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*Phenacoccus manihoti***

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ANALYSIS OF BIOLOGICAL CONTROL OF CASSAVA
PESTS IN AFRICA. II. CASSAVA MEALYBUG
PHENACOCCLUS MANIHOTI

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SUMMARY

(1) The effects of the cassava mealybug, *Phenacoccus manihoti* Mat.-Ferr., on cassava, *Manihot esculenta* Crantz, growth, development and yields as modified by weather, soil water and nitrogen, and natural enemies were examined.

(2) Rainfall-induced mortality and plant carbohydrate stress were the major determinants of *P. manihoti* population patterns prior to the introduction of exotic natural enemies.

(3) The contribution of the introduced parasitoid *Epidinocarsis lopezi* (DeSantis) and indigenous predators of *Hyperaspis* and *Exochomus* to the biological control of *P. manihoti* was assessed. Native coccinellid predators were not important regulating agents of *P. manihoti* before the introduction of exotic parasitoids.

(4) The contribution of native coccinellids to total *P. manihoti* mortality appears largely dispensable after the introduction of *E. lopezi*.

(5) The effect of rainfall on density-dependent regulation of *P. manihoti* by the parasitoid *E. lopezi* in the field was examined.

INTRODUCTION

The parthenogenetic cassava mealybug (*Phenacoccus manihoti* Mat.-Ferr.) is native to South America where it is host-specific to cassava (*Manihot esculenta* Crantz). The introduction of *P. manihoti* to Africa in the early 1970s caused severe damage and threatened to destroy cassava production across the African cassava belt. This area is > 1.5 times the area of the U.S.A. Losses of > 60% attributable to *P. manihoti* were reported from Africa (Herren 1981).

Indigenous natural enemies did not provide effective biological control despite the fact that > 130 species of native natural enemies attack *P. manihoti* (Neuenschwander, Hennessey & Herren 1987). Coccinellid predators of the genera *Hyperaspis* and *Exochomus* (Coleoptera: Coccinellidae) were especially common, but parasitoids were rare.

Classical biological control of coccids has been especially successful (DeBach, Rosen & Kennett 1971), and appeared promising for *P. manihoti*. In 1981 and 1982, the introduced encyrtid parasitoid *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae) was first

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released in southwestern Nigeria by the Africa-wide Biological Control Project (ABCP) (Herren 1987) of the International Institute of Tropical Agriculture (IITA) at Ibadan, Nigeria (Herren & Lema 1982; Neuenschwander & Herren 1987). In 1983, the parasitoid is thought to have reduced the *P. manihoti* population at the initial release site to very low levels (Herren & Lema 1983). The efficacy of the parasitoid has been demonstrated in exclusion experiments (Neuenschwander, Schulthess & Madojemu 1986), and the parasitoid has since been established in different ecological zones in sixteen African countries (Herren *et al.* 1987; Neuenschwander & Herren 1987). However, Odebiyi & Bokonon-Ganta (1986), using laboratory studies, disputed the role of the parasitoid in the observed reductions of *P. manihoti* populations.

A large-scale survey in west Africa showed that, since the introduction of *E. lopezi*, the number of native predators (and parasitoids) associated with *P. manihoti* has declined sharply (Neuenschwander, Hennessy & Herren 1987). In addition, introduced coccinellid predators such as *Hyperaspis jucunda* Muls. have not been established.

This paper presents an analysis of the effects of rainfall, the introduced parasitoid *E. lopezi* and native coccinellid predators on the population dynamics of *P. manihoti*; and assesses the effects of *P. manihoti* on cassava tuber yields as modified by natural enemies and abiotic factors.

MODELLING METHOD

Parameter estimation

The parameters characterizing the biology of the insect species (see Appendix) were estimated from the literature and unpublished data that will be reported in detail elsewhere. Parameters for the *P. manihoti* model were estimated from Fabres (1981), Fabres & Boussienguet (1981), Lema & Herren (1985) and Schulthess (1987); those for *E. lopezi* from Iziquel (1985), Odebiyi & Bokonon-Ganta (1986), Hammond, Neuenschwander & Herren (1987), Kraaijereld & van Alphen (1986), Neuenschwander & Sullivan (1987) and Neuenschwander & Madojemu (1986), Sullivan & Neuenschwander (1988), Löhr *et al.* (in press) as well as unpublished data from P. Neuenschwander & W. N. O. Hammond. The biology of *H. jucunda* is similar to but better known than that of its African relatives (Nsiamia She, Odebiyi & Herren 1984; Nsiamia She 1985), hence its biological parameters were used as surrogates to model predation by native species of the genera *Hyperaspis* and *Exochomus*. The data were made available in an uncommon spirit of international cooperation.

Mathematical model

The basic population dynamics model used in this study was presented in Gutierrez *et al.* (1988a). Since the models of the parasitoid (*E. lopezi*) and the coccinellid predators are conceptually similar to the mealybug model, many of the details are not reported. For the mealybug and predator models, the mass and number dynamics of their life stages and the developing embryos they contain are modelled, but for *E. lopezi* only the number dynamics are considered. In the model, each species accumulates physiological age (Δa , degree days day^{-1} , DD) above its own thermal threshold, but physiological time (Δt) across trophic levels is reported on the plant time-scale.

Cassava mealybug model

The *P. manihoti* population is characterized by attributes such as numbers ($\rho(a,t)$), mass ($M(a,t)$), age (a) and factors that affect birth and death rates which change over time

where θ is the food supply:demand ratio of the *P. manihoti* population, $0 < v([\text{N}]) \leq 1.1$ is a scalar function of leaf nitrogen concentration ($[\text{N}]$) described in detail in Gutierrez *et al.* (1988b) (cf. Wermelinger, Oertli & Delucchi 1985), $\rho_A(a)$ is the density of *P. manihoti* adults of age a , and $F(a)$ is the maximum age-specific fecundity rate displaced to accommodate the fact that the observed eggs (Fabres 1981; Fabres & Boussienguet 1981) were initiated earlier as embryos. A similar model for fecundity minus the effects of v was developed for *E. lopezi* and the predators using the same code for each version of (1).

Components of the mealybug food supply:demand ratio (θ)

Cassava mealybugs prefer the terminal portions of the plant where they feed on the phloem fluids ($P(t)$) in leaves and stem. Parasitized active *P. manihoti* also feed and their demand is included in the mealybug population demand for computing the quantity of plant sap removed. The quantity of photosynthate extracted by parasitized and healthy mealybugs over Δt is Λ , and the relationship between the feeding and the plant is as follows:

$$P(t + \Delta t) = P(t) - \Lambda(t). \quad (3)$$

Λ is computed using the Frazer–Gilbert (1976) functional response model (i.e. $f(\cdot)$, eqn (4) in Gutierrez *et al.* 1988a), where b was defined as the maximum demand rate of P that can be used by parasitized and unparasitized *P. manihoti* (ρ^*) and s is the effective search rate.

$$\Lambda = \theta_p \cdot P(t) f(P, \rho^*, b, s, \Delta t) = \theta_p \Lambda^* \quad (4)$$

The components of the demand rate b in $f(\cdot)$ (eqn (5)) are the sum of the maximum temperature-dependent demands for respiration (z , i.e. Q_{10}), egestion ($0 < \beta \leq 1$), reproduction (R), immature growth (G) and reserves (v) (Gutierrez, Baumgaertner & Hagen 1981). The potential supply rate Λ^* in (4) is factored by the cassava (subscript p) supply:demand ratio (θ_p) (see Gutierrez *et al.* 1988a). This assumes that the mealybug demand b is part of the plant demand and is met in the same proportion and priority rank as plant vegetative growth (Gutierrez *et al.* 1988a).

$$b = (dG/dt + dR/dt + dz/dt + dv/dt)/(1 - \beta) \quad (5)$$

The use of the Frazer–Gilbert model for *P. manihoti* feeding implies that the search for plant sap (P) is a predation process in much the same way as predation by coccinellids and parasitism by *E. lopezi* adults. Of course, the predator form of $f(\cdot)$ is used for *P. manihoti* and the predator, and the parasitoid version which accommodates superparasitism is used for *E. lopezi* (see Gutierrez, Baumgaertner & Hagen 1981; Gutierrez *et al.* 1988a; Baumgaertner, Gutierrez & Klay, in press).

In the assimilation process, Λ is first corrected for egestion (β), and then allocated to respiration (z), and, according to age of the cohort, to reproduction ($R =$ embryo growth) and immature growth (G) and reserves (v). The overall mealybug food supply:demand ratio (index) θ ($0 < \theta = \Lambda/b < 1$) is used to scale the production rate of new embryos as above, but also the age-specific growth rates of *P. manihoti* immatures and the embryos growing within adults. As shown below, θ is a linear component of survivorship. All these factors except x_c are included in an age-specific manner in $\mu_j(a, t, \cdot)$ (eqn (1)). Similar supply–demand indices are computed for the other species in the system (Gutierrez *et al.* 1987), and are measures of intraspecific competition in each trophic level.

The mealybug demand rate b is included in the plant's total demand rate (b^*) for photosynthate ($b^* = b_p + b$), implying that the photosynthetic rate may increase within

limits to compensate for feeding. At low *P. manihoti* densities, there may be complete compensation, but at high densities compensation is incomplete and yield is reduced.

Mealybug age-specific mortality

Among the mortality factors affecting *P. manihoti* population are age-specific intrinsic mortality ($\mu_a(a)$), parasitism and host feeding from *E. lopezi* (μ_E), predation from coccinellid predators (μ_H), the mechanical effects of rainfall (μ_R), and food shortage (μ_θ). Premature death of individuals also kills the embryos or parasitoids they contain.

Age-specific life-table studies on *P. manihoti*, *E. lopezi* and the predator conducted at various temperatures were used to estimate intrinsic mortality rates (Fabres 1981; Nsiama She 1985; Odebiyi & Bokonon-Ganta 1986; Schulthess 1987; B. Löhr & A. M. Varela, unpublished communication) and were characterized in the model via the distribution of outflow rates (y_j) in (1) determined by selecting appropriate species-specific values of the Erlang parameter k . The remaining age-specific mortality was included in ($\mu_i(a, t, \cdot)$). The ability to incorporate them into one term for each population greatly simplifies the problem mathematically. In practice, it is more convenient to think in terms of survival rates (i.e. $lx = 1 - \mu$) during an interval Δt , because they may be readily multiplied as follows:

$$\mu_c(a, t, \cdot) = 1 - lx_E(a)lx_Hlx_\theta lx_R. \tag{6}$$

Mortality from parasitism (μ_E). *E. lopezi* is an arrhenotokous encyrtid parasitoid specific to *P. manihoti*. The adult parasitoid lays its eggs at random in hosts attacked (Iziquel 1985), but it prefers large hosts (Kraaijereld & van Alphen 1986; Neuenschwander & Madojemu 1986). Adult parasitoids also feed on *P. manihoti* active stages, hence the parasitoid's demand for hosts (b_E) has two components: for host feeding and for oviposition. In the model, the host-feeding demand is satisfied as a constant proportion (0.3) of the total hosts attacked. Neuenschwander & Madojemu (1986) found that crawlers are not parasitized; larger *P. manihoti* life stages are preferred for reproduction; and all active stages, but mainly younger ones are host fed. The maximum fecundity of the parasitoid is $c. 85$ eggs female⁻¹ (Iziquel 1985). The mealybug death rate due to parasitoid attack corrected for host feeding is the parasitoid's birth rate (i.e. x_j in (1) of the parasitoid model).

The total number (ρ^*) and the associated mass (M^*) of parasitized and unparasitized *P. manihoti* attacked by the parasitoid (E_A) were computed using the parasitoid version (subscript E) of the Frazer–Gilbert model (7):

$$\rho^* = f_E(\rho_T, E_A, SR, b_E, s_E, \Delta t) \Sigma \rho_i \tag{7}$$

$$M^* = f_E(\rho_T, E_A, SR, b_E, s_E, \Delta t) \Sigma M_i \tag{8}$$

$\rho_T = \Sigma \rho_i$ is the total parasitized and unparasitized *P. manihoti* population of stages $i = I, P, A$ available for attack, SR is the parasitoid sex ratio, b_E is the demand rate, s_E is the parasitoid search rate, and Δt is the increment of elapsed physiological time. ρ_T as used in $f_E(\cdot)$ in (7,8) indicates that the parasitoid searches for individuals and not their mass. The mortality (ρ^*_i) is partitioned among *P. manihoti* immatures (ρ_I) older than the crawler stage, the preoviposition adults (ρ_P) and adults (ρ_A) as follows:

$$\rho^*_I = \rho^*(\zeta_I \rho_I / \rho_w) \tag{9}$$

$$\rho^*_P = \rho^*(\zeta_P \rho_P / \rho_w) \tag{10}$$

$$\rho^*_A = \rho^*(\zeta_A \rho_A / \rho_w) \tag{11}$$

where $\rho_w = \sum \zeta_i \rho_i$ is the weighted sum of all *P. manihoti* stages, and the ζ_i are the stage-specific preference values. The stage (*i*) specific survival due to parasitism (i.e. $0 \leq l_{x_{E,i}} \leq 1$) for the *P. manihoti* life-stages is defined as follows:

$$l_{x_{E,i}} = (1 - \rho_i^* / \sum \zeta_i \rho_i), \quad (12)$$

Individual parasitoid females search, but in the model an aggregate estimate for parasitoid activity is needed. The proportion of the area of search should increase with increasing female (FEM) parasitoid numbers, hence the aggregate search rate chosen is $0 \leq s_E = 1 - e^{-\gamma \text{FEM}} \leq 1$. s_E is the Nicholson-Bailey (1935) model from animal ecology. The parameter $\gamma = 0.05$ for *E. lopezi* was made from laboratory data (P. Neuenschwander, unpublished data). The abundant field data (Neuenschwander, Hennessey & Herren 1987) on the interaction of the parasitoid and *P. manihoti* were used to gauge the aptness of the value. The model is insensitive to the value of γ at high host densities, but very sensitive at low host densities leading to near extinction of both mealybug and parasitoid.

The parasitoid's sex ratio (SR) in (7,8) changes with the average size of available hosts (Kraaijeveld & van Alphen 1986). This is incorporated in the model as follows:

$$\begin{aligned} \rho_w / \rho_T &= (\zeta_1 \rho_1 + \zeta_P \rho_P + \zeta_A \rho_A) / (\rho_1 + \rho_P + \rho_A) \\ 0.3 \leq \text{SR} = \rho_w / \rho_T &\leq 0.75. \end{aligned} \quad (13)$$

Attacks on larger mealybugs are more likely to produce females, hence the preference scalars ζ_i provide a proper weighting of the *P. manihoti* age structure for computing the sex ratio. For example, if only large adults are present in the population, $\text{SR} = 0.75$, but, for a population of small mealybugs, $\text{SR} = 0.3$. The different sets of data give different SR values, but all indicate the same trends. The data are described elsewhere (P. Neuenschwander, unpublished).

The above models estimate the *P. manihoti* death rate and the parasitoid birth rate, but other factors affect the parasitoid's dynamics. Parasitoid emigration and food-related survival rates in the model are regulated by the ratio of hosts attacked: demand for hosts.

E. lopezi immatures are also attacked by native hyperparasitoids and predators. In a large-scale survey, hyperparasitism was linearly related to *E. lopezi* immature densities per cassava tip (P. Neuenschwander & W. N. O. Hammond, unpublished data; hyperparasitoids = $0.28 \times$ parasitoid immatures, $r = 0.776$, $n = 472$). This factor was included in the model as a component of the parasitoid's μ .

Mortality from predation. The native coccinellid predators are small, weighing *c.* 2.5 mg, and attack all mealybug life stages, *E. lopezi* immatures found in active mealybugs, and immature stages younger than themselves. Beetle cannibalism is not considered an important source of nutrient or mortality and is excluded from the model. As with *P. manihoti*, the predator model accounts for both the changes in numbers and mass of the beetle population, and the developing ova the females contain. The proportion of females (0.55), fecundity, development times and thermal threshold were estimated for *H. jucunda* from data by Nsiamia She (1985), but good estimates of its metabolic costs (z_H) and the proportion of food egested (β_H) were not available. The rate ($\beta_H = 0.74$) estimated by Gutierrez, Baumgaertner & Hagen (1981) for the coccinellid *Hippodamia convergens* (G-M) was used as an initial approximation, but this proved to be much too high. A value of 0.25 gave more reasonable results. Lack of good estimates for β_H and z_H is a deficiency of the predator model, but analysis indicates the results are not

seriously affected; z_H depends on temperature which varies little, and β_H scales daily assimilate by a constant and is important at low prey density.

The mass of prey consumed (M^*_H) by the predators (H) includes parasitized and unparasitized mealybug life-stages (i.e. M_T) and is estimated using the predator version of the Frazer–Gilbert model (Gutierrez, Baumgaertner & Hagen 1981; Gutierrez *et al.* 1988a; Baumgaertner, Gutierrez & Klay, in press).

$$M^*_H = f_H(M_T, H, b_H, s_H, \Delta t) M_T \quad (14)$$

The demand parameter b_H in the Frazer–Gilbert model is the sum of all age-specific consumption demand rates computed in a manner similar to that formulated for mealybug (i.e. eqn (5)). The search parameter (s_H) was arbitrarily set to 0.1, but making the search rate a function of the size of the life stages did not alter the results much. Mortality and development rates of predator life stages (e.g. immature development and preoviposition periods) increase proportionally as its supply: demand ratio decreases to zero (i.e. $0 \leq M^*_H/b_H \leq 1$; Gutierrez, Baumgaertner & Hagen 1981).

P. manihoti and *E. lopezi* immature survival from predator attack (lx_H) was computed as follows:

$$lx_H = 1 - M^*_H/M_T. \quad (15)$$

Note that lx_H is used to compute the survival of parasitized and unparasitized *P. manihoti*.

Food-related mortality. The ratio of the food acquired: demanded, lx_θ , was used above to slow organism growth rates; here it is used to scale *P. manihoti* survivorship (Gutierrez, Baumgaertner & Hagen 1981). In the mealybug model, lx_θ affects not only *P. manihoti* but also the embryos and parasitoid life stages they may harbour. A similar ratio was computed for the predator and the host-feeding adult parasitoids.

Survival in rain. The mechanical effects of rainfall ($R = \text{mm day}^{-1}$) has been shown to affect adversely cassava green mite (*Mononychellus tanajoa* (Bondar) s.l., Yaninek 1985; Gutierrez *et al.* 1988b) survival. Similar observations were made for *P. manihoti* by Schulthess (1987), but an empirical relationship was not derived. The effects of rainfall on *M. tanajoa* survival were estimated (Yaninek 1985) as follows:

$$lx_R = 1 - 1.0288R^{-0.319}. \quad (16)$$

The effect on *P. manihoti* was estimated, using simulation, to be 0.6 the *M. tanajoa* rate. Mealybug mortality due to pathogen activity is enhanced by the rain (Le Ru 1986), but here it is lumped in lx_R . Rainfall is also assumed to affect *E. lopezi* immatures in active *P. manihoti* to the same degree that it affects unparasitized *P. manihoti*. No information is available on the effects of rain on mortality to *E. lopezi* pupae and adults or to predator life stages, and it is assumed to be zero.

SIMULATION RESULTS

Field data. *P. manihoti* populations are known to increase during the dry season, and decrease rapidly with the onset of rains. The simulated populations and their impact on cassava yields are related to 1982–83 and 1983–84 field data from Ibadan, Nigeria reported by Schulthess (1987). There were two plantings in 1982–83, and one in 1983–84. Plants were infested at the rate of 1 ovisac (c. 20 eggs) plant^{-1} at 60, 90 or 120 days after planting. Plant dry-matter and *P. manihoti* population densities were estimated from ten

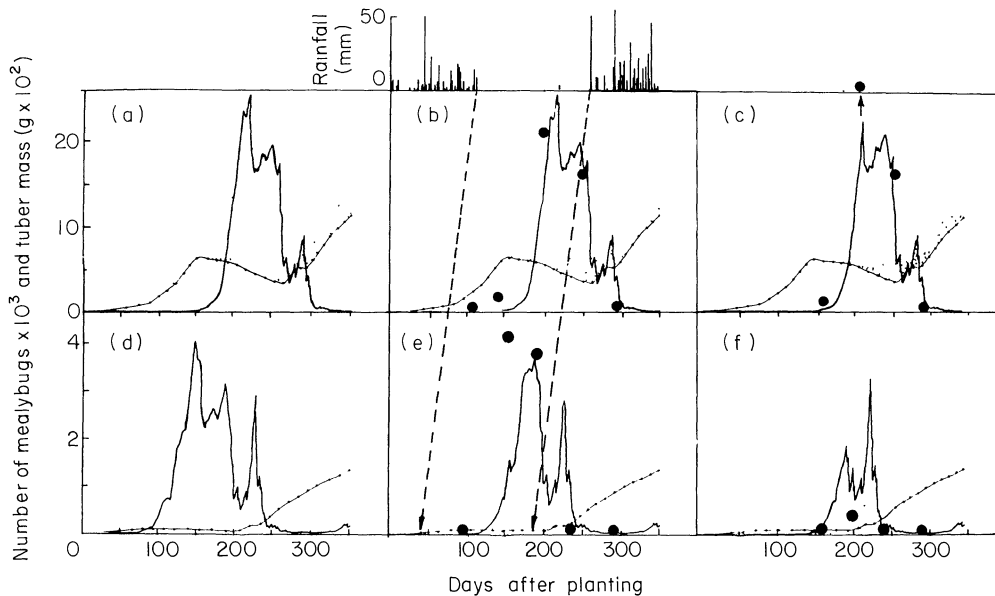


FIG. 1. Simulated cassava tuber growth and mealybug population dynamics in two plantings (July (a)–(c) and September (d)–(f) in 1982–83 at Ibadan, Nigeria. The plantings were exposed to mealybugs 10 ((a), (d)), 60 ((b), (e)) and 120 ((c), (f)) days after planting. Mealybug data from Schulthess (1987) indicated as (●); (---) tuber mass; (—) mealybug population density; □ yield loss. Note that tuber mass in (d), (e), (f) is $\times 10$.

plants taken at 5–6-week intervals. In the simulation studies, the plants were infested 10, 60 and 120 days after planting, and the results compared with the tuber-growth and *P. manihoti* data estimated from the graphs in Schulthess (1987, pp. 86–87).

The plant data provided good measures of plant growth and development (Gutierrez *et al.* 1988a). The *P. manihoti* population data were too sparse to capture the full character of the population dynamics, but provide good measures of mealybug population phenology and density.

1982–83 season

In the 1982 study, native coccinellids but not the parasitoid were present in the experimental fields. An uninterrupted dry season occurred as indicated by the gap in the rainfall pattern in Fig. 1. The effect of the dry season on plant growth and tuber yields in the absence of pests was analysed in Gutierrez *et al.* (1988a). The additional losses due to *P. manihoti* feeding observed by Schulthess (1987) in the July and September 1982 plantings were simulated and are indicated by the stippled area.

In general, the simulated and observed patterns of cassava growth and of size and phenology of the mealybug populations (60- and 120-day treatments, Fig. 1b,c) are similar. Rainfall was the major factor determining dry-matter patterns in cassava, mealybug feeding causing additional losses. Cassava planted in July was well developed until the dry season began, when its growth decreased rapidly. Observed *P. manihoti* populations in the 120-day treatment were higher ($c. 40 \times 10^3$) than those in the 60-day treatment, but the yield losses were similar in all treatments (Fig. 1a–c). The simulated yield losses were $c. 25\%$ less than those reported by Schulthess (1987) for this site and year.

Cassava planted in mid-September 1982 (Fig. 1d-f) was exposed to a much shorter rainy season than the July planting, and so was considerably less vigorous when the dry season began. Drought again affected yield formation and *P. manihoti* densities were less than a fifth of those that developed in the July planting. Simulated depletions of tuber dry-matter were slight and are not shown. Again, the patterns and magnitudes of mealybug dynamics were roughly correct, but discrepancies in tuber yield were observed. The model predicts the same yield for both treatments. Yield in the simulated 60-day infestation was the same as the observed, but that simulated in the 120-day experiment was nearly twice that recorded. It seems unlikely that plants planted at the same time, under the same agronomic practices and experiencing fewer pests would produce half the yield (i.e. 60- vs. 120-day treatment; see Schulthess 1987). Possible causes of the discrepancy are systematic errors in the recording of the data, or differences in soil nutrition.

1983-84 season

Unusually, rain fell during the normally dry period, and the plants suffered little stress (Gutierrez *et al.* 1988a). The parasitoid and native predators were present in all fields during 1983, but we also simulated the crop without natural enemies for heuristic purposes.

Without natural enemies. The observed and simulated interaction between drought and high mealybug numbers was seen in the 1982-83 studies above, but not in 1983-84. After the rains, simulated *P. manihoti* populations grew rapidly to about 10 000 plant⁻¹, with slightly larger numbers predicted in the 60-day infestation (Fig. 2a-c). The simulated patterns of tuber dry-matter accumulation in the three treatments were similar and the predicted yield losses were rather small and hence not shown. In the simulation, *P. manihoti* populations did not reduce cassava yields because the unusual rains during the normally dry period suppressed mealybug populations allowing the plants to grow vigorously and compensate for the damage.

With natural enemies. Cassava infested with *P. manihoti* 60 days after planting was used in this simulation study. As with the 1982-83 data, the model captured the observed growth of plant organs (Gutierrez *et al.* 1988a), as well as the magnitude and phenology of the mealybug populations (see Schulthess 1987). The parasitoid population begun with 0.5 females plant⁻¹ 175 days after planting quickly suppressed the simulated mealybug population to 0.1 of that predicted without parasitism (Fig. 2b vs. 2d). The simulated suppression of *P. manihoti* by the parasitoid alone is less than but similar to that seen in the Schulthess data, and the pattern similar to that reported by Herren & Lema (1982) during the first season at the original release site. Of course the outcome depends on the time and intensity of the initial *E. lopezi* entry into the field.

The simulated action of the parasitoid and the coccinellid predators on mealybug populations produced similar but lower populations (Fig. 2e). However, introducing only the predator (1 adult plant⁻¹) on day 175 and removing the parasitoid had little impact on the initial rate of *P. manihoti* population growth (Fig. 2b vs. 2f), but thereafter, the beetle's numerical response coupled with the onset of rain-induced mortality caused a rapid decrease in *P. manihoti* numbers from 9000. A modest reduction in total mealybug days over the predator-free simulation (Fig. 2b vs. 2f) confirms field observations that coccinellid predators may cause significant mortality in the mealybug population, but not enough to provide timely control (Herren & Lema 1982). The model also predicts that the predators emigrate or die when mealybug populations are greatly reduced (Fig. 2e, f). The

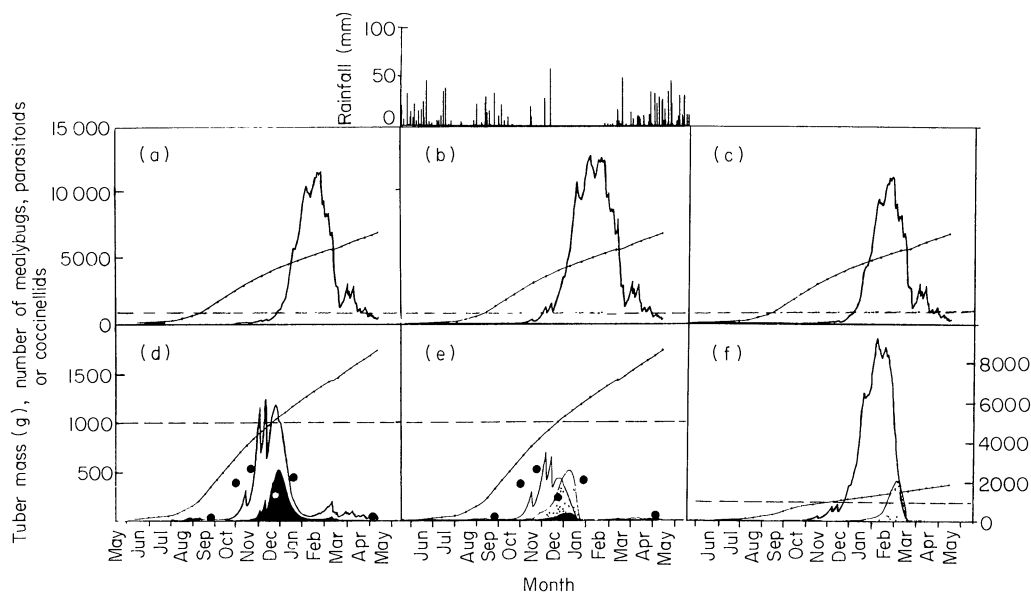


FIG. 2. Simulated cassava tuber growth and mealybug population dynamics in 1983-84 at Ibadan, Nigeria. Cassava was exposed to mealybug populations in the absence of the parasitoid (a) 10, (b) 60 and (c) 120 days after planting; (d) the 60-day mealybug infestation including the parasitoid *E. lopezi* ■, (e) adding coccinellid predators and (f) only the predator. (---) 1000 mealybug plant⁻¹ reference line, (●) data from Schulthess 1987; (---) tubers $\times 4$ for (a), (b) and (c); (—) mealybug population density; □ predator density $\times 10$ in (e) and (f).

interactions between drought and *P. manihoti* were shown above (Fig. 1) to result in larger losses than either factor alone.

Multi-year simulation study

The model is used to examine the effects of rainfall, parasitism and predation on the dynamics of *P. manihoti*. Figure 3 shows the simulated dynamics of *P. manihoti* with and without rain-induced mortality, respectively, over 2 years from 1 January 1982. A reference line of 5000 mealybugs plant⁻¹ is indicated in all figures to facilitate interpretation of the results.

The low mealybug populations predicted during the rainy periods in Fig. 3a are due largely to their suppression by rain. However, plant stress effects in the dry season caused mealybug populations to begin to decline before the second cycle of rains. Removing the rain-induced mortality (Fig. 3e) produced initial rapid mealybug population growth which reached a food-supply-mediated maximum of *c.* 55 000 mealybugs plant⁻¹. The decline in simulated mealybug numbers in the late dry-season was due to drought stress which reduced photosynthesis. Higher peaks observed, in Fig. 3a, in relatively rain-free periods occurred because the plants were more vigorous. The patterns of mealybug build-up in dry periods and declines in the rainy season in Fig. 3a are similar to those observed in the field before the introduction of *E. lopezi*.

The introduction of coccinellid predators into systems Fig. 3a, e produced the results shown in Fig. 3b, f. In early simulation runs, the beetle populations died out at low prey densities, hence a threshold of 300 mg mealybugs plant⁻¹ (*c.* 600 mealybugs plant⁻¹) was used to trigger reinvasion of the field at the rate of 1 adult plant⁻¹. The model excluding

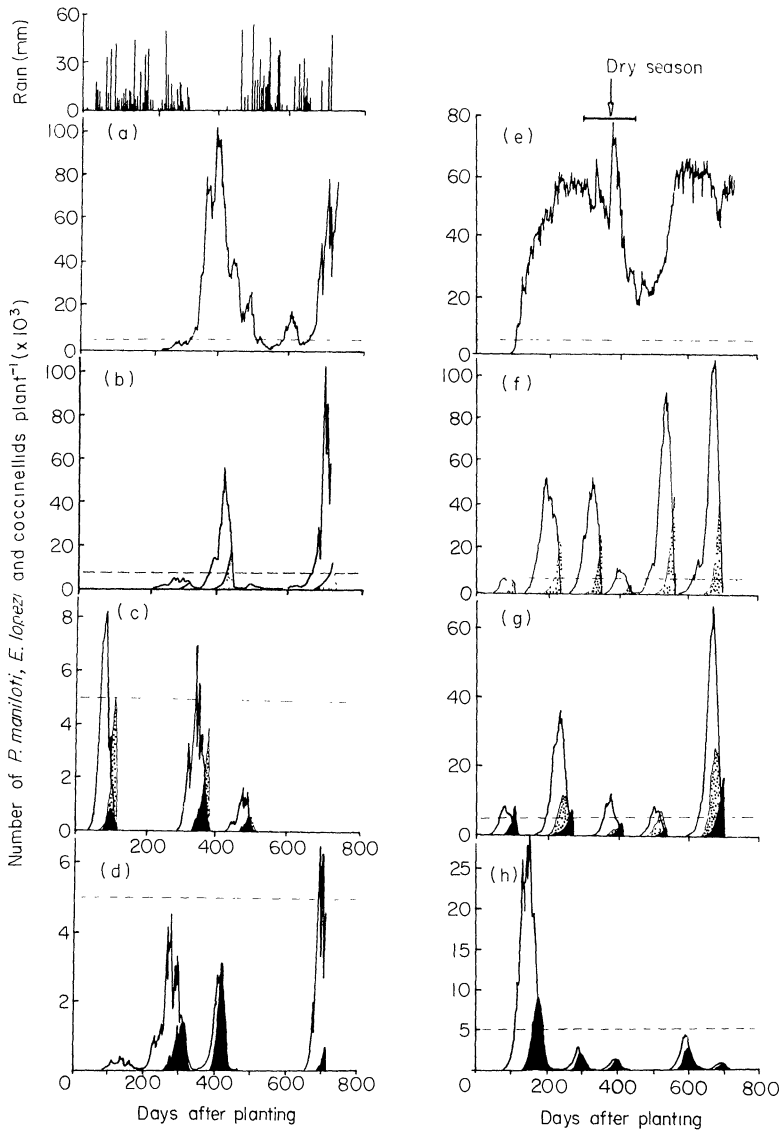


FIG. 3. Simulation of the interactions of parasitoid *E. lopezi*, coccinellid predators and rainfall with mealybug population dynamics using weather for 1 January 1982 to 31 December 1983 in Ibadan, Nigeria with (a)–(d) and without (e)–(h) rainfall-induced mortality to mealybug and *E. lopezi*: (a, e) mealybug alone; (b, f) mealybug and predators $\times 10$; (c, g) all species; (d, h) mealybug and *E. lopezi*. (----) 5000 mealybugs plant^{-1} ; (■) *E. lopezi*; (□) predators $\times 10$; (—) mealybug population density.

rain-induced mortality (Fig. 3f) produced high cyclic outbreaks of mealybugs, the lows occurring during the late drought period. The mealybug pattern with rain-induced mortality included (Fig. 3b) is less cyclic, higher densities occurred during the dry periods and the peaks were about the magnitude seen in Fig. 3f. Raising the reinvasion threshold to 700 mg plant^{-1} caused the mealybug population to tend towards the pattern in 3a, e,

and lowering it to 100 mg plant⁻¹ produced roughly the same patterns as in 3b, f but with lower peaks. The threshold appears to have an important bearing on the beetles' ability to control *P. manihoti* populations.

Evidence of aggregation of natural enemies, especially predators, to areas of high host density is found in the literature (e.g. Hassell 1986). However, there was a low correlation between the number of shoot tips infested with beetles (100 tip samples) and log₁₀ mealybug density tip⁻¹ ($r^2=0.29$, $n=31$) (P. Neuenschwander & W. N. O. Hammond, unpublished data), suggesting that the native beetles are not closely associated with *P. manihoti* densities. Beetles were absent in some mealybug populations as high as 100 tip⁻¹. The correlation between *E. lopezi*-infested tips and log₁₀ mealybug density was much higher ($r^2=0.66$, $n=51$), and the intercept was not different from zero and the slope (17.2) of the regression was twice that for beetles. A plot of the beetle data on the parasitoid data gave a poor correlation and a negative y -intercept, suggesting that the beetles enter the system only after the parasitoid has infested the tips (i.e. at higher mealybug densities).

Including the beetles at the 300-mg threshold and *E. lopezi* in the model caused higher cyclic mealybug populations when rainfall-induced mortality was excluded (Fig. 3g), and fewer but disrupted cycles when included (Fig. 3c). The timing of the peaks appeared to be controlled by predators, but the magnitude and the reduction in the number of peaks were determined by *E. lopezi*. This is similar to the situation for aphidophagous coccinellids found by Gutierrez, Baumgaertner & Summers (1984).

Including only *E. lopezi* produced patterns 3d, h similar to those observed in the field after establishment of the parasitoid (Fig. 4, Hammond, Neuenschwander & Herren 1987). The predicted densities of *P. manihoti* were, for the most part, below those required to maintain significant numbers of beetles in the field, possibly explaining why the numbers of coccinellid predators have been greatly reduced in cassava since the introduction of *E. lopezi*.

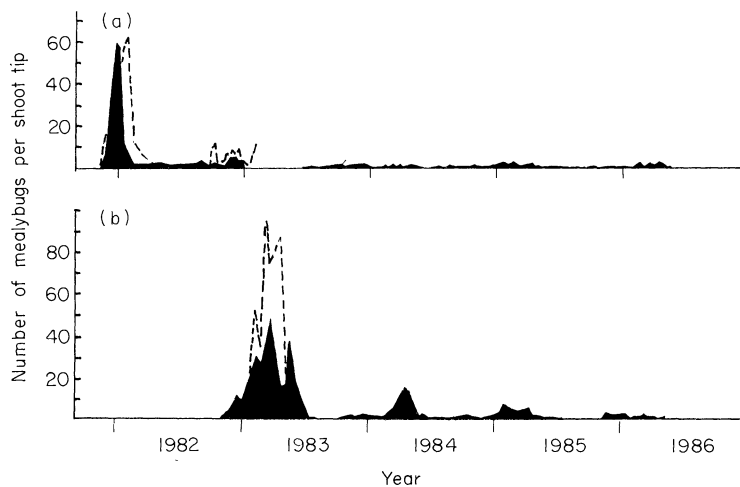


FIG. 4. Dynamics of mealybug in cassava in Nigeria at (a) Ibadan and (b) Abeokuta after the introduction of the parasitoid *E. lopezi* (cf. Hammond, Neuenschwander & Herren 1987). (---) control, (■) with *E. lopezi*.

DISCUSSION

Plant–herbivore interaction

Much has been written on plant–herbivore interactions at the chemical, physiological, behavioural and population levels; see reviews by McNeill & Southwood (1978), Crawley (1983), Enckell & Nilsson (1983) and Strong, Lawton & Southwood (1984). Few have attempted to integrate higher trophic levels and the effects of weather into the analysis. Models are not expected to cover all aspects of the relationship, rather just the dominant ones. Here, we used a model structure for trophic levels that incorporates age structure, distribution of ageing rates, details of physiology, physiological time, nutrient supply: demand and other factors (Gutierrez & Baumgaertner 1984a, b). One would suspect that a large number of parameters are required by our model but, in fact, few are used and most can be easily estimated (see Appendix). It is the generalized structure of the model that enables us to simulate a wide range of species and situations (Gutierrez *et al.* 1987). The work of Gurney, Nisbet & Lawton (1983) and later papers by the same authors tend toward the methods used here, but their focus has been to maintain a rigorous analytical structure. We applaud that work, but press on to examine biological issues keeping the need for sound mathematical underpinnings of our model clearly in mind.

Simulation results

The model was able to simulate the phenology and magnitude of cassava growth and development and mealybug population dynamics in three plantings in two growing seasons. Predicted yield losses in wet years were small because rainfall suppressed mealybug populations directly and enhanced the ability of the plant to compensate for the feeding damage. In contrast, losses in dry years were higher because of direct negative effects of water stress on photosynthesis and were compounded by the much larger mealybug population which developed and depleted the plant's mobile reserves and tubers.

The simulation results incorporating the parasitoid and rainfall-induced mortality are qualitatively similar to the results observed in the field by Herren & Lema (1982) and Hammond, Neuenschwander & Herren (1987). The model confirms field observations that the parasitoid *E. lopezi* is the most important factor controlling mealybug populations in the dry season, and rainfall, directly or possibly via diseases, during the rainy season. The contribution of the predators to mealybug mortality is mostly dispensable and possibly slightly disruptive. This conclusion conflicts with that of Odebiyi & Bokonon-Ganta (1986), who considered that the parasitoid's age-specific, life-table statistics were insufficient to control *P. manihoti*.

Two major factors possibly account for the parasitoid's ability to successfully control *P. manihoti*: host feeding extends the adult parasitoid's life and is an additional source of mortality to the mealybug population, and the parasitoid's preference for the larger mealybug stages has the combined effect of killing not only the mealybug but also the developing ova they contain. From an energy utilization point of view, the mealybug population makes nearly the maximum investment in time and energy in the stages preferred by the parasitoid, and hence suffers near maximum loss. In addition, attacks on preferred stages are more likely to produce female parasitoids which further mitigates against mealybug population growth. The development time of the parasitoid has a large variance (B. Löhner, unpublished data) helping it bridge host-free periods. This factor has been incorporated into the model via the choice of a small parameter, k , of our distributed

delay model. Hyperparasitoids do not appear to be a major constraint on the effectiveness of *E. lopezi* in the field, but biological information is insufficient for us to analyse the interaction confidently.

In contrast, several factors mitigate against the effectiveness of coccinellids in controlling mealybug. The beetle attacks all mealybug stages, hence their contribution to mealybug mortality is not sharply focused; the beetles are only twice the size of an adult mealybug and their consumption demand, relative to the mealybug population's ability to produce biomass, is not large; the beetles cause significant mortality to the mealybug population only via their delayed reproductive numerical response; the beetles have higher total maintenance respiration costs than the parasitoid and these costs must be satisfied before egg production can begin; all mobile life stages require abundant food to meet their minimum respiration costs, otherwise they starve or, where possible, emigrate. Field data show that the minimum mealybug population required to maintain coccinellids in cassava is higher than for *E. lopezi*. This kind of lower food threshold has been demonstrated in aphidophagous coccinellids ($0.34 \text{ mg prey mg}^{-1} \text{ predator}$, Gutierrez, Baumgaertner & Hagen 1981), where adult beetles migrate from the field when insufficient prey for reproduction is captured (Hagen 1976; Ives 1981). If such thresholds operate in the *P. manihoti* system, links between the coccinellids and the mealybug population are likely to be disrupted by an effective parasitoid or rainfall, which may severely deplete prey populations below the critical density. These factors help to explain the failure of the exotic predator *H. jucunda* to establish in Africa, and the great reduction in the numbers of native coccinellids and other predators associated with *P. manihoti* after the introduction of *E. lopezi* (Neuenschwander & Hammond, in press). However, additional field and laboratory studies are needed to provide the missing biological data before our conclusions about the utility of coccinellids in the control of *P. manihoti* can be regarded as fact.

Detecting density-dependent regulation

Density-dependent regulation can be demonstrated by showing that the percentage of hosts attacked increases as the host population density increases, but this is often difficult to demonstrate from field data. In the *P. manihoti* systems, poor correlations of percentage parasitism with mealybug density have been found (W. N. O. Hammond, unpublished data). One way in which the percentage of attacks can increase with host density is for the parasitoids to aggregate in areas of high host density (May 1978). However, Murdoch, Chesson & Chesson (1985) and Reeve & Murdoch (1985, 1986) accumulated evidence that the small aphelinid parasitoids they studied did not aggregate to areas of high host density, suggesting that the parasitoids search at random and that such systems are possibly unstable. Their conclusion rests on the assumption that the predictions of the Nicholson-Bailey (1935) random search model and May's (1978) parasitoid aggregation model provided reasonable hypotheses for comparison with field data that may also be inadequate.

Hassell (1986) suggests that the insights gained from field samples to determine whether density-dependent regulation of hosts by parasitoids occurs may be obscured by differential random abiotic factors. In the mealybug system, we know that variable temperatures and especially mortality due to rainfall add stochasticity by acting differently on different species. Here, we use the simulation model to examine this problem. We chose the weather for 1 January 1983 to 31 December 1984, which predicts

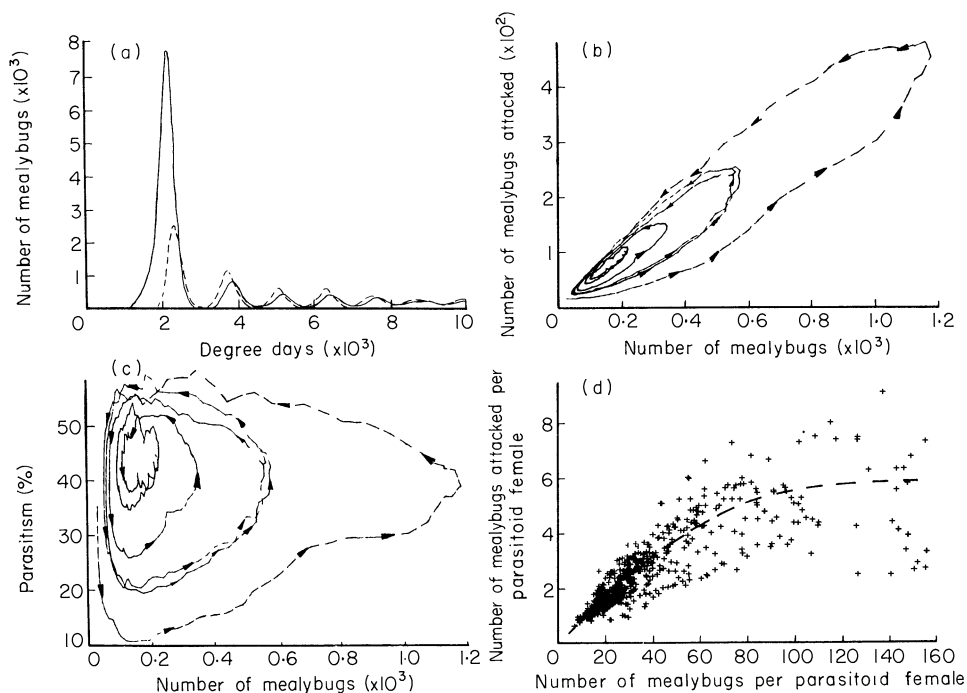


FIG. 5. Simulated interactions of cassava mealybug (—) and its exotic parasitoid *E. lopezi* (---) using weather data for 1 January 1983 to 31 December 1984 in Ibadan, Nigeria with mortality due to rainfall excluded. (a) Population dynamics, (b) numbers of available hosts attacked, (c) parasitism on the number of hosts female⁻¹ and (d) per capita hosts attacked. The arrows in (b) and (c) indicate the direction of the spiral and the (+) in (d) are simulated daily values.

no drought stress on the plants, to examine the effects of rainfall on the *P. manihoti*-*E. lopezi* interaction, with plant effects removed.

In the absence of rain-induced mortality, a cyclic interaction between *P. manihoti* and the parasitoid results, that appears oscillatory stable (Fig. 5a). Clearly, such smooth patterns are not observed in nature. The addition of rain-induced mortality radically alters the pattern (Fig. 6a). A time-series plot of parasitoid-immature numbers on mealybug numbers in both situations yields counterclockwise spirals that have been used to demonstrate density-dependent relationships in systems with discrete generations (Varley, Gradwell & Hassell 1973, Fig. 5b). The spiralling occurs because of the parasitoid's numerical response accruing from reproduction. The pattern in Fig. 5b is altered by rain-induced mortality, but it is still apparent at higher mealybug densities (Fig. 6b). The patterns of percentage parasitism increasing and decreasing with mealybug density also show similar counterclockwise spiralling (Figs 5c, 6c). Rain-induced mortality disrupts the patterns but, as Hassell (1986) demonstrated, the same underlying relationship survived.

The best insights can be gained by examining the per capita response of the parasitoid to mealybug density. Such relationships can be derived from field data. For example, a type II per capita functional response was found by Williams (1981) at two California locations for an egg parasitoid attacking the blackberry leafhopper, *Dikrella californica*

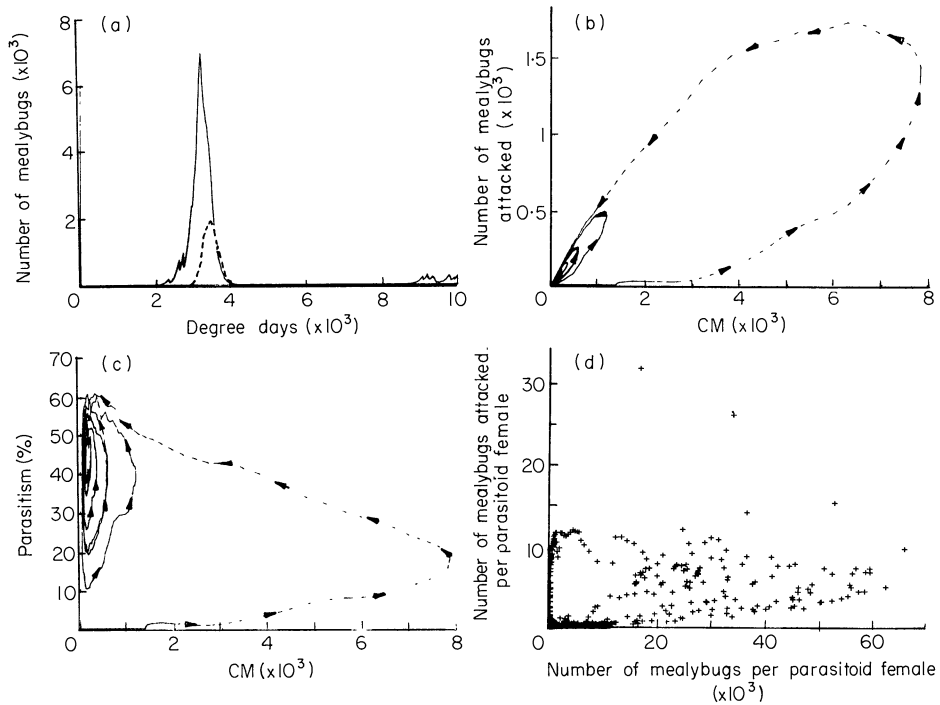


FIG. 6. Simulated interactions of cassava mealybug (CM, —) and its exotic parasitoid *E. lopezi* (---) using weather data for 1 January 1983 to 31 December 1984 in Ibadan, Nigeria with mortality due to rainfall included. (a) Population dynamics, (b) numbers of available hosts attacked, (c) parasitism on the number of hosts female⁻¹ and (d) per capita hosts attacked. The arrows in (b) and (c) indicate the direction of the spiral and the (+) in (d) are simulated daily values.

(Lawson). Leafhopper eggs in that study were embedded in leaf tissue and suffered little mortality from sources other than parasitism. In our mealybug simulation system with rain mortality excluded, a per capita type II relationship was expected and found (Fig. 5d, i.e. the Frazer–Gilbert model), suggesting a per capita inverse density-dependent response to prey density. The net population level response, however, appears to be directly density-dependent, primarily because of a reproductive numerical response by the parasitoid (Fig. 5b). The scatter in the simulated type II data is due to fluctuations in temperatures used to drive the model.

The inclusion of rainfall-induced mortality in our system destroys the type II pattern (Fig. 6d) because it affects mealybug more than the parasitoid and destroys the synchrony of the populations. As a result, there may be few hosts with many parasitoids, and possibly vice versa. Despite these disruptions, the *P. manihoti*–*E. lopezi* relationship remains density-dependent during favourable periods of rapid mealybug population growth (Fig. 6b). Our analysis suggests that *E. lopezi* regulates cassava mealybug in Nigeria, despite the disruptive effect of rain-induced mortality, drought effects on host abundance, and predation by native coccinellid beetles.

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APPENDIX

Unless indicated, degree days (DD) given refer to the species thermal threshold

Phenacoccus manihoti

Initial values plant ⁻¹	
Number of eggs	20
Egg weight (mg)	0.20
Reserves (mg)	0.02
Maximum parameters	
Development threshold (°C)	13.5
Development time (DD)	
Embryos	65.0
Eggs	114.0
Immatures	192.0
Longevity adults	371.0
Embryo shed age (DD)	(0, 50)
Search rate parameter	0.25
Growth demands per unit of age (<i>a</i>) in DD	
Immatures	0.0249*exp(-4.6+0.0249*a)
Reserves (% of growth demands)	10
Embryo (mg DD ⁻¹)	0.000154
Respiration	0.135*exp(0.007*Δt)*active wt
Proportion egested	0.176
Maximum rate of embryo production	[0.47*(a-306)]/[1-0.072***(a-306)]
Rain-induced mortality scalar: see text and Gutierrez <i>et al.</i> (1988b).	
N scaling factor for fecundity: see Gutierrez <i>et al.</i> (1988b).	

Epidinocarsis lopezi

Initial values plant ⁻¹	
Number of adults	0.5
Parameters	
Development threshold (°C)	13.3
Development time (DD)	
Eggs + larvae	100.0
Pupae	86.0
Adult longevity (DD)	280.0
Ratio host feeding: oviposition	0.3
Oviposition rate (eggs DD ⁻¹)	0.9
Host preferences:	
Immatures	0.3
Preoviposition adults	0.75
Adults	0.65
Sex-ratio	See text
Search rate parameter γ	0.05
Rain-induced mortality	See text
Temperature effects on oviposition	1 - [(DD-10)/10] ²

Coccinellid (i.e. *Hyperaspis* sp. and *Exochomus* sp.)

Initial values plant ⁻¹	
Number of adults	1.0
Weight (mg)	2.5
Reserves (mg)	0.5
Parameters	
Development threshold (°C)	14.0
Development time (DD)	
Embryos	109.0
Eggs	58.0
Larvae	105.0
Pupae	98.0
Longevity adults (DD)	962.0
Growth rate larvae (DD ⁻¹)	0.0238
Growth rate embryos (DD ⁻¹)	0.0009
Oviposition rate (eggs DD ⁻¹)	0.41
Sex-ratio	0.55
Proportion egested	0.38
Respiration rate	[exp(0.00607* DD ⁻¹)] active wt
Search rate	0.1
Rain-induced mortality	Not applicable