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The influence of temperature on the life table of *Hyperaspis notata*

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Abstract

The coccinellid *Hyperaspis notata* Mulsant was introduced into Africa for the biological control of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero. Two cohorts of strains, one originating from Southern Brazil and Paraguay feeding on *P. manihoti*, and one from Colombia feeding on *Phenacoccus herreni* Cox & Williams were studied at different temperatures between 15 and 34 °C and age-specific life tables were constructed. Although in the areas of origin the climatical conditions and the food sources are different, the survivorship and developmental times at the same temperature differed little among the two strains, the Colombian strain being slightly more tolerant to high temperatures. Jacknife estimates of the intrinsic rates of increase (r_m) peaked very close to 30 °C for the two strains.

Introduction

In order to control the cassava mealybug, *Phenacoccus manihoti*, Matile-Ferrero (Homoptera: Pseudococcidae), which had been accidentally introduced into sub-Saharan Africa in the early 1970's (Matile-Ferrero, 1977), a solitary parasitic wasp, *Apoanagyrus* (= *Epidinocarsis*) lopezi De Santis (Hymenoptera: Encyrtidae) was imported from South America and released in Africa (Herren & Lema, 1982). *A. lopezi* established itself over a wide range of ecological conditions of the cassava belt and reduced the cassava mealybug to non-pest status (Herren & Neuenschwander, 1991). In about 5% of all cassava fields, however, *A. lopezi* could not control *P. manihoti* efficiently enough to prevent yield losses (Neuenschwander et al., 1991).

To control *P. manihoti* in these 'hot spots' of infestation, indigenous and exotic coccinellids were studied (Umeh, 1982; Fabres & Kiyindou, 1985; Nsiama She, 1985; Nsiama She et al., 1984; Kiyindou & Fabres, 1987; Kanika-Kiamfu et al., 1992). In the early 1980's, *Hyperaspis notata*, Mulsant (Coleoptera: Coccinellidae) was introduced from South America into Africa to complement *A. lopezi* and became established in several east and southern African countries (Herren & Neuenschwander, 1991; Neuenschwander & Zweigert, 1994; Chakupurakal et al., 1994). In South America, *H. notata* was found in two ecologically very different zones on different hosts (Loehr et al., 1990; Sullivan et al., 1991). One strain was found in the Colombian highlands where there are little fluctuations in temperature and day-length throughout the year, and its main-prey is *Phenacoccus herreni* Cox & Williams (Homoptera: Pseudococcidae). The second strain was found in Southern Brazil and Paraguay, where temperatures in winter reach 0 °C under short-day conditions, while temperatures during the hot summer touch 40 °C under long-day conditions. In this region, *H. notata* feeds on *P. manihoti*. The expected differences in response of the coccinellids to temperature are among the factors which could possibly be exploited in the biological control project against the cassava mealybug, and they might help finding an optimal complement to *A. lopezi* in the target sites of introductions.

The purpose of the present study was to quantify possible differences in temperature-dependent survival, development, and oviposition between the two strains of *H. notata*.

Materials and methods

Origin. *H. notata* from two different regions in South America, namely Paraguay/southern Brazil and Valle Cauca, Colombia, was reared in quarantine by the International Institute of Biological Control (IIBC) in the UK. Shipments of *H. notata* were sent to the International Institute of Tropical Agriculture (IITA), in Ibadan, Nigeria. The individuals of the shipments of Paraguay and of southern Brazil were reared in the same rearing unit. The resulting strain is called strain BB throughout this study. In December 1987, *Hyperaspis* (*Cleothera*) *notata* of Colombian origin was received. In this study, the adults and their progeny are identified as strain CC. Cultures of both origins were transferred to the IITA insectary in Cotonou, Benin, in 1988.

Rearing. In the insectary, *H. notata* was reared on *P. manihoti* on potted cassava plants in wooden cages (44 cm × 45 cm × 58 cm) with fine screen sides and glass tops, at 27 °C ± 2 °C. To boost production, females were often kept in small numbers (up to 10) in Petri dishes (100 mm diameter × 15 mm) with cassava mealybug ovisacs in excess.

Experimental set-up. To study temperature-dependent development, different constant temperatures (maximum fluctuations ±1 °C) were chosen: 15, 18, 20, 25, 30, 32 and 34 °C. The photoperiod was kept at L12 : D12. Relative humidities varied between 70 and 90%, but reached 100% for periods of a few hours each day assuming uncontrolled but similar across the treatments.

Cohorts of about 100 eggs of *H. notata*, not older than 24 h, were exposed to one of the seven temperatures and checked every 24 h for hatching. After eclosion, the larvae were reared individually in Petri dishes with cassava mealybug ovisacs in excess. Moulting and mortality were checked every 24 h.

To determine the oviposition capacity, freshly emerged adults were kept as pairs in Petri dishes each at the seven constant temperatures indicated above. The beetles were fed mealybug egg masses in excess every second day, when predator eggs were counted and removed. Dead males were replaced.

Evaluation and statistical analysis. Chi-square tests were done at $P = 0.05$ to evaluate differences in preimaginal survivorship at each temperature.

The developmental rates of eggs, larvae, prepupae and pupae were studied as follows: At constant temperatures T, the rates were fitted to Sharpe & DeMichele's (1977) enzyme kinetics model:

$$r_{(T)} = \frac{r\frac{T}{298.16}\exp\left[\frac{\Delta H_A^{\neq}}{R}\left(\frac{1}{298.16}-\frac{1}{T}\right)\right]}{1+\exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2L}}-\frac{1}{T}\right)\right]+\exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_{1/2H}}-\frac{1}{T}\right)\right]} \quad (1)$$

where r is the developmental rate at $T = 298,16$ K, $T_{1/2L}$ is the absolute temperature [K] at which the enzyme relevant for development is $1/2$ active and $1/2$ low temperature inactive, $T_{1/2H}$ is the temperature (K) at which the enzyme is $1/2$ active and $1/2$ high temperature inactive, $\Delta H_A^{\neq}$ is the enthalpy of activation of the reaction [cal mol^{-1}] and $\Delta H_{L,H}$ is the change in entropy associated with low (L) and with hot (H) temperature, respectively [cal K^{-1} mol^{-1}], and R is the universal gas constant (1.987 [cal K^{-1} mol^{-1}]). This model was chosen because a comparison on the basis of physiological relevant parameters was sought.

The biophysical model was fitted according to Schoolfield et al. (1981) to the developmental rates of eggs, larvae and pupae, to the temperature dependent survivorships and the r_m values.

The life tables were analyzed by means of an algorithm, provided by Dr Fred Hulting (USA). According to Hulting et al. (1990), this algorithm provides a Jacknife estimate of the intrinsic rate of increase, r_m, along with its error (SE) and confidence interval.

Results

Survival. At the extreme temperatures at 15 ° and 34 °C, few individuals survived and highest survivorship for the two strains was recorded at 30 °C (Table 1). The observations suggest differences between developmental rates at low temperature. Nevertheless, no significant difference was found between strains. Survivorship was plotted against temperature and the data points represented by model [1] (Figure 1). The parameters characterizing these curves are presented in Table 2. At most temperatures, the Brazilian strain of *H. notata* survived better than the Colombian strain. This difference was small at 30 °C and disappeared at 34 °C where only individuals of the Colombian strain survived.

Table 1. Proportion (P) of *Hyperaspis notata* of Brazilian origin (BB) and Colombian origin (CC) surviving from egg up to adult emergence, at seven temperatures [N = numbers of individuals]. At P = 0.05, the Chi-square test showed no significance in the proportion of surviving beetles between the strains within the same temperature

Strain	Temperature													
	15 °C		18 °C		20 °C		25 °C		30 °C		32 °C		34 °C	
	P	N	P	N	P	N	P	N	P	N	P	N	P	N
BB	0.000	85	0.483	65	0.792	56	0.718	54	0.865	54	0.821	55	0.000	34
CC	0.000	85	0.480	56	0.544	62	0.508	61	0.808	53	0.681	57	0.027	74

Table 2. Parameter estimates after equation [1] for the survivorship, developmental and Jacknife estimates curves r_m for *Hyperaspis notata* from Brazil (BB), Colombia (CC)

	Strain	Parameter						
		r rate	$\Delta H_A \neq$ cal mol^{-1}	ΔH_L cal mol^{-1}	$T_{1/2L}$ K	$\Delta H_{L,H}$ cal mol^{-1}	$T_{1/2H}$ K	R^2
Survivorship								
	BB	0.79	1086.0	−1712597.0	290.9	1798238.4	305.4	0.99
	CC	0.62	6771.7	−4904495.6	288.4	771842.9	305.4	0.97
Developmental rates								
Eggs	BB	0.163	8717.1	−1864290.5	291.0	1486277.1	306.3	0.99
	CC	0.168	8170.2	−2016109.7	291.0	1666470.1	307.5	0.99
Larvae I-IV	BB	0.085	11896.8	−1928519.0	291.0	2992346.8	306.3	0.99
	CC	0.083	9151.2	−1901843.7	291.0	1745583.9	307.1	0.99
Prepupae and pupae	BB	0.076	11058.8	−6107428.6	291.0	4091343.3	306.3	0.99
	CC	0.073	10878.2	−1706160.7	291.0	1478563.3	307.5	0.99
Egg to adult	BB	0.032	9440.6	−374912.3	291.0	1837996.1	306.3	0.98
	CC	0.031	8704.5	−279735.7	291.0	1364095.3	307.2	0.98
r_m								
	BB	0.552	7176.3	−2046940.2	286.2	214420.0	305.0	0.89
	CC	0.550	9465.0	−1901143.5	291.1	1655275.4	305.1	0.88

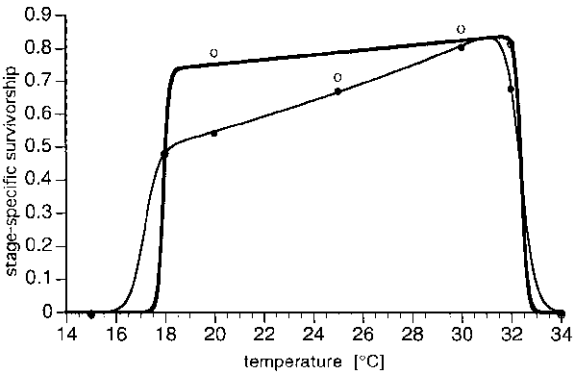

Figure 1. The survivorship of preimaginal *Hyperaspis notata* life stages of different strains (BB and CC) discussed in 'Material and methods'. The observed values (○: BB and ●: CC) were described by equation (1) (——: BB and – – –: CC).

Development. Developmental times at the different temperatures for the two experimental groups are summarized in Table 3. Times needed to complete development from egg to adult ranged from 91 days at 18 °C to 21 days at 32 °C for the Brazilian strain and 88 days at 18 °C to 21 days at 32 °C for the Colombian strain. Generally, the larvae developed uniformly which led to very small variances. It is interesting to note that the few surviving larvae of the Colombian strain needed more time to complete their development at 34 ° than at 32 °C. The Brazilian strain could not complete development at 34 °C. Significant differences between the two strains were found at 30 °C (Table 3).

Figure 2 shows the relationship between developmental rates and temperature and Table 2 gives the corresponding parameters of these curves (see Equa-

Table 3. Average development times (days) ±SE of *Hyperaspis notata* from Brazil (BB), Colombia (CC), the number of replicates is given in parentheses

Instar/	strain	Mean duration (days) ± SE at 18 °C	20 °C	25 °C	30 °C	32 °C	34 °C
Egg							
	BB	14.4 ± 0.14 (50)	7.7 ± 0.07 (50)	6.3 ± 0.11 (50)	5.1 ± 0.10 (50)	4.1 ± 0.04 (50)	4.4 ± 0.15 (16)
	CC	15.5 ± 0.10 (50)	7.3 ± 0.07 (50)	6.2 ± 0.08 (50)	4.9 ± 0.06 (50)	4.1 ± 0.04 (50)	4.6 ± 0.17 (21)
Larvae I-IV							
	BB	36.8 ± 0.82 (34)	15.4 ± 0.26 (44)	12.7 ± 0.32 (39)	9.0 ± 0.20 (48)	7.0 ± 0.19 (45)	**
	CC	33.2 ± 1.39 (30)	15.2 ± 0.19 (34)	12.7 ± 0.19 (33)	9.3 ± 0.31 (46)	8.1 ± 0.17 (40)	10.5 ± 0.35 (2)
Prepupa and pupa							
	BB	38.1 ± 1.20 (33)	18.3 ± 0.21 (33)	13.7 ± 0.30 (39)	9.6 ± 0.14 (47)	9.5 ± 0.22 (45)	**
	CC	35.7 ± 1.50 (27)	19.2 ± 0.17 (34)	14.1 ± 0.30 (31)	9.8 ± 0.30 (43)	9.0 ± 0.26 (39)	8.0 ± 0.71 (2)
Egg to adult							
	BB	91.0 ± 1.11 (32)a[1]	41.4 ± 0.21 (44)a	32.7 ± 0.30 (39)a	23.6 ± 0.17 (47)a	20.9 ± 0.22 (45)a	**
	CC	87.9 ± 0.94 (27)a	41.5 ± 0.26 (34)a	33.0 ± 0.43 (31)a	24.6 ± 0.21 (43)b	21.2 ± 0.48 (39)a	23.5 ± 0.35 (2)

[1] means of a column followed by the same letter do not differ significantly (P = 0.05) from each other; ** no data available because all L1 died.

tion 1). No differences were found among the different strains of *H. notata*. The parameters $T_{1/2L,H,}$ the temperature [K] at which the enzyme is active at $1/2$ low (L) and $1/2$ high (H) temperatures inactive, respectively, refers to the range of temperatures that allow development. *H. notata* BB, e.g., have their maximal development rate reduced by half at 18 °C and 33.3 °C. Hence, the temperature range for optimal development is only 15 °C, i.e., from 18 °C up to 33.3 °C. This temperature range is considered as being quite narrow.

Life table analysis. Longevity, preoviposition and oviposition periods, and the resulting generation times, as well as progeny production and their sex ratio are indicated in Table 4. Life span of adults was generally very long, with a maximum of 592 days by one female at 20 °C. In all groups, some females did not lay any eggs and survived for only about 2 weeks. Daily r_m-values, derived from weekly estimates, were calculated (Table 4). Those females that had stopped laying eggs survived on average for another two and a half weeks (post-oviposition period). Oviposition reached a maximum of 1444 eggs for one female at 20 °C; but declined rapidly at temperatures above 30 °C. Sex ratios were always balanced and no significant deviations from 50% were detected.

The values of r_m were estimated for the two strains at different temperatures (Figure 3) and reported in Table 2; no differences were significant at P = 0.05.

Discussion

The preimaginal survivorships and developmental times of *H. notata* on *P. manihoti* in the present study were similar to those found for *H. jucunda* (Mulsant) (Nsiama She, 1985; Nsiama She et al., 1984) and *H. raynevali* Mulsant (Kiyindou & Fabres, 1987) reared on the same host. Both species are probably synonymous and had been imported from Trinidad, where the main prey was *P. herreni*. The main differences between *H. notata* and the other species concerned high temperatures, where *H. jucunda* larvae survived better, and low temperatures, at which *H. raynevali* needed about 20% more time to complete its development. Among two as yet undescribed species of *Hyperaspis*, which IITA imported also from Brazil and Colombia, species 2 had a lower rate of mortality than *H. notata* (V. Michel, unpubl.).

Our study shows that *H. notata* has virtually the same developmental times and response to temperature as its prey *P. manihoti* (Schulthess et al., 1987). This coincidence is considered one of the factors that render *H. notata* a promising predator for further releases.

On *P. herreni*, the predators *H. notata*, *H. onerata* Mulsant, and *Hyperaspis* sp. were investigated at 28 °C (Sullivan et al., 1991) and *H. notata* at 22, 25, and 30 °C (Carrejo et al., 1991). The developmental times for *H. notata* were practically identical to those found in the present study on *P. manihoti*.

Table 4. Life table parameters for *Hyperaspis notata* from Brazil (BB) and Colombia (CC) at different temperatures

Temperature/ strain	N	Adult longevity (weeks)		Mean generation time (weeks)	Preoviposition period (weeks)	Oviposition period (weeks)	mean total progeny ($n \pm$SE)	sex ratio (proportion females)	Jacknife estimate of r_m per week ($\pm$SE)	Jacknife estimate of r_{m} per day
		mean	max							
18 °C										
BB	30	25.33	74.1	25.5	3.25	13.95	39.90 ± 7.240	0.45	0.122 ± 0.008	0.0174
CC	28	22.61	61.9	25.8	2.71	12.88	30.14 ± 6.650	0.54	0.109 ± 0.007	0.0156
20 °C										
BB	31	48.00	84.6	12.3	1.40	45.01	579.50 ± 36.804	0.43	0.447 ± 0.008	0.0639
CC	30	43.37	76.0	12.6	1.61	39.79	401.51 ± 29.959	0.52	0.424 ± 0.006	0.0606
25 °C										
BB	30	34.90	60.7	9.7	1.02	31.45	533.98 ± 38.227	0.43	0.568 ± 0.011	0.0810
CC	30	39.60	58.3	10.0	1.02	33.91	381.09 ± 26.864	0.47	0.521 ± 0.011	0.0744
30 °C										
BB	30	19.13	39.1	7.0	0.68	16.98	338.04 ± 37.047	0.44	0.717 ± 0.016	0.1024
CC	31	22.39	34.3	6.8	0.53	18.55	354.58 ± 35.885	0.41	0.731 ± 0.010	0.1157
32 °C										
BB	30	7.93	17.9	5.3	1.66	3.90	15.19 ± 2.633	0.45	0.390 ± 0.047	0.0557
CC	30	7.23	12.7	5.6	0.76	4.87	19.70 ± 1.969	0.54	0.516 ± 0.024	0.0757
34 °C										
CC	30	3.10	4.9	0.0	0.79	2.31	0.04 ± 0.015	0.50	0.000 ± 0.000	0.0000

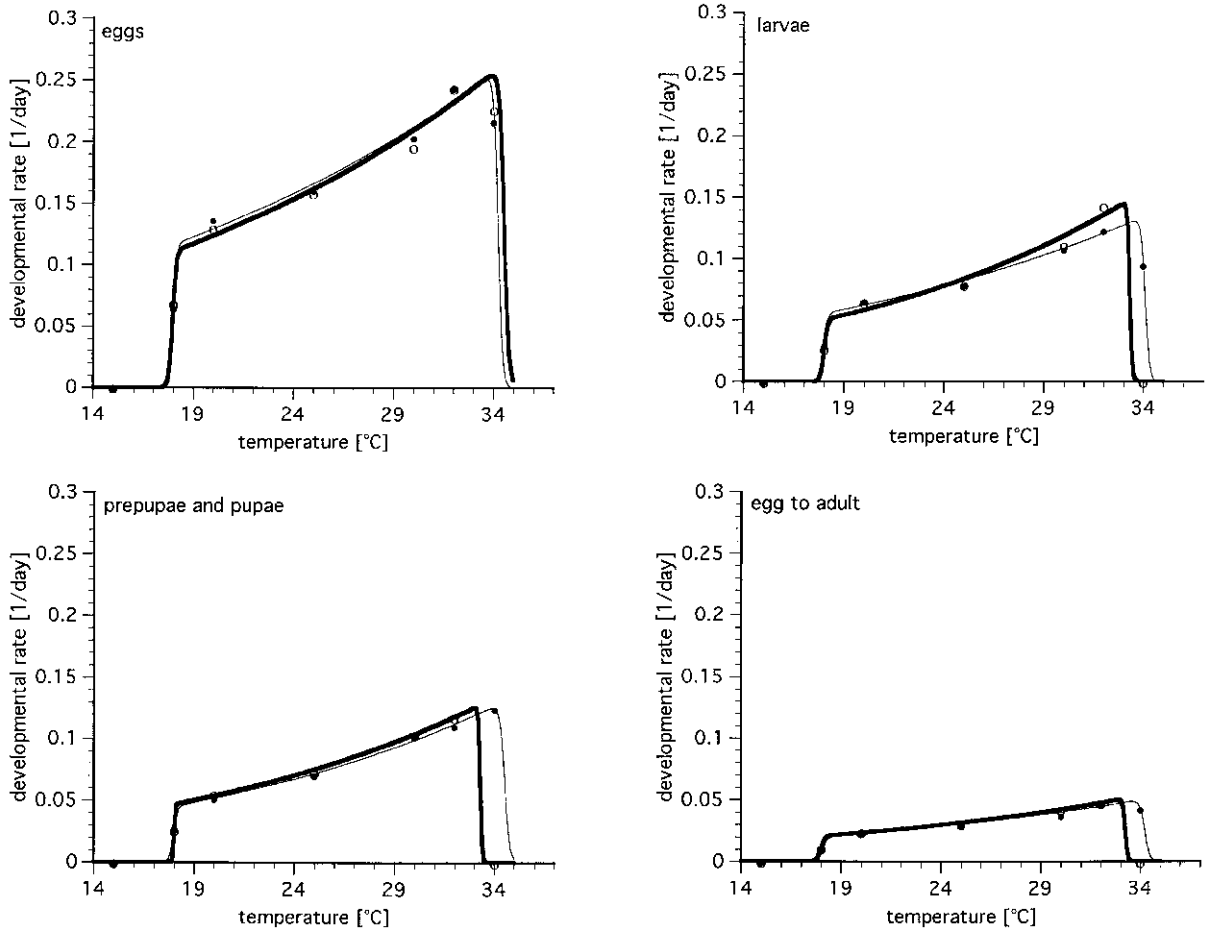

Figure 2. Developmental rate [1/days] of life stages of *Hyperaspis notata* at different temperatures. The lines (——: BB and ——: CC) have been fitted to the observed data (○: BB and ●: CC) according to equation [1]. For the description of the different strains denoted as BB and CC see text.

The highest intrinsic rate of increase, r_m, of *H. notata* was recorded at 30 °C, considerably higher than in the other species. But even at its maximum, r_m of *H. notata* did not reach the corresponding value for its prey, *P. manihoti* namely 0.16 (Schulthess et al., 1987). By contrast, in the study of Carrejo et al. (1991), *H. notata* from Colombia survived for a much shorter time and laid fewer eggs at all temperatures, particularly at 30 °C, than the same strain in our experiment. Whether this is due to the different prey, *P. herreni*, or to the experimental set-up (in our study, males were replaced) remains unclear.

On the basis of the present data, the two strains differ only little in their life table characteristics and do not allow to single out one of the strains for preferential use in the remaining 'hot spots' of mealybug infestation. Possibly, the evaluation of the life-table parameters alone is not sufficient to characterize the two strains of *H. notata* originating from southern Brazil/Paraguay and Colombia. Gutierrez et al. (1993), for example, demonstrated that two parasitoids with equal r_m can be of very different efficiency depending on differences in behaviour. Thus, other aspects, such as searching capacity and choice of host instars are not reflected in the r_m values. Although the life table data presented here demonstrate similar trends between the predator *H. notata* and its prey under different temperature regimes, further studies are required for a complete characterization of the two predator strains.

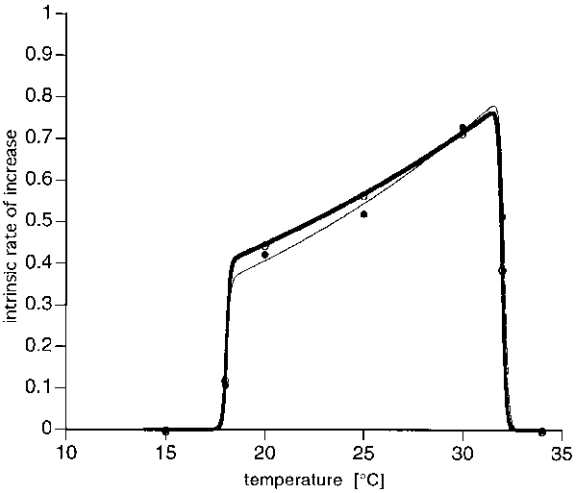

Figure 3. The intrinsic rate of increase r_m per week, for *Hyperaspis notata* as a function of temperature. The lines (——: BB, ——: CC) have been fitted to the observed data (○: BB and ●: CC) for the description of the strains denoted as BB and CC see text.

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References

Carrejo, N. S., A. C. Bellotti & O. R. Gonzales, 1991. Evaluación de algunos factores determinantes de la eficiencia de *Cleothera notata* (Col.: Coccinellidae) como depredador del piojo harinoso de la yuca *Phenacoccus herreni* (Hom.: Pseudococcidae). Revista Colombiana de Entomología 17: 21–27.

Chakupurakal, J., R. H. Markham, P. Neuenschwander, M. Sakala, C. Malambo, D. Mulwanda, E. Banda, A. Chalabesa, T. Bird & T. Haug, 1994. Biological control of the cassava mealybug, *Phenacoccus manihoti* (Homoptera: Pseudococcidae), in Zambia. Biological Control 4: 254–262.

Gutierrez, A. P., P. Neuenschwander & J. J. M. van Alphen, 1993. Factors affecting biological control of cassava mealybug by exotic parasitoids: a ratio-dependent supply-demand driven model. Journal of Applied Entomology 30: 706–721.

Fabres, G. & Kiyindou, A. 1985. Comparaison du potentiel biologique de deux coccinelles, *Exochomus flaviventris* et *Hyperaspis senegalensis hottentotta*, (Col.: Coccinellidae) prédatrices de *Phenacoccus manihoti* (Hom.: Pseudococcidae) au Congo. Acta Oecologica/Oecologia Applicata 6: 339–348.

Herren, H. R. & K. M. Lema, 1982. CMB – First successful releases. Biocontrol News and Information 3: 185.

Herren, H. R. & P. Neuenschwander, 1991. Biological control of cassava pests in Africa. Annual Review of Entomology 36: 257–283.

Hulting, F. L., D. B. Orr & J. J. Obrycki, 1990. A computer program for calculation and statistical comparison of intrinsic rate of increase and associated life table parameters. Florida Entomologist 73: 601–612.

Kanika-Kiamfu, J., A. Kiyindou, J. Brun & G. Iperti, 1992. Comparaison des potentialités biologiques de trois coccinelles prédatrices de la cochenille farineuse du manioc *Phenacoccus manihoti* (Hom. Pseudococcidae). Entomophaga 3: 277–282.

Kiyindou, A. & G. Fabres, 1987. Etude de la capacité d'accroissement chez *Hyperaspis raynevali* (Col.: Coccinellidae) prédateur introduit au Congo pour la régulation des populations de *Phenacoccus manihoti* (Hom.: Pseudococcidae). Entomophaga 32: 181–189.

Loehr, B., A. M. Varela & B. Santos, 1990. Explorations for natural enemies of the cassava mealybug *Phenacoccus manihoti* (Homoptera: Pseudococcidae), in South America for the biological control of this pest introduced in Africa. Bulletin of Entomological Research 80: 417–425.

Matile-Ferrero, D., 1977. Une cochenille nouvelle nuisible au manioc en Afrique équatoriale, *Phenacoccus manihoti* n. sp. (Homoptera, Coccidae, Pseudococcidae). Annales de la Societé Entomologique de France 13: 145–152.

Neuenschwander, P. & M. Zweigert, 1994. Biological control of cassava mealybug and green spider mite in eastern and southern Africa. In: G. Allard, L. G. Skoglund, P. Neuenschwander & R. Murphy (eds.). Proceedings of the Regional Workshop on Root and Tuber Crop Pest Management, 10.–14 Aug. 1992, Mombasa, Kenya. IIBC-CABI, Nairobi, Kenya, 13–28.

Neuenschwander, P., W. N. O. Hammond, O. Ajuono, A. Gado, N. Echendu, A. H. Bokonon-Ganta, R. Allomasso & I. Okon, 1991. Biological control of the cassava mealybug *Phenacoccus manihoti* (Hom., Pseudococcidae) by *Epidinocarsis lopezi* (Hym., Encyrtidae) in West Africa, as influenced by climate and soil. Agriculture, Ecosystems and Environment 32: 39–55.

Nsiama She, H. D. 1985. The bioecology of the predator *Hyperaspis jucunda* Muls. (Coleoptera: Coccinellidae) and the temperature response of its prey, the cassava mealybug *Phenacoccus manihoti* Mat.-Ferr. (Homoptera: Pseudococcidae). PhD Thesis, University of Ibadan, Nigeria, 300 pp.

Nsiama She, H. D., J. A. Odebiyi & H. R. Herren, 1984. The biology of *Hyperaspis jucunda* (Col.: Coccinellidae) an exotic predator of the cassava mealybug *Phenacoccus manihoti* (Hom.: Pseudococcidae) in Southern Nigeria. Entomophaga 29: 87–93.

Schoolfield R. M., P. J. H. Sharpe & C. E. Magnuson, 1981. Nonlinear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. Journal of Theoretical Biology 88: 719–731.

Schulthess F., J. Baumgärtner & H. R. Herren, 1987. Factors influencing the life table statistics of the cassava mealybug, *Phenacoccus manihoti*. Insect Science and its Application 8: 851–854.

Sharpe P. J. H. & D. W. DeMichele, 1977. Reaction kinetics of poikilotherm development. Journal of Theoretical Biology 64: 649–670.

Sullivan, D. J., J. A. Castillo & A. C. Bellotti, 1991. Comparative biology of six species of coccinellid beetles (Coleoptera: Coccinellidae) predaceous on the mealybug, *Phenacoccus herreni* (Homoptera: Pseudococcidae), a pest on cassava in Colombia, South America. Environmental Entomology 20: 685–689.

Umeh, E. D. N. N., 1982. Biological studies of *Hyperaspis marmottani* Fairm., (Col.: Coccinellidae) a predator of the cassava mealybug *Phenacoccus manihoti* (Hom.: Pseudococcidae). Journal of Applied Entomology 94: 530–532.