Functional responses of Neoseiulus idaeus and Iphiseius degenerans (Acarina : Phytoseiidae) feeding on the cassava green mite, Mononychellus tanajoa (Acarina : Tetranychidae)

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The functional responses of larva and female *Iphiseius degenerans* BERLESE and protonymph and female *Neoseiulus idaeus* (DENMARK & MUMA) were determined with different developmental stages of the cassava green mite (CGM), *Mononychellus tanajoa* BONDAR, as food supplied at densities of 1, 2, 5, 10, 20, 30, 40, and 50 individuals per 3.14 cm² cassava leaf disc arena. All functional responses obtained were of the Holling's Type II curve with the highest plateaux when adult females of both *N. idaeus* and *I. degenerans* were preying on CGM eggs. Mean highest number of 14.3 CGM eggs/5-hours consumed by a female *N. idaeus* was not significantly different from the 13.0 CGM eggs/5-hours of *I. degenerans*. There was a significant non-linear positive correlation between predator's search rate and prey density in all treatments. Larvae of *I. degenerans* displayed a unique search rate curve apparently associated with its non-obligatory predatory nature.

INTRODUCTION

Cassava *Manihot esculenta* CRANTZ (Euphorbiaceae) was brought to Africa some 400 years ago (JONES, 1969). Arthropod pests of this crop were not considered to be of economic importance in Africa until the cassava mealybug *Phenacoccus manihoti* MATILE-FERRERO and the cassava green mite (CGM) *Mononychellus tanajoa* (BONDAR) were reported in East Africa in the early 1970s (NYIIRA, 1972; HAHN & WILLIAM, 1973) and later spread rapidly across subsaharan Africa in the absence of their natural enemies and caused devastating losses (HERREN, 1987).

Among several control strategies that have been suggested for the control of the CGM, classical biological control (the use of introduced natural enemies to control exotic pests below their economic injury level) has been recommended, particularly as local predators and parasitoids in Africa were inefficient (LYON, 1973; YANINEK & HERREN, 1988) and insecticidal applications were not effective over extended periods and incompatible with the use of beneficials (BENNETT & YASEEN, 1975). Consequently, several predatory mites of the family Phytoseiidae have been imported into Africa for use in biological control of the CGM. Several of these are valuable natural enemies of tetranychid mites, an economically important group of agricultural pests (HUFFAKER *et al.,* 1970). One of these predators, *Neoseiulus idaeus* (DENMARK & MUMA) (YANINEK, 1985), exists in close association with CGM on cassava on the north coast of Colombia.

The effectiveness of a natural enemy can be measured by its ability to attack and consume prey (functional response), its life history in relation to that of its prey, and tolerance to environmental stresses (MURDOCH, 1973). Functional response has been defined by SOLOMON (1949) as the relationship between the number of prey consumed per unit of time per predator and the prey density. He stressed that this is basically an individual response of predators to the density of their prey. Of the four types of functional responses, the type II response is most common among arthropods. The basic type II functional response equation (the HOLLING disc equation) is represented by the expression:

$$N_a = aT_tN/1 + aT_hN \qquad [1]$$

where N_a = Number of prey eaten, a = rate of predation, T_t = Total time, N = Prey density, and T_h = Handling time (HOLLING, 1959). This equation assumes constant prey density which is often unrealistic. ROGERS (1972) proposed a modification as the random search equation which accounts for changes in prey density over a time scale. Statistical difficulties associated with the use of this equation should be noted particularly when prey depletion exceeds 50% (LIVDAHL & STIVEN, 1983).

The rate at which a functional response appoaches the upper plateau is determined by the area of discovery (a) (NICHOLSON & BAILEY, 1935), expressed by the formula (HASSELL, 1971)

$$a = 1/P \ (\log_e N/S) \qquad [2]$$

where P is the density of predators searching for prey, N and S are the initial and final surviving prey densities. It is a measure of the maximum distance at which a prey can be perceived, speed of predator and prey movements and proportion of attacks that are successful (HOLLING, 1966; BADII & MCMURTRY, 1988).

Phytoseiid predators show a marked preference for various stages of prey (TAKAFUJI & CHANT, 1976), but the interaction involving different developmental prey stages of different predators' stages have not been adequately elucidated. Our study therefore compared the functional response of the protonymph and adult female of the exotic species *N. idaeus* and the larva and adult female of the local species *I. degenerans* on different developmental stages of CGM to assess their predatory potentials and control of CGM. The larva and the protonymph are the first feeding stages of *I. degenerans* and *N. adaeus respectively. Degenerans* is an indigenous species commonly found associated with the two-spotted mite *Tetranychus urticae* KOCH and the red mite *Oligonychus gossypii* (ZACHER) on many plants in western Kenya and recently with CGM on cassava in Africa. It is a cosmopolitan species with a wide range of alternate foods (J. S. YANINEK, pers. comm.; IITA Biocontrol Data Base). *N. idaeus* is an exotic species from Colombia commonly associated with CGM. All mobile stages of *N. idaeus* except the larva require prey, and all mobile stages of *I. degenerans* can also feed although feeding is not obligatory in the larval instar (TAKAFUJI & CHANT, 1976).

MATERIALS AND METHODS

I. degenerans was collected from a cassava field inundated with *N. idaeus* three months earlier on a competition trial within the International Center for Insect Physiology and Ecology Mbita Point Field station. The *N. idaeus* population used was collected from an on-going screenhouse culture at the CABI, Institute

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of Biological Control Station at Muguga, Kenya, having been previously obtained from Centro International Agricultura Tropicale (CIAT), Colombia by the Biological Control Program at IITA, Nigeria. Cultures of both species were maintained separately on McMurtry-Scriven type arenas (MCMURTRY & SCRIVEN, 1975) with all stages of CGM as food in the laboratory. Four cultures of each predator species were simultaneously maintained and the population of each culture exchanged forthnightly to minimize inbreeding.

All experiments were conducted under fluctuating laboratory conditions of 60−90% RH and 20−27 °C. The experiments were performed on 3.14 cm² field-collected cassava leaf discs floating abaxially on water saturated absorbent cottonwool in petri dishes. The water barrier prevented the prey and predators from escaping. Individual mites were placed on these arenas using a slightly moistened camel hair brush.

Cohorts of predators were continuously supplied by obtaining 100 eggs of each species laid within a maximum period of 8 hours each week and reared on McMurtry-Scriven arenas. Only mites which moulted within a two- to four-hour period were used. Adult females were mated immediately after the adult moult. Mating was insured by introducing twice the number of males into each arena.

The first feeding instars (i. e. larva of *I. degenerans* and protonymph of *N. idaeus*) and their adult females were each provided with cohorts of the following developmental stages of CGM at a density of 1, 2, 5, 10, 20, 30, 40, and 50 mites per disc, replicated 20 times.
1. Eggs laid within a maximum of twelve hours before start of experiment
2. Larvae hatched within a maximum of three hours
3. Nymphs (protonymphs and deutonymphs) of indeterminate age
4. Teleiochrysalis
5. Newly moulted adult males (unmated)
6. Newly moulted adult females (unmated).

All adult female predators were starved overnight to maintain a homogeneous hunger state. Observations were done under a binocular microscope at a magnification of 16× every half hour. Consumed prey were replaced during these observations. The total number of prey consumed during a five-hour period was recorded. Mean numbers of prey consumed per 5 hours were plotted against initial prey density. The search rates of each predator for the different developmental stages of CGM were determined as a solid line representing the mean number of prey types killed (i. e. mean of the sum of CGM eggs, larvae, nymphs, teleiochrysalis, males and females eaten) by a single predator at each prey density. This was fitted with a second power polynomial function to determine the maximum search rate (i. e. the y-axis intercept).

The experiment was carried out at the Mbita Point Field Station of the ICIPE during the period of November 1986 to May 1987.

RESULTS AND DISCUSSION

The functional response of larva and adult female *I. degenerans* and protonymph and adult female *N. idaeus* to densities of various stages of CGM showed a monotonic rise reaching a plateau between prey densities 5 and 40 depending on prey and developmental stage; *I. degenerans* females did not attain this plateau on CGM eggs at the densities tested (Fig. 1). All functional response curves were the typical Holling type II curves. The highest consumption was
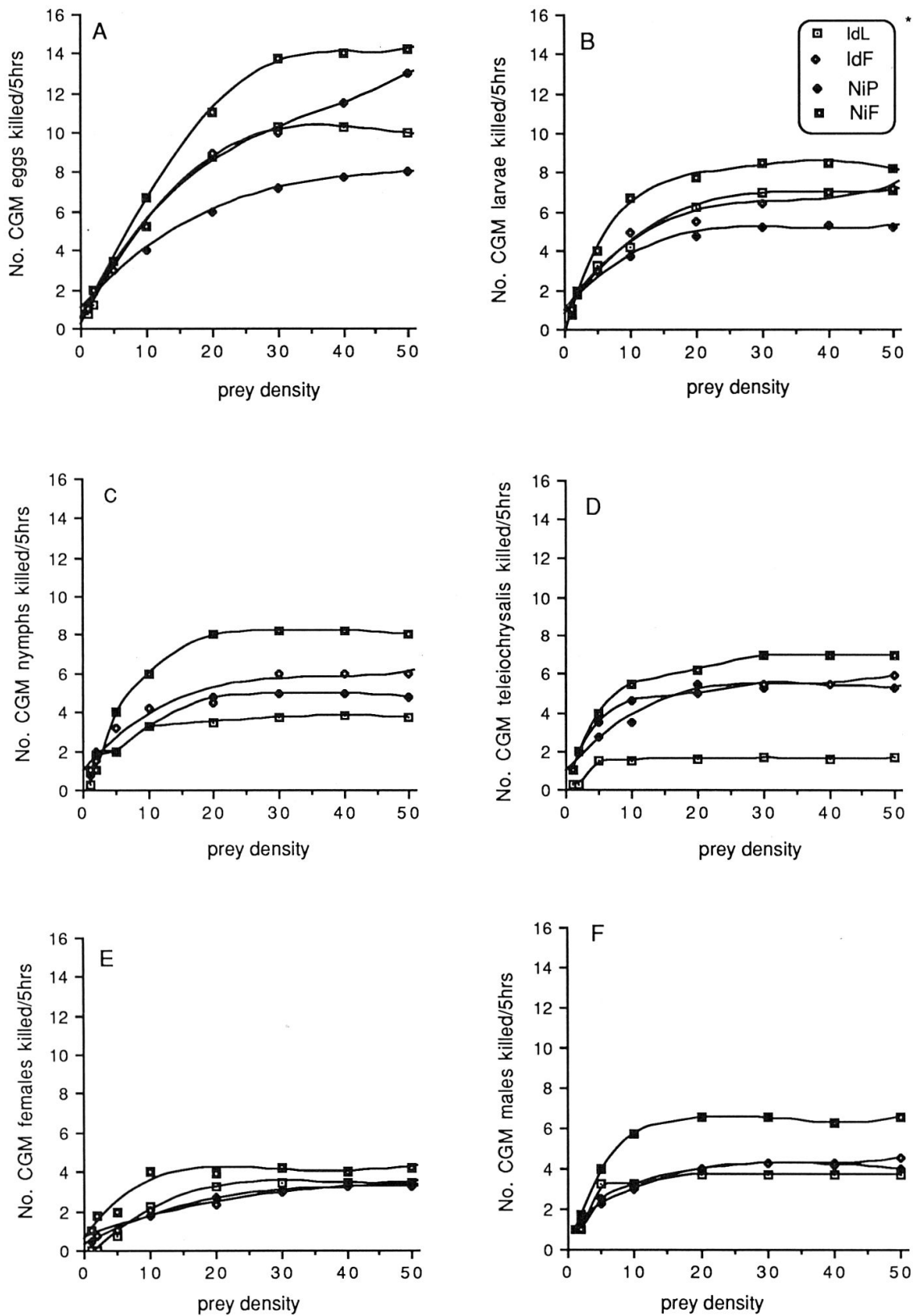
Fig. 1. Functional reponses of protonymph and female *N. idaeus,* and *I. degenerans,* to changes in density of different developmental stages of CGM. IdL = *I. degenerans* larva, IdF = *I. degenerans* female, NiP = *N. idaeus* protonymph, NiF = *N. idaeus* female.

achieved with adult females of *N. idaeus,* followed by adult females and larvae of *I. degenerans* on CGM eggs; lowest by larvae of *I. degenerans* when supplied with 10 CGM teleiochrysalis. Adult female *N. idaeus* attained a plateau 1.5 to 2 times higher than adult female *I. degenerans* for all stages of CGM. Also mature adult females of both species attained higher plateaux than their immature stages when offered the same prey stage. The differences were less obvious when the first feeding immature stages of both predator species were compared. Similar results were obtained from studies on phytoseiids responding to different densities of their tetranychid prey, *Phytoseiulus persimilis* ATHIASHENRIOT (TAKAFUJI & CHANT, 1976; SABELIS, 1981; EVELIEGH & CHANT, 1981), *Typhlodromus occidentalis* NESBITT (SABELIS, 1981) and *Amblyseius bibens* BLOMMERS (BLOMMERS, 1976; SABELIS, 1981). These workers further observed that the age of the female at adulthood and the sex of the predatory mite also determined the level of the plateau. Similar type II functional responses were established for *Amblyseius fallacis* (GARMAN) on two-spotted spider mite egg densities (CROFT & BLYTH, 1979), *Amblyseius potentillae* (GARMAN) on the European red mite larvae (RABBINGE, 1976) and *T. occidentalis* on the spotted spider mite egg and male (FRANTZ, 1974).

The highest predation rate of 14.3 prey/5 hours recorded when adult *N. idaeus* females fed on CGM eggs was not significantly different from 13.0 prey/ 5 hours recorded for adult female *I. degenerans* when given the same prey (Tab. 1). These were however significantly different ($P < 0.05$) from values obtained when the two immature predator stages were fed on the eggs of the prey. Predator stages of both species fed more on eggs than on other stages on CGM; *N. idaeus,* the exotic species, fed significantly more ($P < 0.05$) than the local species *I. degenerans* (Tab. 1). Similarly, both stages of the exotic predator were found to have higher maximum predation rates than their corresponding indigenous predator stages when preying on the mature stages of CGM, with the exception of *I. degenerans* preying on larvae and adult females of CGM. The apparent high prefer-

Tab. 1. Maximum number of CGM eaten by larvae and females of *I. degenerans* and protonymphs and females of *N. idaeus* during a five-hour period searching on a 3.14 cm² cassava leaf disc.

Developmental stage of CGM	N. idaeus[1]		I. degenerans	
	Protonymph	Adult female	Larva	Adult female
Eggs	8.00±0.36c	14.25±0.47a	10.25±0.3b	13.00±0.51a
Larvae	5.30±0.26c	8.55±0.34a	7.10±0.47b	7.25±0.24ab
Nymphs	4.95±0.21cd	8.25±0.30a	3.80±0.35d	6.00±0.36bc
Teleio-chrysalis	5.30±0.26b	7.00±0.36a	1.65±0.26c	5.95±0.34a
Males	4.25±0.20b	6.50±0.26a	3.75±0.26b	4.50±0.16b
Females	3.00±0.21b	4.25±0.21ac	3.60±0.30bc	3.35±0.33bc

[1]Means within a row followed by the same letter are not significantly different (P < 0.05, Duncan multiple range test).
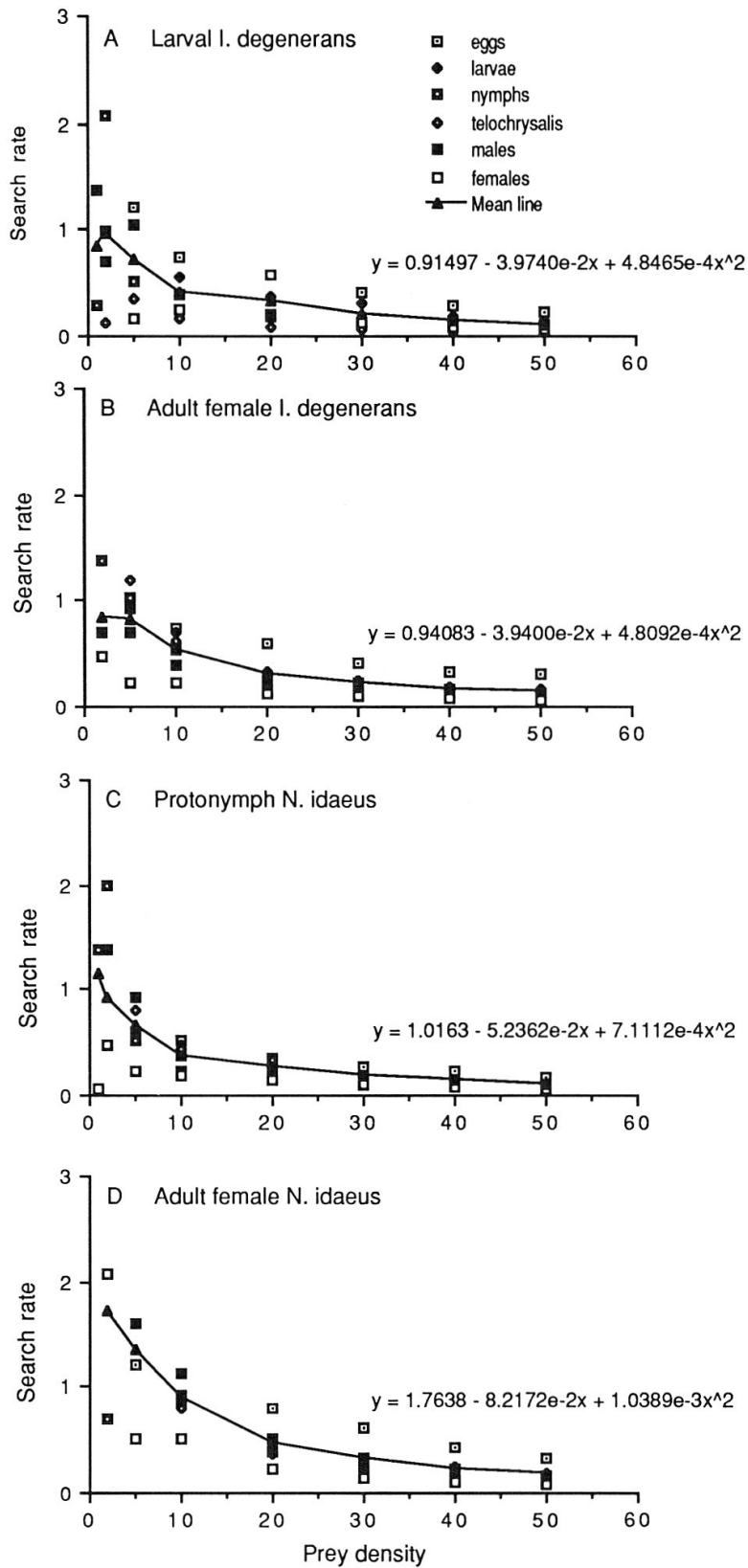
Fig. 2. Relationship between the search rate (= Nicholsonian area of discovery) of the exotic predator *N. idaeus* and the indigenous predator *I. degenerans* at different initial densities of their prey *M. tanajoa*.

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ence for CGM eggs should be viewed with caution as it is generally known that the biomass in an egg of approximately $1\mu g$ wet weight has less food value than that of an adult female (J. S. YANINEK, pers. comm.). In CGM for instance, the female is five times the biomass of its egg (SABELIS, 1981). The mean maximum numbers of prey consumed by the predators represent the different values of the carrying capacity (= constant K) (upper asymptote of the response curve) implying the upper limit of egg laying capacity of the females and the maximum feeding capacity of the immature stages and males within the experimental period inspite of the availability of large numbers of prey (SINGH & SRIVASTAVA, 1989). These results suggest that *N. idaeus* can reduce CGM populations faster than *I. degenerans*, reflecting the higher capability of *N. idaeus* as a biological control agent of CGM.

The area of discovery (as a measure of search rate) decreased within the range of the prey densities tested. The larva of *I. degenerans* depicted a pronounced convex curve (Fig. 2). There was a significant non-linear positive correlation at $P < 0.05$ (r^2 ranging from 0.903 to 0.970) between search rate and prey density for both species. The intercept of this line on the Y-axis depicts the maximum search rate i.e. when a predator is actively searching in an area with zero prey. This value, in order of magnitude, was found to be 1.76 and 1.02 for *N. idaeus* adult female and protonymph respectively and 0.94 for adult female of *I. degenerans*. Larvae of *I. degenerans* had the lowest maximum search rate of 0.91. These results suggest that adult female *N. idaeus* was significantly better (ANOVA, $P < 0.05$) at prey searching than *I. degenerans*. Interestingly, the protonymph of the exotic species *N. idaeus* also had a significantly higher maximum search rate than the adult of the indigenous species *I. degenerans* (ANOVA, $P < 0.05$). The search rate apparently increases as the predator matures showing increasing predatory behaviour. There was no significant difference ($P = 0.05$) between searching rate of adult *I. degenerans* and its larva. These findings are similar to that of the hyperparasitoid *Alloxysta pleuralis* (CAMERON) parasitizing *Trioxys indicus* (SUBBA RAO & SHARMA) (SINGH & SRIVASTAVA, 1989). The unique searching behaviour of the larval *I. degenerans* could be attributed to the fact that feeding is not essential for its growth and development and subsequent moulting to the protonymphal stage (TAKAFUJI & CHANT, 1976).

In conclusion, the indigenous species *I. degenerans* had a similar functional response to that obtained for the exotic species *N. idaeus,* suggesting *I. degenerans* as a potential control factor of CGM particularly if inundated in most African cassava agroecosystems. However, its ability to feed on CGM in the presence of *N. idaeus* in the same arena and when both are present in a cassava field is not known.

ZUSAMMENFASSUNG

Mit verschiedenen Entwicklungsstadien der grünen Cassava-Spinnmilbe (CGM), *Mononychellus tanajoa* BONDAR, angeboten als Futter in den Dichten von 1, 2, 5, 10, 20, 30, 40 und 50 Individuen pro 3,14 cm² grosse Cassavablatt-Arena, wurden die funktionellen Reaktionen («functional responses») der larvalen Stadien und der Weibchen von *Iphiseius degenerans* BERLESE und der protonymphalen

Stadien und der Weibchen von *Neoseiulus idaeus* (Denmark & Muma) ermittelt. Die resultierenden Kurven der funktionellen Reaktionen entsprachen alle dem Holling Typ II mit einem maximalen Plateau, wenn die Weibchen, sowohl von *N. idaeus* als auch *I. degenerans,* sich von Eiern der grünen Cassava-Spinnmilbe ernährten. Die höchste durchschnittliche Anzahl Eier (14,3), die von einem Weibchen von *N. idaeus* in einer 5-Stunden-Periode konsumiert wurde, unterschied sich nicht signifikant von den 13,0 Eiern, die von einem Weibchen von *I. degenerans* in 5 Stunden gefressen wurden. Zwischen der Suchrate des Räubers und der Beutedichte zeigte sich in allen Behandlungen ein signifikant positiver, nichtlinearer Zusammenhang. Die Larven von *I. degenerans* zeigten dagegen eine unterschiedliche Reaktionskurve in ihrer Suchrate, die vermutlich mit ihrer nicht obligaten räuberischen Aktivität zusammenhängt.

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