CONSUMPTION AND OVIPOSITION RATES OF SIX PHYTOSEIID SPECIES FEEDING ON EGGS OF THE CASSAVA GREEN MITE *MONONYCHELLUS TANAJOA* (ACARI: TETRANYCHIDAE)

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ABSTRACT

In Africa the cassava green mite, *Mononychellus tanajoa,* is an important pest of cassava, *Manihot esculenta*. Phytoseiid mites from South America are being evaluated as potential biological control agents of this alien pest. We evaluated six phytoseiid (Acari: Phytoseiidae) species, collected in South America: *Euseius ho*, *Typhlodromalus aripo*, *Typhlodromalus tenuiscutus*, *Neoseiulus californicus*, *Neoseiulus idaeus*, and *Galendromus annectens*. Their effectiveness as a biological control agent was estimated by measuring rates of prey consumption and oviposition in relation to prey density under optimal laboratory conditions. Prey consumption by *E. ho*, *T. aripo* and *T. tenuiscutus* continued increasing linearly up to the highest density of prey evaluated (200 prey eggs) for a maximum of 93, 101 and 59 prey in 24 h. For the other predators, prey consumption levelled off at prey density of 30 or more. Maximum daily consumption was 40, 35 and 18 eggs for *N. californicus*, *N. idaeus* and *G. annectens*, respectively. Except for *T. tenuiscutus*, daily fecundity appeared to reach a plateau at the prey densities tested. Higher maximum daily oviposition rates were registered for *T. tenuiscutus*, *N. californicus*, *N. idaeus* and *G. annectens*, ovipositing 3.9, 3.6, 2.9 and 2.8 eggs, respectively; whereas *E. ho* and *T. aripo* oviposited a maximum of 2.2 and 1.4 eggs in 24 h, respectively. The ratio between oviposition and prey consumption rates was generally higher for *G. annectens*, *N. californicus* and *N. idaeus*. The high prey consumption rate of *E. ho*, *T. aripo* and *T. tenuiscutus* suggests that these species are the best agents in regard to the attack of pest eggs. The high fecundity rate and oviposition/consumption ratio especially at low prey densities (30 prey eggs) of *N. californicus*, *N. idaeus* and *G. annectens* suggests that these species may be able to multiply well at low prey densities.

Key Words: *Euseius ho*, *Typhlodromalus aripo*, *Typhlodromalus tenuiscutus*, *Neoseiulus californicus*, *Neoseiulus idaeus*, *Galendromus annectens*, biological control

RESUMEN

En Africa el ácaro verde de la yuca, *Mononychellus tanajoa*, es una plaga importante de la yuca *Manihot esculenta*. Se están evaluando ácaros fitoseidos de Sur América como agentes potenciales de control biológico de esta plaga. Se evaluarón seis especies de fitoseidos (Acari: Phytoseiidae), colectadas en Sur América: *Typhlodromalus aripo*, *Typhlodromalus tenuiscutus*, *Neoseiulus californicus*, *Neoseiulus idaeus*, y *Galendromus annectens*. Su efectividad como agentes de control biológico se estimó midiendo la tasa de consumo de presa y oviposición en relación con la densidad de presa bajo condiciones óptimas de laboratorio. El consumo de presa por *E. ho*, *T. aripo* y *T. tenuiscutus* continuó incrementando linealmente a la densidad de presa más alta evaluada (200 huevos de la presa) a un máximo de 93, 101 y 59 presas en 24 horas. Para los otros de predadores, el consumo de presa alcanzó un màximo a la densidad de 30 o màs. El consumo diario máximo fue 40, 35 y 18 huevos para *N. californicus*, *N. idaeus* y *G. annectens*, respectivamente. Con excepción de *T. tenuiscutus*, la fecundidad diaria pareció alcanzar una meseta a las densidades de presa probadas. La oviposición diaria máxima más alta se registró para *T. tenuiscutus*, *N. californicus*, *N. idaeus* y *G. annectens*, ovipositando 3.9, 3.6, 2.9 y 2.8 huevos, respectivamente; mientras que *E. ho* y *T. aripo* ovipositaron un máximo de 2.2 y 1.4 huevos en 24 horas, respectivamente. La relación entre la oviposición y la tasa de consumo de presa fue más alta generalmente para *G. annectens*, *N. californicus* y *N. idaeus*. La tasa alta de consumo de presa de *E. ho*, *T. aripo* y *T. tenuiscutus* sugiere que estas especies son los mejores agentes para atacar los huevos de la presa. La tasa de fecundidad alta y el ratio oviposición/consumo especialmente a bajas densidades de la presa (30 huevos de la presa) de *N. californicus*, *N. idaeus* y *G. annectens* sugiere que estas especies pueden ser capaces de multiplicarse bien a densidades bajas de la presa.

The cassava green mite, *Mononychellus tanajoa* Bondar (Acari: Tetranychidae) is an important pest of cassava, *Manihot esculenta* Crantz (Euphorbiaceae) in dry regions of South America (Farias et al. 1982; Byrne et al. 1983; Veiga 1985). In the early 1970s, this mite species was accidentally introduced into Africa, spreading rapidly across the Subsaharan zone in the absence of its natural enemies (Yaninek & Herren 1988) and causing severe yield losses (Yaninek et al. 1990; Bonato et al. 1994). Classical biological control (i.e., through the use of introduced natural enemies) was developed to control *M. tanajoa* in Africa (Mégevand et al. 1987, Yaninek & Herren 1988). Among ten phytoseiid species released in Africa from 1984 to 1993 three of them are now well established but only one is spreading well and affecting the green mite population (Bellotti et al. 1999). It is therefore necessary to release more phytoseiid species or strains from South America. Meanwhile, The International Center for Tropical Agriculture began exploration and evaluation of phytoseiids from coastal Colombia and Ecuador, which has a dry climate similar to target areas in Africa.

Two factors that affect the success of phytoseiid mites in controlling their mite prey are their functional and numerical responses (Sabelis 1985). These factors must be considered when the importance of the phytoseiid species is to be evaluated. First described by Solomon (1949), the functional and numerical responses were defined as follows. The functional response refers to the change in the number of prey consumed per unit time in relation to the change in prey density. The numerical response refers to the increase in numbers of predators in response to increases in prey density and is thus positively correlated with the ovipositional rate. A good candidate for controlling mite populations should have both increased prey consumption and oviposition rates in proportion to the available prey density. Furthermore, Sabelis (1985) theorized that the most efficient (i.e., most co-adapted) predator should be the most efficient at converting their prey into progeny. The ratio between the oviposition and the consumption rates reflects in a straightforward way this theorical efficiency.

The aim of this study was to evaluate, under optimal laboratory conditions, prey consumption and oviposition rates of six phytoseiid predatory mite species in relation to prey density. The objective was to estimate the maximum number of prey consumed and the maximum number of eggs laid as well as their maximum efficiency at converting food energy into egg production of six phytoseiid species.

Materials and Methods

Six phytoseiid mite species (Acari: Phytoseiidae) were collected from coastal areas of Colombia and Ecuador (Table 1). All predatory mite species were maintained in the laboratory on cassava leaves infested by *M. tanajoa* at $25 \pm 1°C$, $75 \pm 5\%$ RH and 12-h photoperiod. Immediately after emergence, individual females were placed with a male in the predation arena, described below, with an uncontrolled egg prey density (generally > 100) for 3 days. Gravid female predators from the predation arenas were then used for the experiments.

For several phytoseiid species, females consume more eggs than mobile stages of their prey (Sabelis 1985). This was also observed with the species used in this study (M. E. Cuellar, unpublished data). Moreover, egg prey is easier to manipulate and control than mobile stages. Consequently, subsequent studies were done with eggs of the prey.

M. tanajoa, the prey for the phytoseiid species, were reared on 2-month-old cassava plants, var. CMC-40, in a greenhouse under natural conditions of temperature and relative humidity and 12-h photoperiod in Palmira, Colombia.

All experiments were conducted under laboratory conditions at $25 \pm 1°C$, $75 \pm 5\%$ RH and 12-h photoperiod [optimal conditions to rear all phytoseiid species studied in laboratory (M. E. Cuellar, unpubl. data)]. The experiments were performed on 3.14 cm² greenhouse-collected cas-

TABLE 1. Origin of six Phytoseiid mite species used in the experiments and collected from different areas of South America.

Species	Country	Region	Location	Altitude (m)	Collection Date
Neoseiulus idaeus Denmark & Muma	Colombia	Guajira	Fonseca	180	2-97
Typhlodromalus aripo De León	Colombia	Magdalena	Pivijay	3	6-97
Galendromus annectens De León	Ecuador	Manabí	Crucita	—	12-95
Neoseiulus californicus McGregor	Ecuador	Manabí	Portoviejo	50	11-94
Typhlodromalus tenuiscutus McMurtry & Moraes	Ecuador	Manabí	Puerto Cayo	40	12-95
Euseius ho De León	Ecuador	Manabí	Rocafuerte	16	12-95

sava leaf discs of var. CMC-40, containing controlled egg densities of *M. tanajoa*. The leaf disc floated abaxially on water-saturated filter paper in plastic dishes (diam., 2 cm, height, 1.5 cm). Individual predatory mite females were placed on the leaf discs, and the predation arena was sealed with transparent plastic wrap.

The number of egg prey consumed per predatory mite female was counted at 24 hours. The same predatory mite female was then transferred to a new predation arena with the same egg density of prey as on previous day, and the number of eggs laid by the predatory female was counted after 24 hours. For each predator species, 14 to 18 predatory mite females were used at each egg prey density.

To obtain different egg densities, gravid *M. tanajoa* females were placed on cassava leaves and left to oviposit until the required egg density was obtained. The following egg densities were tested: 1, 3, 7, 15, 30, 105 or 200 eggs per leaf disc.

Statistical tests were performed with Statview software (Abacus Concept, USA). For two-way analyses of variance (2-way ANOVA), the factors "prey density" and "phytoseiid species" were considered as fixed factors. Homogeneity of variance and data normality were examined by the F-test and Kolmogorov-Smirnov method, respectively, before running the ANOVA. Only the number of eggs consumed was normalized by $\log (X + 1)$ transformation. The Fisher's PLSD (Protected Least Significant Difference) test following the ANOVA was used to compare means post-hoc.

RESULTS

Prey density had a significant influence on the number of eggs consumed regardless of the phytoseiid species [result of 2-way ANOVA: $F = 1177.7$, df = (6, 616), $P < 0.05$ for the factor "prey density"]. There was a general increase in egg consumption with increasing prey density (Table 2). This indicated that all predator species responded functionally to *M. tanajoa* egg density and thus curves of functional responses can be plotted (Fig. 1). Prey consumption by *E. ho*, *T. aripo* and *T. tenuiscutus* continued increasing up to the highest density of prey evaluated (200 prey eggs per leaf disc). In fact, linear regression coefficients (r^2) between consumption and prey density were high for these species, about 0.99, 0.94 and 0.89, respectively. Furthermore, they presented the highest consumption rates, consuming a maximum of 93, 101 and 59 prey in 24 h, respectively. In contrast, lowest correlations were found for *N. californicus*, *N. idaeus* and *G. annectens* (linear regression coefficients: r^2 = 0.79, 0.32 and 0.26 respectively). Nevertheless, at lowest prey densities (≤30 prey eggs per leaf disc), high correlations were also obtained (linear regression coefficient: r^2 = 0.94 to 0.99). This indicated that prey

consumption by these species increased linearly up to 30 prey eggs offered and then leveled off at a plateau (Fig. 1). Consequently, they exhibited lower consumptions, consuming a maximum of 40, 35 and 18 eggs in 24 h, respectively.

Prey density also had a significant influence on the number of eggs laid by all phytoseiid species [result of 2-way ANOVA: $F = 601.6$, df = (6, 614), $P < 0.05$ for the factor "prey density"]. There was a general increase in eggs oviposited by female predator with increasing prey density, regardless of the phytoseiid species (Table 2). Nevertheless, little increase was generally noted at the highest densities evaluated, so daily fecundity appeared to reach a plateau for all species. Highest maximum oviposition rates were registered for *T. tenuiscutus*, *N. californicus*, *N. idaeus* and *G. annectens*, ovipositing a maximum of 3.9, 3.6, 2.9 and 2.8 eggs in 24 h; whereas *E. ho* and *T. aripo* oviposited no more than 2.2 and 1.4 eggs in 24 h, respectively.

The number of eggs laid per prey consumed was calculated (i.e. mean number of eggs oviposited/mean number of prey eggs consumed), and presented in Table 2. As mentioned above, this ratio reflects in a straightforward way the efficiency of a predator at converting their prey into progeny. In general highest ratios were obtained for *G. annectens, N. californicus* and *N. idaeus* showing a maximum of 35.6, 14.5 and 12.0, respectively, suggesting that these species presented highest efficiency at converting prey into progeny. In contrast, lowest ratios were generally registered for *T. aripo*, *T. tenuiscutus* and *E. ho* showing a maximum of 6.7, 9.9 and 11.6, respectively, indicating that these species were the least efficient. The ratio at the first density for *T. aripo* was not considered because this level was obtained only one time for this species and at the lowest prey density. Thus this value appeared to be aberrant.

DISCUSSION

All predator species studied responded functionally to *M. tanajoa* egg density (Fig. 1). Holling (1959) proposed three types of functional response curves: Type 1, a linear rise to a plateau; Type 2, a curvilinear rise to an asymptote; and Type 3, a sigmoid curve rising to an asymptote. These curves, which have been extensively used in predator-prey interactions, are used to evaluate the effectiveness of a predator [see Sabelis (1985) for review]. At lowest prey densities (≤30 prey eggs per leaf disc), curves fitted well to a typical Holling Type-1 functional response for all phytoseiid species. Nevertheless, at higher densities, a flat response was clearly observed and can be regarded as a "plateau" for *N. californicus*, *N. idaeus* and *G. annectens*.

Various factors influence the plateau level of the functional response curve [see Sabelis (1985)

TABLE 2. INFLUENCE OF SEVEN LEVELS OF EGG PREY AVAILABILITY ON THE NUMBER OF EGGS CONSUMED AND NUMBER OF EGGS LAID PER PREDATOR (MEANS[1] + SE) IN 24 H BY FEMALES OF SIX PHYTOSEIID SPECIES AND ON EGGS LAID/PREY CONSUMED RATIO.

Species	Egg prey densities	Eggs consumed	Eggs laid	Ratio (×100)
Euseius ho	1	0.93 ± 0.07 a	0	0
	3	3.00	0.23 ± 0.12 a	7.8
	7	6.30 ± 0.34 b	0.73 ± 0.12 ab	11.6
	15	10.90 ± 0.70 c	1.25 ± 0.21 bc	11.5
	30	23.93 ± 1.30 d	1.60 ± 0.23 c	6.7
	105	52.80 ± 5.73 e	2.23 ± 0.25 d	4.2
	200	93.40 ± 9.84 f	2.07 ± 0.30 cd	2.2
Typhlodromalus aripo	1	0.93 ± 0.07 a	0.30 ± 0.12 a	32.2
	3	2.90 ± 0.08 b	0.20 ± 0.10 a	6.7
	7	6.83 ± 0.12 c	0.40 ± 0.12 a	5.8
	15	14.94 ± 0.06 d	0.62 ± 0.12 a	4.1
	30	28.60 ± 0.40 e	1.30 ± 0.13 b	4.5
	105	81.30 ± 3.40 f	1.22 ± 0.13 b	1.5
	200	101.31 ± 7.60 g	1.40 ± 0.20 b	1.4
Typhlodromalus tenuiscutus	1	0. 91 ± 0.09 a	0.09 ± 0.09 a	9.9
	3	3.00	0	0
	7	6.85 ± 0.11 b	0.30 ± 0.10 *a*	4.4
	15	14.53 ± 0.24 c	1.13 ± 0.21 b	7.8
	30	26.12 ± 1.80 d	2.40 ± 0.40 c	9.2
	105	48.22 ± 4.60 e	2.41 ± 0.30 c	5.0
	200	59.20 ± 5.90 f	3.93 ± 0.21 d	6.6
Neoseiulus californicus	1	1. 00	0	0
	3	3.00	0.07 ± 0.07 a	2.3
	7	6.90 ± 1.12 *a*	1.00 ± 0.09 b	14.5
	15	14.50 ± 0.35 b	1.90 ± 0.30 c	13.1
	30	24.80 ± 1.10 c	3.13 ± 0.32 d	12.6
	105	25.00 ± 1.60 c	3.10 ± 0.30 d	12.4
	200	39.72 ± 5.30 d	3.60 ± 0.20 d	9.1
Neoseiulus idaeus	1	0.92 ± 0.08 a	0	0
	3	3.00	0.25 ± 0.14 a	8.3
	7	6.73 ± 0.15 b	0.60 ± 0.13 a	8.9
	15	12.93 ± 0.93 c	1.40 ± 0.30 b	10.8
	30	24.53 ± 1.20 d	2.94 ± 0.22 d	12.0
	105	34.73 ± 3.61 e	2.90 ± 0.35 d	8.3
	200	18.60 ± 1.61 f	2.12 ± 0.15 c	11.4
Galendromus annectens	1	1. 00	0	0
	3	2.53 ± 0.30 a	0.90 ± 0.20 a	35.6
	7	6.20 ± 0.50 b	1.80 ± 0.20 b	29.0
	15	11.31 ± 0.90 c	2.31 ± 0.22 cd	20.4
	30	15.53 ± 1.40 d	2.80 ± 0.14 d	18.0
	105	18.10 ± 3.21 d	2.70 ± 0.20 cd	14.9
	200	11.50 ± 1.95 c	2.23 ± 0.20 bc	19.4

[1]Means followed by different letters are significantly different at 5% level using Fisher's PLDS test following the ANOVA (when means or SE = 0, no statistical test can be performed then no letter was given).

for review]. For example, it is well known that the plateau level depends to a major extent on the prey stage supplied and the age of the predator. In this study, the prey stage and the age of female predator were held constant. The single factor varying in the experiments was the phytoseiid species. Therefore, the differences in the plateau level of curve are mainly a consequence of differences in the phytoseiid species. The fact that the curves do not rise clearly to a plateau for *E. ho*,
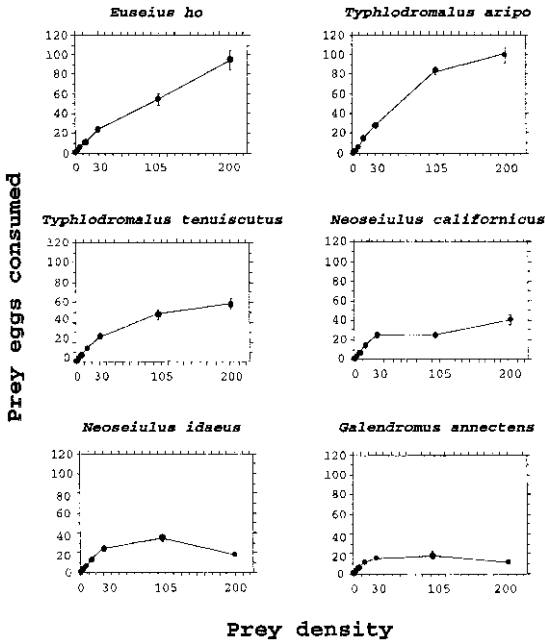
Fig. 1. Functional response of six phytoseiid species to increases in density of *M. tanajoa* eggs (curves were plotted with means ± SE).

T. aripo and *T. tenuiscutus* (Fig. 1) indicates that these species exhibit higher consumption in the range of high prey densities consuming a maximum of 93, 101 and 59 preys in 24 h, respectively. In contrast, *N. californicus*, *N. idaeus* and *G. annectens*, whose curves rose more clearly to a plateau at the density 30, have a low consumption capacity among the high egg densities tested, consuming no more than 40, 35 and 18 eggs in 24 h, respectively. These results suggested that when the prey population is high, *E. ho*, *T. aripo* and *T. tenuiscutus* will be more efficient in controlling *M. tanajoa*.

Nevertheless, among these phytoseiid species, *E. ho* and *T. aripo* had lower maximum daily oviposition rates than *T. tenuiscutus*, *N. californicus*, *N. idaeus* and *G. annectens*. Similar to Ball's (1980) results obtained on four phytoseiid species, the high consumption rate capacities of predators were not reflected in proportionately high reproductive rates. Furthermore, the differences in egg production obtained in our study seems not be correlated with the relative sizes of the predator species or their eggs but more due to the phytoseiid species characteristic. For example, *E. ho* and *G. annectens* had similar body and egg sizes (288 and 189.6 µm, 252 and 175.2 µm body and egg sizes, respectively) but different egg production. As evoked by Eveleigh & Chant (1981) for *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) eating protonymphs of *Tetranychus*

pacificus McGregor (Acari: Tetranychidae), the differences in oviposition rates in our study are more likely due to the fact some species such as *G. annectens* are more efficient in converting food energy into egg production. In fact, highest oviposition/consumption ratios were obtained for this species, regardless of the prey density (Table 2). In contrast, lowest ratios were obtained for *T. aripo*, suggesting that this species is the least efficient in converting food energy into egg production.

Daily fecundity rates at the prey density 30 (the density where functional response curves reached a plateau) were higher for *N. californicus*, *N. idaeus* and *G. annectens*. In fact, it was at 3.1, 2.9 and 2.8 eggs in 24 h for *N. californicus*, *N. idaeus* and *G. annectens*, respectively; whereas it was only at 1.6, 1.3 and 2.4 eggs in 24 h for *E. ho*, *T. aripo* and *T. tenuiscutus*, respectively. This suggests that *N. californicus*, *N. idaeus* and *G. annectens* may be able to multiply well at low prey densities. Furthermore, by their higher oviposition/consumption ratios at this prey density, these phytoseiid species converted prey to predator progeny efficiently at the lower levels of prey eggs availability. As emphasized by Friese & Gilstrap (1982) for three other phytoseiid species, predator species which require fewer prey should be better able to survive as an effective searching population at low prey density and therefore better able to maintain the population at low prey density.

In conclusion, it appeared that among the predatory species studied, when *M. tanajoa* population increases markedly or during at outbreak, the use of *E. ho*, *T. aripo* or *T. tenuiscutus* phytoseiid species should be recommended. In contrast, when the mite population is low on cassava, the use of *N. californicus*, *N. idaeus* or *G. annectens* should be better because they may be able to multiply well. The fact that all phytoseiid strains or populations used in this study came from semi-arid areas of South America suggests that they may establish well in semi-arid areas of Africa to help control cassava green mite populations.

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