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ANALYSIS OF BIOLOGICAL CONTROL OF CASSAVA PESTS IN AFRICA. III. CASSAVA GREEN MITE *MONONYCHELLUS TANAJOA*

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SUMMARY

(1) The interactions of cassava green mite, *Mononychellus tanajoa* (Bondar) s.l., and cassava, *Manihot esculenta* Crantz, under West African weather and soil conditions were examined using a simulation model.

(2) Field studies had demonstrated the effects of plant and leaf age and rainfall-induced mortality on *M. tanajoa* population growth. In the absence of effective natural enemies, the model explains, in order of importance, the effects of rainfall, drought stress via the host-plant, food availability (production and persistence of new foliage) and leaf quality (N concentration) on *M. tanajoa* population growth.

(3) Rainfall-induced mortality greatly reduced *M. tanajoa* populations in the rainy season, drought and N stresses acting indirectly via food availability being most important in the dry season.

(4) The combined effects of *M. tanajoa* feeding and water and N stress on cassava tuber yield were assessed.

INTRODUCTION

The cassava green mite, *Mononychellus tanajoa* (Bondar) s.l. is an important exotic pest of cassava (*Manihot esculenta* Crantz) in the dry season throughout much of the African cassava belt (Yaninek 1985). *M. tanajoa* was discovered on cassava near Kampala, Uganda in late 1971 (Lyon 1973). It has since spread to at least twenty-seven countries in Africa causing damage estimated at 18–80% (Yaninek, Herren & Gutierrez 1987; Yaninek & Herren, in press). Bellotti & van Schoonhoven (1978), Yaninek (1985) and Yaninek & Herren (in press) reviewed aspects of the salient literature on the history of its biology, and outlined its spread in Africa, current economic importance, and attempted biological control.

M. tanajoa is biologically similar (Yaninek 1985) to other agronomically important tetranychids (Huffaker, van de Vrie & McMurtry 1970; McMurtry, Huffaker & van de Vrie 1970). The adult female lays fertilized female eggs and unfertilized male eggs. There are four active stages: a six-legged larva, two nymphal stages (protonymph and deutonymph) and the adult stage. The active stages prefer to feed on the terminal parts of the plant, killing leaf cells and reducing photosynthesis.

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This paper is part of a series evaluating biological control of exotic pests of cassava within the Africa-wide Biological Control Project (ABCP) (Herren, Lema & Neuenschwander 1983) (see Gutierrez *et al.* 1988a, b). In this paper, the biological interactions between cassava and *M. tanajoa* as affected by plant age, leaf age, [N] in leaves of preferred age, drought stress and the direct effects of rainfall are examined using a mathematical model of the cassava system (Gutierrez *et al.* 1988a). Natural enemies are not an important mortality factor to *M. tanajoa* populations in Africa, and temperatures are not limiting in the lowland humid tropics (Yaninek, Herren & Gutierrez 1987).

Mathematical model

A distributed delay model formulated by Gutierrez *et al.* (1988a, b) is used to model the dynamics of the cassava–*M. tanajoa* interaction. Here, only the biological parameters for the model are described, and their values are listed in the Appendix. The model assumes maximum intrinsic values that must be scaled by the different factors affecting *M. tanajoa* population growth rates. In the model, *M. tanajoa* accumulates physiological age (Δa degree-days day^{-1}, DD) above its thermal threshold 14·4 °C, but physiological time (Δt) is reported on the plant time-scale (Yaninek, Herren & Gutierrez 1987).

Cassava–green mite association

Within-plant distribution of M. tanajoa *as a measure of preference*

Absolute population counts of *M. tanajoa* are impractical because large populations often develop. Green mite populations are known to develop primarily in the shoot apices of the plant, and *c.* 10% of the total population on one branching path is found on the first fully expanded leaf (Yaninek 1985). The within-plant frequency distribution of *M. tanajoa* observed by Yaninek (1985) is assumed to be a measure of leaf-age preference.

In the model, leaves are divided into six equal age catagories (0–625 DD), preference values (ζ_i, $i=1,6$ and $\Sigma\zeta_i=1$) for youngest to oldest leaves being 0·05, 0·4, 0·25, 0·15, 0·1 and 0·05, respectively. The preference values are used to calculate the rate of attack on the different-aged leaves, and conversely to estimate the effects of leaf N in them (Gutierrez *et al.* 1988a) on *M. tanajoa* development rates, fecundity and survival. The total mass of leaves available (L_T) in the six age categories may be computed as follows:

$$L_T(t) = \sum_{i=1}^{6} L_i(t). \tag{1}$$

The quantity of leaves attacked (M^*) by *M. tanajoa* was estimated using the Frazer–Gilbert (1976) functional response model ($f(\rho(a,t),b_{cgm},s_{cgm},L_T,\Delta t)$ in eqn (2)) discussed in detail in Gutierrez *et al.* (1988a, b).

$$M^* = f(t,\cdot)L_T(t), \tag{2}$$

In $f(t,\cdot)$, $\rho(a,t)$ is the number density function of *M. tanajoa* of age a at time t, b_{cgm} is the leaf consumption demand rate of the *M. tanajoa* population (subscript *cgm*), s_{cgm} is the search parameter, and Δt is the increment of physiological time. The major parameter determining M^* at time t is b_{cgm}, and it is computed as follows:

$$b_{cgm} = \int g(a)\rho(a,t)\,\mathrm{d}a \tag{3}$$

The age-specific consumption rates ($g(a)$) mite^{-1} of age a in (3) is

$$g(a)=\begin{cases} 0 & 0\leqslant a< 68 \text{ DD egg} \\ 1{\cdot}2\times 10^{-6}(a/154)\text{ g day}^{-1}\text{ mite}^{-1} & 68\leqslant a\leqslant 154 \text{ DD immatures} \\ 1{\cdot}2\times 10^{-6}\text{ g day}^{-1}\text{ mite}^{-1} & 154< a\leqslant 321 \text{ DD adult.} \end{cases} \quad (4)$$

Unfortunately, there is little information concerning $g(a)$, hence we first estimated it by feeding different densities of adult two-spotted mites (*Tetranychus urticae* Koch) on common bean leaf discs (*Phaseolus vulgaris* L.) for varying periods of time. Bean leaves show damage quickly and, not unexpectedly, the estimated consumption rate was too high to simulate field data reported by Yaninek (1985). The feeding rate was scaled to give more reasonable answers. The search parameter (s_{cgm}) in $f(\cdot)$ was arbitrarily set to 0·1.

Green mite damage (M^*) was apportioned to the different leaf age-classes on a weighted frequency basis. The sum of leaves weighted for feeding preference that are available for attack (L^*) is:

$$L^*(t) = \sum_{i=1}^{6} \zeta_i L_i(t), \quad (5)$$

the quantity of leaves consumed in each age-class being $M^*_i = M^*\zeta_i L_i/L^*$.

Effects of leaf N on green mite population growth

The N content of food is known to affect arthropod fecundity and development rates (e.g. McNeill & Southwood 1978; Sharpe & Hu 1980; Crawley 1983). In spider mites, Wermelinger, Oertli & Delucchi (1985) showed that fecundity and development rates in two-spotted mite were strongly correlated with leaf N. Concentrations of N (i.e. [N] = %) in cassava leaves vary through the season and with plant and leaf age (Howeler & Cadavid 1983). Simulation studies in Gutierrez *et al.* (1988a) explained Howeler's results and predicted an increase in [N] in young leaves after the dry season.

Yaninek (1985) found that *M. tanajoa* population growth rates were highest on the first fully expanded leaves but decreased on the same-age leaves on older plants. However, after dry-season defoliation, high green mite fecundity was again observed on the first fully expanded leaves. This suggested a causal relationship between *M. tanajoa* life-table statistics and [N]. In the model, the Wermelinger, Oertli & Delucchi (1985) estimate of the effects of [N] were used to scale *M. tanajoa* fecundity and development rates.

The predicted average [N] in all leaves attacked by green mite was computed as:

$$[\mathrm{N}] = \left(\sum_{i=1}^{6} M_i^*[N_i]\right)\Big/ M^*. \quad (6)$$

This estimate of [N] is used in the Wermelinger, Oertli & Delucchi (1985) functions (ϕ_k, $k=F,I,P$) to determine the reduction in fecundity (F), and the ageing rate of immatures (I) and prereproductive adults (P) in *M. tanajoa*. The Wermelinger, Oertli & Delucchi data suggest a linear relationship between [N] and fecundity of two-spotted spider mites (eqn (7)).

$$0 < \phi_{\mathrm{F}}(t) = 0{\cdot}22[\mathrm{N}] \leqslant 1{\cdot}1 \quad (7)$$

The effects of [N] on immature development rates (ϕ_{I}) and on the preoviposition period (ϕ_{P}) were characterized as follows:

$$1 \leqslant \phi_{\mathrm{I}} = 1{\cdot}63 - 0{\cdot}13[\mathrm{N}] \leqslant 1{\cdot}3 \quad (8)$$

$$0{\cdot}9 \leqslant \phi_{\mathrm{P}} = 3{\cdot}52 - 0{\cdot}52[\mathrm{N}] \leqslant 3. \quad (9)$$

ϕ_I and ϕ_P were incorporated in the model as reductions in available daily physiological time, resulting in an increase in the development time of immatures (Δa^*_I) and prereproductive adults (Δa^*_P).

$$\begin{aligned} \Delta a^*_I &= \Delta t/\phi_I, \\ \Delta a^*_P &= \Delta t/\phi_P. \end{aligned} \tag{10}$$

$\Delta a = \Delta t$ for all other stages. Ageing in the model during a time interval Δt for, say, the immature stage is $a_I(t+\Delta t) = a_I(t) + \Delta a^*_I(t)$. Similar computations were made for the preoviposition period. Thus, [N] affects *M. tanajoa* population growth rates via fecundity and development rates, and indirectly via effects on photosynthesis and leaf production rates (Gutierrez *et al.* 1988a).

Drought effects on M. tanajoa *population growth rates*

Drought may cause defoliation in cassava, reducing the rate of photosynthesis, and plant growth (leaf production) and N uptake resulting in reduced leaf [N]. Reduction in the rate of vegetative growth due to these factors alters not only the age structure of the leaf population, but also the quantity and quality of food, which affects green mite population growth rate. The effects of carbohydrate and N supply:demand ratios ($0 < \theta = L^*/b_{cgm} \leqslant 1$ and $0 \leqslant \phi_F \leqslant 1.1$, respectively) on population reproduction (F^*) via age-specific fecundity ($F(a)$) over Δt were incorporated as follows:

$$F^*_t = \theta \phi_F \Delta t \int F(a)\rho(a),t \; da. \tag{11}$$

The age-specific survival effects of θ and ϕ_F on active green mite populations ($\rho(a,t)$) are included as:

$$\rho(a+\Delta a, t+\Delta t) = \theta \phi_F \rho(a,t). \tag{12}$$

Green mite mortality due to rainfall

Yaninek (1985) derived an empirical relationship between rainfall (R) and *M. tanajoa* mortality (μ_R) due to the mechanical effects of the rain washing the mites off the leaves.

$$\mu_R = 1{\cdot}0288 \; R^{-0{\cdot}3185}, \quad r^2 = 0{\cdot}8. \tag{13}$$

Eggs were found to be slightly less susceptible to rain-induced mortality than were the other stages. Ideally, R should be a measure of intensity but, unfortunately, the duration of rainfall is usually not recorded. Incorporating μ_R in the model is reasonably straightforward.

$$\rho(a+\Delta a, t+\Delta t) = \theta \phi_F (1-\mu_R)\rho(a,t). \tag{14}$$

SIMULATION RESULTS

Simulation studies (Gutierrez *et al.* 1988a) showed that drought and N stress caused only minimal reductions in tuber yields in 1983–84, hence the field and simulation data may be assumed to be reasonable maxima for a non-stressed situation given observed weather and initial conditions. These results may then be used to estimate the effects of *M. tanajoa* population feeding, modified by N and water stress, on yields. Of course, different weather would produce different growth patterns for cassava and the green mite population. Two *M. tanajoa* populations were simulated using one adult female mite per plant starting 50 and 150 days after planting (15 May 1983), well before the dry season.

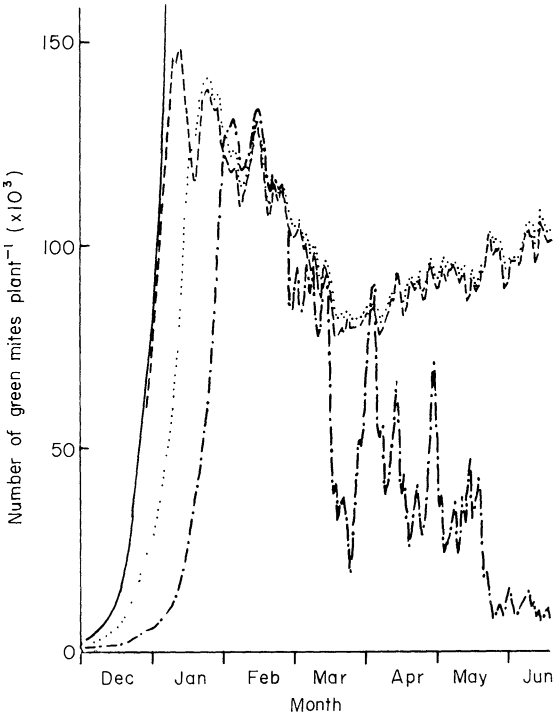

FIG. 1. Simulated dynamics of *M. tanajoa* adult populations (mites plant^{-1}) as influenced by: intrinsic mortality (————), food supply: demand (– – – – –), [N] in leaves (· · · · ·), and rainfall-induced mortality (—•—•—).

Observed temperature, solar radiation, wind, and rainfall data for 1983–84, and the estimated initial soil [N] (Gutierrez *et al.* 1988a) were used to run the model.

Figure 1 shows the expected adult *M. tanajoa* population in the 50-day infestation treatment, including with the following mortality factors: intrinsic mortality, food supply/demand effects (L^*/b_{cgm}), leaf N effects and rainfall. The simulation results suggest that green mite populations would explode exponentially, if only intrinsic mortality were restraining them ((———) on Fig. 1). The addition of food supply/demand mortality imposed a carrying capacity on the green mite population of *c.* 9×10^4 adult mites plant^{-1} ((– – – –) on Fig. 1). The inclusion of leaf N effects retarded early dry-season development ((· · · · ·) on Fig. 1), but the same carrying capacity was reached. The addition of rain-induced mortality caused a dramatic decline in the simulated population ((—·—·) on Fig. 1), conforming to the results of Yaninek & Animashaun (1987).

Interaction of [N] and rainfall on M. tanajoa *population dynamics*

The interaction of different initial soil [N] (nitrates and organic matter, Gutierrez *et al.* 1988a) and observed rainfall on *M. tanajoa* population development was examined via simulation. The cassava plants were exposed to *M. tanajoa* 150 days after planting (Fig. 2); Fig. 2a–c show the effects of observed rainfall and decreasing [N]. The yield loss is estimated from the pest-free yield from Gutierrez *et al.* (1988a). Also shown in the figure is the average expected [N] of the leaves of preferred age.

Maintaining the observed rainfall pattern, but decreasing the soil [N] by 25%, lowers the *M. tanajoa* population by *c.* 40%; lowering [N] by 50% lowers the population by

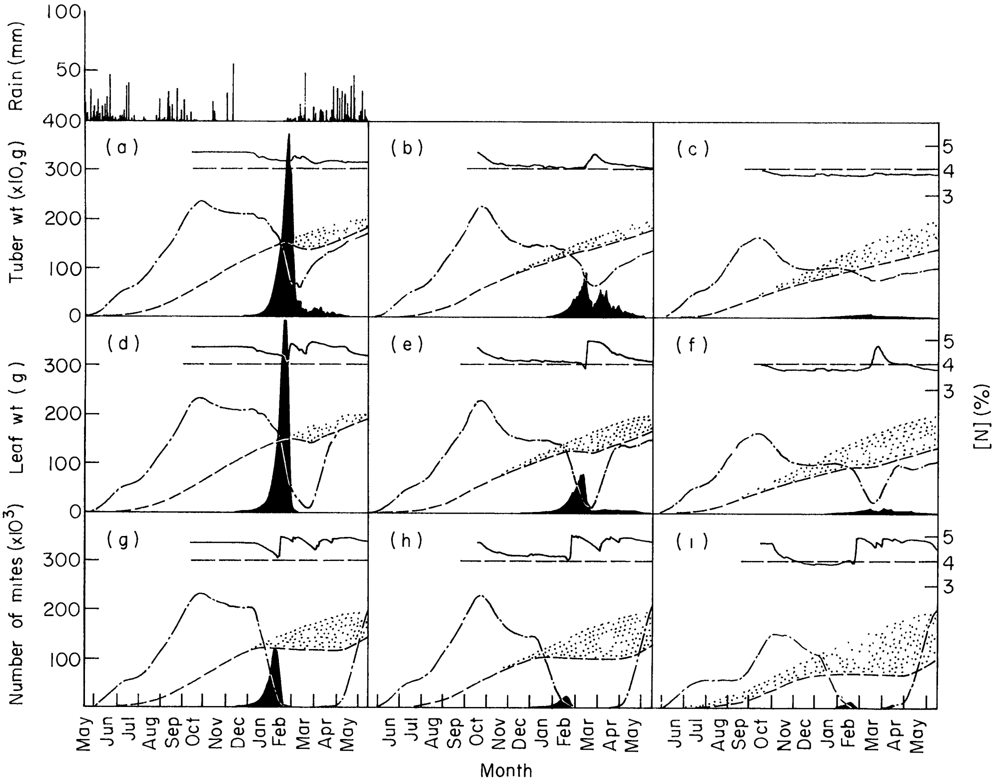

FIG. 2. Simulated effects of initial [N] and observed rainfall on leaf (—·—·—) and tuber (- - - - -) yield biomass (g dry-matter plant^{-1}), green mite population dynamics (■), percentage leaf N (————), reductions in tuber dry-matter (▨) compared with that observed in the field in 1983–84 at IITA, Ibadan, Nigeria. Reference line for 4% leaf nitrogen (— — —). (a) water × 1 : N × 1; (b) water × 1 : N × 0·75; (c) water × 1 : N × 0·5; (d) water × 0·8 : N × 1; (e) water × 0·8 : N × 0·75; (f) water × 0·8 : N × 0·5; (g) water × 0·6 : N × 1; (h) water × 0·6 : N × 0·75; (i) water × 0·6 : N × 0·5.

> 80%. Figure 2a, d, g shows the effects of reducing rainfall but maintaining high soil [N]. Prior results showed that rainfall is the major factor reducing green mite populations (Fig. 1, and Yaninek & Animashaun 1987). The simulations suggest that, despite relaxation in rain-induced mortality, the *M. tanajoa* populations were smaller because of increased defoliation during drought. In general, defoliation was greater and the time of defoliation earlier when rainfall was low. Defoliation during severe drought caused the *M. tanajoa* population pattern to be unimodal, leading to near extinction in the dry season (Yaninek, Herren & Gutierrez 1987).

The interaction of water and N on green mite population dynamics is more difficult to discern (Fig. 2a, e, i). At the lowest levels of water (60%) and N (50%), the population barely develops, defoliation determining its pattern. At 80% water and 75% N, the population remains small and unimodal. In general, the results show that the leaf [N] affects green mite growth rates, while defoliation and drought determine the phenology (see Yaninek 1985).

Predicted increases in leaf [N] after the dry season (Gutierrez *et al.* 1988a) are also seen in Fig. 2; especially in studies with drought stress and lower initial [N] (Fig. 2h, i). The

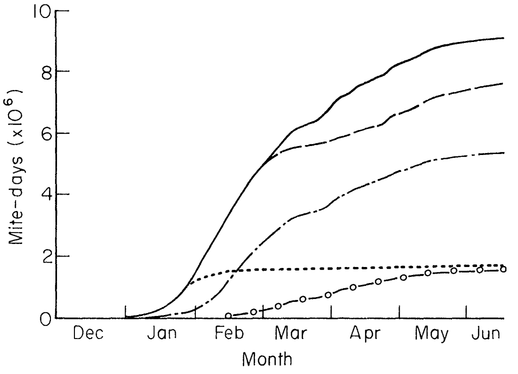

FIG. 3. Simulated cumulative green mite numbers (data from Fig. 2): (————) water × 1 : N × 1; (- - - - -) water × 0·8 : N × 1; (—·—·—) water × 1 : N × 0·75; (· · · · ·) water × 0·6 : N × 1; (—o—o—) water × 1 : N × 0·5.

predicted increases in green mite fecundity after the dry season in response to increased [N] were insufficient to compensate for rain-induced mortality and insufficient leaf mass, which reduced numbers to near extinction.

Figure 3 shows the expected cumulative number of mites over the season when either N or rainfall was allowed to vary and the other was kept at the observed pattern. Drought and N stress each lowered the total green mite population. Nitrogen stress tended to delay the mite's exponential growth phase via reduced fecundity and increased development periods, while water stress determined the phenology.

Effects of M. tanajoa, *[N] and soil moisture on tuber yield*

Biomass formation in pest-free cassava was examined in Gutierrez *et al.* (1988a), and those results are considered the standard in this study. Given observed weather and initial [N], *M. tanajoa* reduced tuber yields by *c.* 10% (Fig. 2a). The declines in leaf and tuber dry-matter accumulation rates in February, March and April were caused by *M. tanajoa* damage.

Drought alone resulted in leaf abscission, and affected photosynthesis and yield, but the interactions were further compounded by green mite feeding. This is seen as the simulated decrease of tuber growth rates in Fig. 2a, d, g. In the 80% water and 100% N treatment (Fig. 2d), the mite population was smaller and the leaf loss greater than in 100% water and N treatment (Fig. 2a), but the net reduction in tuber yields was about the same. At 60% water and 100% N (Fig. 2g), the direct effects of drought on tuber formation were more important than the effects of green mite. The rate of dry-matter accumulation in tubers was slightly negative in Fig. 2g because of respiration costs compared with treatments reported in Fig. 2a where green mite feeding was considerably more intense.

The effect of soil [N] was more subtle. Reduced N decreases photosynthesis and dry-matter accumulation in tubers. In the model and probably in nature, N reserves and reallocation of N from ageing leaves buffer the system from the sharp changes in photosynthate production that occur with defoliation. At 100% water and 75% N, the green mite population was greatly reduced (Fig. 2b), and the pattern of tuber dry-matter accumulation was smooth. Reducing N to 50% nearly eliminated green mite, but also reduced yield by 20% (Fig. 2c).

The compounding effects of N and rainfall on tuber yield formation are best seen by comparing Fig. 2c, g with Fig. 2i. This comparison shows that tuber yield was reduced a further 20% by the interaction, but that *M. tanajoa* damage was inconsequential under these extreme conditions.

DISCUSSION

Several workers have examined the effects of mite feeding damage on crop yields, or on leaf photosynthetic rates (Andrews & LaPre' 1979; Allen 1981; Sances *et al.* 1981, 1982; Smith & Mozingo 1983; Welter *et al.* 1984; Hardman, Herbert & Stanford 1985). However, only the work of Allen (1981) on citrus rust mite (*Phyllocoptruta oleivora* (Ash.)) integrates the two levels of analysis. Our crop model is biologically more complete (Gutierrez *et al.* 1988a) and abiotic factors affecting mite population growth rates have been included. Accurate estimates of mite feeding rates on leaves are generally lacking, and consequently a conservative estimate was used here.

Water and N effects on plants are well known, but these factors have important effects on pest populations as well. For example, the 1983–84 crop had adequate N and unusually heavy rainfall occurred during the normally dry period; predicted green mite impact on tuber yields was moderate (*c.*10%) due primarily to the high rain-induced mortality on *M. tanajoa*. The effects of reducing either the observed 1983–84 N or water on *M. tanajoa* are shown in Fig. 4; 50% reduction in either N or rainfall caused an estimated reduction of >90% in total mite-days, but reduced yields only 15–20%. Rainfall is the primary factor determining numbers of green mites in the wet season (Yaninek 1985; Yaninek, Herren & Gutierrez 1987), and induced leaf abscission determines the green mite pattern in the dry season (Yaninek & Animashaun 1987), but it is [N] in leaves that determines the maximum *M. tanajoa* population growth rate.

The simulation data suggest that *M. tanajoa* would not be a severe problem on N-poor soils even with low rainfall-induced mortality. This observation has been made by R. Hennessey (US/AID, personal communication) in the field in Zaire. Unfortunately, the predicted yield reduction caused by poor soils is greater than the expected losses from green mite feeding on plants grown in good soils (Fig. 2a vs. 2c). The results further suggest that growing cassava under intensive irrigation and fertilization in an extended

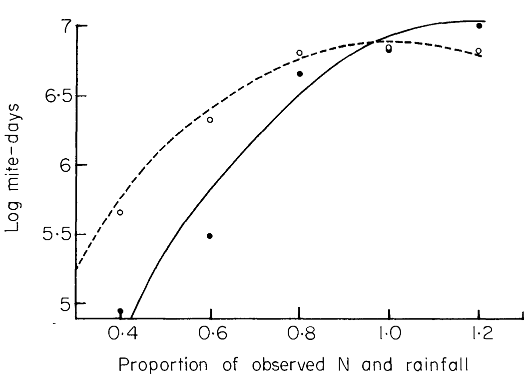

FIG. 4. Simulated relationship between $\log_{10}$ mite-days and multiples of initial N and rainfall patterns. (- - - - -) water, (————) N.

dry season exacerbates the green mite problem because mortality due to rainfall is removed, reproductive rates increase, and development times shorten.

The biological realism of this model enables us to use it as a basis for the evaluation of the biological control of *M. tanajoa* from several perspectives. In this study, we have examined the components of yield as affected by N, rainfall and *M. tanajoa* but, just as easily, we could incorporate all the other species discussed in Gutierrez *et al.* (1988b). The effects of these various factors can be separated more efficiently by simulation than by standard agronomic trials, but field studies are the standard with which the simulation model must be compared.

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APPENDIX

Mononychellus tanajoa

Initial values	
Adult number (plant^{-1})	1·0
Maximum parameters*	
Development threshold (°C)	14·4
Development time (DD)	
Eggs	68·0
Immatures	86·0
Preoviposition period (DD)	12·0
Longevity adults (DD)	141·0
Damage rate per adult ($\mu\text{g DD}^{-1}$)	1·2
Oviposition rate (eggs DD^{-1})	0·32
Sex-ratio (female bias)	0·7
Search rate	0·1
Mortality due to rain	$0 \leqslant 1{\cdot}0288\ \text{mm}^{-0{\cdot}3185} \leqslant 1$
N scaling factors	
Preimaginal development	$1 \leqslant 1{\cdot}63 - 0{\cdot}13{*}[\text{N}] \leqslant 1{\cdot}3$
Preoviposition time	$0{\cdot}9 \leqslant 3{\cdot}52 - 0{\cdot}52{*}[\text{N}] \leqslant 3$
Fecundity	$0 \leqslant 0{\cdot}22{*}[\text{N}] \leqslant 1{\cdot}1$

* Cf. Yaninek (1985).