Biological Control of the Cassava Mealybug, Phenacoccus manihoti, by the Exotic Parasitoid Epidinocarsis lopezi in Africa [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1988 **318**, 319-333
doi: 10.1098/rstb.1988.0012

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Printed in Great Britain

Biological control of the cassava mealybug, *Phenacoccus manihoti*, by the exotic parasitoid *Epidinocarsis lopezi* in Africa

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Since its accidental introduction into Africa, the cassava mealybug (CM) has spread to about 25 countries. The specific parasitoid *Epidinocarsis lopezi*, introduced from South America, its area of origin, into Nigeria in 1981, has since been released in more than 50 sites. By the end of 1986 it was established in 16 countries and more than 750000 km^2.

In southwestern Nigeria, CM populations declined after two initial releases, and have since remained low. During the same period, populations of indigenous predators of CM, mainly coccinellids, have declined, as have indigenous hyperparasitoids on *E. lopezi*, because of scarcer hosts. Results from laboratory bionomic studies were incorporated into a simulation model. The model, field studies on population dynamics, and experiments excluding *E. lopezi* by physical or chemical means demonstrate its efficiency, despite its low reproductive potential.

Introduction

Some of the first introductions of biological control agents against pests were made in Africa. But only 15 insect pests have been controlled in nine countries, mostly in East Africa, a meagre record considering the opportunities and importance of biological control to African agriculture (Greathead 1986). This paper describes a large-scale biological control effort on cassava (*Manihot esculenta*), a prime source of carbohydrates (from the roots), and proteins and vitamins (from the leaves) (Sylvestre & Arraudeau 1983). The mealybug project covers most of tropical Africa from its centre in the lowland, humid tropics of West Africa and is executed and coordinated by the Africa-wide Biological Control Programme (ABCP) of the International Institute of Tropical Agriculture (IITA), which collaborates with numerous institutions worldwide. The project's targets are a complete biological control programme including introduction of exotic beneficials and monitoring them after they are established, studying both their biology and their interactions with indigenous insects, particularly their host-finding capacity, then thoroughly assessing their impact on the host and on farmers' incomes.

Accidental introduction and spread of the cassava mealybug in Africa

In 1973 an unknown species of mealybug causing serious damage to cassava in Congo (Sylvestre 1973; Matile-Ferrero 1978) and Zaire (Hahn & Williams 1973) was reported. The new pest, reproducing parthenogenetically, spread rapidly through most of the African cassava belt which extends from 15° N to 20° S (maximum distribution shown in figure 1) (Herren *et al.* 1988). Within a few years it became the major pest on cassava. Matile-Ferrero (1977) described the insect as a new species, *Phenacoccus manihoti* (Homoptera, Pseudococcidae).

In Zaire, general CM outbreaks occurred in the Bas-Zaire, Bandundu and Shaba regions; the

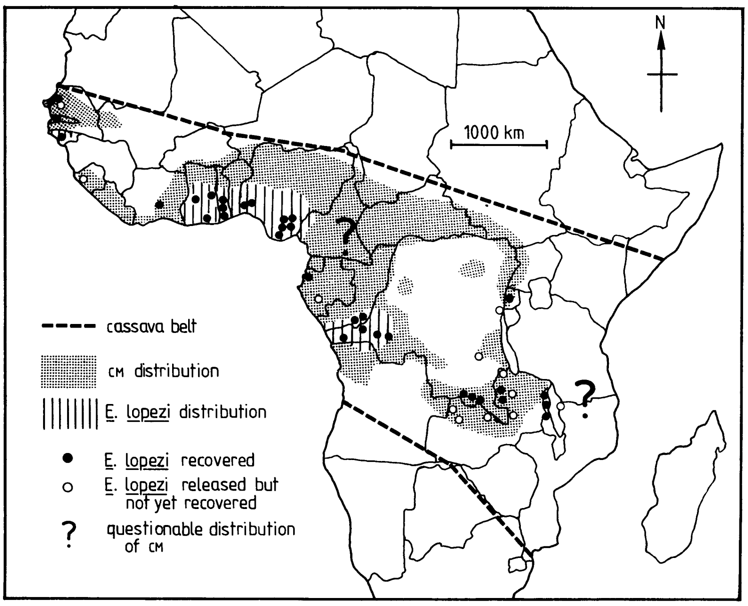

FIGURE 1. Maximum distribution of CM (shaded) and *Epidinocarsis lopezi* (stripes) in Africa showing the situation at the end of 1986.

pest gained new footholds in Senegal and Gambia in 1976, in Nigeria and Benin Republic in 1979 (Akinlosotu & Leuschner 1981), and in Sierra Leone and Malawi in 1985. From those sites, the pest spread up to 300 km per year. By the end of 1986 it had reached about 25 countries and covered about 70% of the African cassava belt. In most countries CM caused severe damage by stunting the growth points of cassava plants, sometimes totally defoliating the plants. Tuber yield losses of 84% were documented (Nwanze 1982). Weed and erosion problems, after plant growth was crippled, sometimes led to total destruction of the crops. Additionally, the poor quality of cuttings from infested plants, used as planting material, led to cassava disappearing in some regions.

Because the pest spread over large areas that are difficult to approach and mostly mixed-cropped by subsistence farmers, biological control seemed a particularly appropriate approach, needing no input by the farmers. So an effort, corresponding to the scale of the problem, was undertaken to introduce beneficial species from the original home of the CM into Africa.

EXPLORATION FOR NATURAL ENEMIES

Since cassava, the only natural host of the CM in Africa, was introduced from South America (in the 1500s) and the genera *Manihot* and *Phenacoccus* are particularly rich in species in central and northern South America, searching for beneficial insects started there. From 1977 to 1980 the Commonwealth Institute of Biological Control (CIBC) searched in the Carribean, Venezuela, the Guyanas and northeastern Brazil; then in 1980 and 1981 IITA explored the southern U.S.A., Mexico, Central America, northern Colombia and Venezuela (figure 2). A mealybug in this region was causing the same symptoms, so it was initially thought to be identical with *P. manihoti* (Bennett & Yaseen 1980). Several parasitoid species collected failed to reproduce on CM in an insectary in the Congo (Bennett & Yaseen 1980) or on another mealybug in Trinidad (Yaseen 1988). Because of small morphological differences and the bisexual nature of the mealybug on cassava in northern Latin America, it was newly described as *P. herreni* (Cox & Williams 1981).

FIGURE 2. Exploration for mealybug natural enemies by the Africa-wide Biological Control Project in latin America (thick lines represent the exploration route). Recovery of *Phenacoccus manihoti* (dots) and *P. herreni* (shaded).

P. manihoti was finally discovered in 1981 in Paraguay by the Centro Internacional de Agricultura Tropical (CIAT). Several predators and parasitoids were collected by CIBC and sent, via quarantine at CIBC London, to IITA. The shipments were approved by the Inter-African Phytosanitary Council and passed through Nigerian Plant Quarantine.

Among the parasitoids was *Epidinocarsis* (= *Apoanagyrus*) *lopezi* (Hymenoptera, Encyrtidae), described in 1963 from northern Argentina from an unidentified mealybug. Further explorations in Paraguay, Brazil and Bolivia were sponsored by the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ) under the umbrella of IITA. Between 1983 and 1986, two entomologists covered extended regions, but discovered only eight areas where CM occurred: four in Paraguay (Löhr & Varela 1987), one in Bolivia and three in Mato Grosso do Sul, Brazil (figure 2) (Löhr 1987). In all areas CM populations were low, with peaks up to 16 CM per tip in the dry season and below 1 CM per tip during the rainy season: populations so low, that trap plants loaded with CM from a laboratory culture had to be placed into fields to attract natural enemies. That led to the collection of *E. lopezi* (and several more parasitoids and predators) from Brazil and Bolivia (Löhr 1987).

Release, establishment, and dispersal of *E. lopezi*

E. lopezi (an endophagous, solitary encyrtid) was, and still is, reared at IITA on its only known host, *P. manihoti*, on potted cassava plants. First releases at IITA were made in November 1981 at the beginning of the dry season (Herren & Lema 1982) and one year later in nearby Abeokuta (figure 3) (Lema & Herren 1985). *E. lopezi* was permanently established, i.e. it was recovered after the next rainy season, which is its most difficult survival period because of low host density. By March 1983 (about 10 generations after the release) *E. lopezi* was recovered from almost all sampled fields within 100 km from where they were released, and some 170 km north of the release site in the Guinea Savannah zone. They spread more slowly south and southeast into the rain forest. At the end of 1984, three years after the first release, *E. lopezi* was found in 70% of all fields on more than 200000 km^2 in southwestern Nigeria and up to the northern limit of regular CM distribution (figure 3) (Herren *et al.* 1988). This dispersal, among the fastest recorded for microhymenoptera (Tooke 1955; De Bach & Argyriou 1967; van den Bosch *et al.* 1970), occurred mostly in traditional farming environments on local cassava varieties. We do not know which mode of transport was most important: active flight, passive transport by wind, or by man transporting cassava cuttings and leaves.

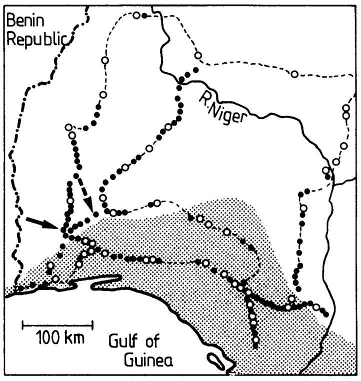

FIGURE 3. Distribution of *Epidinocarsis lopezi* in southwestern Nigeria during the survey in December 1984. The solid arrow shows the release near Abeokuta in November 1982, the broken arrow the release at IITA in November 1981; dots show where *E. lopezi* was recovered, circles show where only CM was found, and broken lines where no CM was found; shaded area represents rain forest.

On request from different governments, and in collaboration with the local agronomists and entomologists, we exported *E. lopezi* to other African countries, by the end of 1986 to more than 50 sites (confirmed distribution shown in figure 1). Although we sometimes released several thousand wasps at a site, on several occasions we used fewer than one hundred. *E. lopezi* proved to be established in almost all accessible sites the next dry season, and spread into several neighbouring countries. It is now established in 16 African countries, from north to south and west to east: Senegal, Gambia, Guinea-Bissau, Côte d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Gabon, Congo, Zaire, Angola, Rwanda, Zambia and Malawi. Recent releases in Sierra Leone and Zambia have not yet been monitored.

The area of distribution in Africa is estimated to be 750000 km^2. Approximately 1% of the area (750000 ha†) is under cassava cultivation in a wide range of ecological zones (Sudan savannah, Guinea savannah, equatorial rainforest, East African highlands). The distribution already exceeds that of any other agent introduced into Africa for biological control of insect pests, and the adaptability of *E. lopezi* to different ecological conditions is without precedent in Africa (Greathead *et al.* 1971). Few other biological control agents have been spread over similarly large areas or more countries (Schuster *et al.* 1971; Bartlett 1978; Sailer *et al.* 1984).

Currently, CM is spreading farther into the East African highlands, with unconfirmed reports from Uganda, Tanzania and Mozambique. Though maximum dispersal rates of more than 100 km per dry season for *E. lopezi* were confirmed from other countries of the humid lowlands, the wasp seems to spread more slowly under the East African highland conditions of southern Shaba province in Zaire and Zambia's Luapula valley. It appears, therefore, that the strategy (ground and aerial releases) for East Africa must be changed to more numerous and closer release sites.

RELATIONSHIP BETWEEN INDIGENOUS INSECTS AND THE INTRODUCED *E. LOPEZI*

E. lopezi is not the only parasitoid attacking CM. Other primary parasitoids and predators compete, and hyperparasitoids are direct antagonists. In South America, Löhr (1987) found five species of primary parasitoids on CM, but the five were attacked by six, sometimes very abundant, species of hyperparasitoids. Another 11 species of mostly polyphagous insect predators, mainly coccinellids, were attacked by five species of hymenopterous parasitoids.

Although cassava was introduced into Africa in the 16th century, it reached its current distribution in this century. Until recently it had a remarkably poor insect fauna. After CM was introduced and spread, the arthropod fauna of cassava rapidly increased in abundance and complexity. Many workers compiled lists of new insects: for Congo (Matile-Ferrero 1977; Fabres & Matile-Ferrero 1980), Nigeria (Akinlosotu & Leuschner 1981), and Gabon (Boussienguet 1986). After the introduction of *E. lopezi*, the fauna associated with CM were studied again in many countries, and more than 130 species were reported (Neuenschwander *et al.* 1987). Apparently, indigenous coccinellid predators adopted the newly arrived CM as an alternative host. A few encyrtids of the genus *Anagyrus*, parasitoids of other mealybugs like *Phenacoccus madeirensis* Green and *Ferrisia virgata* Cockerell, also adapted to the new pest, but not often. They, in turn, were followed by their own complex of parasitoids and hyperparasitoids. Simultaneously, insects of other species occupied shoot apexes that CM feeding had distorted. Polyphagous predators attracted to the enriched insect fauna added still more links to the developing food web. After *E. lopezi* was established, a complex of about 10 species of hyperparasitoids of *Anagyrus* spp. or of coccinellid parasitoids also shifted to this host.

In southwestern Nigeria, hyperparasitoids destroyed up to 50% of all *E. lopezi* mummies the first season *E. lopezi* was established and parasitoid populations were large on the still abundant CM hosts. Similar observations were reported from Congo (Ganga 1984), Ghana

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† 1 hectare = 10^4 m^2.

(Korang-Amoakoh *et al.* 1988), and Zaire (Hennessey & Muaka 1988); but the 50% fell to 20% when *E. lopezi* and CM populations in southwestern Nigeria declined in the next few years, indicating density dependence in hyperparasitism (Neuenschwander *et al.* 1988). The 20% are below the percentage reported from the same hyperparasitoids on the inefficient indigenous *Anagyrus* sp. on CM in Gabon (Boussienguet 1986), from similar species on *E. lopezi* in South America (Löhr 1987), or from many other successful biological control programmes (Bennett 1981). Finally, mathematical models predict more stability with, than without, hyperparasitoids (Luck *et al.* 1981; Hassell & Waage 1984). So, the *E. lopezi*-hyperparasitoid system seems unlikely to change suddenly for the worse and critically affect *E. lopezi*'s performance in the future.

Establishing *E. lopezi* also influenced the abundance and composition of indigenous CM predators. On the large CM populations that existed before the exotic parasitoid was introduced, beneficial fauna consisted almost entirely of predators (98%). But within a few months after *E. lopezi* was released, it and its hyperparasitoids accounted for 61% of all specimens collected, and 84–86% of all natural enemies early in the next two dry seasons (P. Neuenschwander & W. N. O. Hammond, unpublished results). Though predators probably indiscriminately destroy active CM containing parasitoid larvae, the high percentage of *E. lopezi* indicates that it stands up well to competition.

BIOLOGICAL STUDIES

Since the project started, the biology of *E. lopezi* had been studied for various reasons: (1) to acquire information to improve rearing, storage, and transport; (2) to understand the parasitoid's life-history and interactions with the CM host; and (3) to study the evolution of host-finding behaviour of *E. lopezi*, which seemed particularly promising for the understanding and evaluation of this and other biological control programmes. The experiments on host finding were done by the University of Leiden in collaboration with the ABCP.

Biology of the immatures

E. lopezi is a solitary, internal parasitoid with four larval instars; it passes its nymphal stage inside the mummified CM often in sheltered places between leaves. Its egg and larval morphology were described (Odebiyi & Bokonon-Ganta 1986; B. Löhr, A. M. Varela & B. Santos, unpublished results). Most *E. lopezi* develop within two weeks at 27 °C, twice as fast as their host. Optimum temperature is 27 °C, and the lower thermal threshold is 13.3 °C (from Lema & Herren 1982). Male larvae grow faster than females (B. Löhr, A. M. Varela & B. Santos, unpublished results) and become smaller adults than females (Kraaijeveld & van Alphen 1986; B. Löhr, A. M. Varela & B. Santos, unpublished results). When a second instar serves as host, development is much slower. The delay affects only larval development, particularly the second instar parasitoid larvae; nymphal development remains unaffected. Thus a small proportion of *E. lopezi* emerges only after four weeks, or one parasitoid generation later, (B. Löhr, A. M. Varela & B. Santos, unpublished results), a feature that might have survival value when host populations are small. In one third of the CM with delayed development, however, the immature parasitoids die (B. Löhr, A. M. Varela & B. Santos, unpublished results). The dead parasitoid larvae are usually encapsulated within the first two weeks of development, but they reach only about 12–16% of the total (Neuenschwander &

Sullivan 1987; B. Löhr, A. M. Varela & B. Santos, unpublished results). Living parasitoid larvae that are being encapsulated can often free themselves. Most melanization, however, is restricted to wounded tissue of the host and, in the experiments that allowed the same CM to be stung several times, the supernumerary larvae have been killed (Neuenschwander & Sullivan 1988).

Biology of the adults

After emerging, the females mate. Olfactometer experiments showed them attracted to CM-infested cassava leaves but not to CM alone. As they were also attracted to uninfested leaves from partly infested cassava plants but not to clean leaves of uninfested plants, they obviously home in on the odours (synomones) of attacked cassava to locate CM-bearing plants (Nadel & van Alphen 1986). This mechanism apparently helps the females locate very small host populations. Once they reach the plant, they are arrested by CM wax acting as contact kairomone (Langenbach & van Alphen 1986), but seem to find their hosts by chance (B. Löhr, A. M. Varela & B. Santos, unpublished results). Jerking movements of the abdomen give larger hosts a stronger defence, so attacks are concentrated more on third instar CM (Kraaijeveld & van Alphen 1986; Neuenschwander & Madojemu 1986; B. Löhr, A. M. Varela & B. Santos, unpublished results). The CM's defence is particularly strong if it has been previously attacked by a wasp, which reduces superparasitism (Iziquel 1985). Kraaijeveld & van Alphen (1986) also observed a weak rejection of already parasitized CM by a parasitoid female when testing their suitability as hosts with her antennae.

After a sting, the female parasitoid often turns and feeds on the host. Second instars are preferred, and almost as many such instars are killed as are killed by the parasitoid larva (Neuenschwander & Madojemu 1986; B. Löhr, A. M. Varela & B. Santos, unpublished results). Host-feeding is less important on older instars, and increases only slightly with increased oviposition. Eggs are rarely laid in host-fed CM (B. Santos & P. Neuenschwander, unpublished results).

The proportion of stings that leads to oviposition is highest on early fourth instars (B. Löhr & A. M. Varela, unpublished results) but varies greatly in different experiments. Younger host instars are preferred for male eggs, old ones for female eggs (Kraaijeveld & van Alphen 1986; B. Löhr & A. M. Varela, unpublished results). Mean oviposition at 25 °C was reported as high as 85 eggs per female (Iziquel 1985), but reproduction averaged 40–67 offspring per female with a maximum of 10 per day and a mean longevity of approximately 10 days. Longevity increased substantially at lower temperatures (Ganga 1984; Odebiyi & Bokonon-Ganta 1986; B. Löhr, A. M. Varela & B. Santos, unpublished results; P. Neuenschwander, unpublished results). Oviposition increased as numbers of hosts offered increased, but percentage parasitism in these experiments tended to decrease (Odebiyi & Bokonon-Ganta 1986), except at very small host populations (when it increases with an increase in host numbers) (P. Neuenschwander, unpublished results). Overall, larger females lived longer and reproduced better, which demonstrated the advantage of larger hosts for oviposition (Kraaijeveld & van Alphen 1986). The reproductive capacity of *E. lopezi* is limited, but mortality of the host also includes host-feeding and mutilation apart from larval parasitism. Moreover, 30% of once stung, second instar CM, whether they contained a parasitoid egg or not, showed retarded growth and lay an average of only 37 eggs (compared with several hundred eggs by healthy CM) (B. Löhr, A. M. Varela & B. Santos, unpublished results). Collectively the other mortalities, depending on the CM instar, can far surpass mortality through mummy formation (Neuenschwander & Madojemu 1986).

Impact assessment

Methods of evaluating the effectiveness of biological control agents have been reviewed (Hodek *et al.* 1972; Kiritani & Dempster 1973; van Lenteren 1980). To assess the efficiency of *E. lopezi* we chose three approaches.

Exclusion experiments

Physical exclusion experiments by sleeve cages were done at IITA. They demonstrated (figure 4) that, two months after artificial infestation of cassava tips, CM populations were 7.0 and 2.3 times lower on tips covered with open cages than on tips in closed cages that excluded most parasitoids. On similarly infested but uncovered tips CM populations were 24.3 and 37.5 times lower, and parasitization rates were higher (Neuenschwander *et al.* 1986). In a chemical exclusion experiment, an artificially infested field treated weekly with carbaryl had a peak CM infestation of 200 per tip because the adult parasites were killed by the insecticide. In the untreated plot, parasitism was much higher and CM populations were mostly fewer than 10 per tip (figure 5) (Neuenschwander *et al.* 1986). Those experiments were difficult, but they demonstrate the efficiency of *E. lopezi* in the field in such conditions.

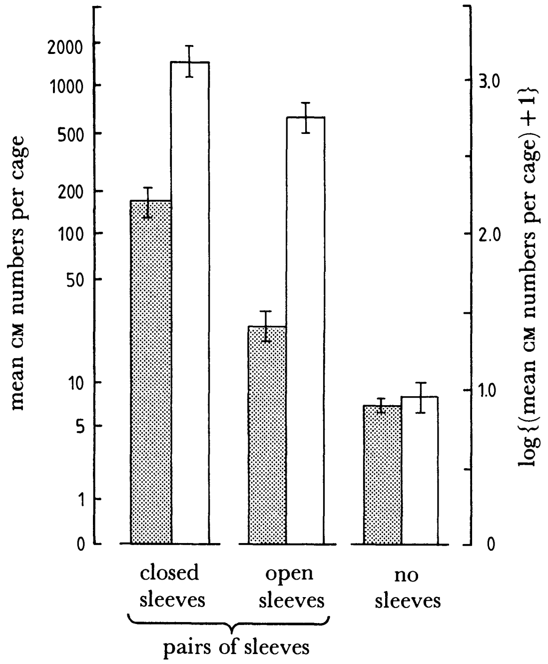

Figure 4. CM densities about two months after infestation in closed and open-sleeve cages, and from uncovered cassava tips without artificial infestation, in the second half of the 1983/84 dry season (shaded) and the first half of the 1984/85 dry season (white).

Studies on CM population dynamics

CM monitored after two early releases in southwestern Nigeria (Herren & Lema 1982; Lema *et al.* 1984) showed slight differences in the CM population dynamics in the release field and control fields (figure 6). But the so-called control fields were also invaded by *E. lopezi*, probably

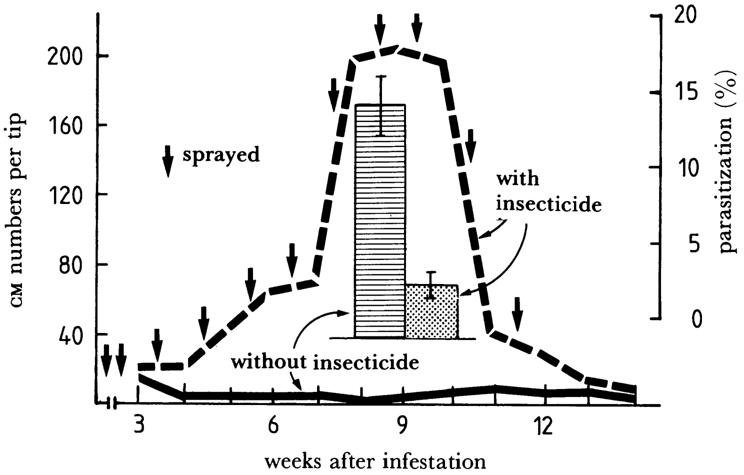

Figure 5. Cassava mealybug population development in insecticide treated (arrows, broken line) and untreated plots (solid line), together with mean parasitization rates for weeks 3–12 (± the standard error) by *Epidinocarsis lopezi*.

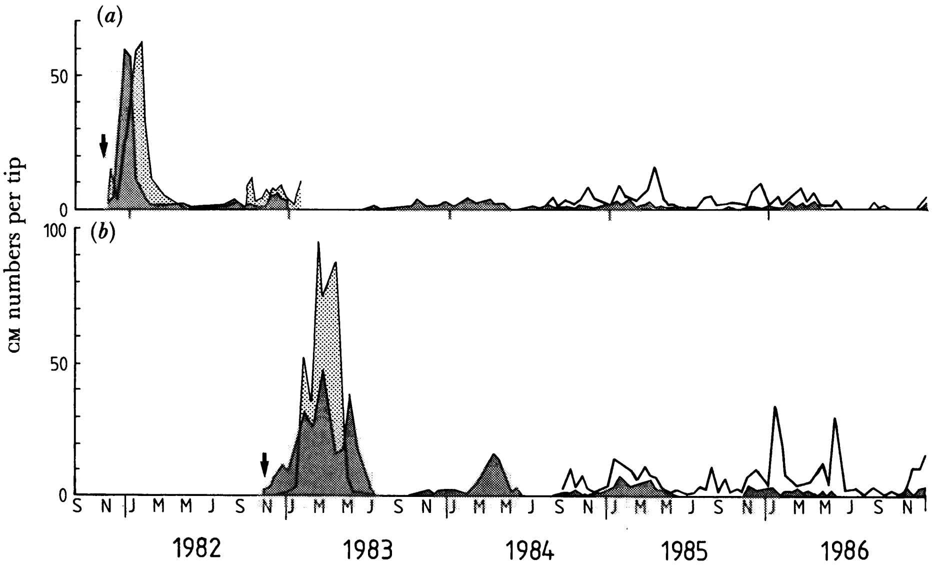

Figure 6. Population dynamics of CM on IITA improved (darker shade) and farmers' (white) varieties after the introduction of *Epidinocarsis lopezi* (arrows) in (*a*) Ibadan and (*b*) Abeokuta, in southwestern Nigeria. The original control field, with IITA improved variety, (lighter shade) was invaded by *E. lopezi* within 1–2 months. (Mean of 2–3 fields, 50 tips each, every 2 weeks.)

during the first month (see above under dispersal). Collapse of CM populations at the end of the dry season has also been reported where no parasitoids were established (Fabres 1982; Leuschner 1978).

Monitoring near Ibadan and Abeokuta continued on 12 fields, half planted with farmer's varieties, half with improved IITA variety TMS 30572 (figure 6) (Hammond *et al.* 1988). Every year CM populations peaked in the second half of the dry season. Peaks were generally higher near Abeokuta than in Ibadan's more humid area, averaging two to three times more on farmer's varieties than on the IITA disease-resistant variety, which grows more vigorously.

Occasional sharp peaks of 20–40 CM per tip were registered but, overall, CM populations remained much smaller than during the year when *E. lopezi* was released.

In surveys covering 200000 km^2 and hundreds of randomly chosen fields in southwestern Nigeria, CM damage symptoms declined from 88% of the plants at the end of the first dry season after *E. lopezi* was released to 23% the next year. By then the average CM population in 100 infested fields was only 11±1.7 CM per tip, and only 16 fields had more than 20 CM per tip (P. Neuenschwander & W. N. O. Hammond, unpublished results).

In other countries, CM often exceeding 1000 on a heavily infested cassava tip were observed in the absence of the parasitoid but seldom quantitatively assessed. In a recent CM outbreak in Malawi, CM from 13 fields averaged 554 per tip (calculations from 50 tips per field, log of the mean density equal to 2.74±0.13 standard error) (P. Neuenschwander & R. D. Markham, unpublished results). Reductions in CM populations were documented after *E. lopezi* was introduced in Ghana (Korang-Amoakoh *et al.* 1988; P. Neuenschwander & W. N. O. Hammond, unpublished results), in the Rift valley of Rwanda (B. Birandano, unpublished results), in Bas-Zaire (Hennessey & Muaka 1988), and in the Luapula valley of Zambia (C. Klinnert, unpublished results) despite considerable hyperparasitism. Important reductions in CM infestation were observed but not documented in Gambia and Guinea-Bissau. We still do not have long-term quantitative studies from areas outside southwestern Nigeria.

In southwestern Nigeria, at least, CM is no longer the severe pest insect it was before *E. lopezi* was introduced. But it still occasionally damages farmers' fields, mainly on poor soil and heavily diseased plants.

Computer simulation model

The systems-analysis component of ABCP, executed in collaboration with the University of California, Berkeley, and the Swiss Federal Institute of Technology, Zürich, aims at linking previously mentioned results. It examines the dynamics of the various components of the cassava agro-ecosystem, estimates CM effects on tuber yields and effects of natural enemies, including *E. lopezi*, on CM dynamics. Gutierrez *et al.* (1988) evaluated effects of abiotic factors (temperature, rainfall, solar radiation, soil nitrogen and water) on the population dynamics and interactions of the different species. A model by Gutierrez & Baumgärtner (1984*a b*) and Gutierrez *et al.* (1987) was modified to simulate the population dynamics of all species. The model is driven by observed weather and simulates the number and mass dynamics of each species much like a life-table analysis. It is based on the idea that each population must acquire resources, so acquisition and demand rates determine whether the population grows or declines.

Many, but not all, of the parameters for *E. lopezi* listed in the biology section and obtained mostly in the laboratory, were superimposed on cassava and mealybug data (Nwanze *et al.* 1979; Fabres & Boussienguet 1981; Fabres & Le Rü 1986; Le Rü & Fabres 1986; Le Rü & Papierok 1986; Schulthess *et al.* 1988) and incorporated in the first simulations of the computer model (Gutierrez *et al.* 1987). Figure 7, which includes also unpublished results by A. P. Gutierrez, shows the simulated cassava yield loss due to CM during the 1983/84 season at Ibadan by introducing CM on day 50 (which gives highest loss) and reduction in yield losses due to *E. lopezi* assuming two search parameters. Though the model needs some refinement, the population curves it describes correspond well with those found (figure 6), and it predicts the impact of *E. lopezi*. Further simulations that included the effect of coccinellid predators show

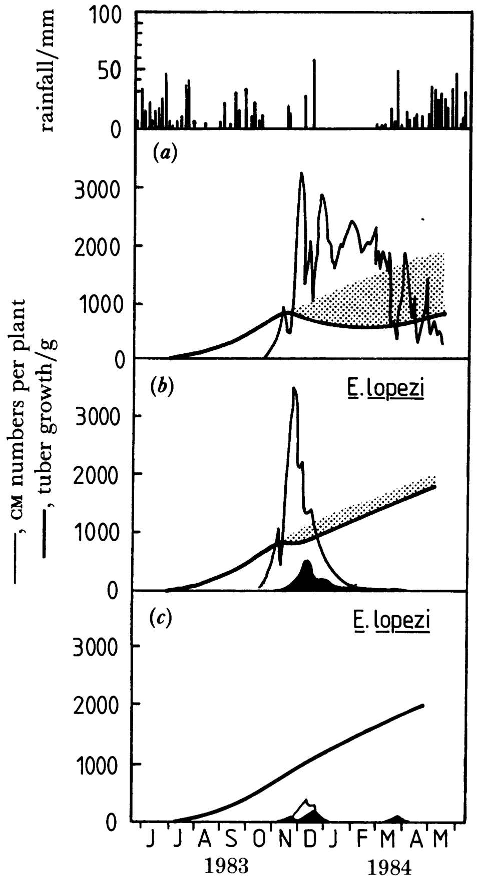

FIGURE 7. Simulated cassava tuber growth (in grams per plant) (thick line) during the 1983/84 season at Ibadan with CM populations per plant (*a*) without natural enemies (shaded area represents yield loss), (*b*) with *E. lopezi* (parasitized CM shown in black) with medium search rate assumed, and (*c*) with *E. lopezi* with a high search rate assumed.

that, contrary to the reports by Iziquel (1985) and Odebiyi & Bokonon-Ganta (1986), the introduced parasitoid is responsible for the observed small CM populations. Crop losses are now being measured directly in Ghana and Côte d'Ivoire by comparing yields in areas where the parasitoid has been established during the full or part of the growing season, or not yet. The growth characteristics of the plant, abiotic and biotic factors, farmers' opinions, and market situations are all incorporated in the simulation model.

CONCLUSION

Results so far show that *E. lopezi*, introduced from a few localities in South America, established very successfully in several ecological zones of Africa. From the release sites it spread rapidly, at least in the lowland, humid tropics. That it displaced competing, indigenous predators attests to its efficiency. Hyperparasitism was less on the reduced parasitoid and CM populations, which reached equilibrium during the second dry season after *E. lopezi* was released. Exclusion experiments, population dynamics studies, and preliminary results of a computer-simulation model show that *E. lopezi* is an efficient biological control agent across several, but perhaps not all, ecological zones of the African cassava belt. Although *E. lopezi* cannot substantially lower large host populations, it can maintain the small CM populations that exist after the rainy season. Because it homes in on infested host plants rather than directly on CM it has a good host-finding capability. The economic impact of *E. lopezi* is being investigated now as the last major step in documenting this biological control programme.

IITA's ABCP gratefully acknowledges financial support of the International Fund for Agricultural Development, Rome; the International Development Research Centre, Canada, and governmental donor agencies of Austria, Switzerland, West Germany, and, since 1984–5, those of Denmark, Italy, The Netherlands, as well as the Food and Agriculture Organization of the United Nations, and since 1986 those of Norway. Work in Zaire and Guinea-Bissau was partly supported by the United States Agency for International Development. We thank all agencies mentioned in the text and, particularly, our collaborators in the field for their help. We also thank J. van Alphen (Leiden), L. Brandner, and L. E. N. Jackai (IITA) for reviewing the manuscript.

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Discussion

I. **Harpaz** (*Department of Entomology, Hebrew University of Jerusalem, Israel*). My question relates to the hyperparasites mentioned in the paper. Have these been identified, and if so, then has it been established whether these are indigenous African species that had adapted themselves to the newly introduced parasite, or that they were accidentally introduced from South America together with the primary parasite? The latter possibility seems most unlikely because the introduced material went through quarantine in London, as stated by Dr Neuenschwander.

P. **Neuenschwander**. Professor Harpaz is right; all hyperparasitoids of *E. lopezi* in Africa that we found are indigenous African species. The commoner ones, in fact, had already been reared previously from mummies of other mealybugs. About 10 species have been recorded up to now and identified by the British Museum (Natural History), belonging to six genera but, where identified to that level, they are different species from those in South America.

D. **Badulescu** (*Faculty of Agriculture, University of Reading, U.K.*). Dr Neuenschwander said one of the goals of these kinds of programme is to leave trained teams to tackle similar problems in future; it seems to me that these programmes are very costly. Do you think that without much support from western European and American institutions such projects can be successfully repeated, such are the financial constraints in the Third World?

P. **Neuenschwander**. Yes, if the political will is there, but I hope the donors will continue to provide finance, because assisting in the execution of biological control programmes is a particularly good approach to achieve long-term solutions that do not make these countries even more dependent on the industrialized countries. I agree, biological control programmes are expensive to implement, because they require high quality research. Classical biological control programmes derive their benefits not from cheap initial implementation but from accruing benefits once they are successful.

A. E. **Akingbohungbe** (*Department of Plant Science, University of Ife, Nigeria*). Compared with the other African countries, it would appear that the mealybug outbreak in Nigeria is less severe. This I would like to think could be attributed to several factors. Firstly, the rainfall pattern within the past five years had been much better than in the late 1970s when CM was first found in the country; such rainfall removes the drought stress that helps epizootic development of CM. Secondly, within the context of a national control programme, an integrated pest management package involving date of planting, insecticide disinfestation of planting material and appropriate fertilizer application was formulated and has been implemented. Thirdly, there has been considerable shift in planting of improved, more tolerant cultivars. How do we put all of these together and account for their joint effects in assessing the efficiency of *E. lopezi* releases?

P. **Neuenschwander**. Without belittling other IPM components, I think we showed that *E. lopezi* was the key factor in maintaining small CM populations in southwestern Nigeria. The influence of planting time and cultivars can be tested in the simulation model as it is being developed. I would like to add that other countries, where *E. lopezi* was not established, continued to experience severe CM problems despite vastly increased rainfall compared with the early 1980s.