Biocontrol Science and Technology (1995) 5, 95–107

Impact of the Biological Control Agent *Gyranusoidea tebygi* Noyes (Hymenoptera: Encyrtidae) on the Mango Mealybug, *Rastrococcus invadens* Williams (Homoptera: Pseudococcidae), in Benin

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(*Received for publication 11 May 1994; revised manuscript accepted 20 October 1994*)

The distribution of Rastrococcus invadens *among different host plants and the impact of the mealybug on mango growth were investigated on 2067 trees in three surveys across all the ecological zones of Benin. The first survey started in 1989, less than 1 year after the first release of the exotic parasitoid* Gyranusoidea tebygi. *Within 3 years,* G. tebygi *had colonized the entire area of infestation, and was found on practically all infested mango trees as well as other infested host plants. By 1991, the incidence of* R. invadens *on the secondary host plants had declined significantly. The percentage of infested mango trees declined from 31.0% in 1989 to 17.5% in 1991, highest populations being found in the coastal savanna. During the same period, the mean percentage of infested mango trees having indigenous predators declined from 42.3 to 20.9%. Average mealybug densities declined steadily from 9.7 females/48 leaves in 1989, with 3.2% of all mango trees having densities above 100 mealybugs, to 6.4 females/48 leaves in 1991, with 1.3% of all trees having densities above 100 mealybugs. In multiple regression analyses, based on 23 meteorological, agronomic and plant variables, the duration of the parasitoid's presence proved to be a major factor. It influenced mealybug population densities and sooty mould incidence, which, in turn, affected the production of new leaves. In all analyses, the impact of rainfall, for example, on the sooty mould or the mealybug was less important than the effect of* G. tebygi. *The present study demonstrates for the first time on a large scale the impact of* G. tebygi *on* R. invadens *and, indirectly, on its main host plant, mango.*

Keywords: *biological control, mango, mango mealybug, Benin,* Rastrococcus invadens, Gyranusoidea tebygi

INTRODUCTION

In August 1986, an unknown species of mealybug was reported to cause serious damage to various fruit trees, particularly mango (*Mangifera indica*, Anacardiaceae), in southern Benin (Agounké *et al.*, 1988). The species was described as *Rastrococcus invadens* Williams (Homoptera: Pseudococcidae) from South-East Asia, which had been introduced accidentally,

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probably on infested plant material, into Ghana and Togo (Williams, 1986). It has since invaded Congo, the Ivory Coast, Gabon, Nigeria, Sierra Leone and Zaire (Boussienguet & Herren, 1992; Matokot *et al.*, 1992; Neuenschwander *et al.*, 1994).

In a biological control programme, the parasitic wasp, *Gyranusoidea tebygi* Noyes (Hymenoptera: Encyrtidae) was imported from India (Narasimham & Chacko, 1988) and studied in quarantine (Willink & Moore, 1988). It was reared, released and successfully established in Togo (Agricola *et al.*, 1989). This programme was later extended to the whole region (Neuenschwander *et al.*, 1994). In Benin, first releases were carried out in 1988 in collaboration between the IITA Biological Control Programme and the National Plant Protection Service. The spread of *R. invadens*, the establishment of *G. tebygi* and the impact of this parasitoid on mango were assessed in three surveys from 1989 to 1991, the results of which are presented here.

MATERIALS AND METHODS

Surveys and General Protocol

Benin is situated in West Africa between latitude 6°30′ and 12°30′N and longitude 1°00 and 3°40′E, with a total land area of 112 622 km^2. The country is divided into six departments, Ouémé, Atlantique and Mono in the south; Zou in the centre; and Borgou and Atacora in the north. In 1992, about 4 600 000 inhabitants were registered, with an average population density of 43 km^{-2}. Sixty per cent of the population is concentrated in the three southern departments, with an average density of 207 km^{-2}.

The surveys reported here on the spread and dispersal of mango mealybug covered all the areas of the country known to be infested during the years of survey (Figure 1). There were three major surveys from 1989 to 1991 (together with casual observations) at the end of each dry season, when mealybug infestations are highest: 20 February–11 March 1989, 15 February–23 March 1990 and 13 February–9 March 1991. At this time, mango trees in Benin carry young fruits of the main yearly harvest.

Trees were selected at fixed distances while driving along roads to ensure that the results were without bias, and were thus representative of large areas and comparable between surveys. In urban areas, groups of mango trees were selected every 5 km, and in rural areas, every 10 km. Each group consisted of four mango trees close to each other. In the southern departments, stops were also made along dirt roads in order to achieve a better coverage of the area. In the northern departments, sampling was concentrated around towns known to be infested by *R. invadens*. Sampling along the main roads leading away from these towns was discontinued after several stops without *R. invadens*. Trees that were partially destroyed by bush fire or were difficult to access were not surveyed.

Whenever possible, other plant species that were known to be hosts of *R. invadens* were also assessed. The most important ones were citrus (*Citrus* spp., Rutaceae), banana (*Musa* spp., Musaceae), guava (*Psidium guajava*, Myrtaceae), breadfruit (*Artocarpus altilis*, Moraceae), frangipani (*Plumeria* spp., Apocynaceae) and fig (*Ficus* spp., Moraceae).

Abundance of *R. invadens, G. tebygi* and its local antagonists and competitors were estimated, and plant growth, soil and weather parameters were assessed according to a protocol tested on the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae) (Neuenschwander *et al.*, 1989, 1990, 1991). The 1989, 1990 and 1991 surveys covered 147, 166 and 204 localities, where 587, 664 and 816 mango trees were sampled respectively.

Survey Variables

Environmental and agronomic factors. In southern Benin, the rainfall pattern is bimodal. The long rainy season lasts from the end of March to the end of July, peaking in June; it is followed by a short dry season. The short rainy season lasts from the end of September until November, peaking towards the end of September. From the end of November until the beginning of March, the weather is dry, with frequent periods of 'harmattan', a dry, dusty wind originating in the Sahara desert. Further north, the rainfall pattern is unimodal. From about 9°N, the rainy season

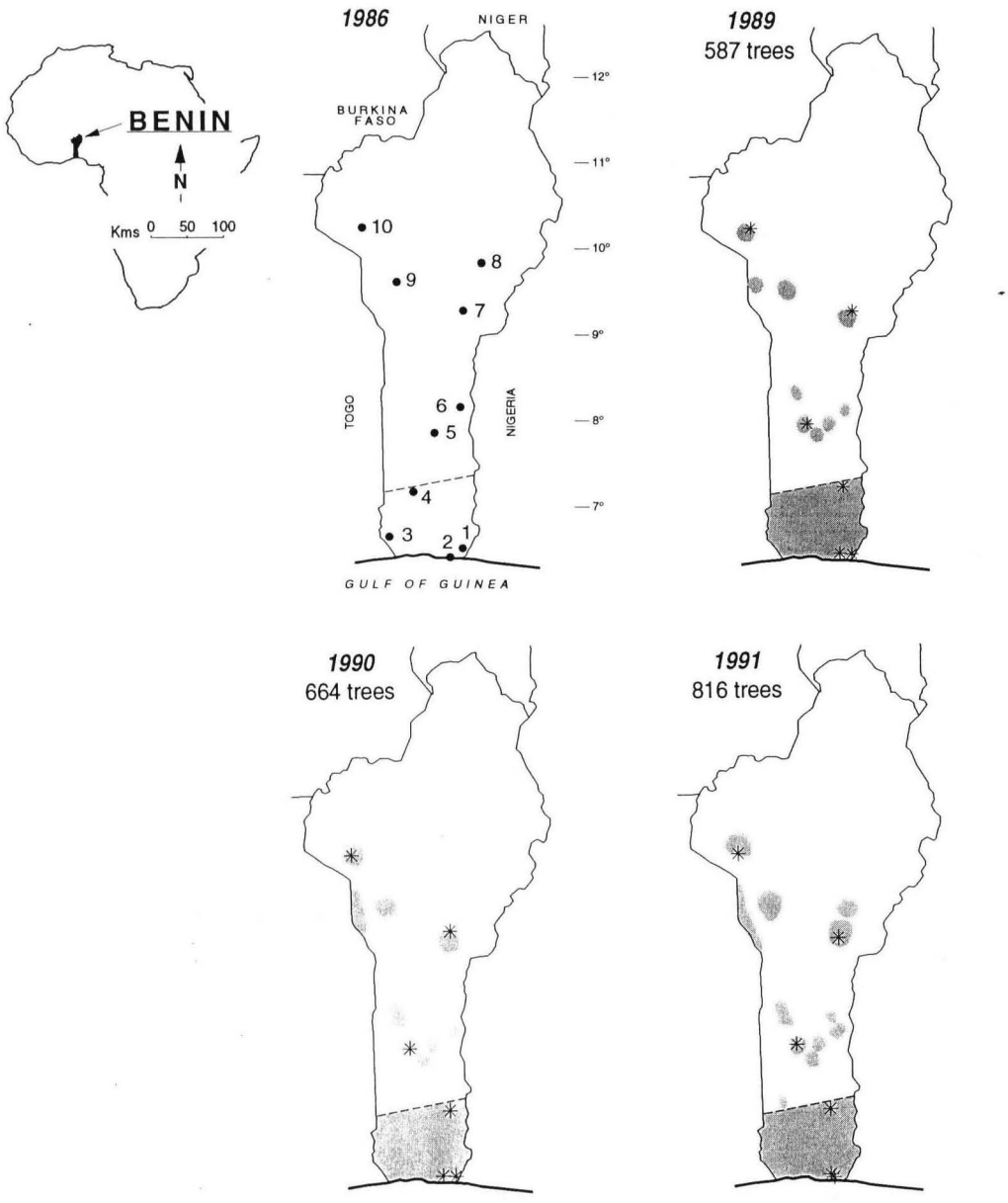


FIGURE 1. The distribution of mango mealybug *R. invadens* and its exotic parasitoid *G. tebygi* in Benin from 1989 to 1991, compared with the situation in 1986 (Agounké *et al.*, 1988) showing the approximate northern limit of contiguous distribution of insect pest (broken lines). Important towns: 1 = Porto-Novo; 2 = Cotonou; 3 = Lokossa; 4 = Abomey; 5 = Dassa; 6 = Savè; 7 = Parakou; 8 = N'Dali; 9 = Djougou; 10 = Natitingou. The distribution of *G. tebygi* is marked by shading and the release sites are marked by asterisks.

lasts from May to October, with a peak in early September. The dry season is from November to April (Adam & Boko, 1983).

Data on the annual rainfall for the years of survey were obtained from government meteoro-

logical stations nearest to survey points. The data covered the period preceding the surveys, from 1 February to the end of January the following year, and computations were made from 98 weather stations with complete monthly data sets (variable 1). Yearly totals (means of 3 years) varied from 609 mm rainfall in the north-west to 1717 mm in the south-west.

Long-term rainfall patterns are reflected in the plant cover. The area surrounding each locality was classified, on the basis of the vegetation, into four ecological zones (variable 2). The first area, (a), was the coastal savanna zone, extending up to about 10 km inland. This is the most densely populated area with degraded sandy soils and marked bimodal rainfall pattern. The second area, (b), was the forest and transition zone in the south, with patches of forest with tall grasses. The third area, (c), comprised the Guinea savanna zone, characterized by open forest with grass, covering nearly the whole country up to 10°30′N. The fourth area, (d), was the Sudan savanna zone, characterized by scattered trees, in a dry belt in northern Borgou and Atacora departments, above latitude 10°30′N with a unimodal rainfall pattern.

The soil around each sampled tree was scored according to increasing water retention capacity (variable 3) as sand (1), loamy sand (2) or sandy loam with or without clay (3) (Sanchez *et al.*, 1982). The content of organic matter on the soil surface (mulch) (variable 4) was scored from low (1) to high (3). Weed cover (variable 5) was scored as none (1) to high (3) and human population density (variable 6) as farm (1), village (2) or town (3).

Plant factors. Although the names of different imported mango varieties were recorded, trees were only categorized (variable 7) as local (fruits small and fibrous, the so-called mangotiers) or grafted varieties (big fruit without fibres).

The trunk circumference (cm), 80 cm above ground, was used as a measure of tree age (variable 8). In addition, tree height (m) (variable 9) was estimated.

To describe plant growth, 11 phenological stages of terminal shoot development (Laroussihle, 1980) were distinguished on four branches, randomly selected in the four quadrants of the tree (north, west, south, east). All leaves on the freshly grown part of the stem (i.e. young leaves) (phenological stages D, E_1, E_2 and E_3) (variable 10) and on the second growth (i.e. medium-aged leaves) (E_3) (variable 11), were counted. On branches with a dormant bud (stage A) or where leaf development had just started (stages B and C), the number of young leaves was noted as zero. The total number of leaves counted on the young, medium-aged and old growths on all four branches of each tree was used as an additional variable (variable 12).

The percentages of physiologically active trees (i.e. trees bearing fruit) (stages G and H), fresh foliage (stages D, E_1 and E_2) and/or flowers (stages F_1 and F_2) on at least one of the four branches were calculated for each year and ecological zone, but not included in the multiple regression analysis.

Pest insects and their antagonists. On the same branches used to quantify plant growth, all adult female mealybugs were counted on four randomly chosen leaves of each of the three age classes. Counting females, the most conspicuous and easily recognizable stage, was justified by the fact that the numbers of adult and immature *R. invadens* are closely correlated because of the complete overlap of generations (Boavida *et al.*, 1992). Counts on leaves of different ages were compared. For the multiple regression analysis, however, the $\log(x + 1)$-transformed number of adult female *R. invadens* on the 48 leaves inspected/tree (variable 13) was taken as the variable characterizing mealybug population density. Since immatures proved to be difficult to count in the field, only the presence or absence of younger instars of *R. invadens* (variable 14) and, in addition, dead mealybugs (variable 15), were noted.

On each tree, the presence or absence of mummies and adults of *G. tebygi* (variable 16) was recorded. All indigenous and exotic parasitoids and predators were identified, but only those thought to have some influence on *R. invadens* were taken into account, as judged from the food web of *P. manihoti* (Neuenschwander *et al.*, 1987). Thus, the presence or absence of larvae, pupae and adults of local predators (e.g. coccinellids and *Spalgis lemolea* Druce (Lepidoptera: Lycaenidae)) (variable 17) and live ants (variable 18) were noted for each tree.

Empty mealybug mummies and exuviae of coccinellids and *S. lemolea* were not included in these counts.

All other mango pests were scored according to the presence or absence of either live insects or their damage on the tree. The scale *Aulacaspis tubercularis* Newst. (Homoptera: Diaspididae) (variable 19) and leaf-feeding insects (variable 20), mostly *Zonocerus variegatus* L. (Orthoptera: Pyrgomorphidae), were scored separately. All fungal and bacterial diseases (variable 21) were considered together.

The duration (in months) that *G. tebygi* had been present in the area (variable 22) was estimated from the release and dispersal records (Neuenschwander *et al.*, 1994).

Damage to host plants. Besides sucking sap, mealybugs cause damage to mango trees by secreting honeydew. The ensuing sooty mould inhibits photosynthesis, with reduction in the growth of new leaves and flowering. Sooty mould was quantified according to the following scale: no damage, no sooty mould (1); slight damage, 1–25% of the upper leaf surface covered by sooty mould (2); moderate damage, 26–50% covered (3); marked damage, 51–75% covered (4); and heavy damage, 76–100% covered (5). On the chosen branches, damage was recorded as an estimated average for all four inspected leaves of a given growing period. Later, the highest score among the four quadrants and all age classes (variable 23) was judged to best reflect the situation of the tree at that moment. This was retained for the final analysis.

Statistical Analysis

Percentages of trees having mealybugs were compared using χ^2 tests with correction for continuity. According to the question asked, mealybug numbers were added up among all quadrants or leaf ages of a single tree. Where four leaves could not be found in a given age class, numbers were corrected accordingly. For the multiple regression analyses, these numbers were $\log(x + 1)$ transformed, but for the description of the distribution of mealybugs, means obtained from untransformed data are presented.

To determine the relative importance of different factors, econometric multiple linear regression analyses (Drapper & Smith, 1981; Wrigley, 1985) were carried out, each tree occupying one line in the matrix. Variables X and Y were characterized by the corresponding subscript numbers. Only those parameters that were biologically meaningful and thought to influence directly the dependent variables (mealybug population density, damage score or number of young leaves) were included in the calculation. All factors subjected to strong feedbacks were excluded, as discussed by Neuenschwander *et al.* (1990). For the final analysis, only factors contributing significantly, that is with a significant slope, were retained. Factors were ranked according to the t-values of the slope, b.

All statistical tests were judged at $P = 0.05$, and significant results were marked with an asterisk.

RESULTS

Spread of *R. invadens* and *G. tebygi*

In a preliminary survey in July–August 1986, *R. invadens* was restricted mainly to the southern part of Benin, with important sites around Cotonou, Porto-Novo and Lokossa (Figure 1). The infestation extended 30 km inland in the east and 50 km in the west, occurring only locally further north. In August 1986, the northern limit of the insect was located in Abomey, 120 km from the coast, on a few plants of breadfruit and mango. These plants had been introduced into the region from a horticultural centre in Porto-Novo. Numerous plant species were seriously damaged by *R. invadens*.

In 1989, *R. invadens* was found frequently on plants other than mango, mainly citrus, banana, guava, fig, frangipani and breadfruit, in 71.4% of the 147 localities (Table 1). In 1991, the incidence on each of these plant species was significantly lower than in 1989, the overall

TABLE 1. Percentages of localities where different plant species (mango trees excluded) were infested by *R. invadens*. Data were obtained from a total of 147, 166 and 204 localities surveyed in Benin, in February–March 1989, 1990 and 1991 respectively

	1989		1990		1991		
Host plant	Total	Percentage infested	Total	Percentage infested	Total	Percentage infested	χ^{2a}
Citrus	67	57	67	73	66	32	7.2*
Banana	22	86	39	31	36	22	22.2*
Guava	16	81	18	56	25	28	9.1*
Fig	11	73	13	46	7	29	NA
Frangipani	8	75	9	89	8	25	NA
Breadfruit	7	86	8	88	7	43	NA
Others	16	94	15	53	11	18	NA

[a] χ^2 test comparing 1989 with 1991.
*Significant at $P = 0.05$.
NA = non applicable (expected value < 5).

percentage being reduced to 28.1%. *G. tebygi* was recovered from all plant species mentioned in Table 1.

A total of 2067 mango trees was inspected in all ecological zones (Figure 1, Table 2). Mealybugs were not found in the Sudan savanna, though mango trees are abundant there. Throughout the 3 years, the percentage of infested mango trees was highest in the coastal savanna, where it declined from 85.0% of all the surveyed trees in 1989 to 70.8% and 71.9% in 1990 and 1991 respectively. The percentage of infested trees in all the zones together declined from 31.0% in 1989 to 23.2% and 17.5% in 1990 and 1991 respectively.

Among the infested mango trees, the percentage with *G. tebygi* rose from 96.7% ($N = 182$) only a few months after their release in 1988 to 99.4% ($N = 154$) and 100% ($N = 143$) in 1990 and 1991 respectively. In contrast, the percentage of infested trees having indigenous predators

TABLE 2. Percentage of mango trees in Benin infested with mango mealybug (MM), *R. invadens*, its exotic natural enemy, *G. tebygi* and local predators in different ecological zones. Data were obtained from a total of 2067 trees surveyed in Benin in February–March 1989, 1990 and 1991

Year and ecological zone	Number of trees (= 100%)	Percentage of trees having			Percentage of physiologically active trees
		MM[a]	*G. tebygi*[b]	Predators[b]	
1989					
Forest	44	13.6	100.0	50.0	86.4
Savanna	523	30.4	96.2	42.1	87.4
Coast	20	85.0	100.0	41.2	65.0
1990					
Forest	68	17.6	100.0	8.3	69.1
Savanna	572	21.8	99.2	28.0	71.3
Coast	24	70.8	100.0	41.2	75.0
1991					
Forest	60	1.7	100.0	100.0	75.0
Savanna	724	164	100.0	17.6	82.0
Coast	32	71.9	100.0	34.8	81.2

[a] Based on all surveyed trees.
[b] Based on infested trees only.

declined from an average of 42.3% less than 1 year after the release of *G. tebygi* to 27.9% and 20.9% in 1990 and 1991 respectively.

R. invadens Population Densities and Plant Condition

Taking into account infested as well as uninfested trees from the 1989, 1990 and 1991 surveys, the following mean population densities were observed on leaves of the different age classes. Mealybugs were most abundant on young foliage with a mean of 5.5 females/16 leaves (maximum 252 females; for trees with young leaves, $N = 494$). The corresponding means for medium-aged leaves were 3.8 females (maximum 240, $N = 1498$) and for old leaves, 3.2 females (maximum 132, $N = 644$).

The number of females (expressed as $\log(x + 1)$) found on medium-aged leaves (Y_m) was closely linked to the number of mealybugs found on old leaves (X_o), from where they had probably migrated: $Y_m = 0.061 + 1.035\ X_o$ (the number of trees that had both types of leaves = 629, $t_b = 45.3$*). Similarly, mealybug population densities on young leaves (Y_y) were determined by the ones on medium-aged leaves (X_m): $Y_y = 0.037 + 0.934\ X_m$ ($N = 290$; $t_b = 31.5$*). These results justify the pooling of mealybug counts from all sampled leaves of the three age classes to obtain one count/tree, based on 48 leaves, for further analyses.

Since many trees had no mealybugs on the sampled branches, mealybug population densities overall were low, highest means being found along the coast. Across all the zones, population density (untransformed data) averaged 9.7 females/48 leaves in 1989, with only 3.2% of the trees having population densities above 100 mealybugs/48 leaves. The corresponding values in 1990 were 7.1 females and 1.7% of trees respectively; in 1991, values were 6.4 females and 1.3% of trees respectively.

Impact of Biotic and Abiotic Factors on *R. invadens* Populations

The contributions of various biotic and abiotic variables on mealybug population density (Y_{13}) were quantified in a multiple regression analysis (Table 3). On the basis of infested trees only, two independent factors significantly influenced *R. invadens*, namely the presence of *A. tuberculariis*, followed by the number of young leaves. The two variables accounted for only 6.5% of the variance. On the basis of all trees, two other factors became pre-eminent in explaining population densities: mealybugs were more abundant in towns than in villages, and lowest on farms. They increased slightly the longer *G. tebygi* had been present in the area (X_{22}). Detailed inspection of these data revealed, however, that mealybug population densities (Y_{13}) peaked 16 months after the introduction of *G. tebygi* into an area, with a steep decline thereafter ($Y_{13} = 0.809 - 0.015X_{22}$; $N = 532$, $t_b = 2.84$*).

Other factors, like rainfall, number of young and medium-aged leaves and the presence of *A. tubercularis*, contributed significantly, but to a lesser degree. The explained variance was 14.1%. Still other factors, such as variety, soil or ecological zone, did not contribute significantly.

Influence of Biotic and Abiotic Factors on *R. invadens* Damage to Mango Trees

To assess the influence of biotic and abiotic variables on damage score (Y_{23}) on infested trees, four independent variables were retained, which accounted for 32.7% of the variance (Table 4). The duration of *G. tebygi*'s presence was the most important, followed by mealybug population density, human population density and *A. tubercularis*. Factors such as rainfall, variety and ecological zone had no significant impact on sooty mould.

When uninfested trees were included in the analysis, mealybug population density was by far the most important variable, each 10-fold increase in number adding 1.18 units to the damage scores. The duration of *G. tebygi*'s presence was the third most important factor, coming before human population density, soil factors and rainfall. Again, *A. tubercularis* presence was important.

TABLE 3. Multiple regression analysis for assessing the importance of factors influencing mango mealybug populations from infested mango trees only ($N = 479$) and from all ($N = 2067$). Data obtained in Benin, during February–March 1989, 1990 and 1991

	Regression statistics			
	Infested trees		All trees	
Variables	b	t_b	b	t_b
Dependent variable				
Y_{13} Mealybugs[a] in $\log(x + 1)$				
Independent variables[b]				
X_1 Rainfall $\times 10^4$			2.872	5.56*
X_6 Human population density			0.195	11.66*
X_{10} Young leaves[c]	0.003	2.82*	0.003	5.00*
X_{11} Medium-aged leaves[c]			0.003	3.84*
X_{19} *A. tubercularis*	0.237	4.46*	0.047	1.97*
X_{22} Duration *G. tebygi*			0.009	7.57*
Intercept	0.721		− 0.020	
Explained variance, R^2	0.065		0.141	

[a]Total number of adult female mango mealybugs, estimated on four leaves of each of the three growing periods of four randomly selected branches (north, west, south, east) (i.e. 48 leaves).

[b]Within each category (infested trees and all trees), all independent variables that had a significant b are shown with asterisks.

[c]Number of leaves of the indicated age, counted on four randomly selected branches (north, west, south, east).

The relatively high explained variance of 46.9% indicates that, in the present data set, damage score is far better explained by the various factors quantified in the surveys than was the case for mealybug population density. This was despite the fact that average sooty mould scores (with the exception of trees along the coast in 1989) were low.

Both mealybug population densities and damage scores were affected by human population density, both variables having generally higher values in towns than in villages and farms. Means of both variables declined markedly from 1989 to 1991 (Figure 2).

Impact of *R. invadens* and its Biological Control on Plant Growth

The number of young leaves (Y_{10}) was the only variable that allowed us to quantify the impact of various factors on plant growth. Results of both analyses (with or without uninfested trees) gave similar results (Table 5). When all trees were included, leafiness (estimated by the number of medium-aged leaves), the age of the tree (estimated by the circumference of the trunk) and mango variety were important factors, more so than on infested trees alone. The negative slopes show that older and bushier trees, particularly 'mangotiers', have fewer young leaves than younger and grafted trees.

The population density of mealybugs was positively correlated with the growth of the trees. This could indicate a stimulatory action by the mealybugs, although it is more probable that it is due to the attraction of mealybugs to the young leaves for food. In this case, the implied cause–effect relationship of the regression is reversed, which warrants the exclusion of the mealybug variable. Exclusion led to the following changes in comparison to Table 5, which are not presented in detail here: On infested trees, the results were practically the same, all t_b values being slightly lower. For all trees, a few t_b values were marginally higher, the one for *G. tebygi* duration being substantially higher, namely $t_b = 3.36$*.

TABLE 4. Multiple regression analysis for predicting damage (score for sooty mould) by mango mealybug from 2067 mango trees, among them 479 infested trees, in Benin, February–March 1989, 1990 and 1991

	Regression statistics			
	Infested trees		All trees	
Variables	b	t_b	b	t_b
Dependent variable				
Y_{23} Damage score				
Independent variables[a]				
X_1 Rainfall $\times 10^4$			4.581	5.37*
X_3 Soil texture			− 0.219	5.23*
X_4 Soil fertility			− 0.137	3.47*
X_5 Weediness			0.076	2.19*
X_6 Human population density	0.570	6.42*	0.181	5.64*
X_{13} Mealybugs[b] in $\log(x + 1)$	0.706	7.78*	1.183	33.09*
X_{19} *A. tuberculatis*	− 0.523	4.73*	− 0.309	7.95*
X_{22} Duration *G. tebygi*	− 0.055	9.92*	− 0.013	6.49*
Intercept	4.469		2.319	
Explained variance, R^2	0.327		0.469	

[a]Within each category (infested trees and all trees), all independent variables that had a significant b are shown with asterisks.

[b]Total number of mango mealybugs, estimated on four leaves of each of the three growing periods, of four randomly selected branches (north, west, south, east) (i.e. 48 leaves).

In all analyses, the duration of *G. tebygi*'s presence was positively correlated with plant growth as measured by the production of new leaves. This improvement of the growth of trees also occurred when the percentage of physiologically active trees was calculated for the different ecological zones and years (Table 2). Overall, only a few per cent showed any new growth during the sampling periods; many more trees had young fruit. The percentage of trees with either young leaves, fruit or flowers increased from 1990 to 1991 and, along the coast, from 1989 to 1991. The two highest values were found in the savanna and forest in 1989, when infestations by *R. invadens* in these areas were still very recent.

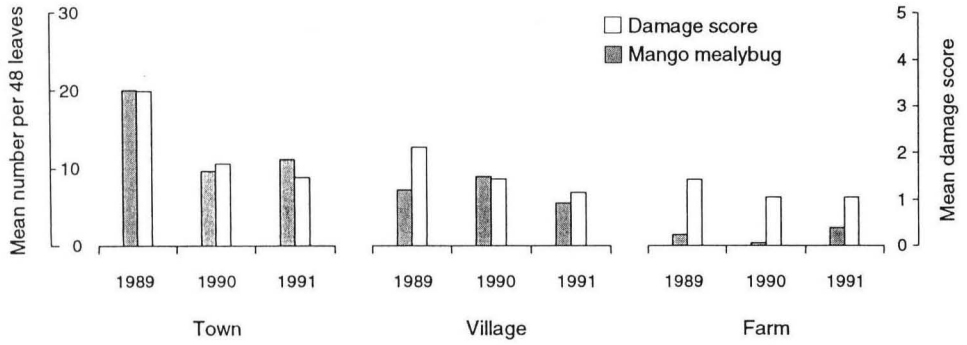


FIGURE 2. The mean number of mango mealybugs, *R. invadens*, per 48 leaves, and mean damage score in different localities in Benin from a total of 2067 trees surveyed in February–March 1989, 1990 and 1991. Of trees surveyed, 630 were located in towns, 915 in villages and 522 on farms.

TABLE 5. Multiple regression analysis for assessing the importance of factors influencing the growth of mango tree, as measured by the number of young leaves/tree, from 2067 mango trees, among them 479 infested trees, in Benin, in February–March 1989, 1990 and 1991

	Regression statistics			
	Infested trees		All trees	
Variables	b	t_b	b	t_b
Dependent variable				
Y_{10} Young leaves[a]				
Independent variables[b]				
X_1 Rainfall	0.013	2.45*		
X_3 Soil texture	− 7.275	3.13*	− 3.131	3.06*
X_4 Soil fertility	7.589	3.70*	4.113	4.44*
X_6 Human population density			2.182	2.80*
X_7 Variety	− 5.320	2.58*	− 4.852	4.30*
X_8 Circumstance	− 0.063	3.59*	− 0.072	8.90*
X_{11} Medium aged leaves[a]			− 0.257	9.57*
X_{13} Mealybugs[c] in $\log(x + 1)$	6.176	3.81*	4.733	5.40*
X_{22} Duration *G. tebygi*	0.609	4.87*	0.131	2.71*
Intercept	15.422		45.134	
Explained variance, R^2	0.141		0.108	

[a]Number of leaves of the indicated age, counted on four randomly selected branches (north, west, south, east).

[b]Within each category (infested trees and all trees), all independent variables that had a significant b are shown with asterisks.

[c]Total number of mango mealybugs, estimated on four leaves of each of the three growing periods, of four randomly selected branches (north, west, south, east) (i.e. 48 leaves).

DISCUSSION

The capability of *G. tebygi* to reduce populations of *R. invadens* has been demonstrated in Togo (Agricola *et al.*, 1989), Congo (Matokot *et al.*, 1992) and Benin (Boavida *et al.*, 1992, 1995), but in all these studies only a few trees were sampled. The present work demonstrates, for the first time, a large-scale impact.

R. invadens was found to be very polyphagous (Agounké *et al.*, 1988), but, after the establishment of *G. tebygi* and the concomitant decline in mealybug populations, the range of host plants was drastically reduced and mango remained the only important host (Boussienguet & Mouloungou, 1993). This was confirmed in the present study.

In Benin, the spread of *R. invadens* was slower and less regular in the forest and savanna zones than along the coast. The speed of dispersal leading to a continuous distribution in southern Benin was similar to the one in Gabon (Boussienguet & Herren, 1992). The northern cities of Benin with isolated mealybug populations were reached much later than similar localities in Togo (Agounké *et al.*, 1988).

Across all ecological zones, mealybug population densities and damage on trees were higher in towns than in villages and farms, confirming previous observations made shortly after the introduction of the pest (Agounké *et al.*, 1988). Local foci of high infestations remained, particularly in towns, notwithstanding the presence of *G. tebygi*. They are the sites of releases of another exotic parasitoid, *Anagyrus mangicola* Noyes (Hymenoptera: Encyrtidae) (Neuenschwander *et al.*, 1994).

While the host-specific *G. tebygi* was recovered from practically all trees, whatever the mealybug infestation level, indigenous predators disappeared from trees which were infested little. This illustrates the relative inefficiency of the indigenous predators to adapt and control

populations of the newly introduced mango mealybug. This conclusion is similar to observations made on cassava mealybug (Neuenschwander *et al.*, 1989, 1991; Hammond & Neuenschwander, 1990), which were backed up by a simulation model (Gutierrez *et al.*, 1988). These rather polyphagous predators fluctuated irregularly in time and space, probably because their numbers were influenced by other hosts not sampled in the present study.

The present study represents the first evaluation of the interacting abiotic and biotic factors affecting *R. invadens* populations, their damage and their influence on the growth of mango trees. Similar multiple regression analyses have been used in studies on rice pests (Baumgärtner *et al.*, 1990), cassava mealybug (Neuenschwander *et al.*, 1989, 1990, 1991; Chakupurakal *et al.*, 1994) and stem and ear borers of maize (Gounou *et al.*, 1994). These studies offer general conclusions which cannot be obtained from small-scale, controlled experiments. The cassava studies showed the overwhelming impact of the establishment duration of the introduced parasitoid. The present study gives similar results for *G. tebygi*, though significance levels are generally lower. This is attributable to the fact that the basic unit in the cassava studies was a cassava field, whereas on mango the unit is the individual tree. Similar differences in infestations by *R. invadens* among mango trees, even of the same variety, have been described before (Boavida *et al.*, 1992; Boussienguet & Mouloungou, 1993).

In several analyses, the presence or absence of *A. tubercularis* played a relatively important role. Yet, this scale insect was never seen to interfere in any way with the mealybug. The effect of *A. tubercularis* in the regression analysis is probably due to a third factor which also benefits *R. invadens*.

There was only little impact of rainfall on the sooty mould. This suggests that, contrary to the statements by the extension services, rain cannot be considered to be a key factor in sooty mould reduction, since sooty mould on mango leaves appeared too thick to be washed off by rain. It seems that any reduction due to the control of *R. invadens* by *G. tebygi* becomes evident only after the affected leaves have been shed.

The growth of mango trees was assessed by various parameters. Only the number of young leaves on the sampled branches was quantified in a way adaptable to a regression analysis. Mealybug population density was higher on trees with dense canopies. The same observation often led mango producers to cut off branches of dense trees, sometimes drastically affecting the growth, and consequently the production, of these trees.

The main contribution of the present study lies in the direct demonstration of the impact of *G. tebygi* on populations of *R. invadens* over large areas in Benin. Reduction of mealybug populations led to significant reductions in damage, as estimated by sooty mould. Considering the heterogeneity of mango trees, this demonstration of significant correlations across two trophic levels is remarkable. These regressions are interpreted as impact by a parasitoid on its host and the physiology of the host plant.

The percentages of physiologically active trees showed a slight increase from 1990 to 1991, after *G. tebygi* had been present in the area for more than a year. Other variables that would be closer to commercial interests, such as the production of fruit, were also assessed. The semi-quantitative data on fruit were, however, not sufficient for inclusion in the regression analysis on the impact by *G. tebygi*. Fruit production during the last 5 years was, therefore, assessed in a socioeconomic impact study, which will be presented elsewhere.

ACKNOWLEDGEMENTS

This work was carried out in partial fulfilment of a PhD thesis by A. H. B.-G. at the University of Leiden under Professor J. J. M. van Alphen, and financed through the Biological Control Programme of IITA by the Gesellschaft für Technische Zusammenarbeit, Germany. We thank all the donors of IITA's Biological Control Programme for their financial and material support. We also thank Ira Olaleye for drawing the maps, our colleagues for reviewing the manuscript and the late Abou Gado for his assistance. We are grateful to the staff of the Direction de l'Agriculture, especially the Plant Protection Service, for their encouragement, support and assistance during

the execution of this programme, and the agents of the extension services (CARDER) for their collaboration and hospitality.

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