Comparison of biological and demographic parameters for *Mononychellus progresivus* and *Oligonychus gossypii* on cassava: influence of temperature

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Abstract

The effect of five constant temperatures (16, 22, 26, 31 and 36 °C) on biological (survival and duration of developmental stages, fecundity and longevity of females, sex-ratio) and demographic parameters (R_o, G, r_m and λ) of the two main phytophagous mites that attack cassava in Africa, *Mononychellus progresivus* Doreste and *Oligonychus gossypii* (Zacher), was studied in the laboratory. Experiments were performed simultaneously on the two mite species reared on the same cassava variety (1M20) under controlled conditions: 70 ± 10% r.h. and 12L:12D. The lower thermal threshold was 13 °C for *M. progresivus* and 11 °C for *O. gossypii*. Both species developed in the range from 22 to 36 °C. The shortest development time was obtained at 31 °C for both species; it was 7.2 days for *M. progresivus* and 8.2 days for *O. gossypii*. Maximum fecundity of both species was recorded at 26 °C with 42.1 eggs for *M. progresivus* and 36.3 eggs for *O. gossypii* The highest intrinsic rate of increase (r_m) was obtained at 31 °C for both species with 0.289 and 0.214 for *M. progresivus* and *O. gossypii*, respectively.

Introduction

The cassava green mite *Mononychellus progresivus* Doreste (= *tanajoa* (Bondar)) (see Gutierrez, 1987) and the cotton red mite *Oligonychus gossypii* (Zacher) are the most frequently observed phytophagous mites in cassava plantations in Africa (Matthysse, 1978; Yaninek & Onzo, 1988; Gutierrez & Bonato, 1994). Yield losses due to *M. progresivus*, a neotropical species introduced into Africa in the early 1970s, are between 13 to 80% (Yaninek & Herren, 1988; Yaninek *et al.*, 1990). Peak densities of *M. progresivus* are usually observed during the transitions from dry to rainy season and vice versa (Yaninek *et al.*, 1989b; Bonato, 1993). Damage caused by *O. gossypii*, an African polyphagous mite mainly found in plantations during the dry season, is widely unknown. A recent study in the Congo (Bonato *et al.*, 1994) showed that *O. gossypii* population sizes during outbreaks and

their impact on yield losses were comparable to those of *M. progresivus*.

A pest management program should be built on an adequate knowledge of the main factors responsible for changes in a pest's population dynamics. Life tables under different abiotic conditions and the biological parameters required to develop them form basic tools for, e.g., understanding changes in the status of a pest species (Poole, 1974; Dempster, 1975; Krebs, 1978; Southwood, 1978). Studies on developmental biology of *O. gossypii* have been done by Ezulike & Odeyibi (1978), and of *M. progresivus* by Yaninek *et al.* (1989a). In the present work, simultaneous investigations on the development of both species using cohorts reared together under identical experimental conditions, including the same cassava variety, were carried out. For calculation of the demographic parameters of both species the method described by Hulting *et al.* (1990) was used which enables statistical comparisons of parameters. The present work was part of a

programme for the control of the major cassava pests in Central Africa, initiated in the early 1980s by the Institut Français de Recherche pour le Développement en Coopération (ORSTOM). It was part of a 2-year investigation of the biology and ecology of the two major tetranychid mites found on cassava in the Congo.

Materials and methods

Mite rearing and host plant production. Experiments were carried out using the progeny of several females taken from an experimental field located in Brazzaville (Congo), in which neither acaricide nor insecticide had been applied. Mites were reared on 6-month-old cassava plants (variety 1M20), grown in pots and placed outside under natural climatic conditions (28 ± 2 °C, $75 \pm 10\%$ r.h.). Leaf disks were taken from the first fully developed leaf (Yaninek, 1985) of cassava plants (variety 1M20) grown under the above mentioned conditions.

Experimental conditions. Studies were performed on both tetranychids *M. progresivus* and *O. gossypii* at 5 constant temperatures: 16, 22, 26, 31 and 36 ± 0.5 °C. Because of significant differences between leaf surface and ambient temperatures (Saito & Suzuki, 1987; Bonato *et al.*, 1990), temperature was measured on the leaf disk surface using a thermocouple (copper-constantan) connected to a digital multimeter (Keithley No. 197) accurate to within a microvolt. All experiments were carried out in air-conditioned rooms with relative humidity kept at $70 \pm 10\%$. Light (12L:12D) was provided by fluorescent tubes. The illuminance was 3,500 to 4,000 lx.

Survival rate and development. Seven to eight females were placed per leaf disk. After one hour, the females and excess eggs were killed to obtain one egg per disk. One hundred and fifty leaf disks were kept per species at the above temperatures. The eggs were monitored to determine the development and survival rate of immature stages: larvae, protochrysalis, protonymph, deutochrysalis, deutonymph and teliochrysalis, respectively l, q_1, p, q_2, d and q_3. Each individual was examined 3 times a day (at 7 a.m., 1 p.m. and 7 p.m.) and the transition from one stage to another was noted. The lower thermal threshold for development (TD) was calculated by the ratio: $TD = a/b$ where a and b were determined by linear regression of the equation $DR = a + bT$, with DR being the development rate per

day, T the temperature in °C, and a and b the regression coefficients.

Oviposition. One female teliochrysalis and two males were placed on a leaf disk. The males were removed 48 h after the female had emerged. The number of eggs laid per female was monitored daily. Disk were changed every 4 days.

Sex ratio. Sex ratio is defined as the proportion of female in the progeny. The method was the same as that used for oviposition, except that the females were placed on a new leaf disk every day and disks with eggs were maintained under the same experimental conditions as for females. The sex ratio was determined on the basis of a count of adults originating from those eggs. Non mated females, i.e., producing only males, were not taken into account. Constant survival of the sexes was assumed in the experiment.

Demographic parameters. The net reproductive rate (R_o), the mean generation time (G), the intrinsic rate of natural increase (r_m), and the finite rate of increase (λ) were determined using a program developed by Hulting *et al.* (1990) in which the parameters are calculated using the method recommended by Birch (1948). The program of Hulting *et al.* (1990), based on Jacknife's procedures, gives a variance and hence a standard error to each parameter calculated, thus enabling statistical comparison of the values. The influence of temperature on the r_m was described by the modified model proposed by Logan *et al.* (1976):

$$r_m = p_1[\exp[p_2(T - T_b)] - \exp[p_2(T_m - T_b) - 1/p_3(T_m - T)]]$$

where T_b is the lowest temperature tested and T_m is the upper developmental threshold derived from the observations. The model was validated using the r_m calculated for each temperature. The parameters p_1, p_2 and p_3 were estimated by least square regression techniques. Analysis covered only the intrinsic rate of natural increase r_m as this integrates all the biological parameters and their relations with temperature.

Results and discussion

Survival rate and development
M. progresivus. At 16 °C, none of the 117 eggs hatched: 7 contained embryos (ocular patches were vis-

Table 1. Duration in days of the egg (e), larva (l), protonymph (p), deutonymph (d), and quiescent stages (q_1, q_2, q_3) of *Mononychellus progresivus* and *Oligonychus gossypii* and total mortalities at 5 constant temperatures. Standard deviation is in parentheses. Values in the same row followed by the same letter are not significatively different (ANOVA and multicomparison Scheffé *F* tests, $\alpha = 0.05$)

Species	Stage	Temperature				
		16 °C	22 °C	26 °C	31 °C	36 °C
M. progresivus	e	—	7.3 (0.5)	4.7 (0.3)	3.3 (0.2)	3.5 (0.5)
	l	—	1.4 (0.6)	1.1 (0.3)	0.8 (0.2)	1.0 (0.3)
	q_1	—	1.1 (0.3)	0.8 (0.3)	0.4 (0.2)	0.6 (0.3)
	p	—	0.9 (0.3)	0.8 (0.2)	0.7 (0.2)	0.9 (0.6)
	q_2	—	1.2 (0.2)	1.0 (0.3)	0.4 (0.2)	0.6 (0.2)
	d	—	1.1 (0.3)	1.0 (0.1)	1.0 (0.3)	1.2 (0.5)
	q_3	—	1.3 (0.3)	0.8 (0.1)	0.6 (0.2)	0.6 (0.4)
	Total	—	14.3 (0.8) a	10.1 (0.3) b	7.2 (0.6) c	8.3 (1.0) d
	Mortality (%)	100	21	15	31	88
O. gossypii	e	20.2 (1.0)	7.5 (0.5)	5.0 (0.4)	3.4 (0.4)	3.4 (0.2)
	l	—	2.4 (0.9)	1.2 (0.4)	1.2 (0.4)	1.2 (0.4)
	q_1	—	0.9 (0.4)	0.7 (0.2)	0.6 (0.2)	0.6 (0.2)
	p	—	1.4 (0.4)	0.9 (0.4)	0.8 (0.4)	1.2 (0.5)
	q_2	—	0.8 (0.3)	0.8 (0.2)	0.6 (0.2)	0.6 (0.4)
	d	—	1.5 (0.5)	1.2 (0.2)	1.0 (0.5)	1.6 (0.6)
	q_3	—	1.0 (0.2)	0.8 (0.1)	0.7 (0.2)	0.4 (0.2)
	Total	—	14.8 (1.4) a	10.5 (0.5) b	8.2 (1.0) c	8.9 (1.0) d
	Mortality (%)	100	38	28	32	87

Table 2. Duration in days of various adult stages and ovipositional rates of *Mononychellus progresivus* and *Oligonychus gossypii*. Standard deviation in parentheses. Values in the same row followed by the same letter are not significatively different (ANOVA and multicomparison Scheffé *F* tests, $\alpha = 0.05$). Only Longevity Eggs/female/day and Total eggs/female were tested

Species		Temperature				
	16 °C	22 °C	26 °C	31 °C	36 °C	
M. progresivus	Preoviposition	7.9 (1.4)	2.7 (0.3)	1.0 (0.1)	0.5 (0.2)	0.3 (0.2)
	Oviposition	4.1 (2.1)	12.5 (1.7)	9.1 (1.3)	5.6 (0.7)	4.0 (0.6)
	Postoviposition	13.1 (2.8)	1.2 (0.5)	0.6 (0.3)	0.5 (0.3)	0.6 (0.4)
	Longevity	22.1 (4.7) a	16.4 (1.8) b	10.7 (1.4) c	6.5 (0.8) d	4.3 (0.7) e
	Eggs/female/day	0.3 (0.2) a	2.0 (0.2) b	4.5 (0.3) c	5.3 (0.6) c	3.5 (0.7) d
	Total eggs/female	0.8 (0.6) a	25.6 (4.7) bd	42.1 (7.4) c	31.4 (5.6) dc	15.3 (4.2) b
	No. of females	18	46	42	48	44
O. gossypii	Preoviposition	4.9 (0.4)	2.3 (0.2)	2.2 (0.3)	1.5 (0.3)	1.2 (0.2)
	Oviposition	7.6 (1.3)	8.7 (1.0)	8.3 (1.3)	4.6 (0.7)	4.4 (0.7)
	Postoviposition	1.6 (0.6)	1.3 (0.4)	0.5 (0.2)	0.8 (0.4)	1.0 (0.4)
	Longevity	12.3 (1.7) a	12.3 (1.0) a	10.8 (1.4) a	6.7 (0.7) b	5.6 (0.9) b
	Eggs/female/day	1.1 (0.2) a	3.7 (0.4) bc	4.3 (0.5) b	3.1 (0.5) c	2.3 (0.5) d
	Total eggs/female	8.9 (2.6) a	34.1 (6.1) b	36.3 (8.5) b	16.4 (4.1) c	11.3 (3.4) a
	No. of females	47	49	36	56	46

ible through the chorion) whereas the others remained translucent. This temperature is very close to the lower biological threshold (see below). Between 22 °C and 31 °C, the rate of development displayed linear positive temperature dependence; development time was 14.3 days at 22 °C and 7.2 days at 31 °C. The lowest mortality (15%) was recorded at 26 °C. At 36 °C, the increase of development time (8.3 days), indicates the proximity of the upper thermal threshold. This hypothesis is confirmed by the high mortality (88%) observed at this temperature. Development time recorded at 22, 26, 31 et 36 °C were significantly different according to analysis of variance (ANOVA) ($\alpha = 0.05$; $F = 1671.1$; df $= 242$; P<0.0001) followed by Sheffé's F tests. The theoretical lower threshold of development calculated from the development time observed in the range 22–31 °C is 13 °C ($a = 0.0995$, $b = 0.00767$, $r^2 = 0.99$, P< 0.001).

O. gossypii. At 16 °C, 14 of the 97 eggs monitored remained translucent, 62 contained embryos which did not hatch and 11 yielded larvae after an average of 20 days. All the larvae died within 48 h of hatching. This recorded mortality may have been an artifact. Although 16 °C was close to the lower thermal threshold, it is an average figure obtained from temperatures oscillating because of air-conditioning, to which the larvae must have been sensitive. The results obtained at 16 °C with *O. gossypii* and *M. progresivus* underline the need for caution in the interpretation of results when working close to the theoretical biological thermal threshold of a species; because the mortality is high, the rate of development is derived from a small cohort.

Durations of development recorded at 22, 26, 31 and 36 °C were significantly different according to analysis of variance (ANOVA) ($\alpha = 0.05$; $F = 516.7$; df $= 221$; P<0.0001) followed by Sheffé's F tests (Table 1). As in the case of *M. progresivus*, a decrease in average duration of development was observed from 22 to 31 °C. The shortest development time determined experimentally (8.2 days) was at 31 °C. In the 22–31 °C temperature range, the death rates (38, 28 and 32% at respectively 22, 26 and 31 °C) were higher than in *M. progresivus* and generally higher than in other mites, e.g., 5% for *Panonychus citri* (McGregor) and 11% for *Tetranychus urticae* Koch reared at 25 °C-52% r.h. (Saito, 1979); 3% for *Eotetranychus uncatus* Garman and 16% for *E. tiliarium* Herman reared at 25 °C-60% r.h. (Gotoh, 1987); 7, 2 and 10% for *Tetranychus neocaledonicus* André and 8, 7 and 20% for *T. urticae* reared respectively at 20, 25

and 30 °C-50% r.h. (Gutierrez, 1976). This high mortality may be a result of the experimental procedures or poor adaptation of the species to the plant. Similar results obtained with other procedures and the temporary presence in time and space of *O. gossypii* on cassava support the second hypothesis (Bonato, unpubl.). The phenomenon has been observed for other tetranychids reared on substitute plants (J. Gutierrez, unpubl.). At 36 °C, the 8.9 days of development were significantly greater than the 8.2 days observed at 31 °C (Sheffé F value $= 2.78$, $\alpha = 0.05$). This indicates that the upper thermal threshold (increased mortality and duration of development) had been approached. The theoretical lower threshold calculated here was 11 °C ($a = 0.0644$, $b = 0.00601$, $r^2 = 0.99$, P<0.001). In conclusion, the temperature range within which *O. gossypii* can develop is broader than that of *M. progresivus*, and the lower thermal threshold for development is lower and the upper threshold slightly lower but very close to that of *M. progresivus*.

Oviposition

M. progresivus. In the 16–36 °C range, adult longevity, encompassing the three phases pre-oviposition, oviposition and post-oviposition (Table 2), decreased with increasing temperature, with significant differences between each temperature, ($\alpha = 0.05$, $F = 72.43$; df $= 218$; P< 0.0001). Maximum longevity of 22.1 days was recorded at 16 °C. At 36 °C, adult longevity was only 4.3 days and was probably near the upper threshold as also shown by the high mortality (see above).

Daily fecundity increased according to temperature. It was practically nil at 16 °C with 0.3 eggs per female per day. The maximum was attained at 31 °C with an average of 5.3 eggs per female, and then decreased to 3.5 eggs per female at 36 °C (Table 2). Total number of eggs laid per female increased from 0.8 to 42.1 (the highest value) between 16 and 26 °C, then decreased to only 15.3 eggs at 36 °C. Total fecundity depends on both daily fecundity and duration of oviposition. Of the five temperatures tested, 26 °C appeared to be the optimum.

O. gossypii. From 16 to 26 °C, although life spans were not significantly different, a tendency for a shorter life was noted with 10.8 days at 26 °C in comparison with 12.3 days at 16 ° and 22 °C. The adult longevity decreased from 6.7 to 5.6 days between 31–36 °C, respectively (Table 2).

Table 3. Sex-ratio (percentage females) of progeny of *Mononychellus progresivus* and *Oligonychus gossypii* at 4 constant temperatures. Values followed by the same letter are not significatively different (χ^2 test, $\alpha = 0.05$)

Species		Temperature			
		22 °C	26 °C	31 °C	36 °C
M. progresivus	Adult progeny	207	144	100	14
	% female progeny	61 a	70 a	72 a	71 a
O. gossypii	Adult progeny	163	190	100 16	
	% female progeny	66 a	70 a	75 a	81 a

Table 4. Parameters related to potential rates of population increase of *Mononychellus progresivus* and *Oligonychus gossypii* at 4 constant temperatures. Standard error in parentheses. Values followed by the same letter are not significatively different (Newman-Keul tests, $\alpha = 0.05$)

Temperature	Species							
	M. progresivus				*O. gossypii*			
	Ro	G	r_m	λ	Ro	G	r_m	λ
22 °C	15.7 (2.5)	23.5	0.117 (0.004)a	1.12	16.1 (2.6)	21.1	0.132 (0.006)a	1.14
26 °C	27.3 (4.6)	14.7	0.224 (0.008)b	1.25	20.7 (4.3)	16.4	0.185 (0.010)b	1.20
31 °C	19.0 (2.7)	10.2	0.289 (0.012)c	1.34	12.8 (2.6)	11.9	0.214 (0.016)c	1.24
36 °C	1.4 (0.4)	11.2	0.028 (0.026)d	1.03	1.6 (0.4)	12.4	0.036 (0.024)d	1.04

The smallest number of eggs per female per day (1.1) was observed at 16 °C. Maximum laying (4.3) was recorded at 26 °C. In the range 16–36 °C, daily fecundity increased from 16 to 26 °C, then decreased to 36 °C. Multiple comparisons showed no significant differences between 22 and 26 °C, and between 22 and 31 °C experiments (Scheffé *F* values are respectively, 0.846, and 0.811, $\alpha = 0.05$). The total number of eggs laid per female at 22 and 26 °C was similar with 34.1 and 36.3 eggs, respectively (Table 2). The lowest figure of 8.9 eggs per female was observed at 16 °C.

At 16 °C and 22 °C, daily and total fecundity of *O. gossypii* were greater than those of *M. progresivus* but the situation was reversed in the 26 °C to 36 °C range. *O. gossypii* appeared to be less sensitive to low temperatures than *M. progresivus*. The lower thermal threshold for development of *O. gossypii* seems to confirm this hypothesis.

Sex-ratio

In *M. progresivus* and *O. gossypii*, the proportion of females in the progeny was always female-biased at all temperatures. The smallest proportion of females was measured at the lowest of the 4 tem-

peratures tested (Table 3) and therefore seems to be temperature-dependent but no significant difference between species at the various temperatures could be found (χ^2 test; df=3; $\chi^2_{P_c}$ = 1.3 for *M. progresivus* and 3.3 for *O. gossypii*, α= 0.05). The sex-ratio of both species calculated at 36 °C should be treated with caution as the mortality at each stage was very high at this temperature; it was calculated for only a small number of eggs (14 and 16 for *M. progresivus* and *O. gossypii*, respectively). The sex-ratio of both *M. progresivus* and *O. gossypii* appeared to be approximately 0.70 in the non-limiting temperature range of 22 to 31 °C (Table 3).

Demographic parameters

M. progresivus. Except for 16 °C where the values were nil, the lowest r_m (0.028) was found at 36 °C (Table 4). This very low figure confirms the proximity of the upper thermal threshold. The highest r_m (0,289) was calculated for 31 °C with an average generation time of 10.18 days and with 19.01 females per female (Table 4). This r_m value is comparable to the results of Yaninek *et al.* (1989a) for the same species although no statistical comparison could be done. All values were
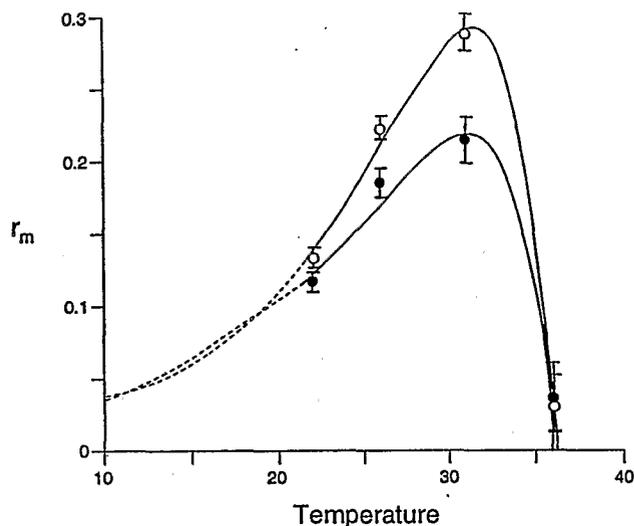
Fig. 1. Influence of temperature on rate of natural increase (r_m) of *Mononychellus progresivus* (○) and *Oligonychus gossypii* (●) after Logan's model (1976), $T_b = 16$ °C, $T_m = 36.5$ °C. Symbols correspond to the calculated values after Hulting *et al.* (1990) with their confidence interval ($\alpha = 0.05$).

significantly different (Newman-Keuls test; $\alpha = 0.05$, $q = [9.1, 7.2, 13.6, 11.9, 3.4, 4.5]$, $q_\alpha = 2.9$).

O. gossypii. The r_m values were all significantly different from each other, increasing from 16 to 31 °C, then falling very sharply at 36 °C (Newman-Keuls test; $\alpha = 0.05$, $q = [6.2, 4.8, 4.5, 3.5, 5.7, 3.9]$, $q_\alpha = 2.9$). The highest r_m (0.214) was at 31 °C, while the lowest (0.036) was at 36 °C. As for *M. progresivus*, the upper thermal threshold was in the region of 36 °C, and it can be estimated that the highest rm occurred at temperatures close to 31 °C (Table 4).

The use of Logan *et. al.* (1976) model (Fig. 1) allowed estimation of the upper thermal threshold for population development: 36.4 °C for *O. gossypii* and 36.2 °C for *M. progresivus*. It confirmed that in the range of temperatures within which populations develop, the r_m values of *M. progresivus* were mostly greater than that of *O. gossypii*. The values of Logan's model parameters, estimated by least square regression techniques, are $p_1 = 0.145$, $p_2 = 0.121$, $p_3 = 3.002$ for *M. progresivus* (P<0.0001) and $p_1 = 0.132$, $p_2 = 0.096$, $p_3 = 3.017$ for *O. gossypii* (P<0.0001).

Studies on the influence of temperature on biological parameters enabled a characterisation of the two phytophagous mite species. *O. gossypii* develops within a broader temperature range compared to *M. progresivus*, although its biological parameters are lower and the amplitude of its response to the ther-

mal factor is smaller. The r_m values and study of their variations according to temperature are not limited to comparisons of biological characteristics; the results provide complementary information facilitating the understanding of population dynamics. For example, the difference in the r_m values between both species could also partly explain the observed distribution of *M. progresivus* in the apical and mid part and of *O. gossypii* in the mid and basal part of the plant when they are simultaneously present on cassava (Yaninek *et al.*, 1991; Bonato, 1993). *M. progresivus* should be more effective than *O. gossypii* for plant occupation since it has higher growth rates. Its populations increase more rapidly than *O. gossypii* populations and occupy first the available uninfested leaves. As plant colonizations usually occur when a large portion of mites disperses from the focus of initial colonization to the upper strata of the plant (Kennedy & Smitley, 1985), *M. progresivus* tends to be concentrated in the apical and mid part of cassava plant. Similarly, in the republic of Congo, main factors such as decline of rainfall mortality, or asynchronous predation can prompt outbreaks of *O. gossypii* in the middle of the dry season (Bonato, 1993). Interestingly, during this period, average daily temperatures are the lowest of the year (25–26 °C) and correspond to the range where the rm values of *O. gossypii* are equivalent of those of *M. progresivus*. Consequently, *M. progresivus* is less competitive and effective for plant occupation and cannot achieve its dominance during this period, thus allowing better development of *O. gossypii* populations as shown by Bonato (1993).

Acknowledgments

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