Impact assessment of the biological control of the cassava mealybug, Phenacoccus manihoti Matile-Ferrero (Hemiptera: Pseudococcidae), by the introduced parasitoid Epidinocarsis lopezi (De Santis) (Hymenoptera: Encyrtidae)

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Impact assessment of the biological control of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae), by the introduced parasitoid *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae)

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Abstract

The impact of *Phenacoccus manihoti* Matile-Ferrero on growth and tuber yield of cassava, and the results of its biological control by the exotic parasitoid *Epidinocarsis lopezi* (De Santis) were investigated in a survey of 60 farmers' fields in Ghana and Ivory Coast over an area of 180 000 km^2 of the savanna and forest ecosystems. Twenty-nine variables associated with plant growth, agronomic and environmental factors, and insect populations were recorded. Densities of *P. manihoti* were closely correlated with stunting of the cassava shoot tips and, less so, with the rate of stunting early in the growing season. With increasing mealybug infestations, average harvest indices declined and populations of *E. lopezi* and of indigenous coccinellids increased, but parasitoids were found at lower host levels than were predators. The length of time *E. lopezi* had been present in an area was the most important factor influencing mealybug densities. Thus, *P. manihoti* populations were significantly lower where *E. lopezi* had been present for more than half the planting season than in areas where *E. lopezi* was lacking or had been only recently introduced. A significant proportion of the farmers in the savanna zone, where *P. manihoti* populations were much higher than in the forest zone, had observed this decline due to *E. lopezi*. Tuber yield losses due to *P. manihoti* in the absence of *E. lopezi* were tentatively estimated at 463 g/plant in the savanna zone. No significant effect was found in the forest region. When *E. lopezi* was present, average *P. manihoti* damage scores were reduced significantly, both in the savanna and forest regions. The increase in yields was 228 g/plant or about 2·48 t/ha in the savanna region.

Introduction

In the early 1970s, the mealybug *Phenacoccus manihoti* Matile-Ferrero was accidentally introduced from South America to Africa where it spread and became the major cassava pest (Matile-Ferrero, 1977; Herren 1981; Fabres & Boussienguet, 1981; Nwanze, 1982; Herren & Lema, 1983). Tuber losses due to it have been measured in experimental fields (Nwanze, 1982; Schulthess, 1987) and estimated for different regions of Africa by the International Institute of Tropical Agriculture (IITA) (unpubl. results), FAO (1985) and Walker *et al.* (1985), but these estimates are controversial.

In a large-scale biological control project against this pest, undertaken by IITA's Biological Control Programme in collaboration with numerous international agencies (Herren, 1987), the solitary, host-specific encyrtid parasitoid *Epidinocarsis lopezi* (De Santis) was imported from South America and first released in Nigeria in 1981 (Herren & Lema, 1982). By July 1988, it had been successfully established in 19 African countries and had spread over an area of over 1·5 million km^2 (Herren *et al.*, 1987; Neuenschwander & Herren, 1988 & unpubl. results). Regular monitoring in two areas in Nigeria showed that *P. manihoti* populations declined after the releases of the exotic parasitoid and remained low (Hammond *et al.*, 1987). Large-scale surveys in south-western Nigeria (Neuenschwander & Hammond, 1988) and exclusion experiments (Neuenschwander *et al.*, 1986) also documented the efficiency of *E. lopezi* in preventing *P. manihoti* outbreaks in most fields. A computer simulation model for the growth of cassava (Gutierrez *et al.*, 1987; 1988*a*, *b*) predicted that *E. lopezi* is capable of preventing tuber yield losses, while the impact of the native coccinellids (Fabres & Matile-Ferrero, 1980; Boussienguet, 1986; Neuenschwander *et al.*, 1987) in suppressing *P. manihoti* populations is small. Yield and *P. manihoti* population data from a wide geographical area were, however, lacking.

The two objectives of the present survey therefore were to assess the impact of *P. manihoti* on tuber yields at the farm level over a wide range of conditions and to measure the effects of the introduction of *E. lopezi* on *P. manihoti* and tuber yield. Ecological zones in Ghana and Ivory Coast where *E. lopezi* was well established were contrasted with areas where *E. lopezi* was not present at the time of the survey. A description of individual biotic factors is followed by a multiple regression analysis assessing the relative importance of biotic and abiotic factors, and summed up by a general production function for cassava tubers.

Materials and methods

Survey area and choice of fields

All field data were collected during a 5000-km-long survey through 180 000 km^2 of the most important cassava production centres in Ghana and parts of Ivory Coast during February–March 1986 (Fig. 1). Sixty fields were sampled at fixed 10-km intervals (1-km intervals in two areas) in the areas indicated in Fig. 1 through a wide range of ecological conditions (from 200 to more than 1800 mm rainfall). Individual fields were sampled only if the owner came to the field to be interviewed. Cassava fields with crops less than nine months of age or severely infested with weeds were not included. Most fields were *ca* 0·1 ha in size.

Survey variables

Twenty-nine factors concerning plant growth, agronomic and environmental character-

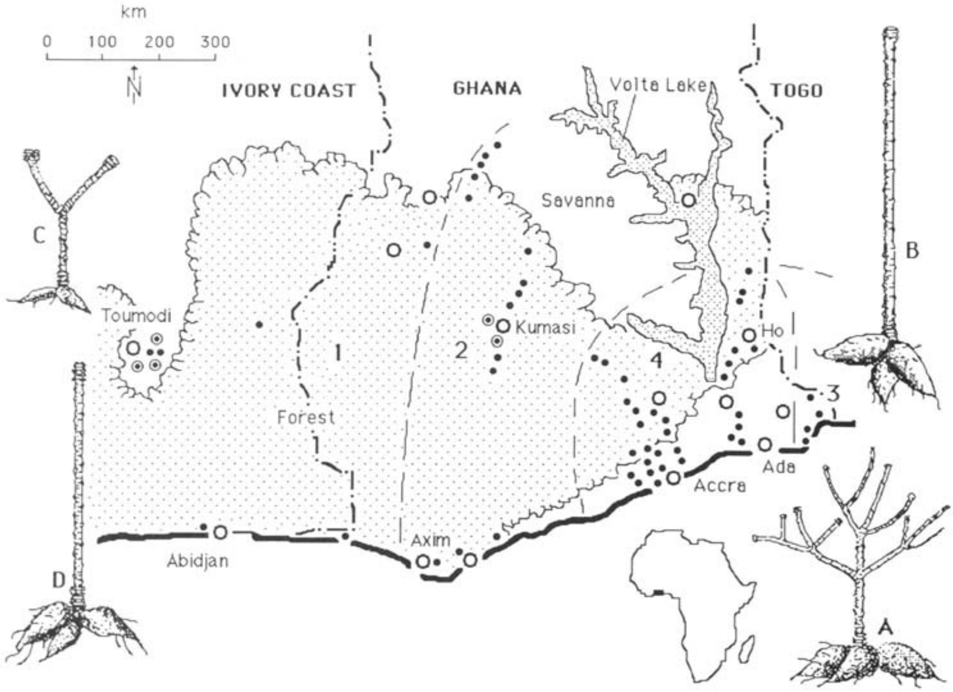

Fig. 1.—Map of survey area in Ghana and Ivory Coast with rain forest-transition zone (stippled) and approximate limits of distribution of *Epidinocarsis lopezi* (broken lines) separating Zones 1–4 (parameter 29, Appendix), together with schematic cassava plants showing mealybug damage typical for the area. (*A*, Savanna with *E. lopezi*, branching varieties with little stunting; *B*, forest with *E. lopezi*, non-branching varieties with almost no stunting; *C*, savanna without *E. lopezi*, branching varieties with high degree of stunting; *D*, forest without *E. lopezi*, non-branching varieties with some stunting; ●, surveyed fields with *Phenacoccus manihoti* uncommon; ◉, surveyed fields with relatively high *P. manihoti* densities (>10/tip); ○, weather stations.) Inset: Africa, with survey area black.

istics of the field, as well as abundance of *P. manihoti*, its natural enemies and other cassava pests were measured or scored (see Appendix).

Plant factors.—To characterize plant growth, ten plants were chosen in each field at equal intervals along a straight line across the entire field in the direction of an arbitrarily chosen tree on the horizon. Plants with mechanical injuries or with roots damaged by rodents were not selected.

The total number of nodes was calculated by counting nodes along a single branching path which was assumed representative of the others. The path was chosen starting at the bottom, with subsequent choices alternating between branches in the direction of the sampler and in the opposite direction. Along this branching path, the numbers of healthy and stunted internodes were assessed separately for each branching level, and the total number of branches at each level was registered. The nodes on lateral shoots were counted separately. The plants had up to seven branching levels with two to three branches at eacn branching point.

The plants were harvested and the number and the fresh weights of all leaves (with petioles) and tubers were determined. Fresh green stems, the wooden grey parts of the stems and the planting stick used for vegetative propagation were also weighed. Later analyses showed no benefit in separating green and grey stem weights, hence the two values were added to give the total stem weight per plant.

Agronomic and environmental factors.—Three groups of varieties with different growth forms were distinguished: *A*, varieties grown mainly in the savanna zones, which have profuse branching and are usually harvested after 9–10 months, *B*, varieties which are intermediate in character, and *C*, rain forest varieties with only one or two branching levels, which are harvested after about 15 months. At the time of the survey, plants were approximately 9(*A*), 12(*B*) or 15(*C*) months old, and harvesting of all varieties had begun.

The plant density was assessed by measuring mean distances between plants, damaged or dead plants which would not contribute to the yield not being counted. The degree of intercropping was estimated from residues of harvested crops (maize or cowpea, as well as plantain and cocoyam in the forest zone) and from farmer interviews.

Weediness was classified between fields with only single herbaceous weeds (group 1) and those with a dense carpet of herbaceous weeds up to 30 cm high (group 3). Fields with dense high grasses or with numerous low tree weeds were rejected.

Organic matter of the top soil was classed between rich mulch (high, group 1) and uncovered sand, loam, clay or gravel (low, group 3), and the moisture-holding capacity of the soil was ranked according to expert opinion.

Data on total rainfall during the 1985 planting season were obtained for 12 weather stations in southern Ghana from the Meteorological Services Department at Legon and for two weather stations in Ivory Coast (Fig. 1). Data from the nearest weather station in the same ecological zone were assigned to each field. Rainfall data were also obtained for 1979 to 1985 in order to distinguish drought years and those with good rainfall.

Finally, the area surrounding each field was classified on the basis of vegetation to one of four ecological zones: rain forest with a closed canopy of high trees; transition zone where the forest canopy in patches is opened up to give way to elephant grass (*Pennisetum purpureum*); Guinea savanna with patchy open forest with understorey grasses, predominantly Guinea grass (*Panicum maximum*); and coastal savanna with open grassland and a few scattered trees, often baobab (*Adansonia digitata*). The vegetation in the coastal savanna in Ghana is similar to that of the Sudan savanna further north.

Pest insects, mites and their antagonists.—The presence of and damage by the variegated grasshopper, *Zonocerus variegatus* (L.), and the cassava green mite, *Mononychellus tanajoa* (Bondar), were scored on a graded scale, as described in the Appendix.

Population density of *Phenacoccus manihoti* in each field was estimated from inspection of 50 plant terminals. These tips were chosen at equal intervals along several lines across the field in the direction of randomly chosen trees on the horizon. In the field, *P. manihoti* numbers per tip were estimated as falling into one of the following categories: 0, 1–9, 10–99, 100–999 and ≥1000. The $\log(x+1)$-transformed upper limits of mealybugs in each category are 0, 1, 2, 3 and 4, and the mean numbers in each category are assumed to be 0, 0·5, 1·5, 2·5 and 3·5, respectively. From the latter, the means per 50 shoot tips were calculated. Such transformation is justified by the high degree of aggregation of *P. manihoti* (Schulthess *et al.*, 1989).

The same shoot tips were also scored according to the shoot tip damage scale described by K. F. Nwanze in PRONAM (1978): 1 = no damage, 2 = slight curling of leaf margins, 3 = slight bunching of the tip, 4 = pronounced distortion of the tip (=bunch top), 5 = severe defoliation.

Because the number of predators and parasitoids could not be counted under the conditions of the survey, the proportion of shoot tips containing ants, coccinellids (larvae and adults), *E. lopezi* (mummies and adults) and its hyperparasitoids was used as a surrogate for their numbers. This proportion is known to increase as the absolute number of organisms increases (Wilson & Room, 1983; Schulthess *et al.*, 1989).

Fields were classified for the time *E. lopezi* had already been present in the area, according to information from previous surveys in Ghana (Korang-Amoakoh *et al.*, 1987; IITA, unpublished data) and Togo (Herren *et al.*, 1987). In areas where *E. lopezi* had not yet been recovered, samples of ten infested bunch tops were taken per field and held in sealed paper bags in the laboratory for three weeks for parasitoid and predator emergence.

Farmers' interviews.—The farmers were interviewed in their own language about the pest problems during the last seven years and about their opinions concerning the causes for changes in the severity of pests, particularly *P. manihoti*. Care was taken to phrase questions so as not to bias the answers. Farmers who had started their farms recently were not polled. If an owner had more than one field in the survey, his opinion was counted only once. Overall, 50 of the interviewed farmers expressed views about cassava pest problems.

Statistical analysis

All analyses were done with fields as units. Variables characterizing individual plants were summarized as means of ten plants per field and examined in a correlation matrix.

For the description of some well-known biological relationships, simple regressions were calculated. To specify the independent variable X or the dependent variable Y, the ordinal number from the Appendix was used as a subscript. Means based on different numbers of fields with unequal variances were compared using adjusted t' values. Correlation coefficients for quadratic equations were calculated using provisional means. If not stated otherwise, regressions concerned all 60 fields.

In order to determine the relative importance of different factors, multiple linear regression analyses were done. To predict separately yield, stunting and *P. manihoti* density, only those variables and interactions which were biologically relevant were included. The analyses followed the model:

$$Y_i = a + \Sigma b_i X_{ij} + \Sigma c_n X_{ij} X_{il} + U_i \qquad (1)$$

where i is the field subscript, j and l are the subscripts of different variables, n is the set of $j \times l$ interactions and U_i is the unknown error term.

Some data were grouped as follows and treated as dummy variables: *E. lopezi* present in the area either before or after the midpoint of the current cassava season; the two major ecological zones, namely the forest-transition zone and the savanna zones. Soil types (X_{19}) were also treated as dummy variables, but the contribution to R^2 was so low that this parameter was excluded from the model. All statistical tests were judged at $P = 0{\cdot}05$, and significant results in the text are indicated with an asterisk.

Results

Description of selected biotic variables

Plant growth variables.—The complete correlation matrix concerning plant growth

TABLE I. *Correlation matrix for plant growth parameters from a survey of 60 fields in Ghana and Ivory Coast in February–March 1986*

	Parameter	1	2	3	4	5	6	7	8	9
1	Tuber yield	1·00								
2	No. of tubers	0·71*	1·00							
3	Wt of planting stick	0·64*	0·63*	1·00						
4	No. of leaves	0·52*	0·49*	0·52*	1·00					
5	Wt of leaves	0·46*	0·45*	0·55*	0·81*	1·00				
6	Wt of stems	0·66*	0·70*	0·83*	0·47*	0·54*	1·00			
7	No. of nodes	0·68*	0·55*	0·54*	0·75*	0·51*	0·57*	1·00		
8	No. of shoot nodes	0·33*	0·26*	0·38*	0·62*	0·45*	0·27*	0·49*	1·00	
9	No. of branching levels	0·32*	0·34*	0·31*	0·55*	0·19	0·26*	0·65*	0·37*	1·00

For description of parameters see Appendix.
*r values $\geq 0{\cdot}26$ have $P < 0{\cdot}05$.

parameters is given in Table I. The numbers and/or masses of tubers, leaves and stems were often only weakly correlated with each other, demonstrating the degree to which plant growth is allometric. The weakness of this linear relationship across all 60 fields was particularly evident for the number of branching levels, which varies between varieties, and the number of lateral shoots, which are a reaction to previous defoliation.

Groups of cassava varieties were characterized generally by branching architecture, the time of tuber growth to harvest and the ecological zone in which they are grown. Given the variation introduced by other factors, the mean weights of tubers were not significantly different among varieties (nine-month variety (A) used in the savanna zones: 897 g, n = 27; 12-month variety (B): 1101 g, n = 10; 15-month variety (C) used in the forest zones: 1034 g, n = 23; F = 0·67). Averages in individual fields varied between 235 g/plant in the savanna zone of Ivory Coast and 2379 g/plant in the forest zone in Ghana.

The total number of nodes (X_7) predicted tuber yield (Y_1) for all varieties with an r^2 of 0·464* ($Y_1 = 206{\cdot}4 + 1{\cdot}885\,X_7$). For stem weight ($X_6$), the corresponding regression equation was $Y_1 = 368{\cdot}7 + 0{\cdot}500\,X_6$ (r^2 = 0·439*). Average stem weights varied between 331 and 3122 g, but yields stopped increasing when stem weights were above 1750 g.

The ratios between tuber weights and total weights of the plants, i.e. the mean harvest indices (HI) and standard errors were 0·431 ± 0·017 for variety A, 0·373 ± 0·029 for variety B, and 0·331 ± 0·018 for variety C. The only significant difference in the harvest indices was between variety A and variety C (t' = 4·06*).

Mealybug variables.—There was a very close correlation (Fig. 2) between *P. manihoti* densities (X_{25}) and the shoot tip damage (stunting) score (Y_{24}): $Y_{24} = 1{\cdot}136 + 2{\cdot}457\,X_{25} - 0{\cdot}475\,X_{25}^2$ (r^2=0·832). Shoot tip damage itself was only weakly correlated with the earlier stunting observed at the first branching level (X_{11}): $Y_{24} = 1{\cdot}652 + 0{\cdot}033X_{11}$ (r^2 = 0·205*). Early *P. manihoti* damage was evident on 16·8% of the nodes in areas where *E. lopezi* had been absent during the first half of the growing season, but only on 3·3% of the nodes in areas where *E. lopezi* had been present longer (t = 3·30*, comparison with arc sin $\sqrt{p}$ transformed values).

Plants attacked by *P. manihoti* were not only smaller, they also had a lower harvest index (proportion of tuber to total weight). In the savanna zones, harvest indices (Y_{HI}) declined from 0·491 on uninfested plants to 0·299 on plants infested with 100 mealybugs per tip ($Y_{HI} = 0{\cdot}491 - 0{\cdot}096\,X_{25}$; n = 24, r^2 = 0·400*) (Fig. 3). In the forest zones, the HI data from all 8 fields with *P. manihoti* log(x+1) densities above 0·5 fitted the curve obtained from savanna fields very well (+ symbol in Fig. 3) (r^2 = 0·608*), while harvest indices at lowest *P. manihoti* infestation levels varied widely (not shown in Fig. 3).

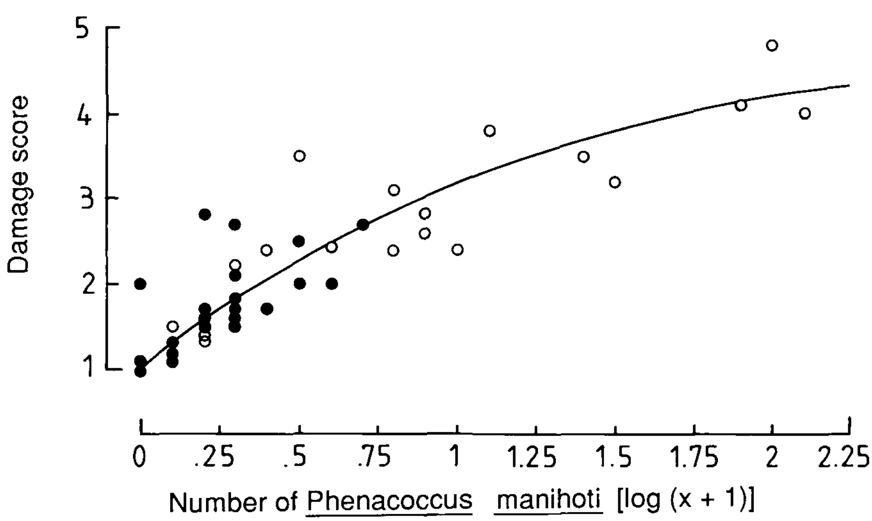

Fig. 2.—Damage score of cassava shoot tips (parameter 24, Appendix and text) as a function of present *Phenacoccus manihoti* density in 60 fields in Ghana and Ivory Coast in February–March 1986. (○, Fields in areas where *Epidinocarsis lopezi* was lacking or had been introduced only recently; ●, fields in areas where *E. lopezi* had been present since the first half of the cropping season.

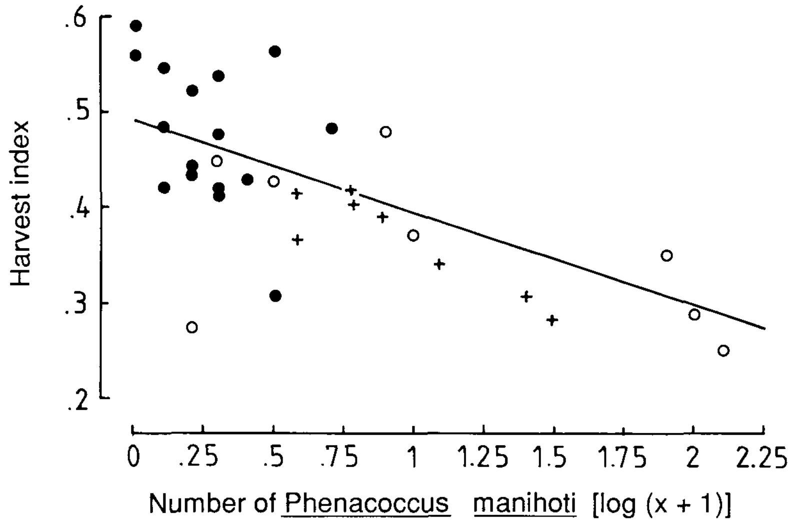

Fig. 3.—Harvest index (ratio of tuber yield to total weight) at different densities of *Phenacoccus manihoti* in 24 fields in the savanna zones of Ghana and Ivory Coast in February–March 1987. (○, Fields in areas where *Epidinocarsis lopezi* was lacking or had been introduced only recently; ●, fields in areas where *E. lopezi* had been present since the first half of the cropping season; +, fields from the forest zones with *P. manihoti* densities above 0·5 not included in regression calculation.)

Natural enemies variables.—In all fields from areas where *E. lopezi* had become established, the proportion of shoot tips containing this parasitoid (Y_{28}) was related to the *P. manihoti* damage score as follows: $Y_{28} = -7{\cdot}55 + 7{\cdot}887\ X_{24}$ ($r^2 = 0{\cdot}625^*$, $n = 51$). This straight line starts at damage score 1, i.e. no damage by *P. manihoti*, suggesting that *E. lopezi* was present even at the lowest host densities. By contrast, coccinellid numbers (Y_{27}) increased much less with increasing damage scores ($Y_{27} = -6{\cdot}24 + 4{\cdot}851\ X_{24}$; $n = 21$ fields where coccinellids were found) and the r^2 was much lower ($0{\cdot}250^*$). In fact, with the exception of one shoot tip, no coccinellids were found at mean damage scores ≤ 2. When damage scores were substituted by $\log(x+1)$ counts, the results were similar and the r^2 marginally higher. Fig. 4 summarizes these relationships and covers all fields which had either *E. lopezi* or predators or both. In most fields, *E. lopezi* was more abundant than coccinellids and predators did not occur before parasitoids had occupied on average 10% of all shoot tips.

Multiple regression analysis and production function

The analysis was divided into two steps. In the first, the effect of biotic and abiotic factors were examined, and the contribution of *P. manihoti* to yield losses was estimated. In the second step, the effects of various factors on *P. manihoti* were analysed.

The effects of abiotic and biotic factors on yield.—The results of a multiple regression of yield as a function of the variables that were judged to be important are presented in Table II. The selection of the variables included in the model was based first on biological considerations and second on some preliminary test runs. Factors that were allometrically related to tube yield (e.g. stem weight) were not included in the analysis.

A major factor in the analysis is the different behaviour of the model between the two ecological regions. The insignificant effect of the rainfall variable can be attributed to its strong correlation with the regional variable. The effect of the region (X_{21}) is the additional

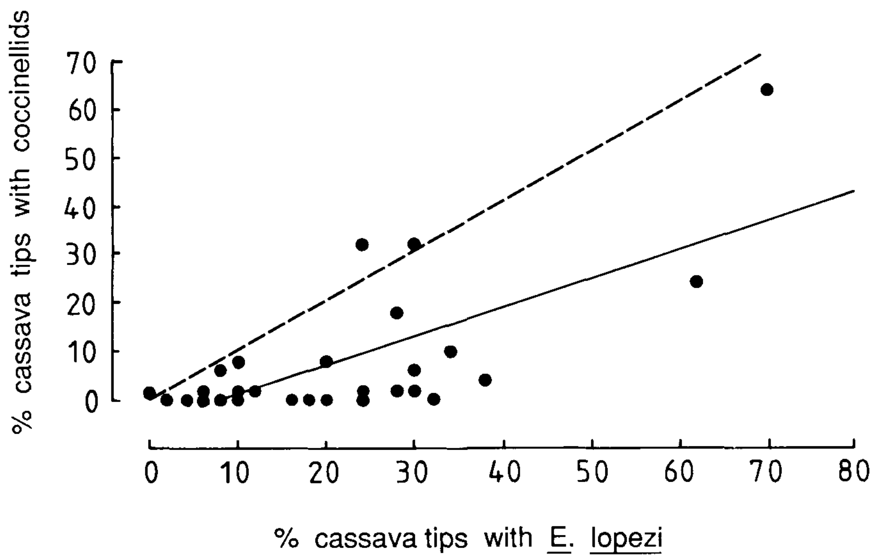

Fig. 4.—Percentages of cassava shoot tips with *Epidinocarsis lopezi* and coccinellids, based on 50 shoot tips per field in Ghana and Ivory Coast in February–March 1986. Fields which had neither *E. lopezi* nor coccinellids were excluded. (– – –, equal proportions of tips with *E. lopezi* and coccinellids.)

TABLE II. *Multiple regression and analysis of variance for predicting tuber yield from survey data from 60 fields in Ghana and Ivory Coast in February–March 1986*

Variable		Regression statistics b_j	t	Mean	±SE
Dependent variable					
Y_1	Tuber yield			982·65	541·40
Independent variables					
$X_{(21)}^{+}$	Savanna zone	314·454	0·77	0·400	0·494
X_{20}	Rainfall	−0·092	0·45	1187·90	400·49
$X_{3,20}$	Planting stick × rain	0·00172	4·99*	0·33 × 10^6	0·21 × 10^6
$X_{20,21}$	Ecological zone × rain	0·758	2·03*	334·5	438·7
X_{18}	Organic matter	151·662	2·11*	1·80	0·61
X_{17}	Weeds	105·119	1·96	1·75	0·84
X_{24}	*P. manihoti* damage score	−151·600	1·52	1·96	0·95
$X_{24,21}$	*P. manihoti* score × ecol. zone	−237·647	2·30*	0·905	1·32
$X_{24,7}$	*P. manihoti* score × nodes	0·566	3·88*	766·4	410·1

$\sqrt{MSE}$ = 312·31695 with 50 degrees of freedom.
Explained variance R^2 = 0·718.
Intercept = −245·609 with t = 0·72.

b_j = regression coefficient.
SE = standard error.
MSE = mean square error.
+Treated as dummy variable.
*$P<0{\cdot}05$.

yield (δY_1) in the savanna region as predicted by the model. This can be read from Table II as:

$$\delta Y_1/\delta X_{21} = 314{\cdot}5 + 0{\cdot}758\ X_{20} - 237{\cdot}647\ X_{24} \quad (2)$$

The difference in the yield between the two regions, predicted by the model for the same average value of 1188 mm annual rainfall (X_{20}) and 1·96 units on the *P. manihoti* scoring scale (X_{24}), is very high, namely 750 g/plant. Its 95% confidence interval, calculated from the variance/covariance matrix of the coefficients, is ±311 g.

Larger planting sticks contributed significantly to higher yield, provided sufficient rain was available ($X_{3,20}$). More organic matter in the soil significantly improved yields (X_{18}), and such soils were also more likely to be weedy. Thus, while truly weedy fields with reduced yields were excluded from the survey, higher weediness was positively linked with higher yields (X_{17}).

If the analysis was stopped at this point, the total explained variance was 0·555. Inclusion of other agronomic, environmental, or biotic factors than those used in Table II contributed only negligibly to the R^2. However, when variables concerning the mealybug infestation were added, this value jumped to 0·718, indicating the importance of *P. manihoti* in determining the yield.

This high total R^2 was achieved with the mean shoot tip damage score (X_{24}) and two significant interactions ($X_{24,21}$ and $X_{24,7}$). The first one indicates that *P. manihoti* damage influenced yield mainly in the savanna zone. Average yield losses per unit increase on the scoring scale were 151 g/plant in the forest and 388 g/plant (i.e. 151 + 237 g) in the savanna. The second interaction indicates that yield loss per scoring unit was reduced by 0·57 g for each additional node, suggesting that a unit increase on the scoring scale causes less yield reduction in a bigger plant.

When *P. manihoti* population density expressed as log $(x+1)$ (X_{25}) was used instead of the scoring scale, the R^2 was only 0·662. But the t values, though slightly lower, indicated the same priorities of factors responsible for yield as in the analysis with damage scores.

The following change in yield due to a unit increase in *P. manihoti* score is derived from Table II:

$$\delta Y_1/X_{24} = -151{\cdot}60 - 237{\cdot}65\, X_{21} + 0{\cdot}566\, X_7 \tag{3}$$

$$\delta Y_1/X_{24} = \begin{cases} \text{Forest} \quad 90{\cdot}62 \quad \mathrm{SE} = 79{\cdot}85\ t = 1{\cdot}13\ (\text{n.s.}) \\ \text{Savanna} \quad -147{\cdot}02 \quad \mathrm{SE} = 70{\cdot}87\ t = 2{\cdot}07\ (P<0{\cdot}06) \end{cases}$$

These values were calculated from Equation 3 by replacing X_7 by the corresponding average number of nodes in the forest and savanna zones, respectively. Given an average yield in the savanna zone of 1000 g/plant and an average *P. manihoti* score of 2·26, these results imply that the average yield loss in this region due to *P. manihoti* damage (across all fields, of which some had no *E. lopezi* and some were in the zone of *E. lopezi* distribution) was 147 g × 2·26 = 332 g/plant. The *P. manihoti* damage in the savanna zone was much higher in the eight fields where *E. lopezi* was absent, namely 3·15 on the scoring scale, corresponding to a yield loss of 463 g/plant. By comparison, in the 16 fields where *E. lopezi* had been present for a long time, the average *P. manihoti* score was only 1·80 and the average yield loss 265 g/plant. The resulting difference, which is attributable mostly to the presence of *E. lopezi*, was 1·35 units on the scoring scale or 199 g/plant. In this type of calculation, the estimate of *P. manihoti* impact without *E. lopezi* was, however, based on only a few fields in each category and has to be viewed with caution. A better way to calculate the average yield difference between fields with and without *E. lopezi*, though not the absolute yield levels, is applied in the next section.

The effects of abiotic factors and natural enemies on mealybug populations.—The multiple regression analysis (Table III) summarizes the variables which best predict the *P. manihoti* damage on shoot tips, as expressed by the damage score. The time *E. lopezi* had been present (X_{29} and $X_{29,21}$) contributed most to prediction of *P. manihoti* damage scores (Y_{24}). Abiotic factors proved to be poor predictors of *P. manihoti* damage.

The proportions of shoot tips with *E. lopezi* (X_{28}) and, to a lesser degree, those with coccinellid predators (X_{27}) and ants (X_{26}) were positively linked with *P. manihoti*. This indicates the influence of host densities on predators and parasitoids. Such a feedback mechanism is not taken care of by a multiple regression analysis in which the influence of different factors on *P. manihoti* populations is described.

TABLE III. *Multiple regression and analysis of variance for predicting* Phenacoccus manihoti *damage score from survey data from 60 fields in Ghana and Ivory Coast in February–March 1986*

Variable		Regression statistics b_j	t	Mean	±SE
Dependent variable					
Y_{24}	*P. manihoti* damage score			1·96	0·95
Independent variables					
$X_P{}^+$	*E. lopezi* presence	−0·451	2·10*	0·583	0·497
$X_{(21)}{}^+$	Savanna	1·215	4·44*	0·400	0·494
$X_{P,21}$	*E. lopezi* presence × savanna	−1·103	3·11*	0·267	0·446
X_{27}	Predators	0·759	0·67	0·039	0·105
X_{26}	Ants	3·701	2·78*	0·054	0·065
X_{28}	*E. lopezi* density	2·201	2·67*	0·118	0·149

$\sqrt{MSE} = 0{\cdot}61387$ with 53 degrees of freedom.
Explained variance $R^2 = 0{\cdot}623$.
Intercept = 1·545 with $t = 8{\cdot}66$*.

b_j = regression coefficient.
SE = standard error.
+Treated as dummy variable.
**P*<0·05.

The importance of *E. lopezi*'s presence as a predictor of *P. manihoti* damage scores in the present model is shown by the reduction in R^2 from 0·623 to 0·327 when *E. lopezi* parameters were removed from the analysis.

Except for a few fields in the savanna zones where counts of 100 individuals of *P. manihoti* per tip were encountered, actual *P. manihoti* densities were generally low. Since $\log(x+1)$ population counts varied more than damage scores, the R^2 of the analysis with the same factors as in Table III but with *P. manihoti* counts instead of damage scores was reduced to 0·597. All variables contributed roughly the same share to the explained variance as before.

From Table III, the effects of the presence of *E. lopezi* (X_p) on *P. manihoti* scores (Y_{24}) can be estimated as −0·451 units for the forest and −1·554 units (i.e. −0·451–1·103 units) for the savanna zones, both values being significant, with t values of 2·10 and 5·70 and 95% confidence intervals of ±0·430 and ±0·096 units, respectively.

When incorporated into Equation 3, these results imply that, on average, *E. lopezi* significantly reduced *P. manihoti* damage in the savanna regions by 228 g/plant, i.e. 1·554 × 147 g. At an average planting density of 10 878 plants/ha in the savanna zones, this amounts to 2·48 t/ha.

Farmers' interviews

Among the 50 farmers volunteering information about pests and their damage, 46 knew *P. manihoti* and were aware in which year (1980–83, according to region) the pest had invaded their area. Farmers in the savanna zones considered *P. manihoti* to be a devastating pest, but many in the forest zones doubted whether it did much damage. The four farmers who did not recognize the mealybug typically were from the forest zone.

Among the 46 farmers recognizing the pest, 36 could say whether *P. manihoti* had increased, remained the same or decreased in 1985–86 as compared to previous years (the others having no opinion). Where *E. lopezi* had been present longer than half the planting season, all ten farmers of the savanna zones had observed a dramatic decline in damage caused by *P. manihoti*, while nine farmers in the rain forest zone had observed a decrease and four reported about the same mealybug levels as in previous years. Where *E. lopezi* was either lacking or newly introduced, four farmers reported higher, five the same and four lower *P. manihoti* infestations. In summary, 82·6% of all knowledgeable farmers from areas where *E. lopezi* had been established for a long time (n = 23) reported decreases in *P. manihoti*-related damage, as compared to 30·8% (n = 13) from areas where *E. lopezi* was lacking or only newly established ($\chi^2 = 5{\cdot}68$*).

Discussion

Crop loss assessment in a biological control programme is essential for comparing costs with potential gains. While the present biological control project established a world-wide network of collaborators and financial donors (Herren, 1987), the extent of the damage by *P. manihoti* inflicted on subsistence farmers in Africa remained controversial. From small-scale field experiments, Nwanze (1982) estimated tuber yield loss due to *P. manihoti* of 84%, not taking into account the loss of leaves which are often eaten as a vegetable. Schulthess (1987) measured 9–75% loss depending on the time of tuber harvest. It was widely observed that weed and erosion problems, after plant growth was crippled, led sometimes to total destruction of the crops. The poor quality of cuttings from infested plants, used as planting material, made cassava disappear in some regions. Thus crop losses due to *P. manihoti* were dramatic but often patchy over much of the savanna belts in Africa, while damage was less severe in the rain forest zones. In the absence of reliable government statistics on cassava production, average losses were estimated at 30% by IITA (unpubl. results), FAO (1985) and Walker *et al.* (1985).

The present study represents the first attempt to obtain an unbiased measure of yield losses in cassava based on field survey data on subsistence farms. The effects of *P. manihoti* on yield were separated from those of other factors, which is not the case when farmers' questionnaires and non-differentiable national statistics (Walker *et al.*, 1985) or subjective assessments by experts (Norgaard, 1988) are used. Even yield loss calculations derived from simple regressions with one explanatory variable only must be considered statistically biased, though easily understandable. Thus, on the basis of simple regressions and interpolations it can be estimated tentatively from the present data set that yields of ten-month-old plants in the savanna zones declined from 15 704 kg/ha in uninfested fields to 534 kg/ha in those with the highest *P. manihoti* damage score, a 96·6% yield reduction.

The correct evaluation requires, however, the complete production function (Table II), in which the various interacting abiotic and biotic factors affecting yield in different ecological zones are evaluated. Such a multiple regression analysis, similar to that in a study on rice in Madagascar (Baumgärtner *et al.*, in press), offers general conclusions not obtainable by extrapolating results from small-scale controlled experiments. It also overcomes the inherent heterogeneity present in data from subsistence farms, which has historically stymied quantitative investigation (Oldfield & Acorn, 1987). While such survey data describe only one point in time, their interpretation has to take into account the dynamics of yield formation and yield reduction (Cock *et al.*, 1979; Schulthess, 1987).

The present yield data correspond well to long-term experience in Ghana (E. V. Doku, pers. comm.). As expected, yield proved to be determined to a large extent by soil moisture and nutrition (Shanmugavelu *et al.*, 1973; Hahn *et al.*, 1979; Connor & Cock, 1981; Connor *et al.*, 1981; Njoku & Odurukwe, 1987; Schulthess, 1987). Thus, rain and organic matter on the soil surface, which affects soil moisture and fertility, increased yields as well as the weed cover. From Equation 2, it is estimated that yields in the savanna zone would be 7·5 t/ha higher than those in the forest zone if the savanna zone received the overall average rainfall of 1188 mm/year recorded over the entire study area. This is a strong indication of how limiting rains are in the savanna zones. Where rains were sufficient to avoid die-back of the cuttings, yields were higher if large sticks, which provide more reserves to carry the young plant through stress periods, were planted.

P. manihoti was the major pest, and its importance in determining yields rivalled the one of abiotic and agronomic factors. Its impact was higher in the savanna than in the forest and higher on smaller, i.e. younger, plants than on older ones. Since the survey had probably missed the peak of the sharply fluctuating *P. manihoti* populations in some fields (Fabres, 1981; Hammond *et al.*, 1987; Schulthess, 1987), the damage caused on the growing shoot tips provided higher explained variances than density estimates and was therefore preferred as a variable. This damage score was considered to reflect the accumulated *P. manihoti* numbers of the previous few months. Unexpectedly, stunting at the first branching level, which reflects an early *P. manihoti* attack, influenced yield only weakly, due most likely to later compensation. Contrary to the notion that the harvest index is a genetic constant

(Boerboom, 1978; Dahniya *et al.*, 1982), its reduction following *P. manihoti* attack was significant, at least in the savanna zone. In the forest zone at lowest mealybug densities, however, other unidentified factors influenced tuber formation.

Yield loss due to *P. manihoti* is expected to be greater in other areas for the following reasons: in Ghana, the crop is usually harvested at the end of the dry season, i.e. during the period of the survey. In Nigeria, however, harvest is staggered, and yield losses due to *P. manihoti* increase in the first part of the rainy season because of mobilization of carbohydrates from the roots for new growth (Schulthess, 1987).

Among the other pests, the mite *M. tanajoa* did not show strong gradients in severity of attack. Hence its considerable potential for yield reduction (Yaninek & Herren, 1988) could not be substantiated. The grasshopper *Z. variegatus*, the most important indigenous cassava pest insect (Chapman *et al.*, 1986), caused some defoliation, for which the plants compensated by new growth of side shoots. This effect was too patchy to be significant.

The main contribution of the present study lies in the direct demonstration of the impact of *E. lopezi* on *P. manihoti* (or the substitute measure of damage scores) under the conditions of subsistence agriculture. As in other mealybug systems (Le Pelley, 1943; Bartlett, 1978), ants played an important role. They are first attracted by the mealybug and then protect it against parasitoids and predators, almost exclusively coccinellids (Neuenschwander & Hammond, 1988). The attraction of coccinellids and *E. lopezi* to the mealybug, i.e. the food supply, explains the positive relationship between *P. manihoti* and beneficial arthropods. *E. lopezi* was attracted to the mealybug even at the lowest host densities and reacted strongly to an increase in host density, whereas coccinellids arrived only later on the growing *P. manihoti* populations and reacted only weakly to changes in their densities. This difference between parasitoids and predators is commonly observed in homopteran systems (Hagen, 1976), though rarely quantified.

Since feed-back mechanisms between attraction and host reduction surpass the simple relationship inherent in the analysis with dependent and independent variables, the relative importance of *E. lopezi* and indigenous coccinellids cannot be demonstrated with the present data set. Population dynamics studies (Hammond *et al.*, 1987) and a simulation model (Gutierrez *et al.*, 1988*a*) have, however, clearly shown that mortality of *P. manihoti* caused by coccinellids is relatively low and that *E. lopezi* is the key factor in determining *P. manihoti* population levels.

The beneficial impact of the introduced biological control agent, *E. lopezi* (presence/absence), was estimated as an increase in yield of 228 g/plant in the savanna zone, i.e. at roughly 2·48 t/ha. This constitutes a 50% loss reduction which can be used for estimating the global impact of this biological control programme, thereby replacing subjective assessments (Norgaard, 1988).

TABLE IV. *Total rainfall in 1979, 1983 and 1985 for areas in different ecological zones in Ghana and Ivory Coast where* Epidinocarsis lopezi *in 1985 had been present for a long or a short time*

Ecological zone	*E. lopezi* present for	Meteorological station	Annual rainfall (mm) 1979	1983⁺	1985
Savanna	Long[1]	Akuse	465	203	366
		Ada	886	493	632
		Accra	917	333	681
		Akatsi	1678	726	1207
	Short[2]	Toumodi	1191	721	1227
		Wenchi	1283	668	1492
Forest	Long[1]	Ho	1415	956	1253
		Koforidua	1505	966	1513
	Short[2]	Sunyani	1131	808	1294
		Kumasi	1538	951	1676
		Takoradi	1656	481	956
		Axim	2951	1148	1833

⁺1983 was the year of severe drought.
[1]*E. lopezi* had been present since the first half of the planting season or longer.
[2]*E. lopezi* was absent or present only for the second half of the planting season.

The interviews revealed that the farmers in the savanna zone were aware of the reduction in *P. manihoti* following the establishment of *E. lopezi*, of which they knew nothing. All farmers attributed the decline of the mealybug to higher rainfall during the rainy part of the 1985 cassava season. The low rainfall recorded at the height of the 1983 drought when *P. manihoti* infestations were particularly severe is shown in Table IV, which also shows that rainfall, despite an overall long-term decline (Bradley *et al.*, 1987), had improved during 1985 in all areas, including areas of high *P. manihoti* incidence.

The present data, which are unique in biological control, show that, in 1986, the difference in *P. manihoti* populations between eastern Ghana and central Ivory Coast under equally favourable rain patterns was attributable to the establishment of *E. lopezi*.

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APPENDIX. NUMBERED VARIABLES, ESTIMATED FOR EACH OF 60 CASSAVA FIELDS IN GHANA AND IVORY COAST IN FEBRUARY–MARCH 1986

Characters concerning plant growth (mean of ten plants per field)

1 Tuber yield, fresh weight (g)
2 Number of tubers
3 Fresh weight of planting stick (g)
4 Number of leaves per plant
5 Total fresh weight of leaves and petioles (g)
6 Total fresh weight of stems[1] (g)
7 Total number of nodes[2]
8 Total number of nodes on lateral shoots[2]
9 Number of branching levels
10 Total number of stunted internodes[2]
11 Percentage stunted nodes on first branching level
12 Percentage stunted nodes on second branching level
13 Percentage stunted nodes on third and subsequent branching levels

Agronomic and environmental factors (determined for each field)

14	Crop age[3]:	9 months for short-term variety *A*	=1
		12 months for intermediate variety *B*	=2
		>15 months for long-term variety *C*	=3
15	Planting density (plants/ha)		
16	Intercropping:	<10% (monocrop cassava)	=1
		10–30%	=2
		31–50%	=3
		>50%	=4
17	Weeds[4]:	None to very few	=1
		Few	=2
		Moderate	=3

[1]The weights of green, fresh stems and grey, woody stems were determined separately.

[2]Calculated from the number of nodes, stunted internodes and shoot nodes, respectively, along one branching path and the number of branches on each branching level.

[3]Age and growth form (variety) were independently assessed but, with very few exceptions, fell into the same three categories indicated.

[4]Thoroughly weedy fields were excluded from the survey.

18 Organic matter: High =1
Medium =2
Low =3

19 Moisture-holding capacity—texture of soil: Sand =1
Sandy loam-silt =2
Sandy loam with gravel =3
Clay =4
Clay with gravel =5

20 Total rainfall in 1985 rainy season, in mm (measurements from nearest weather station, see Table IV)

21 Ecological zone: Rain forest =1
Transition zone =2
Guinea savanna =3
Coastal savanna =4

Pest insects and their antagonists (estimated in each field)

22 *Zonocerus variegatus*, none observed =1
Grasshoppers present at low levels, doing no damage =2
Grasshoppers present, causing some defoliation =3
Grasshoppers present, doing heavy damage by decorticating stems =4

23 *Mononychellus tanajoa*, same as *Z. variegatus*, but with complete defoliation instead of decortication in score 4

24 *Phenacoccus manihoti* mean damage score, from 50 tips per field (see text)

25 Mean number of *P. manihoti* per tip, from 50 tips per field, estimated and calculated as $\log(X+1)$ (see text)

26 Total number of tips with ants, out of 50 tips

27 Total number of tips with coccinellids, out of 50 tips

28 Total number of tips with *Epidinocarsis lopezi* in mummies or as adults, including hyperparasitoids, out of 50 tips

29 Duration of *E. lopezi* presence in this area:
E. lopezi not established =1
Since second half of cropping cycle =2
Since first half of cropping cycle =3
E. lopezi arrived in the area before planting =4

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