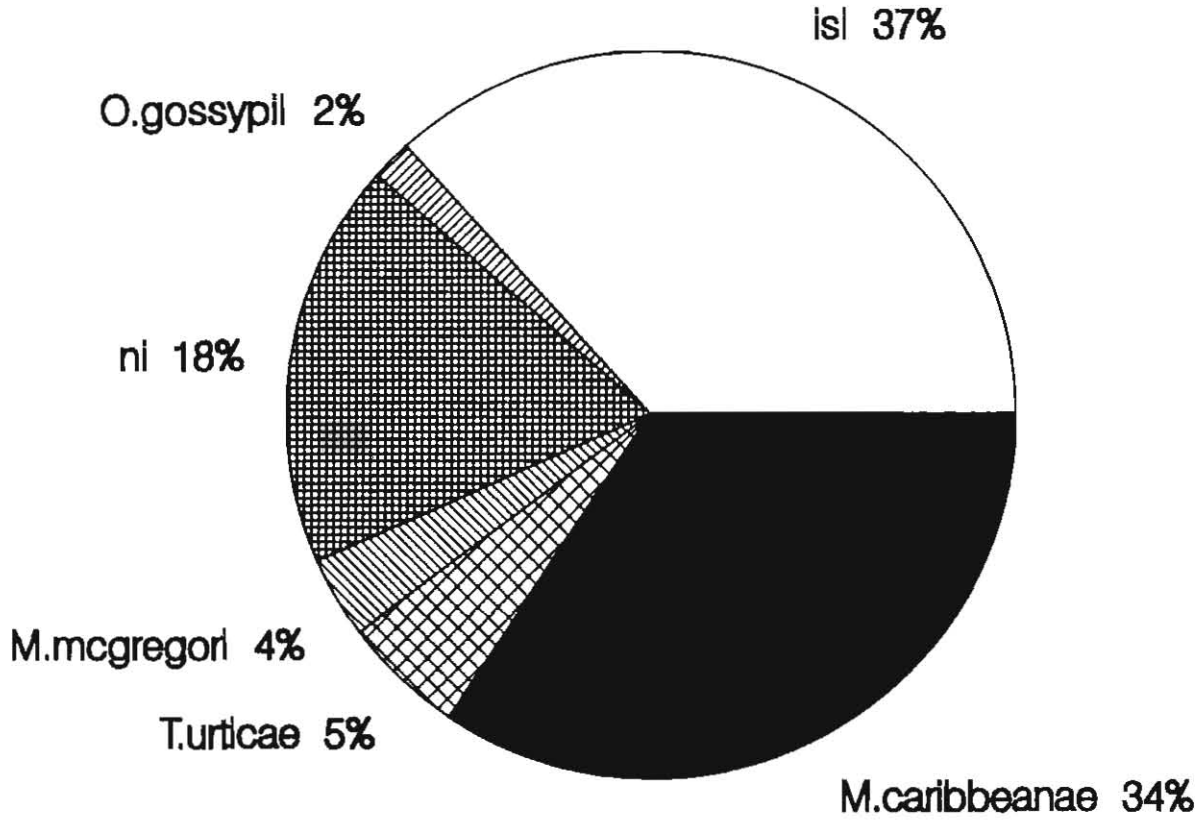


Figure 16. Fractions of gut contents of phytoseiids collected in Ecuador and identified by means of electrophoresis.

n = 166
isi = insufficient staining intensity
ni = unknown esterase pattern

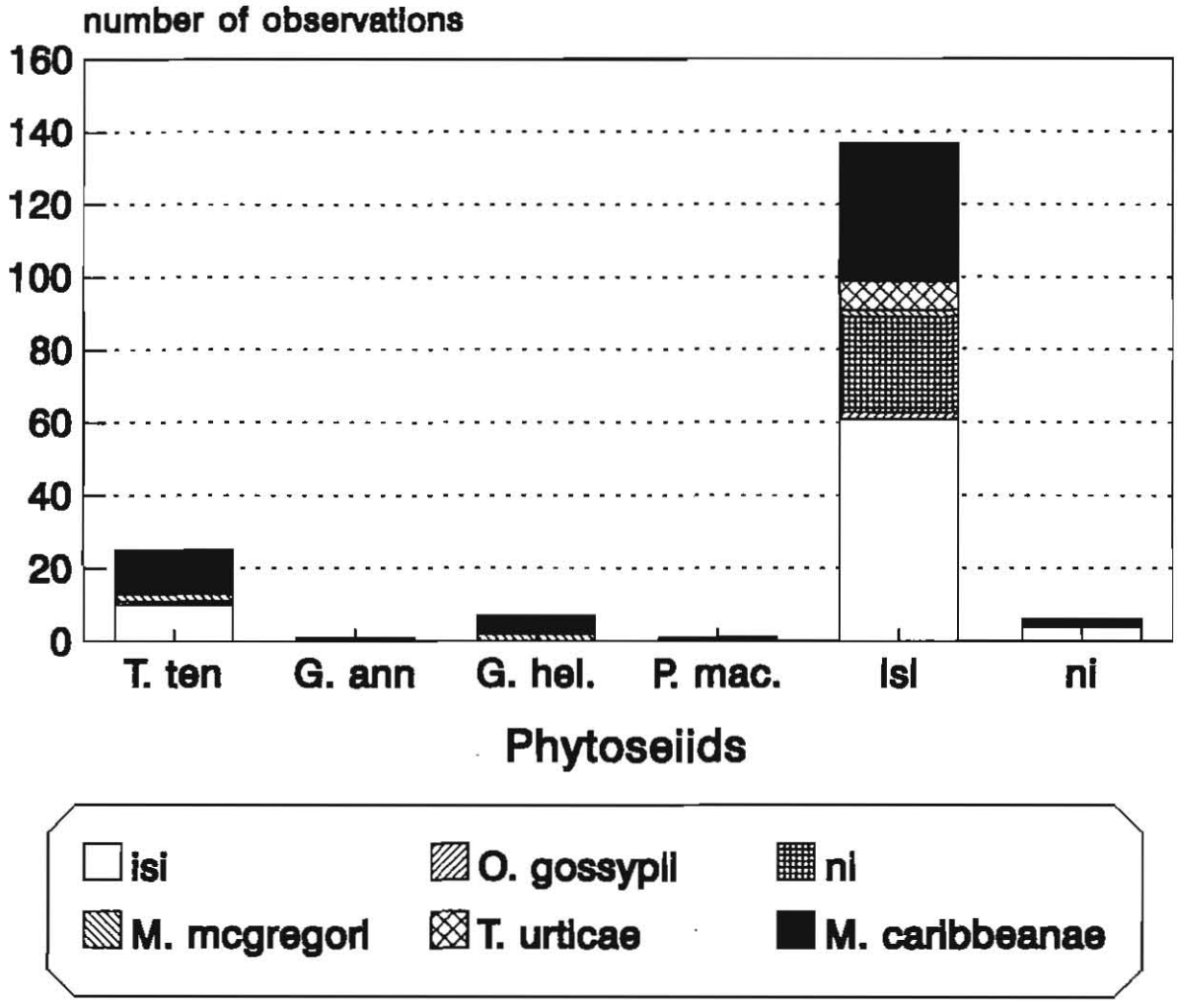


Figure 17. Gut contents of phytoseiid mites collected in Ecuador (n = 166).

Abbreviations:
T. ten = T. tenuiscutus
G. ann = G. annectens
G. hel = G. helveolus
P. mac = P. macropilis
isi = insufficient staining intensity
ni = unknown esterase pattern

LS total = 170

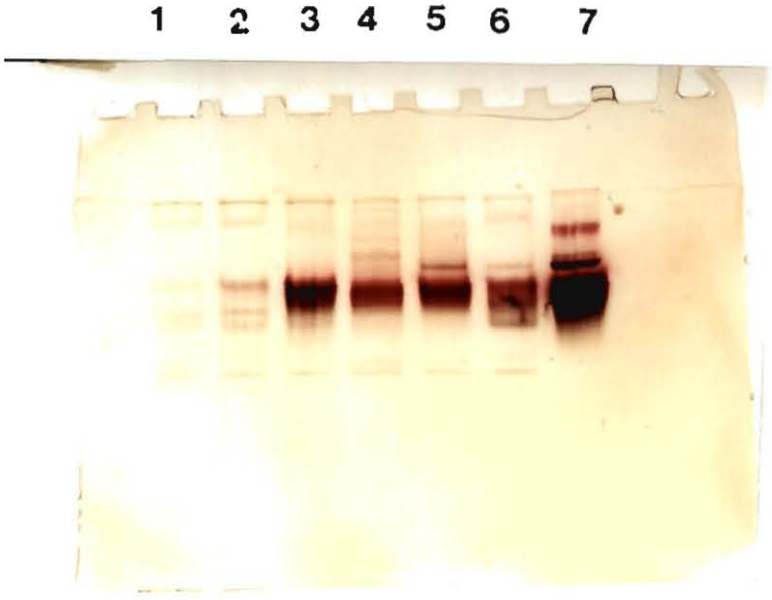


Figure 18a. Influence of prey stage on the staining intensity of the gut content of *T. manihoti* (Palmira) after feeding for five hours on different stages of *M. caribbeanae* (the females were starved for 48 hours prior to the experiment). Two females were used per sample. The number of consumed individuals and the calculated ingestion of biomass is given below (15 % homogenous gel, 0.5 M Tris/HCl (pH 8.2) as tank puffer, 120 V, 120 minutes running time).

1 : starved for 48 hours
2 : consumed 22 eggs (15 µg)
3 : consumed 21 larvae (38.9 µg)
4 : consumed 24 protonymphs (50.9 µg)
5 : consumed 11 deutonymphs (40.2 µg)
6 : consumed 3 adults (29.4 µg)
7 : 1 ♀ *M. caribbeanae*

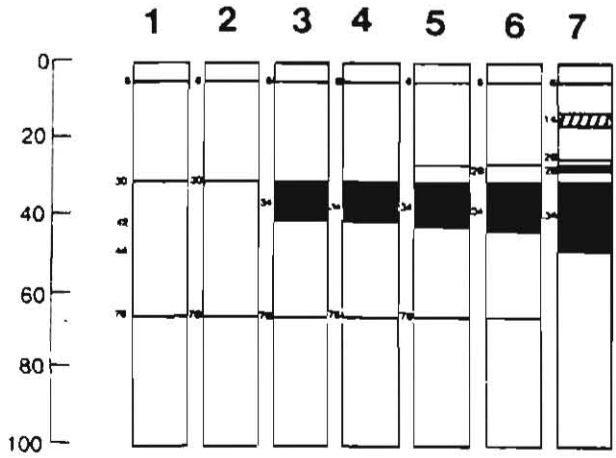


Figure 18b. Schematic illustration of Figure 19a.

1 : starved for 48 hours
2 : consumed 22 eggs (15 μg)
3 : consumed 21 larvae (38.9 μg)
4 : consumed 24 protonymphs (50.9 μg)
5 : consumed 11 deutonymphs (40.2 μg)
6 : consumed 3 adults (29.4 μg)
7 : 1 ♀ *M. caribbeanae*

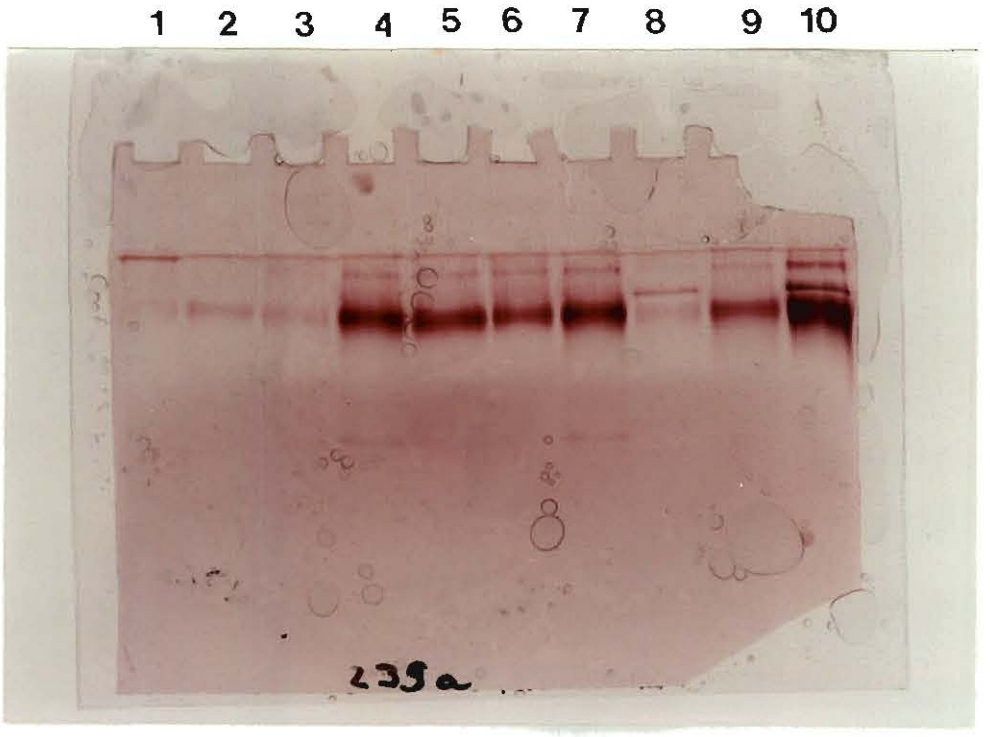


Figure 19a. Influence of consumed biomass on the staining intensity of the gut content of *T. tenuiscutus*. Larvae of *M. caribbeanae* were offered as prey (15 % homogenous gel, 0.5 M Tris/HCl (pH 8.2) as tank puffer, 120 V, 120 minutes running time). For each sample one female was processed.

1 : 2 ♀♀, starved for 24 hours
2 : consumed 2 larvae
3 : consumed 3 larvae
4 : consumed 4 larvae
5 : consumed 4 larvae
6 : consumed 8 larvae
7 : consumed 8 larvae
8 : consumed 14 larvae
9 : consumed 17 larvae
10 : *M. caribbeanae*

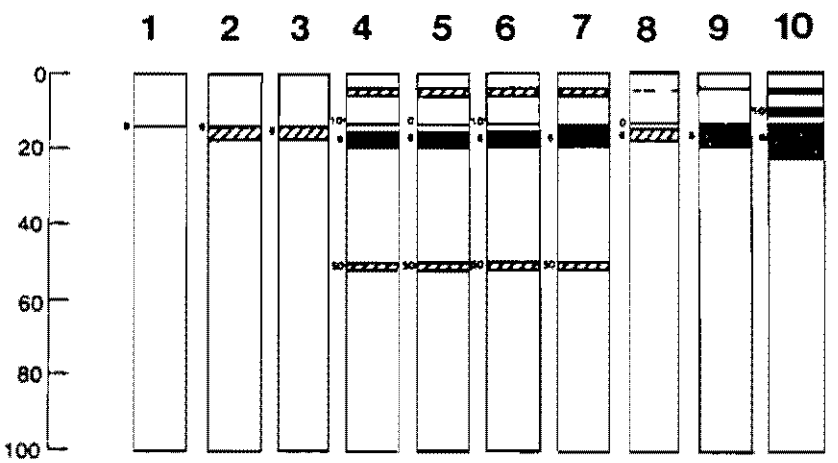


Figure 19b Schematic illustration of Figure 19a

1 2 ♀♀, starved for 24 hours
2 consumed 2 larvae
3 consumed 3 larvae
4 consumed 4 larvae
5 consumed 4 larvae
6 consumed 8 larvae
7 consumed 8 larvae
8 consumed 14 larvae
9 consumed 17 larvae
10 *M caribbeanae*

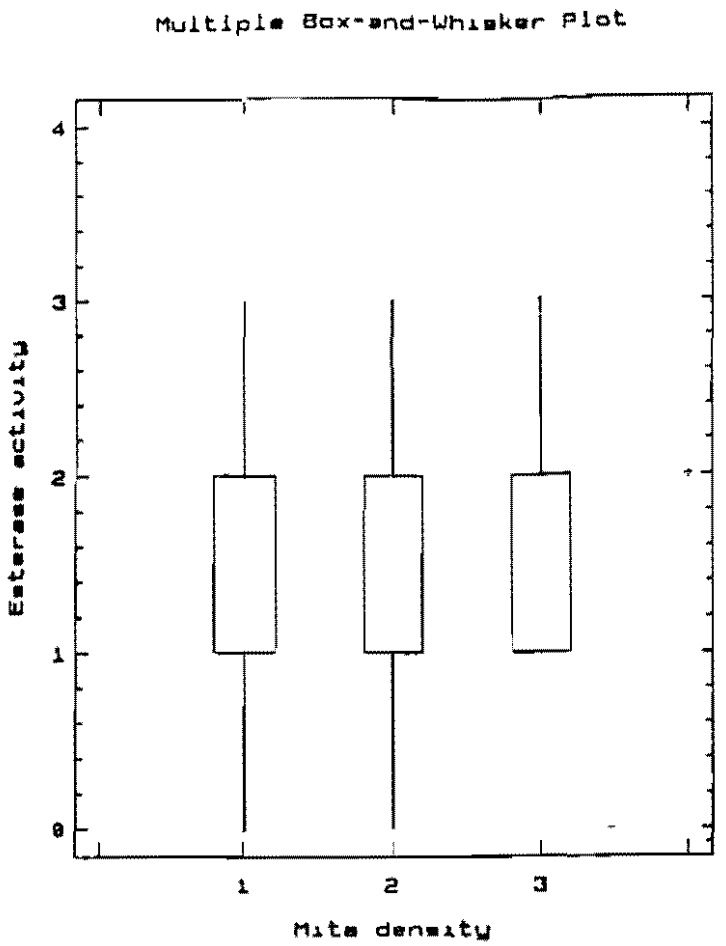


Figure 20 Effect of prey density (1 = no mites, 2 = less than 25 mites per leaf, 3 = more than 25 and less than 200 mites per leaf and 4 = more than 200 mites per leaf, Yaninek *et al* , 1989) on staining intensity (scale 0-6, where staining intensity increases from 0 (invisible) to 4 (saturated banding pattern)) of gut content n = 163

The bottom and top of the box indicate the sample 25th and 75th percentiles The center horizontal line represents the sample median The central vertical lines indicate the data range (SAS, 1989, see also Tukey, 1977) The median does not appear when it is identical with one of the lower or upper border of the box When no box appears the values were concentrated at one point Range 4 of mite density was never observed

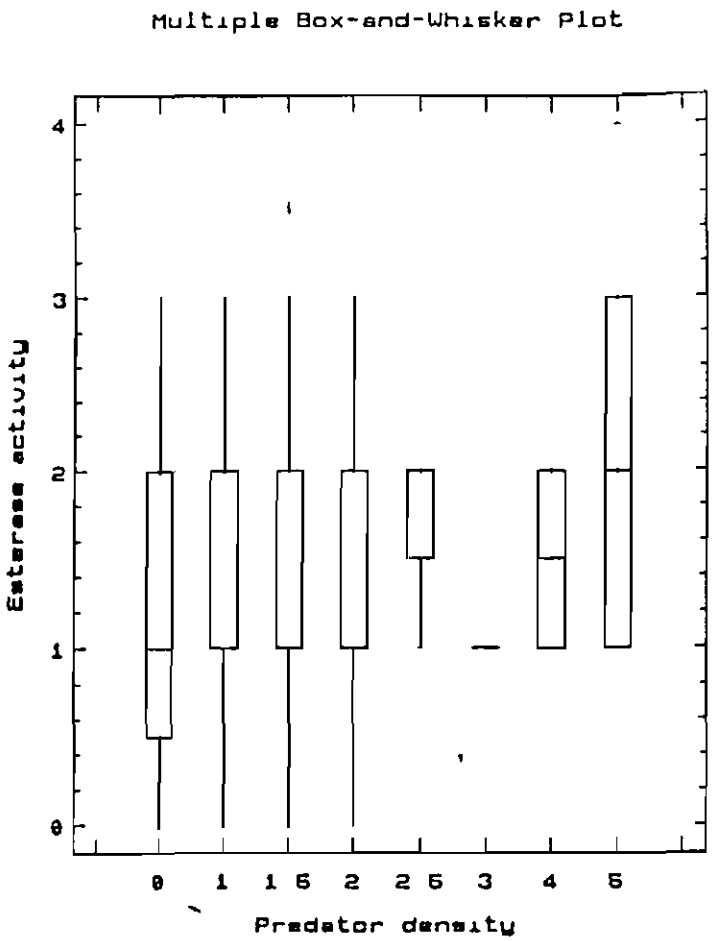


Figure 21 Effect of predator density predators (no per leaf) on staining intensity (scale 0-6, where staining intensity increases from 0 (=invisible) to 6 (=oversaturated banding pattern)) of gut content (for more explanations of "box-and-whisker-plots" see Fig 17) n = 163

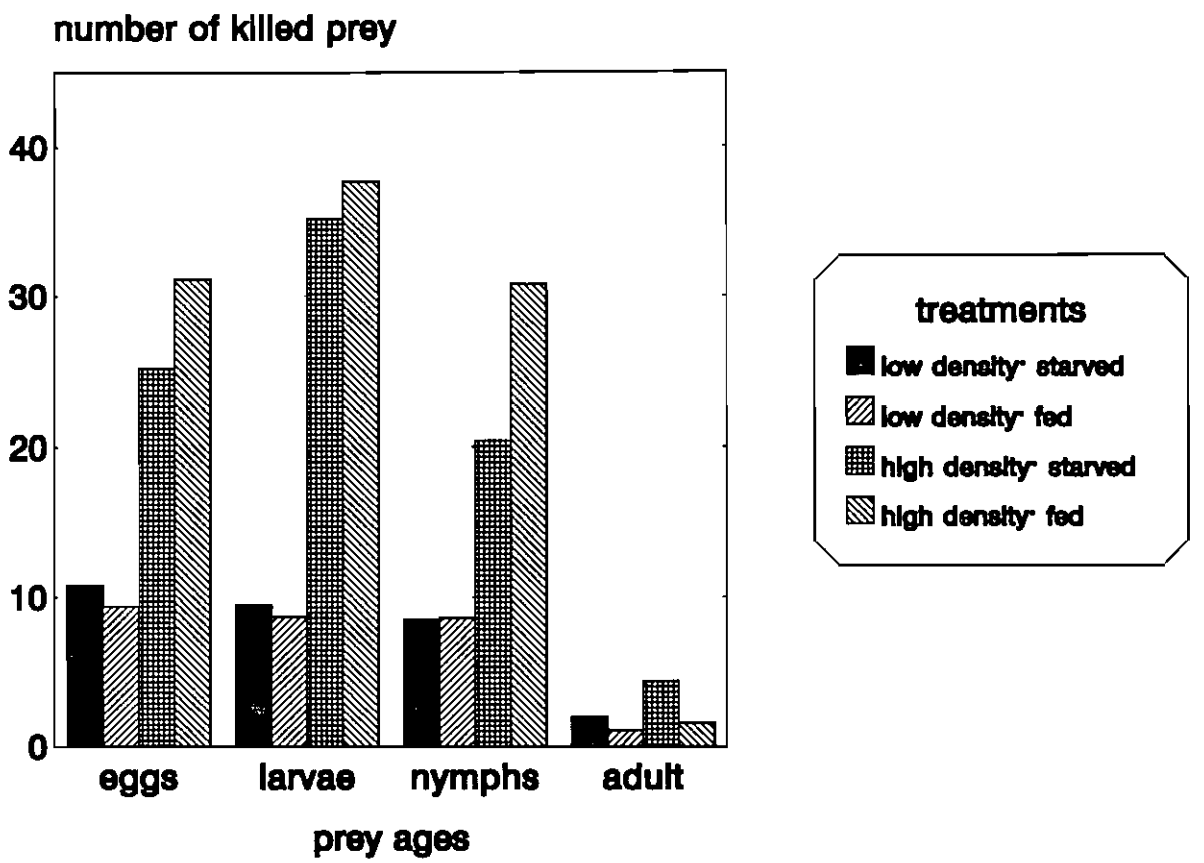


Figure 22 Influence of feeding history and prey density on killing rate of adult females of *N idaeus* (Fonseca) ($11 \leq n \leq 46$) 10 individuals of each prey stage were offered as low density, 61 eggs, 40 larvae, 40 nymphs and 30 adults as high density

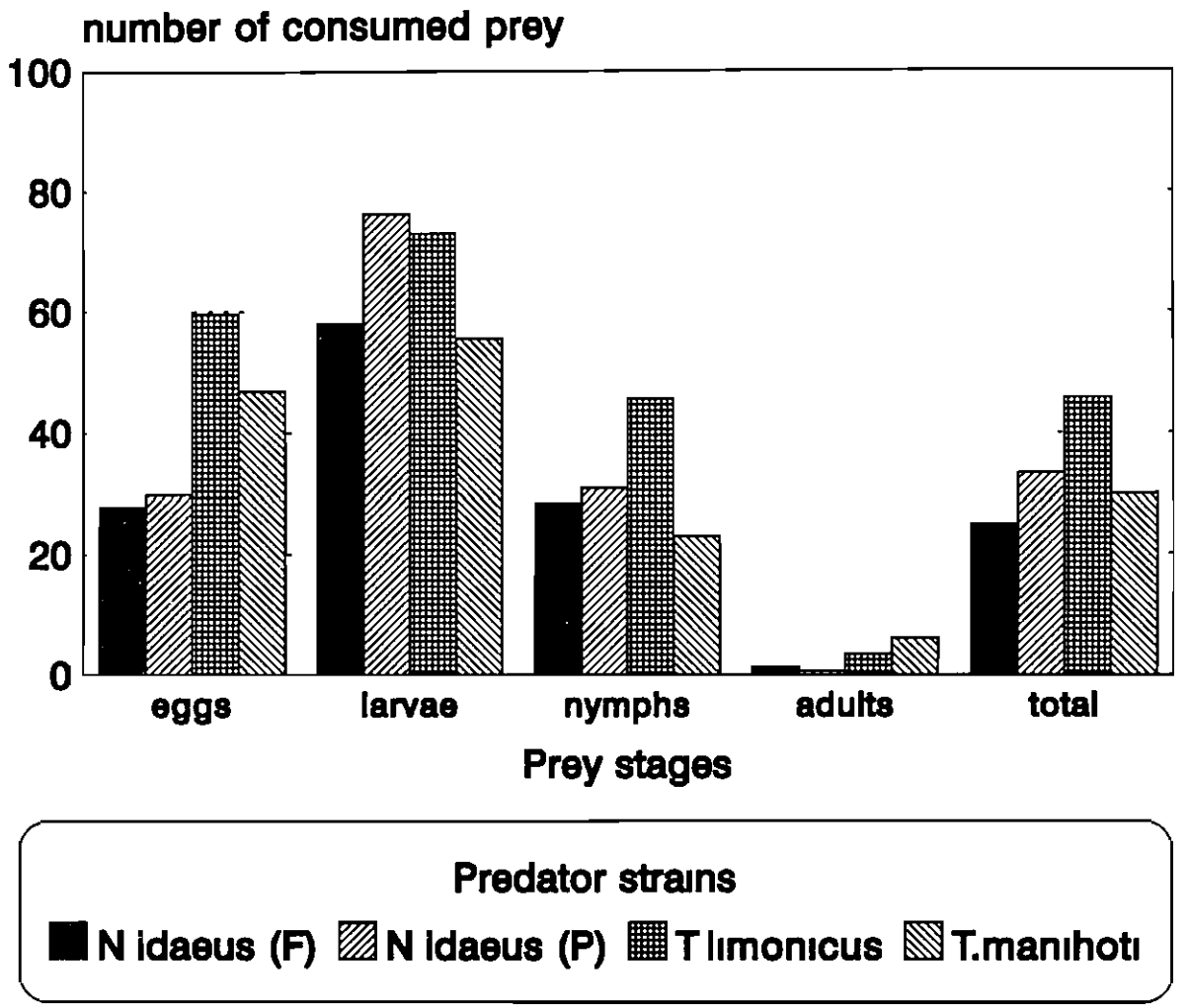


Figure 23 Means of consumption by the phytoseiids *N idaeus*, *T limonicus* and *T manihoti* of various developmental stages of *M caribbeanae*

N idaeus (P) = *N idaeus* from Petrolina
N idaeus (F) = *N idaeus* from Fonseca

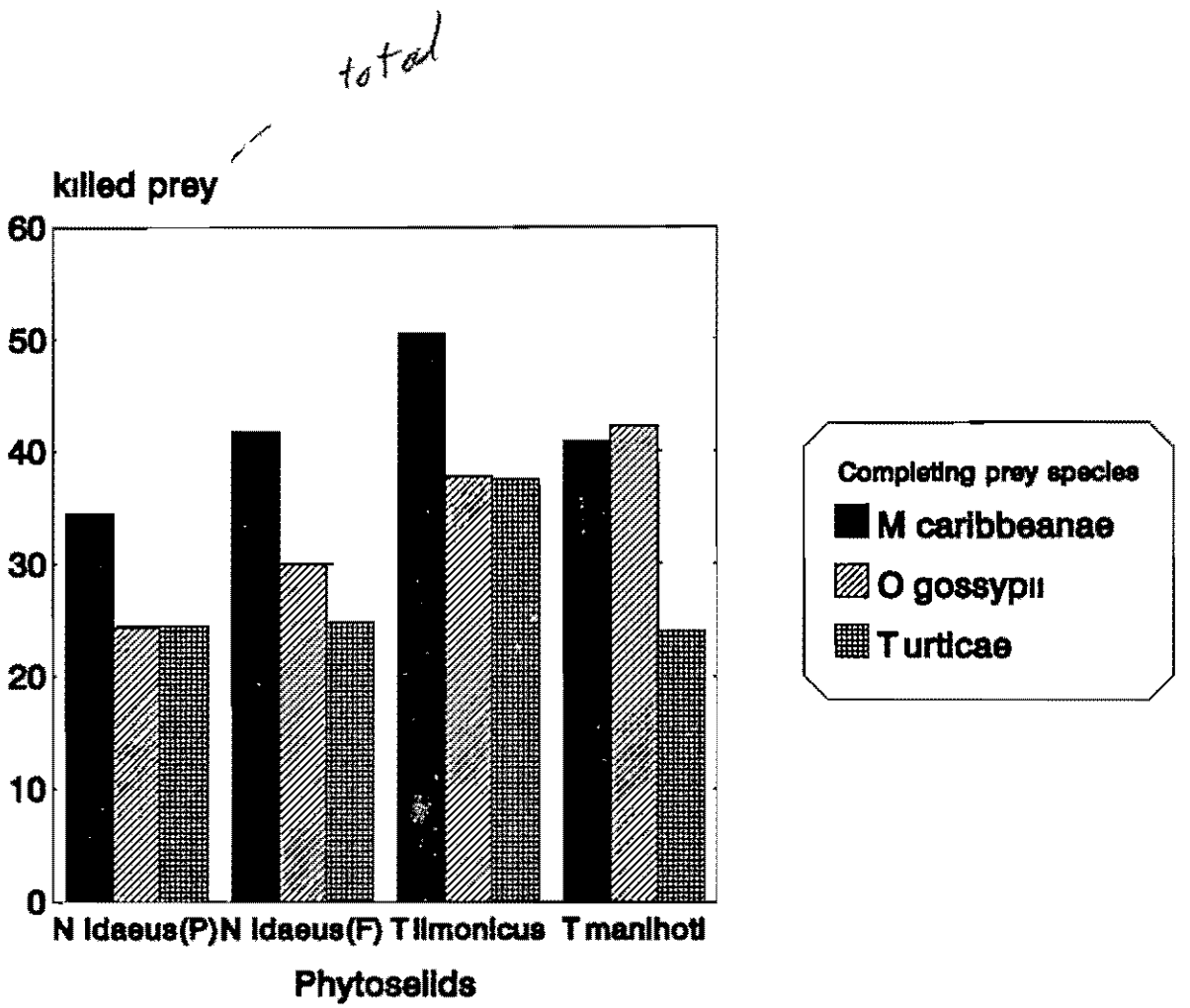


Figure 24 Consumption by *N idaeus*, *T limonicus* and *T manihotae* on *M tanajoa* combined with *M caribbeanae*, *O gossypii* and *T urticae*

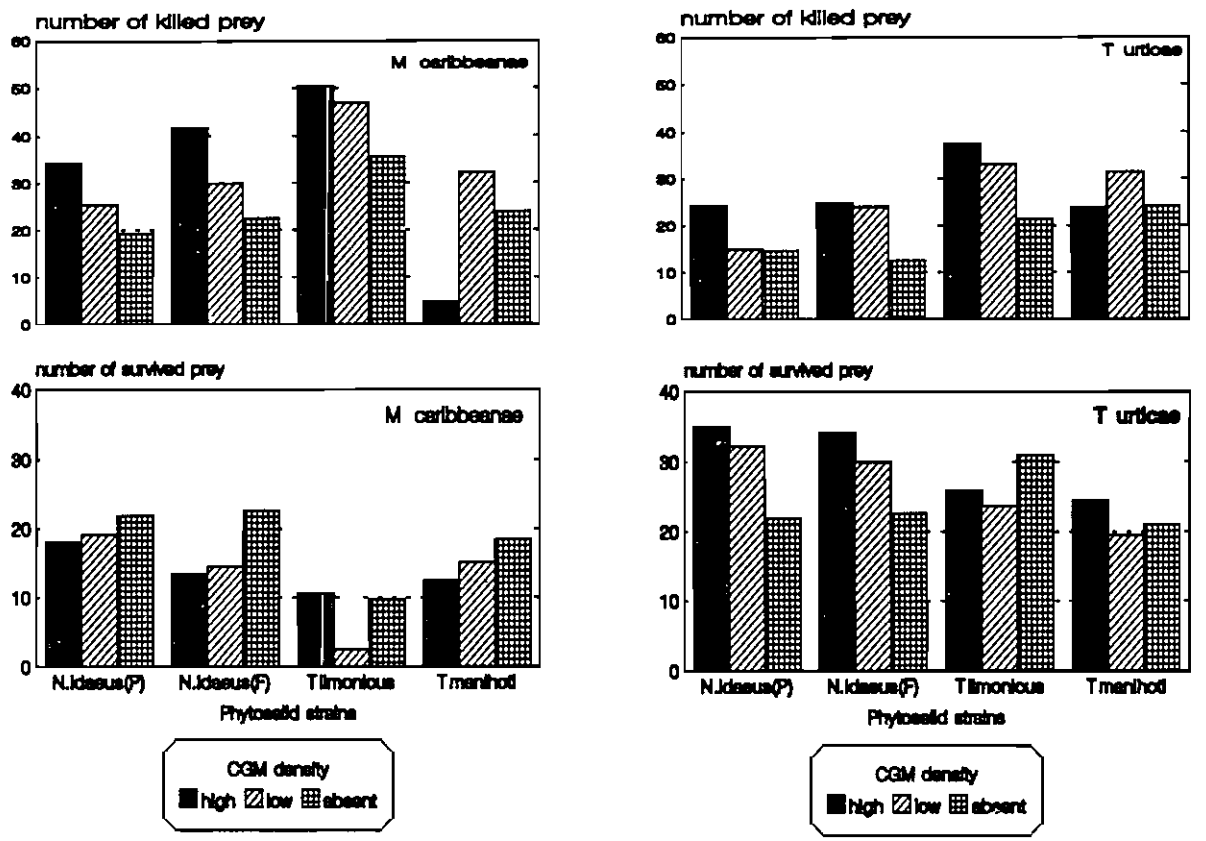


Figure 25 Predation rate of phytoseiids on *M caribbeanae* and *T urticae* at three different CGM densities (50, 10, and 0 protonymphs) Means of killed and survived prey are presented ($10 \leq n \leq 12$ for *M caribbeanae* at high density, $38 \leq n \leq 50$ for low density or absence of *M caribbeanae*)

all spp ?

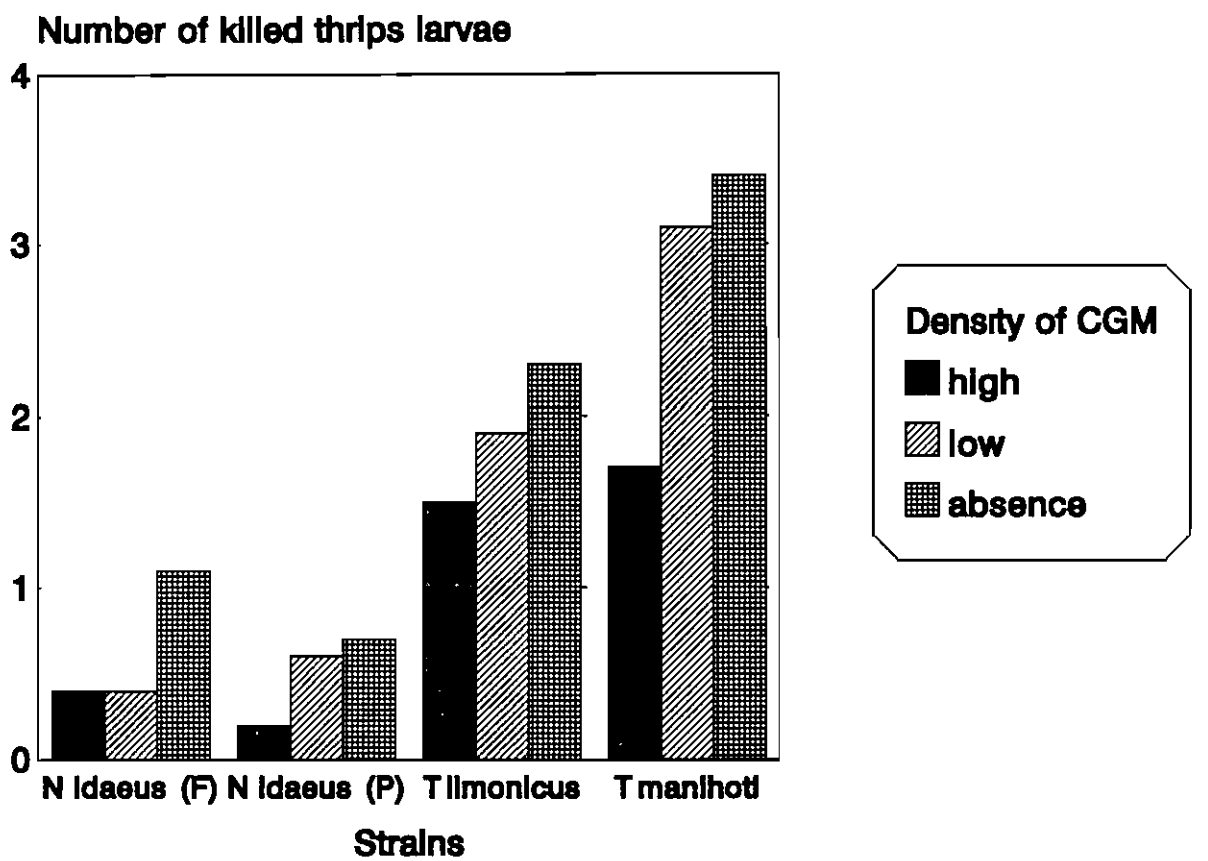


Figure 26 Killing rate of phytoseiid species on thrips at three densities of CGM (50, 10, 0 protonymphs) ($11 \leq n \leq 46$)

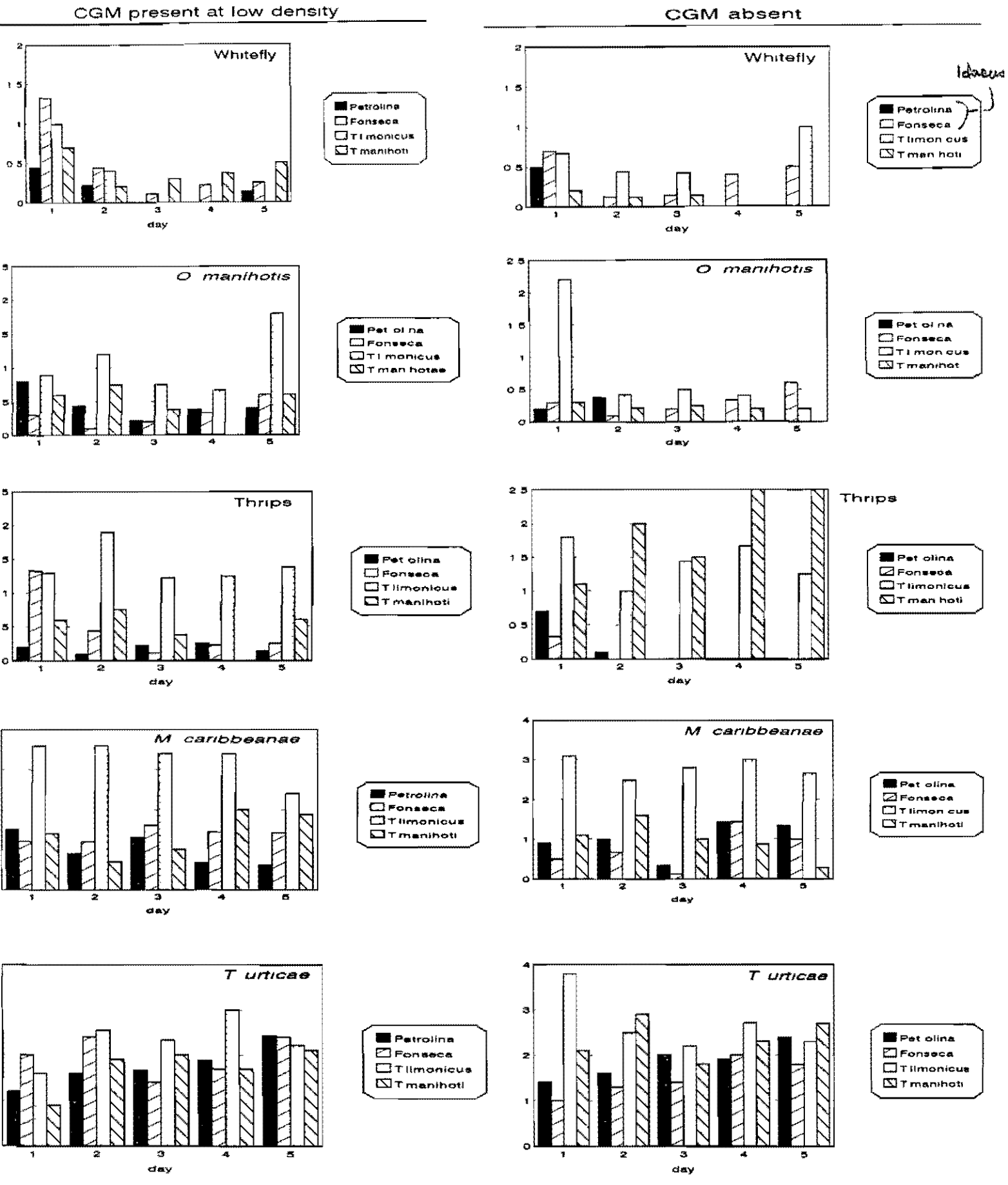


Figure 27 Daily mean oviposition of phytoseiids in relation to food item ($45 \leq n \leq 79$)

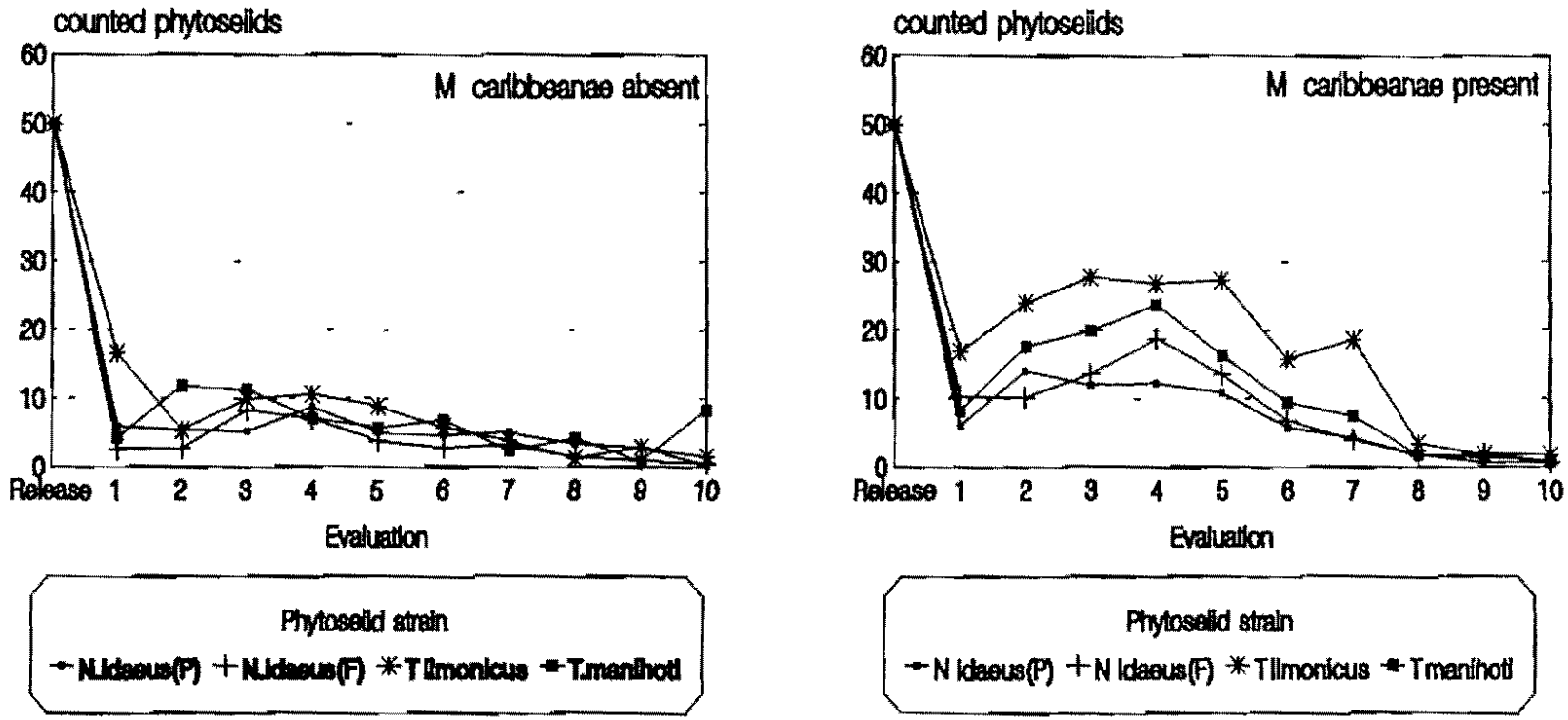


Figure 28 Population dynamics of phytoseiids in field experiment The chart shows the influence of the presence of *M caribbeanae* on the density of phytoseiidae Values represent means of all treatments (n = 12)

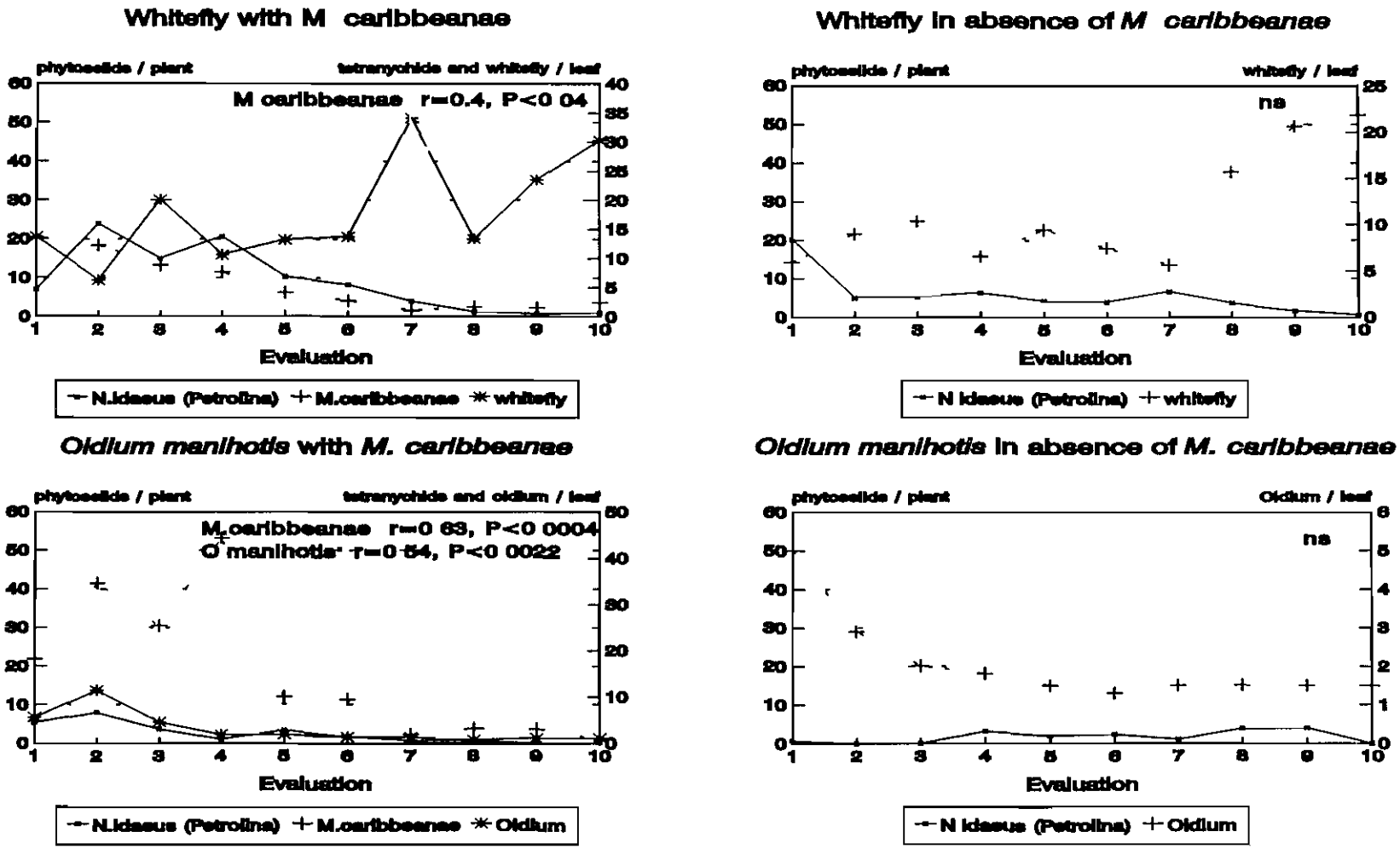


Figure 29 Density of *N idaeus* (Petrolina) on two different food types (n=3) Correlation data refer to population densities of phytoseiids and indicated food item Densities of whitefly and oidium were estimated as infested area per leaf

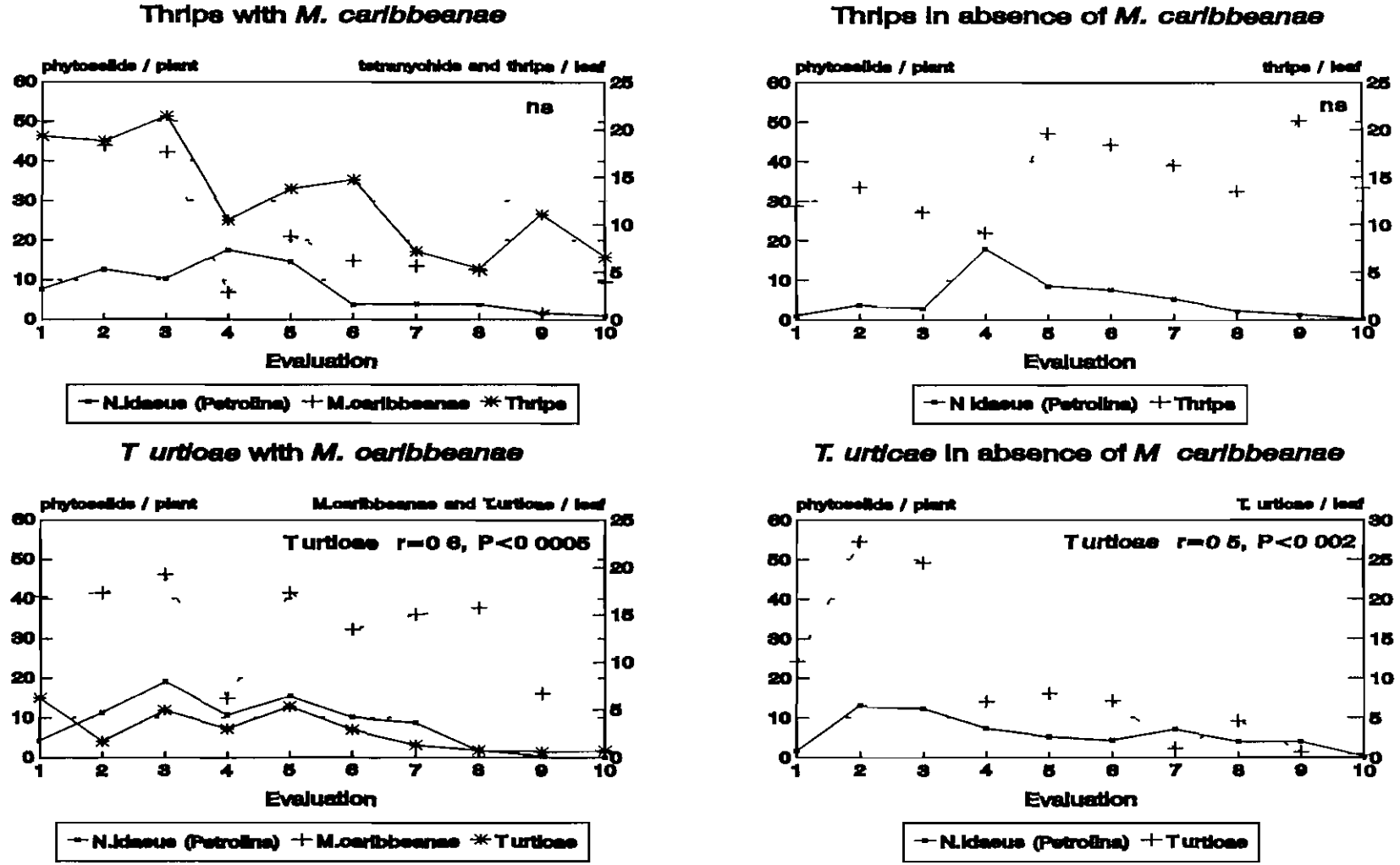


Figure 30 Density of *N idaeus* (Petrolina) on two different food types (n = 3) Correlation data refer to population densities of the phytotosiids and indicated food items

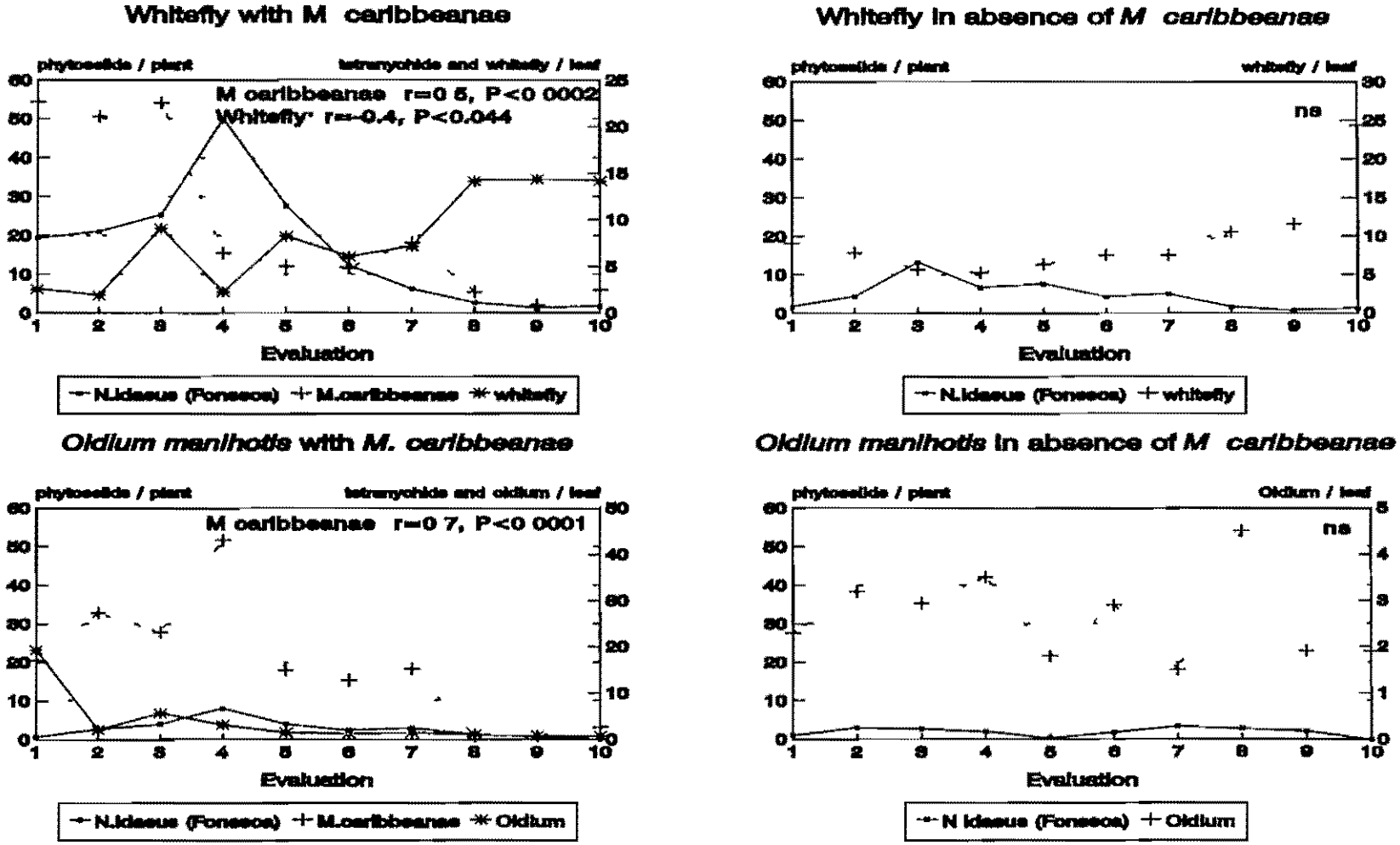


Figure 31 Density of *N idaeus* (Fonseca) on two different food types (n=3) Correlation data refer to population densities of phytoseiids and indicated food item Densities of whitefly and oidium were estimated as infested area per leaf

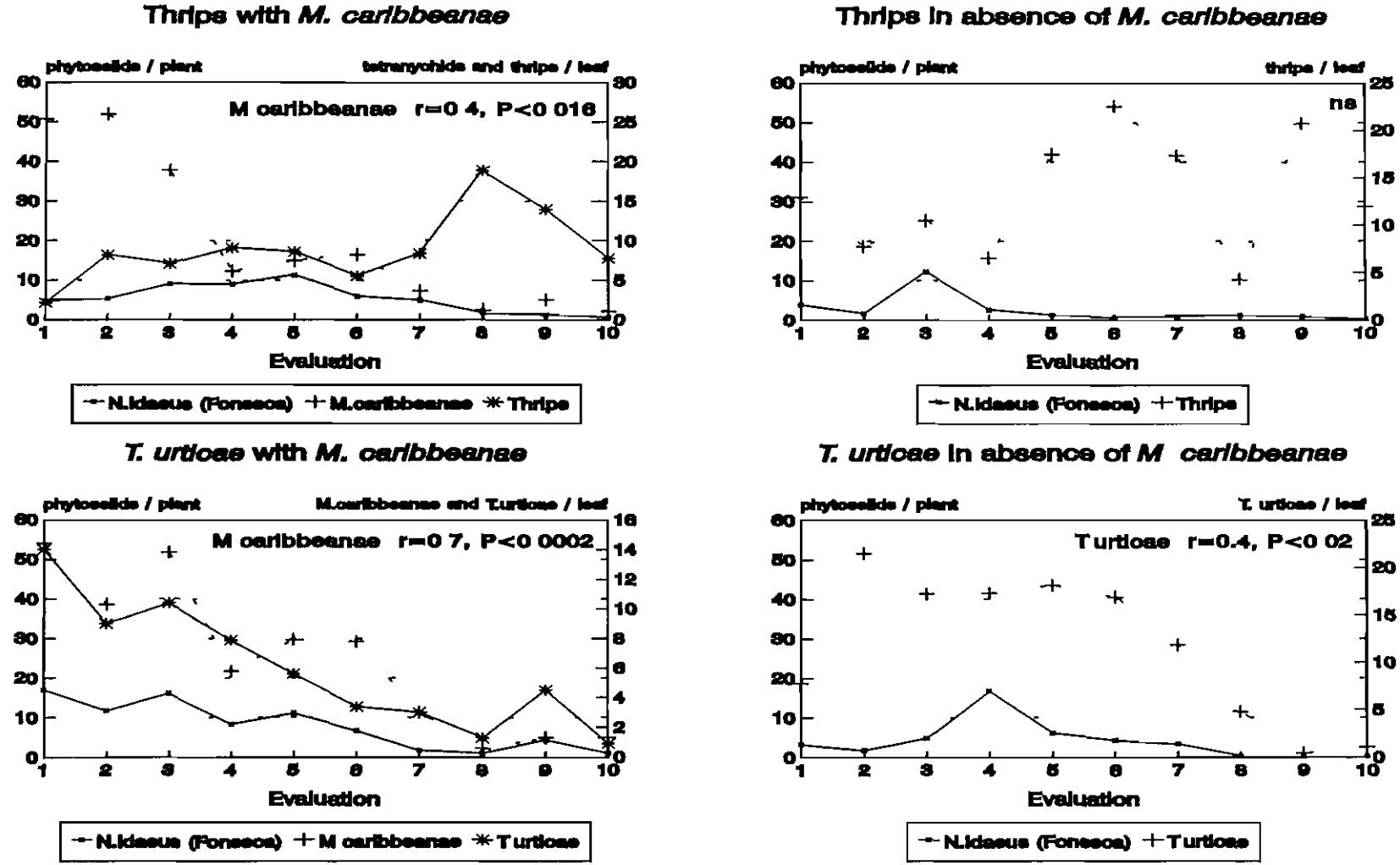


Figure 32 Density of *N idaeus* (Fonseca) on two different food types (n=3) Correlation data refer to population densities of phytoseiids and indicated food items

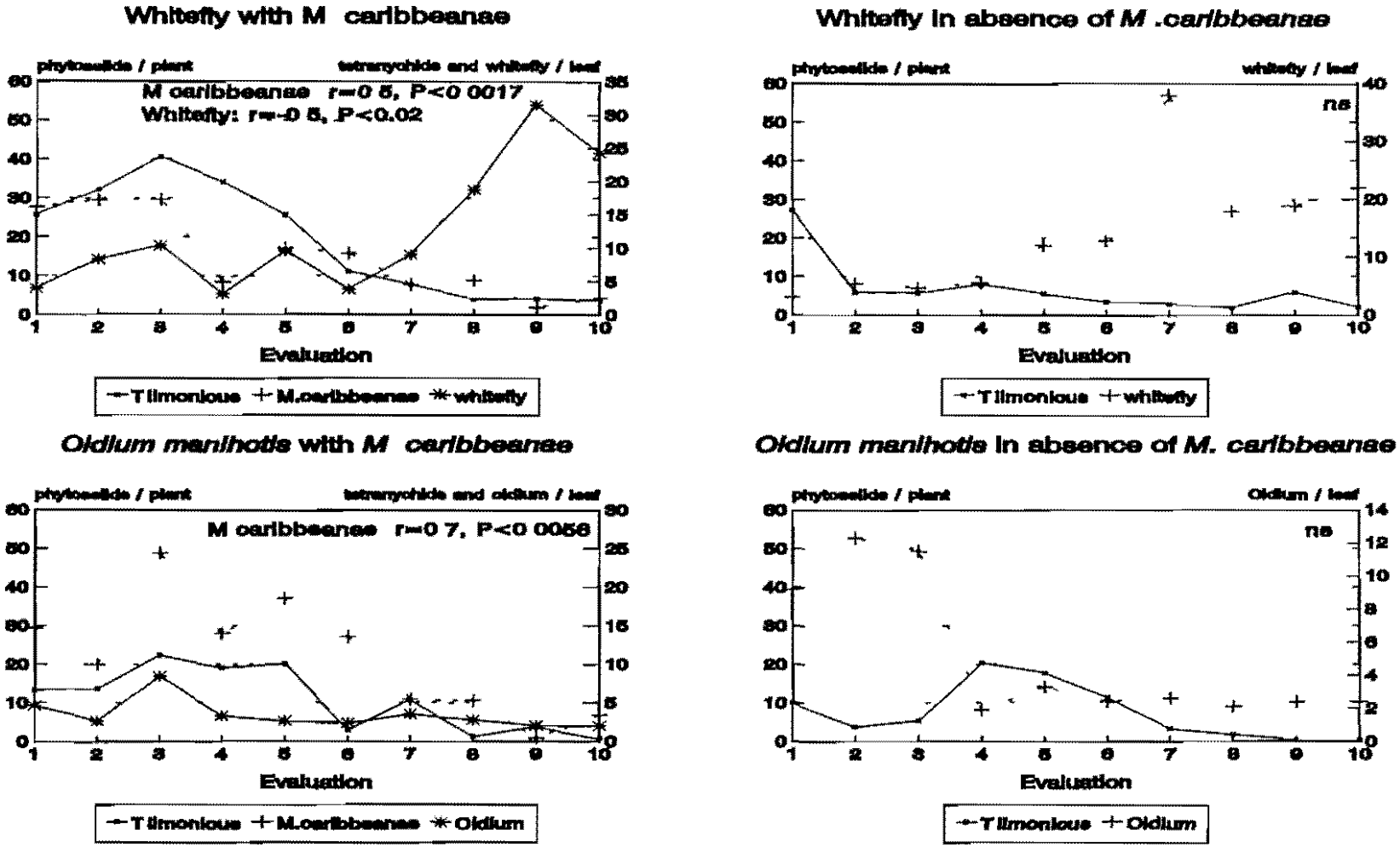


Figure 33 Density of *T limonicus* on two different food types Correlation data refer to population densities of phytoseiids and indicated food items Density of whitefly and oidium were estimated at infested area per leaf

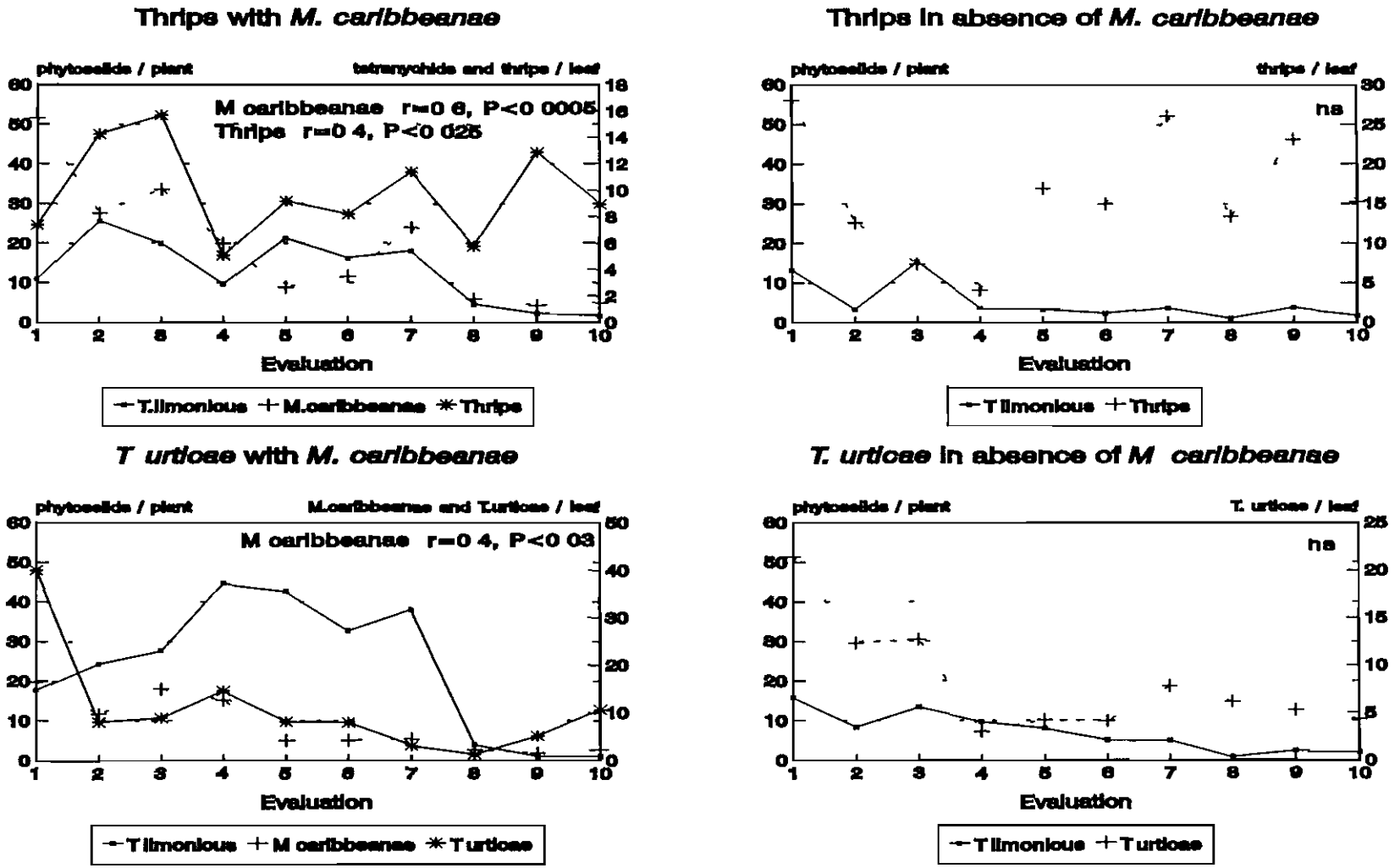


Figure 34 Density of *T limonicus* on two different food types (n=3) Correlation data refer to population densities of phytoseiids and indicated food items

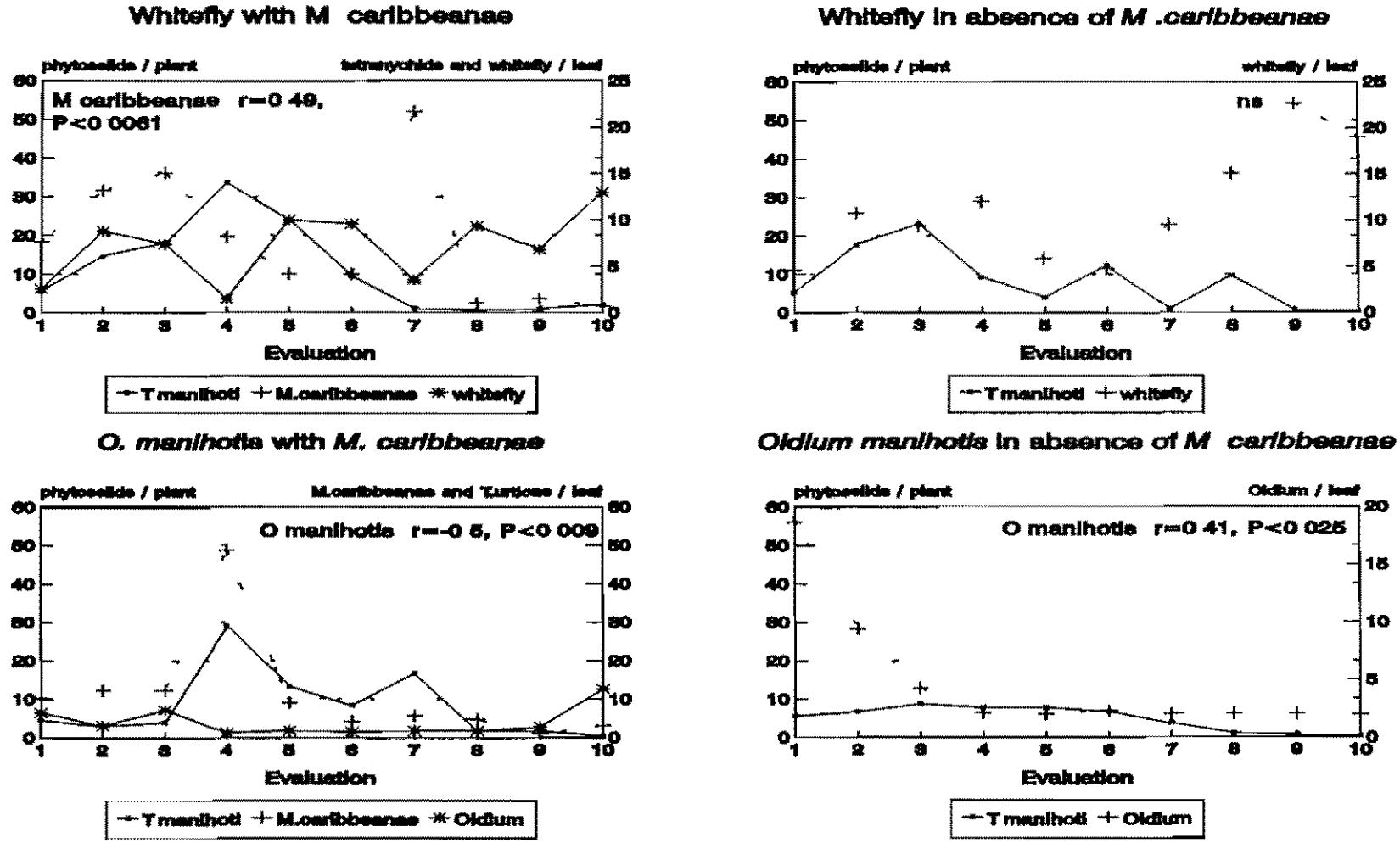


Figure 35 Density of *T manihoti* on two different food types (n=3) Correlation data refer to population densities of phytoseiids and indicated food items Densities of whitefly and oidium were estimated as infested area per leaf

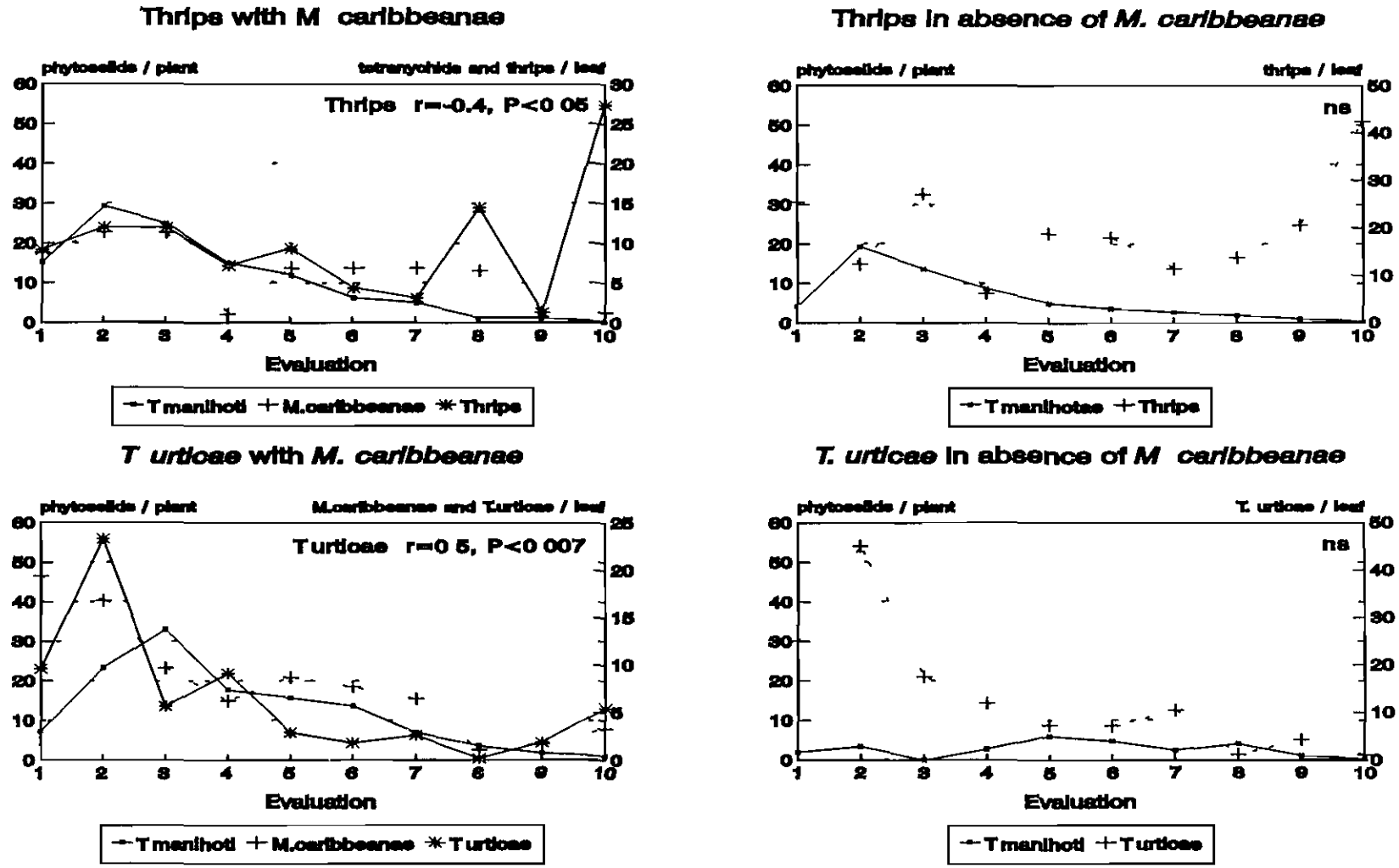


Figure 36 Density of *T manihoti* on two different food types (n=3) Correlation data refer to population densities of phytoseiids and indicated food item

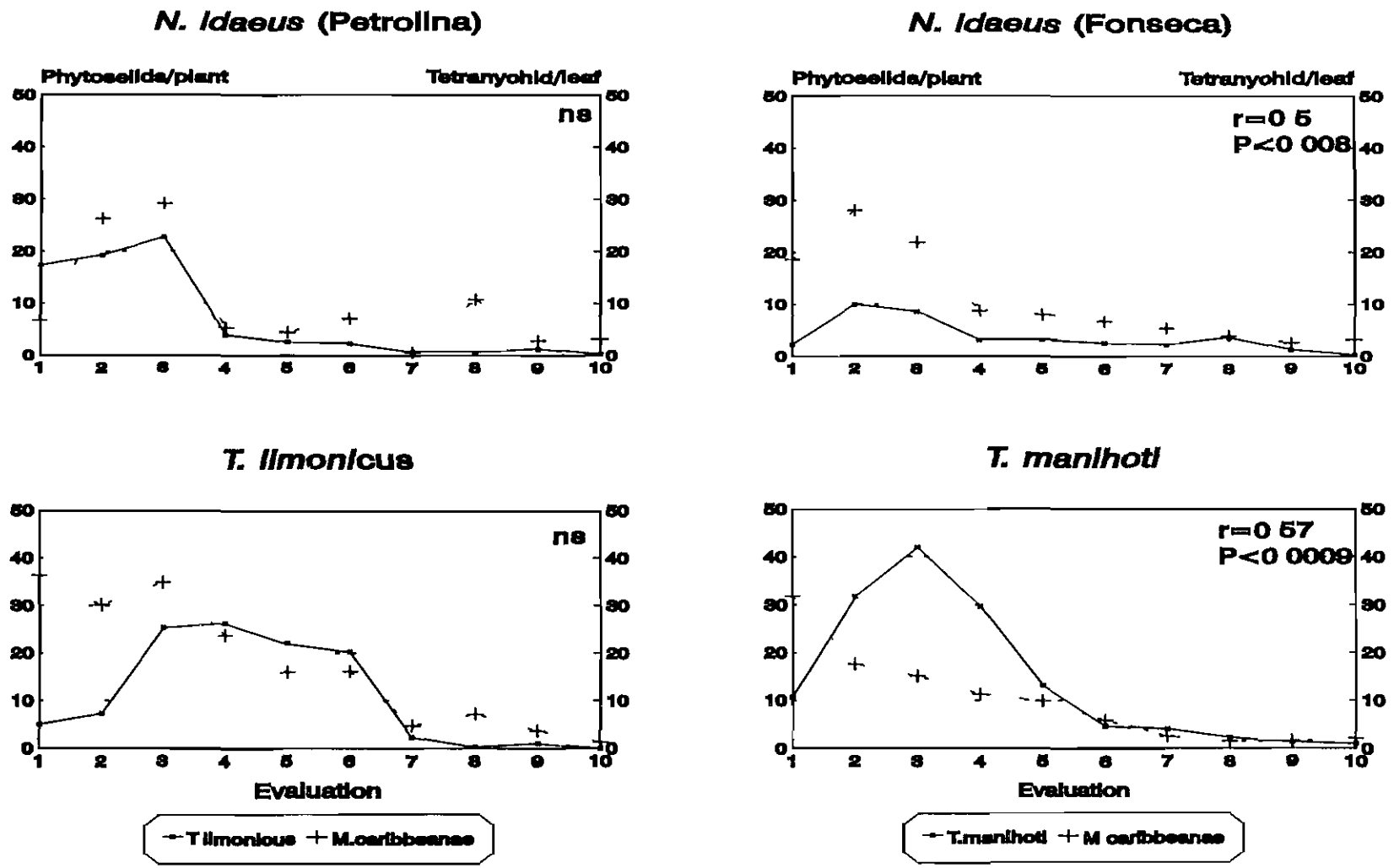


Figure 37 Correlation of population density of phytoseiids and *M caribbeanae*, when no alternative food items were present

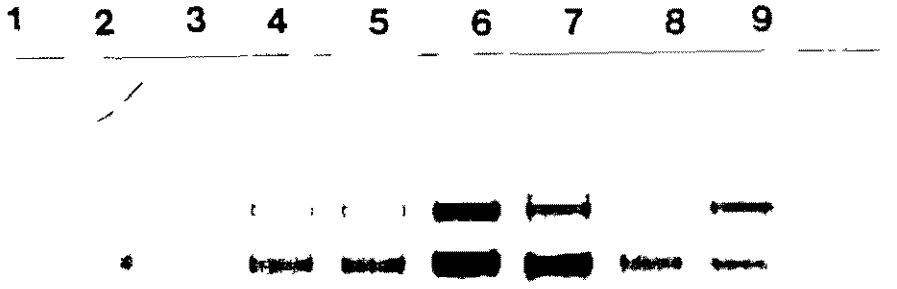


Figure 38 Esterase activity of stages of *M tanajoa*

1 4 eggs
2 1 protonymph (♀)
3 1 protonymph
4 1 deutonymph
5 1 deutonymph
6 1 adult (♀)
7 1 adult (♀)
8 1 protochrysalis
9 1 adult (♂)

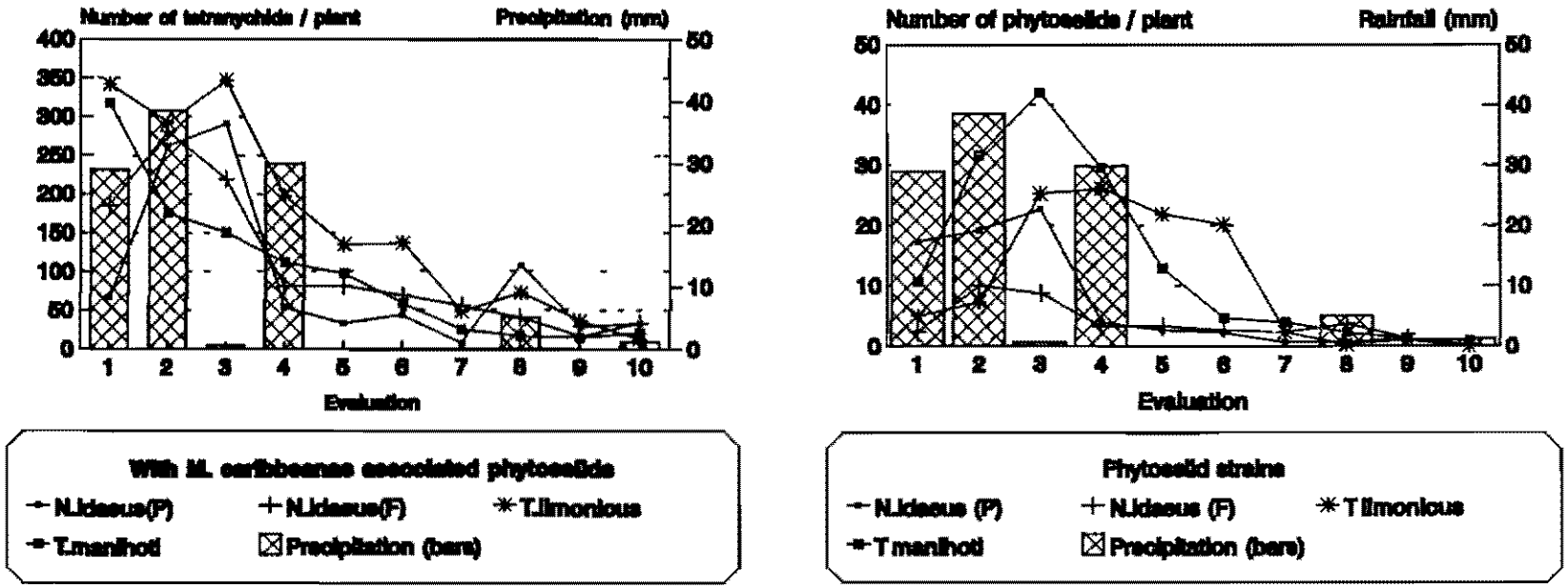


Figure 39 Density of *M caribbeanae* and the four phytoseiid strains in treatments without alternative food (n=3) Densities of *N idaeus* (r=0 5, P<0 002) and *T manihoti* (r=0 6, P<0 0009) correlated with prey

10 Conclusions and recommendations for future research including necessary follow-up through national agriculture research stations (NARS) and farmers' practice

The electrophoretic analysis of field-collected predators did not provide a reliable means for identification of their diet We concluded that low food intake was one of the reasons why enzyme activity of the analyzed samples was generally low For this reason we recommend for studies where it is necessary to use only one individual, to restrict electrophoresis on controlled laboratory experiments--where predators find optimal conditions--and/or taxonomic identification of tetranychid species It seems of interest to study, whether more sensitive biochemical tools like polymerase chain reaction (PCR, Mullis *et al*, 1986 and Mullis & Faloona, 1987) can provide more reliable data

The preference tests conducted in the laboratory identified *T limonicus* as the most voracious predator Furthermore, this species had the highest fecundity among the tested predator types These attributes and its ability to survive on alternative food like thrips and even to oviposit on pure *O manihotis* diet recommend this species as a highly promising candidate for the biological control of CGM In the field experiment this species reached the highest average population density with significant differences to *N idaeus*

One of the future interests is to study the predation behaviour of *T limonicus* in more detail including agroecological aspects such as relative humidity An intense field survey of the

interaction of predator and prey populations should be conducted The focus on only two or one types should allow the design of an experiment with more replicates than we could conduct due to the quantity of predator and food types

Comparisons of plots where *T limonicus* is present with plots where it is excluded should be conducted in order to know the effect of this candidate on yield Furthermore, it is of crucial importance to test his adaptability to the climatic conditions of the target regions Sabelis (1985b) stressed the influence of relative humidity on the effectiveness of phytoseiids The problem of *T limonicus* is that its regions of collection (e g Jaguariuna) are characterized by a humid climate (CIAT, unit of agroecological studies), whereas CGM is a dry season pest (CIAT, 1990) Bakker *et al* (1993) found in laboratory experiments that 50% of the eggs of this phytoseiid strain did not hatch when relative humidity was lower than 72 3%

In contrast to this species, *N idaeus* is well adapted to dry zones (CIAT, 1992, Bakker *et al*, 1993) Dinh *et al* (1988) reported that under lab conditions the eggs of this species hatched at 30% RH This predator is associated with CGM in seasonally dry NE Brazil It is one of three phytoseiid species which could be established successfully in Africa The other candidates are Brazilian strains of *T limonicus* and *T aripo* (CIAT, 1994) However, reliable data on the efficiency of this species are still not available Preliminary observations in Brazil showed that the results are variable from year to year, depending on the density of *N idaeus* In one experiment, where density was high, 30% higher yield was found in plots with this predator compared to plots without predators (de Moraes, 1994, pers communication) More research

is needed to study the efficiency of this species

As in any case of Classical Biological Control it is recommended to realize studies on possible undesirable ecological effects of the candidates in the target areas where they do not occur

Another challenge was created by the sudden collapse of the CGM colony caused by a virus If it would be possible to identify, isolate and rear this virus a milestone in the control of CGM would be laid We observed that this virus is very specific since adjacent colonies of *T urticae* and *M caribbeanae* were not affected Preliminary analyses in the virology unit of CIAT identified virus-like polyhedrical particles (Calvert, pers communication) This interest of virological control was reinforced by findings of another type of virus-like particles in *M caribbeanae*, collected in Ecuador (Guerrero, pers communication) Various reports corroborate that virus(es) can be a spectacular control agent of pests The cabbage semi-looper *Trichoplusia ni* ceased to be a serious problem in cotton in Colombia when a nuclear polyhidrosis virus was introduced from California (Bustillo, 1989) Bellotti *et al* (1992) reported a mortality of 99 8% of the hornworm *Erinnyis ello* on cassava when a granulosis virus of the family Baculoviridae was applied Since the viruses against CGM and *M caribbeanae* seem to be very specific, it seems to be a promising natural enemy if it would be possible to find an effective way of its propagation among healthy individuals

References

Akpokodje, G O, J A Odebiyi, R S Ochieng, and H R Herren 1990 Functional response of *Neoseiulus idaeus* and *Iphiseius degenerans* (Acarina Phytoseiidae) feeding on the cassava green mite, *Mononychellus tanajoa* Mitteilungen der schweizerischen entomologischen Gesellschaft 63 327-335

Avise, J C 1974 Systematic value of electrophoretic data Systematic Zoology 23 465-481

Ayala, F J 1978 Chemical genetics and evolution In Biochemistry of insects Edited by M Rockstein 579-616 New York, San Francisco, Los Angeles Academic Press

Bakker, F 1993 Selecting phytoseiid predators for biological control, with emphasis on the significance of tri-trophic interactions Ph D , 132 pp , University of Amsterdam

Bakker, F M , and M E Klein 1990 The significance of cassava exudate for predaceous mites Symp Biol Hung 39 437-439

Bakker, F M , and M E Klein 1993 Host plant mediated coexistence of predatory mites the role of extrafloral nectar and extrafoliar domatia on cassava In Selecting phytoseiid predators for biological control, with emphasis on the significance of tri-trophic interactions Frank Bakker, Ph D thesis, University of Amsterdam, 132 pp

Bakker, F M , M E Klein, N C Mesa, and A R Braun 1993 Saturation deficit tolerance spectra of phytophagous mites and their phytoseiid predators on cassava Exp Appl Acarol 17 97-113

Buth, D G 1984 The application of electrophoretic data in systematic studies Ann Rev Ecol Syst 15 501-522

Bellotti, A C , and A V Schoonhoven 1978 Mite and insect pests of cassava Ann Rev Entomol 23 39-67

Bellotti, A C , B Arias, and O L Guzman 1992 Biological control of the cassava hornworm *Erinnys ello* (Lepidoptera Sphingidae) Florida Entomologist 75(4) 506-515

Braun, A R , J M Alvarez, M E Cuellar, M C Duque, J R Escobar, C Franco, A Gaigl, J M Guerrero, J I Lenis, E L Melo, N C Mesa, and R Zuñiga 1993 Inventario de acaros fitofagos y sus enemigos naturales en el cultivo de la yuca en Ecuador In Bases fundamentales para investigacion sobre los acaros plagas y sus enemigos naturales en Ecuador Documento de trabajo No 126 Edited by A R Braun pp 1-51 CIAT, Cali, Colombia

Bustillo, A 1989 Utilizacion de agentes microbiologicos In Manejo integrado de plagas insectiles en la agricultura Estado y futuro Edited by K L Andrews and J R Quezada Departamento de proteccion vegetal Escuela agricola panamericana, EL Zamorano, Honduras, Centroamerica Chapter 13, pp 211-228

CIAT, 1990 Annual report 1990 Working Document No 95 Cassava Program Chapter 4 Cassava Entomology and Acarology pp 119-172

CIAT, 1993 Annual report 1993 Cassava program Cassava Entomology and Acarology Working Document 146

CIAT, 1994 Annual report 1994 (Draft) Cassava program Acarology

Cloutier, C , and S G Johnson 1993 Interaction between life stages in a phytoseiid predator western flower thrips prey killed by adults as food for protonymphs of *Amblyseius cucumeris* Exp Appl Acarol 17 441-449

Cuellar, M E 1992 Biosistimatica de poblaciones de *T limonicus* Garman & McGregor *sensu lato* y *sensu stricto* (Acarina Phytoseidae) y su importancia en el control del acaro verde de la yuca Undergraduate thesis Universidad del Valle, Facultad de Ciencias, Departamento de Biologia, Cali Colombia 127 pp

Dicke, M , M de Jong 1988 Prey preference of the phytoseiid mite *Typhlodramus pyri* 2 Electrophoretic diet analysis Exp Appl Acarol 4 15-25

Dinh, N V , M W Sabelis, and A Janssen 1988 Influence of humidity and water availability on the survival of *Amblyseius idaeus* and *A anonymus* (Acarina Phytoseiidae) Exp Appl Acarol , 4 27-40

Evans, G O 1992 Principles of acarology CAB International, Wallingford, UK 563 pp

Eveleigh, E S , and D A Chant 1981 Experimental studies on acarine predator-prey interactions the numerical response of immature and adult predators (Acarina Phytoseiidae) Can J Zool 59 1407-1418

Eveleigh, E S , and D A Chant 1982 Experimental studies on acarine predator-prey interactions the effects of predator density on prey consumption, predator searching efficiency, and the functional response to prey density (Acarina Phytoseiidae) Can J Zool 60 611-629

Fitzgerald, J D , M G Solomon, and R A Murray 1986 The quantitative assessment of arthropod predation rates by electrophoresis Ann Appl Biol , 109 491-498

Florkin, M , and C Jeuniaux 1974 Hemolymph composition In Physiology of insecta

Edited by M Rockstein pp 256-307 New York and London Academic Press

Gaigl, A , A R Braun, and H -M Poehling Electrophoretic gut analysis of phytoseiid predators associated with cassava Methodology development (submitted)

Giller, P S 1984 Predator gut state and prey detectability using electrophoretic analysis of gut contents Ecological Entomology, 9 157-162

House, H L 1974 Digestion In The physiology of insecta Edited by M Rockstein pp 63-117 New York and London Academic Press

Hoy, C W , and C S Glenister 1991 Releasing *Amblyseius* spp (Acarina Phytoseiidae) to control *Thrips tabaci* (Thysanoptera Thripidae) Entomophaga, 36(4) 561-573

McMurtry, J A and G T Scriven (1966) Studies on predator-prey interactions between *Amblyseius hibisci* and *Oligonychus punicae* (Acarina Phytoseiidae, Tetranychidae) under greenhouse conditions Ann Entomol Soc Am 59 793-800

McMurtry, J A 1992 Dynamics and potential impact of 'generalist' phytoseiids in agroecosystems and possibilities for establishment of exotic species Exp Appl Acarol , 14 371-382

Maisonneuve, J C , T Queraud, A Vitre, and G Fournier 1985 Tomate une methode de lutte biologique contre l'aleurode des serres Phytoma 371 42-43

Mesa, N C , A R Braun, and A C Bellotti 1990 Comparison of *Mononychellus progresivus* and *Tetranychus urticae* as prey for five species of phytoseiid mites Exp Appl Acarol , 9 159-168

Mesa, N C , and J I Lenis 1993 Importancia de los metodos de la cria masiva en un programa de control biologico In Bases fundamentales para investigacion sobre los acaros plagas y sus enemigos naturales en Ecuador Documento de trabajo No 126 Edited by A R Braun pp 116-138 CIAT, Cali, Colombia

Moraes, G J de, N C Mesa, A R Braun, and E L Melo 1994 Definition of the *Amblyseius limonicus* species group (Acari Phytoseiidae), with descriptions of two new species, new records and measurements of related species Internat J Acarol 20(3) (in press)

Mori, H , and D H Chant 1966 The influence of the prey density, relative humidity, and starvation on the predacious behaviour of *Phytoseiulus persimilis* Athias-Henriot (Acari Phytoseiidae) Can J Zool 44 483-491

Murray, R A , and M G Solomon 1978 A rapid technique for analyzing diets of invertebrate predators by electrophoresis Ann Appl Biol 90 7-10

Mullis, K B , F A Faloona, S Scharf, R Saiki, G Horn, and H Erlich 1986 Specific enzymatic amplification of DNA *in vitro* the polymerase chain reaction Cold Spring Harbour Symp Quant Biol 51 263-273

Mullis, K B and F A Faloona 1987 Specific synthesis of DNA *in vitro* via a polymerase-catalyzed chain reaction Methods Enzymol 155 335-350

Ohnesorge, B 1981 Populationsdynamische Untersuchungen in einem Rauber-Beute-System *Phytoseiulus persimilis* A -H (Acarina, Phytoseiidae) und *Tetranychus urticae* Koch Z ang Ent 91(1) 25-49

Pritchard, A E , and E W Baker 1955 A revision of the spider mite family tetranychidae Edited by P D Hurd, Jr 472 pp San Francisco Pacific Coast Entomological Society

Rao, N V , A S Reddy, and K T Rao 1989 Natural enemies of cotton whitefly, *Bemisia tabaci* in relation to host population and weather factors Journal of Biolocical Control 3(1) 10-12

SAS, 1990 SAS/STAT User's Guide Rel 6, 4th edition, SAS Institute Inc , Cary, NC, pp 1685

Sabelis, M W 1985a Predation on spider mites In World Crop Pests Spider Mites, their biology, natural enemies and control Vol 1B Edited by W Helle and M W Sabelis pp 103-129 Amsterdam, Oxford, New York Elsevier Science Publishers

Sabelis, M W 1985b Development In World Crop Pests Spider Mites, their biology, natural enemies and control Vol 1B Edited by W Helle and M W Sabelis pp 43-53 Amsterdam, Oxford, New York Elsevier Science Publishers

Shipp, J L , and G H Whitfield 1991 Functional response of the predatory mite *Amblyseius cucumeris* (Acari Phytoseiidae) on Western Flower Thrips, *Frankliniella occidentalis* (Thysanoptera Thripidae) Environ Entomol 2(20) 694-699

Solomon, M G , R A Murray, and L P S van der Geest 1985 Analysis of prey by means of electrophoresis In World Crop Pests Spider mites, their biology, natural enemies and control Vol 1B Edited by Helle and Sabelis pp 171-173 Amsterdam, Oxford, New York Elsevier Science Publishers

Sula, J , and F Weyda 1982 Esterase polymorphism in several populations of the two-spotted spider mite *Tetranychus urticae* Koch Experientia 39 78-79

Swirski, E and N Dorzia 1968 Studies on the feeding development and oviposition of the predacious mite *Amblyseius limonicus* Garman and McGregor (Acari Phytoseiidae) on various kinds of food substances Israel J agric Res 18(2) 71-75

Takafuji, A , and D A Chant 1976 Comparative studies of two species of predacious phytoseiid mites (Acarina Phytoseiidae), with special reference to their responses to the density of the prey Res Popul Ecol 17 255-310

Takafuji, A , Y Tsuda, and T Miki 1983 System behaviour in predator-prey interaction, with special reference to acarine predator-prey system Res Popul Ecol Suppl 3 75-92

Tanigoshi, L T , B Megevand, and J S Yaninek 1993 Non-prey food for subsistence of *Amblyseius idaeus* (Acari Phytoseiidae) on cassava in Africa Exp Appl Acarol 17 91-96

Toko, M , R J O'Neil, and J S Yaninek 1994 Effect of cassava exudate and prey densities on the survival and reproduction of *Typhlodromalus limonicus* (Garman & McGregor) *s l* (Acari Phytoseiidae), a predator of the cassava green mite, *Mononychellus tanajoa* (Bondar) (Acari Tetranychidae) Exp Appl Acarol 18 221-231

Tukey, J W 1977 Exploratory data analysis Reading, Massachusetts Addison-Wisley, 688pp

Wagner, R P , and R K Selander 1974 Isozymes in insects and their significance Ann Rev Ent 19 117-138

Waterhouse, D F 1957 Digestion in insects Ann Rev Entomol 2 1-18

Wysoki, M , and M Cohen 1983 Mites of the family Phytoseiidae (Acarina Mesostigmata) as predators of the Japanese bayberry whitefly, *Parabemisia myricae* Kuwana (Hom , Aleyrodidae) Agronomie 3(8) 823-825