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# Biological Control of Cassava and Mango Mealybugs in Africa

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## Introduction

In the 1970s, the exotic mealybug *Phenacoccus manihoti* Matile-Ferrero (Homoptera, Pseudococcidae) (Plate 3) was inadvertently introduced into Africa. It quickly spread across almost all the continent and, in the absence of efficient adapted natural enemies, became the prime pest on cassava. Fifteen years later, *P. manihoti* was under complete biological control thanks to an international collaborative effort across three continents, but mainly in Africa. The story of this well-documented success in classical biological control illustrates the different stages of such a project, from desperate, though inefficient, attempts by farmers to control the pest, through collaborative research to implement classical biological control on a large scale. It is also the story of winning over the minds of the various people in the research establishment and government to allow introductions of exotic species, of monitoring the ups and downs of the pest populations, and of communicating these results back to the client farmers, local collaborators and government officials. Finally, the international community and the donor agencies had to be convinced that despite the slowness of the process, classical biological control was a good investment, deserving long-term external support. More recently, dangers of these interventions to the environment through possible effects on non-target organisms had to be evaluated and the results used in the effort to codify the conduct of biological control practitioners.

On the strength of this model of biological control in Africa, several other projects with the same international organizations and national collaborators were executed. These projects profited from established procedures and the trust already achieved among colleagues. One of these projects, the fight against the mango mealybug, *Rastrococcus invadens* Williams (Homoptera, Pseudococcidae) (Plate 6), which invaded West Africa in the early 1980s, shows striking parallels, but also a few highly interesting differences.

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Biological control of cassava mealybug has been reviewed on several occasions (for complete bibliographies, see Herren and Neuenschwander, 1991; Neuenschwander, 2001). The mango mealybug story, by contrast, is much less well known (Neuenschwander *et al.*, 1994; Neuenschwander, 1996). Here, we review the parallels and explore the impact in a larger context of IPM, citing only a few recent papers.

## Origin of Host Plants and Invading Mealybug Species

Cassava, *Manihot esculenta* Crantz (*Euphorbiaceae*), was introduced to Africa from South America by the Portuguese in the 16th century, but penetrated into the interior of the continent only in the 20th century. Today, this hardy plant is the main staple for about 200 million Africans, with a particular importance in poor countries.

Because of its plant defences, namely a high cyanide and latex content in leaves, stems and tubers, it had few pest insects attacking it in Africa. By contrast, the list of co-evolved arthropods in its native South America comprises some 200 species. In Africa, several diseases of African origin also affected yields before breeding provided resistant or tolerant varieties. The situation changed dramatically when, in the early 1970s, the cassava mealybug was accidentally introduced into the Republic of Congo and D.R. Congo (then Zaire). *P. manihoti* was described as a new species of presumably Neotropical origin, but it took several years of search before this mealybug was discovered in its original home land, Paraguay, and later in Brazil and Bolivia. In most instances, the densities of the few infestations that were found in South America were low.

As *P. manihoti* spread across most of Africa, its high infestation levels immediately made it the number one pest of cassava on the continent, severely affecting the livelihood, particularly of poor people. New foci of infestation were discovered in Senegal/Gambia in 1976, Nigeria/Bénin in 1979, and in Sierra Leone in 1985. In West Africa, the mealybug spread at 300 km year$^{-1}$; but in East Africa barriers like the Rift Valley or vast areas with little cassava led to a slower spread and an initially sporadic distribution. New pest outbreaks, sometimes hundreds of kilometres away from the next infestation, were found in Malawi in 1985, Mozambique in 1986, Tanzania in 1987 and Kenya in 1989. By 2000, the entire cassava belt south to the Lowveld of the Republic of South Africa, with the main exceptions of Madagascar and the Indian Ocean islands, was infested.

Where infestations were high, crawlers of cassava mealybug also settled on the surrounding vegetation, where they sometimes even reproduced. Without a high population on cassava, these infestations on other host plants ceased, however, within a short time. Two *Manihot* spp. and their hybrid, all introduced from South America, proved to be the only lasting host plants. Recent studies shed light on the adaptation of cassava mealybug to its host plant. *P. manihoti* is capable of metabolizing cyanogenic glycosides and three flavonoid glycosides, among them rutin, which are translocated in the phloem sap with seasonal fluctuations (Catalayud *et al.*, 1994a,b). These compounds are responsible for the antibiosis that cassava mealybug, unlike other insects, is capable of counteracting to a large extent.

In the 1980s, another exotic mealybug, the mango mealybug, was observed for the first time in massive infestations in Lomé, Togo, and Cotonou, Bénin. This new plague then spread rapidly along the coast west to Ghana and Côte d'Ivoire and east to Nigeria. By the mid-1990s, it had invaded most of West and Central Africa, from Senegal to D.R. Congo. In the urban environment, this mealybug attacked indiscriminately mango, citrus, shade trees (mainly *Terminalia* spp.), but also plants of many other families; over 100 host plant species were registered. In Bénin, for instance, *R. invadens* was observed most often in and around large cities, being less abundant in commercial orchards and even less so on local mango varieties in farmers' fields.

After its introduction into Africa, a renewed search led to the identification of this species within a complex of mealybug species on mango on the Indian sub-continent. *R. invadens* is now known from India to Indonesia, where it seems to be of minor economic importance. Interestingly, it is still absent from East Africa. Similarly to the situation with cassava mealybug, once the populations of mango mealybug had crashed due to biological control, it also became restricted to mango as its main host.

## Impact of Mealybugs on Farming Communities and First Control Measures

Damage by cassava mealybug is mainly due to the distortion of shoot tips, which are colonized preferentially. Because leaf production stops, carbohydrate accumulation in the tubers ceases and, in the following season, early mobilization of sugars causes severe quality decline of tubers. Early tuber losses were estimated at 80%. In addition, stems became contorted and unfit for use as planting material, so that cassava production collapsed over vast areas. In countries where leaves are consumed as vegetable, this food source also disappeared. This combined effect sometimes led to famine conditions requiring food aid from abroad.

Due to the adaptation of local predators to this new food source and due to farmers' selection of less susceptible cassava varieties, these losses declined within 5 years so that losses were about 40% of pre-invasion conditions in the savannah and highlands and an estimated 20% in the rainforest zone. In most countries, farmers and extension services experimented with insecticide applications. These invariably did not give satisfactory results because of the habit of the insect to hide and find protection in the mass of contorted leaves at the shoot tips.

By contrast, when the mango mealybug first appeared, the first victims were urban home owners and the damage concerned not only the loss of a widely consumed fruit, but also the spoilage of shade trees used as meeting places, by black sooty mould and dripping honeydew. The initial panic reaction of the homeowners consisted of cutting down affected trees. Insecticide spraying on these, sometimes huge, shade trees proved difficult and inefficient, and a quick move to less susceptible varieties was impossible because of the slow growth of these trees. As a result, mango production in the southern part of Bénin, for instance, stopped almost completely in the early 1990s. Mango mealybug infestation then moved quickly north into the commercial production zones.

Both mealybugs invaded a production system based on exotic crops that had been mostly free of important pests and therefore without plant protection measures. In both cases, early local interventions did not offer any relief and losses were catastrophic, though mostly non-quantified.

## Initiating a Biological Control Project: From Discovery to Release

As both species were evidently of exotic origin, classical biological control was the method of choice. Lengthy foreign exploration was undertaken by three international institutions in Central and South America, but was not immediately successful. The first recovery of natural enemies from northern South America from a purported cassava mealybug consisted in parasitoids that, when tested, did not accept *P. manihoti* as host. Later, this mealybug was described as a new species, *Phenacoccus herreni* Williams, and the search had to be continued. Eventually, in 1981, *P. manihoti* was found serendipitously in Paraguay and later in neighbouring provinces of Brazil and Bolivia. The first recovered parasitoid, (*Anagyrus, Epidinocarsis*) *lopezi* De Santis (Hymenoptera, Encyrtidae) (Plate 4), which had already been described earlier from an unknown host from northern Argentina, i.e. from the same general area of the La Plata valley, later proved to be the key species for successful biological control in Africa.

Following rearing and host specificity tests in quarantine in England by what is now CABI *Bioscience*, wasps from several different sources were sent to the IITA in Ibadan, Nigeria, and, later, to IITA in Cotonou, Bénin, for further study and mass-rearing. This transfer was sanctioned by permits from the Nigerian (and later Bénin) Plant Quarantine and executed under the umbrella of the IAPSC. A national biological control committee was established to guide activities, with the IITA representative as the only non-Nigerian member.

At the same time, the non-glamorous task of producing enough *A. lopezi* for release was pursued. Because, according to quarantine regulations, it was not possible to transport cassava plants infested with parasitized mealybugs across borders, enough adult wasps had to be produced and delivered within a short time to assure survival and establishment. After some experience with specially designed high-technology equipment for rearing, eventually a special, decidedly low-tech, rearing cage consisting of a central plastic column filled with coconut husks and watered by drip irrigation equipment, into which 150 cassava sticks could be placed, the whole frame being covered with gauze, gave a simple and efficient rearing unit (Plate 5). Over 1.6 million wasps were produced for releases all over Africa.

First releases in 1981 led to immediate establishment and rapid spread (up to 20 km per generation). Subsequently, the same procedures were used for another 125 releases of *A. lopezi* across Africa (Fig. 3.1). With a few exceptions, these releases were done from the ground. Though a novel release system by airplane had been developed, it was eventually used only rarely in the operational phase of the project because *A. lopezi* proved to be such a good disperser. Within about 10 years, *A. lopezi* was established across all ecological zones from Senegal to the Republic of South Africa.

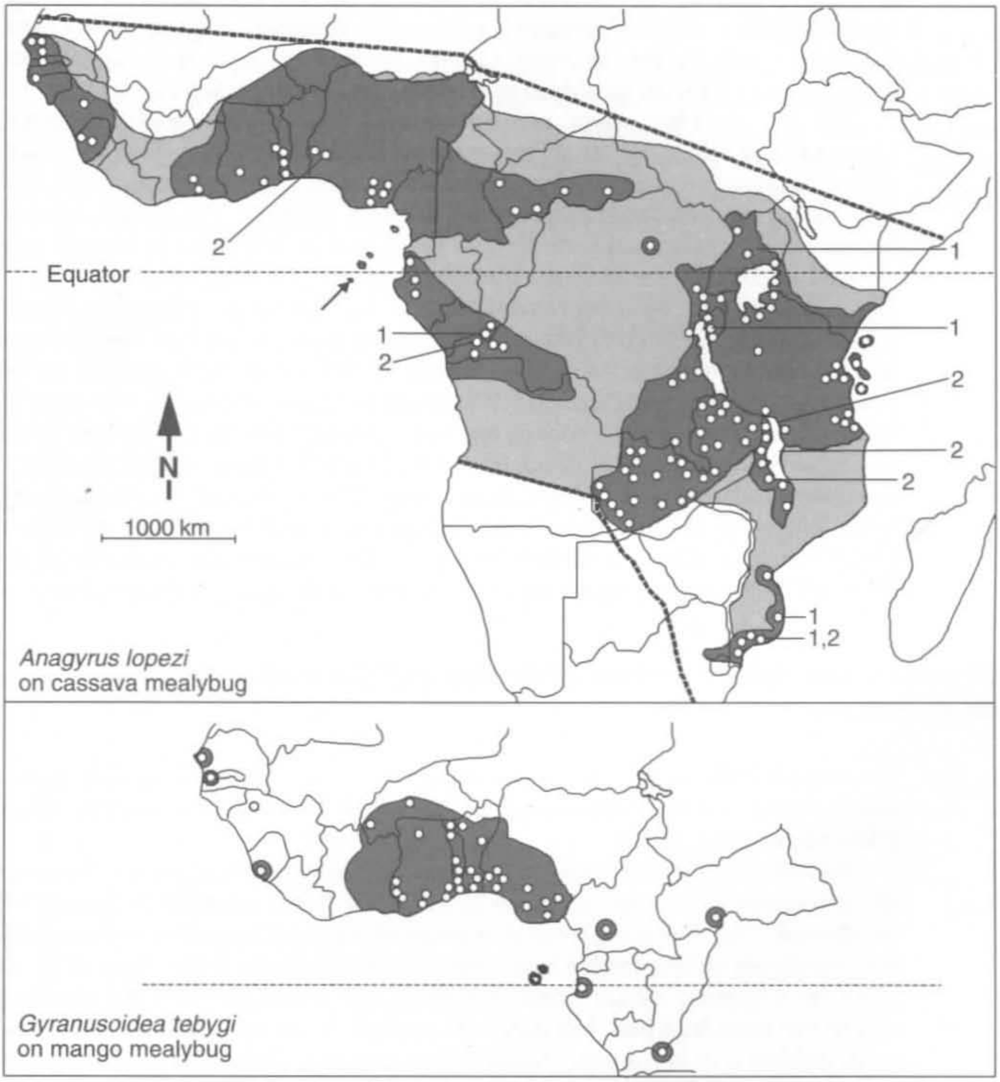

**Fig. 3.1.** Distribution of two hymenopterous parasitoids and their respective hosts in Africa. White dots: release sites (sometimes one dot covers two sites); dark grey: establishment confirmed; light grey: establishment expected; 1: establishment of *Hyperaspis notata*; 2: establishment of *Diomus hennesseyi*.

A few years later, a sister species, *Anagyrus diversicornis* (Howard), was recovered from mealybug infestations set out on potted plants in Brazil. It was brought to Africa, but despite releases in 14 countries, no long-term recoveries were ever made. Several exotic coccinellids and one hemerobiid predator were also imported from Paraguay and/or Brazil. They were released in various African countries (see list in Neuenschwander, 2001), but mostly without establishing permanently (i.e. with recoveries after more than 1 year). Only *Hyperaspis notata* Mulsant and *Diomus hennesseyi* Fürsch (both Coleoptera, Coccinellidae) persisted locally in central and eastern Africa. In most places, indigenous coccinellids and other predators became more numerous on cassava mealybug, which constituted a new and abundant food source. These indigenous natural enemies were capable of reducing peak populations, but they could not stabilize mealybug populations at acceptable levels.

On *R. invadens* two new parasitoids were discovered in India. *Gyranusoidea tebygi* Noyes (Hymenoptera, Encyrtidae) (Plate 7) was passed through quarantine in England and released through a project supported by the Gesellschaft für technische Zusammenarbeit and the FAO. The project was led by the national programme in Lomé, Togo, and in 1987 the parasitoid was released in six localities in Togo. The following year, *G. tebygi* was also sent to IITA Cotonou, to be complemented later by *Anagyrus mangicola* Noyes (Hymenoptera, Encyrtidae) (Plate 8). Both were reared in normal rearing cages and released from the ground. Of *G. tebygi*, 59,000 adults were released on 48 occasions, and of *A. mangicola*, 15,000 wasps were released on 57 occasions, in another ten countries. Both species are now established on all *R. invadens* infestations in West and Central Africa (Fig. 3.1). While *G. tebygi* established immediately in all situations, *A. mangicola* was more difficult because its adults proved to be highly fragile and short-lived. When parasitized mealybugs on potted plants from local rearing units were brought to the field, the species finally established on the remaining high mealybug populations, mainly in urban centres.

## Impact Assessment: Effect of Biological Control on Host Populations

The impact of the exotic parasitoids on their hosts was assessed by IITA and its collaborating national programmes in Africa and has been reviewed in detail (Neuenschwander, 1996).

As a first step, it was necessary to determine whether *A. lopezi* was capable of suppressing its host and to prove its efficiency to the scientists involved and the donors. This was done through a series of exclusion experiments, whereby the parasitoids were excluded from host colonies by sleeve cages, by ants or by chemical treatment. In each case, the result was compared with the situation where the parasitoid had free access to its host. Chemical exclusion gave the most striking and immediate results with population explosions of 40–80-fold over the control plots where parasitoids were active. In three physical exclusion experiments using sleeve cages, which had the advantage of repetitions, parasitoids that had entered through the open base of the sleeve reduced mealybug populations to a mean of 43.5% and 2.3% for *P. manihoti* and 37.0% for *R.*

*invadens*. Where ants were prevented from protecting the mealybugs, whose sweet honeydew they crave, parasitoids lowered population levels to 66.7% of the mealybug population found in the closed sleeves.

Long-term population dynamics studies were started immediately following the release (Fig. 3.2). Of course, such studies should start a long time before the releases in order to develop baseline data, but in the heat of implementing a promising biological control project, we succeeded in capturing an early high host population in only four long-term studies, two on cassava and two on mango. Sampling procedures initially were developed to the best knowledge of the scientists involved, but were later revisited by scientifically developed sampling plans, which gave confidence intervals for different sample sizes. In retrospect, the previously chosen sampling procedure proved to be acceptable. Larger sample sizes would certainly have given better resolution, but were unacceptable because of time limits. In all study sites, samples were taken from physiologically different host plants: susceptible versus relatively unsusceptible cassava varieties in the case of *P. manihoti*, young, susceptible versus old and relative unsusceptible mango leaves in the case of *R. invadens*.

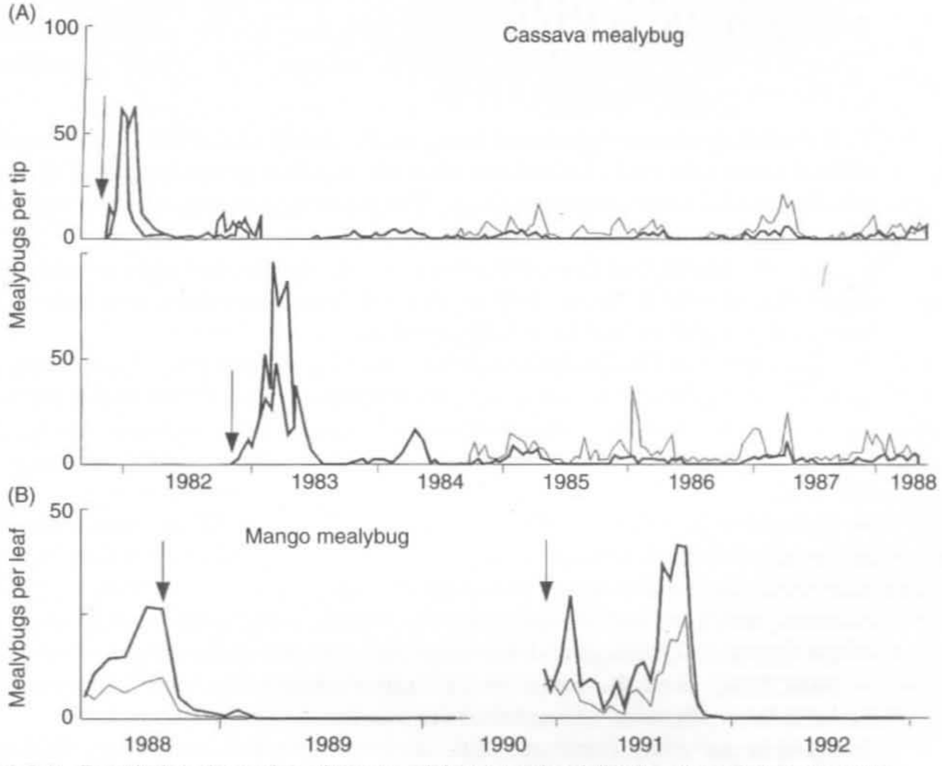

**Fig. 3.2.** Population dynamics of two mealybug species following the release of exotic parasitoids (arrow). (A) Cassava mealybug in Ibadan (top) and Abeokuta (below), both Nigeria; thick line: on IITA cassava variety; thin line: on farmers' variety. (B) Mango mealybug in Ouega (left) and Calavi (right), both Bénin; thick line on young mango leaves, thin line: on old mango leaves.

Overall, populations of *P. manihoti* crashed after the last peak following the release of *A. lopezi* and within 2 years reached low levels with irregular peaks that were about one-tenth as high as the former population peaks just following the releases (Fig. 3.2).

On mango mealybug, which eventually spread across all of West and some parts of Central Africa (Fig. 3.1), the newly established *G. tebygi* immediately reduced host numbers. *A. mangicola* was more difficult to establish and became mostly restricted to mealybug infestations in towns. Population densities of *R. invadens* crashed within 1–2 years, but in contrast to the punctuated equilibrium shown during 7 years of monthly samples of two cassava varieties each, in two locations, mango mealybug populations collapsed totally, leading to local extinction. This was indicated by no recovery of mealybugs during all sampling dates throughout a full year (Fig. 3.2).

Between 1983 and 1995, repeated surveys on cassava were conducted in 11 African countries, and from 1989 to 1991, a survey on mango and other host plants of *R. invadens* was repeated yearly in Bénin. At fixed intervals, regular samples were taken and evaluated in order to document establishment of the exotic species, quantify mealybug populations together with those of their natural enemies and hyperparasitoids, and assess host plant parameters, including yield. The results of the surveys were analysed by multiple regression analysis, published and reviewed (Neuenschwander, 1996, 2001). The following points emerged from these surveys:

**1.** Establishment of *A. lopezi* was highly successful (close to 100%), even under difficult conditions and sometimes with small numbers (a few hundred) of long-travelled and already weakened wasps. The same success was observed with *G. tebygi*. All other species were far less successful, as already mentioned.

**2.** Both *A. lopezi* and *G. tebygi*, once established, immediately spread. The detailed studies of *A. lopezi* indicate that this spread occurred long before the local host population had been fully exploited.

**3.** Mealybug populations collapsed only after 2 (in highlands in East Africa, 4) years. With a generation time of the parasitoid of about 2 (to 3) weeks, this is a strikingly slow effect. We hypothesize that *A. lopezi* starts having an impact on host populations only when emigration rates are compensated for by immigration rates.

**4.** Astonishingly, establishment and good impact by *A. lopezi* were observed across all ecological zones from the Sahel to the rainforest to the East African highlands, despite the rather restricted ecological zone of collection in South America, which did not always match the climate in the establishment zones in Africa. Similarly, *G. tebygi* and *A. mangicola* cover the entire range of their host in West Africa from the forest to the Sudan savannah, except for some dry areas in the north, where invasion of the pest has occurred only recently.

**5.** Most importantly, in surveys that had been repeated many times (Malawi: five yearly surveys; Zambia: ten half-yearly surveys), the duration of *A. lopezi*'s presence in an area proved to be the single most important factor predicting suppression of cassava mealybug populations. This factor was more important than rainfall or other ecological or plant factors. For mango mealybug population densities, the duration of the presence of G. *tebygi* (Bénin: three yearly surveys) was the second most important factor, after 'human population density'. That mango mealybug is particularly abundant on mangos near taxi stands and is a more important pest in urban conditions than in villages or farmers' fields might in fact be attributable to air pollution (Bell *et al.*, 1993).

While sampling both mealybug systems, care was taken to also quantify populations of indigenous natural enemies and competitors. On cassava, 135 species were linked with *P. manihoti*. On mango, the food web was much more restricted, but covered essentially the same species. Though other Homoptera were found, neither exotic mealybug species seemed to have important competitors and, before biological control had been achieved, both mealybugs were the dominant insect species on their host plants across the entire range. Other, indigenous, mealybug species were not attacked by the released exotic wasps, which indicates that both biological control projects against mealybugs in Africa did not endanger biodiversity through unwanted non-target effects. Indigenous parasitoids of mealybugs, mostly *Anagyrus* spp. (Hymenoptera, Encyrtidae), were recovered only occasionally from *P. manihoti* or *R. invadens*; they evidently could not adapt to these new hosts either. Their hyperparasitoids, however, transferred successfully to the three introduced primary parasitoids. The same dozen or so African hyperparasitoid species, though in different proportions, were recovered from both mealybugs, sometimes already on the first sampling date. Exotic hyperparasitoids had been excluded by quarantine, and none were ever recorded in Africa. On *P. manihoti*, the strict density dependence of these hyperparasitoids could be demonstrated. This was highly evident when, in each new establishment area of *A. lopezi*, hyperparasitism rates were in the order of 50%, which worried the local communities. As mealybug populations collapsed and parasitism rates fell, hyperparasitism rates dropped to around 10%. It is worth mentioning that all the above estimates of impact of *A. lopezi* were achieved in the presence of these hyperparasitism rates.

With the arrival of these exotic mealybugs, which both immediately built up huge population densities, indigenous predators of mealybugs, like coccinellids, neuropterans, and the predatory caterpillar of the lycaenid butterfly *Spalgis lemolea* Druce, immediately became abundant. A total of 32 species of coccinellids were recovered from *P. manihoti*, and many of them later on *R. invadens*. They were reducing peak populations of the mealybugs, but could not stabilize host populations at an acceptable level. A simulation model credited them with an overall reduction of *P. manihoti* of about 25%. Once the encyrtid parasitoids exerted control and kept mealybug populations low, these predators (and also the few indigenous *Anagyrus* spp. parasitoids) lost these abundant hosts and their populations became again inconspicuous on cassava and mango. Only two exotic coccinellid species could be established. While the large *H. notata* had to compete with other, abundant *Hyperaspis* spp., *D. hennesseyi* found a particular niche, as indigenous small coccinellids of the tribe Scymnini are relatively rare on cassava. Both released coccinellids remained, however, rather local and never seemed to play an important role in the reduction of cassava mealybug populations.

## Understanding Impact: From Observational Studies to Simulation Models

Field studies across the entire range of the cassava mealybug in Africa unequivocally demonstrated the impact of *A. lopezi* and this project was correctly classified as a major success in biological control. From the beginning, there was, however, skepticism about this claim coming from two angles.

First, *A. lopezi*, though present on all mealybug infestations, was not equally effective in all conditions. On several occasions, our own countrywide surveys indicated that about 5% of all randomly chosen fields had unacceptably high mealybug infestations even after *A. lopezi* had reduced populations. Such fields, invariably, were associated with extremely poor cassava because the soil was pure sand and had no mulch cover whatsoever. In experiments, mulching of such poor soils improved water retention capacity of the soil and the nutrient status of cassava and had a measurable effect on parasitism.

Second, performance measurements of *A. lopezi* in the laboratory and the field initially did not reveal a promising biological control agent. In fact, throughout the indicated field studies, observed parasitism rates remained relatively low (below 50%). Detailed analysis showed that mean parasitism rates slightly increased up to about 25% at a host density of 10 mealybugs per tip, and that the percentage of tips with at least one parasitoid steeply increased to reach a plateau of 70% at the same density of 10 mealybugs per tip. This indicates a density dependent reaction of the parasitoid in response to its host population in this population range, a condition that is considered an important attribute of efficient parasitoids. Above this population density, parasitism rates dropped, however, sharply. In fact, it was observed that highly infested leafless tips with hosts exhibiting strong jerking defence reactions became unattractive to searching parasitoid females. Similarly, life-table parameters were not impressive.

Detailed observations, particularly of the host selection behaviour of the female, gave important clues as to the biological mechanisms that would explain *A. lopezi*'s success. As common in many encyrtids, *A. lopezi* was shown to be a frequent host feeder, particularly on young host stages for which host mortality due to host feeding equalled and was additional to the one through egg laying. In addition, observation of the behaviour of released females in relation to different (manipulated) host colony sizes demonstrated the high host-finding capacity of this species, in relation to other species of natural enemies that were also released in the same experiment. Anecdotal evidence of this high host-finding capacity had already been accumulated from observations following releases. On several occasions, the initial isolated release field had been harvested soon after the release; yet the few survivors of the first generation had still managed to find new fields, sometimes tens of km away. Several laboratories have now reported that *A. lopezi* responds to the odours of the host plant (Nadel and van Alphen, 1987; Souissi and Le Rü, 1999), which is not the case for its coccinellid competitors.

The attributes that made *A. lopezi* special were placed into relief in a parallel study with a sister species, *A. diversicornis*, which was released widely, but could not establish. That *A. diversicornis* is a poor competitor to *A. lopezi* was explained by the small range of host stages on which it could produce female offspring compared with *A. lopezi*, which can produce females even from small hosts. Also, *A. diversicornis* showed a comparatively low host-finding capacity and, in the larval stage, a low intrinsic capacity to compete in multiparasitized hosts.

These observations were integrated into a weather-driven simulation model that predicted plant and tuber growth as well as *P. manihoti* populations. The model has recently been expanded to include a spatial component, accounting for the irregular distribution of mealybug colonies (Gutierrez *et al.*, 1999). Adding *A. lopezi* in this model lowered mealybug populations to 10%, which corresponded to observed field data. The same model also indicated that *A. diversicornis* was competitively displaced by *A. lopezi* in all circumstances. Prior release of this weaker competitor would allow temporary establishment and some impact on *P. manihoti*; but the immigration of *A. lopezi* into *A. diversicornis* territory would still lead to *A. diversicornis*' extinction. These predictions confirm the lack of establishment of *A. diversicornis* in Africa. As for South America, it is predicted that this species, which had only been recovered from *P. manihoti*-infested potted plants, probably has other mealybug hosts of larger size.

By contrast, on mango mealybug, the two parasitoids *G. tebygi* and *A. mangicola* co-exist, both in the field and in cage studies. This is possible because their niches do not totally overlap: *A. mangicola* is far larger than *G. tebygi*, which allows it to overpower large hosts (fourth instars). *G. tebygi* prefers third instar hosts, but uses much time in handling them and grooming after oviposition. As a result, its fitness return is greatest on first instars. This means, that in a new host colony, *G. tebygi* can pre-empt an attack by *A. mangicola*. Both species accept hosts already parasitized by the other species, but inside the same host, *A. mangicola* larvae win more often. As a result of these subtle differences between the two species, where the advantage does not rest on the same side in all conditions, both species co-exist in the field. Thus an early prediction by another simulation model, based on preliminary data, which warned against the release of *A. mangicola*, was refuted.

## Economic Impact: What Does it Mean for the Farmer?

An early economic study with preliminary data predicted a high return on investment (146 to 1). This study was taken up again (Zeddies *et al.*, 2001) with new data on yield losses in different conditions, which also included the initial reduction of yield loss due to indigenous predators and the farmers' choice of relatively tolerant varieties. The impact of *A. lopezi* in different ecological zones, with the now known slow impact of the parasitoid, was superimposed. While yield loss in the first year can be expressed in tons of cassava, the action of the farmer in the following year cannot. Different scenarios were discussed, like the farmer growing a larger acreage of cassava to compensate for loss, or growing maize, or buying maize or cassava, or even receiving food aid. For all scenarios, a dollar value was attributed and added up with depreciation taken into account. Interestingly, the result from this much larger study essentially confirmed the previous one, with returns, depending on the scenario, estimated at between 200 and over 500 for each dollar from donors invested.

For mango mealybug biological control, the returns from southern Bénin alone gave a return on investment in Bénin and Togo, where this project had originated, of 145 to 1. The survey also demonstrated the good knowledge about biological control and the appreciation of its impact by mango producers (Bokonon-Ganta *et al.*, 2002).

In both cases, this is, however, not the whole story. Both projects had brought a sustainable and environmentally friendly solution without any health hazards, at no costs to the farmer and with benefits accruing directly to the farmers, without additional administrative expenditures. As is customary with most biological control projects, these ecological and social benefits had not been taken into account in the above calculations. In addition, the training and awareness building that accompanied particularly the cassava mealybug project had a beneficial effect on the acceptance of other biological control projects in Africa. Today, most African entomologists working in plant protection have at one time or the other profited from courses in biological control given by IITA staff working on the biological control of cassava mealybug.

## The Future: IPM Considerations

Both exotic mealybugs were and are sustainably controlled by their specific exotic parasitoids, introduced in the framework of a classical biological control programme. Interactions with African hyperparasitoids and competition with indigenous coccinellids and other predators were described; they are principally outside the scope of farmers' interventions.

In the case of cassava, there was a high degree of experimenting with new varieties at the height of the cassava mealybug infestation. As *A. lopezi* started to exert control, switchover to other varieties slowed down considerably. Of course, IITA and national institutes tested their varieties for resistance. Some varieties that were less attacked by *P. manihoti* and suffered less damage, were distributed by institutes and extension services, but their popular acceptance was based more on other favourable attributes than on their tolerance towards *P. manihoti*. It is interesting to note that varieties with some antibiosis against *P. manihoti* had a negative effect also on life-table parameters of *A. lopezi* (Souissi and Le Rü, 1998) and negatively influenced life-table parameters of coccinellids feeding on them (Le Rü and Mitsipa, 2000).

Pest population levels, even after biological control had stabilized, were much higher under bad agronomic conditions, for instance on extremely poor sandy and unmulched soils, than where plants were healthy. This opens up the opportunity for advocating IPM measures, like mulching, which – while reducing mealybug infestations – also strengthens plant growth and improves yields.

It has now been shown in the laboratory that mineral fertilization increases resistance of cassava to *P. manihoti* (Le Rü *et al.*, 1994). In the field, it was shown that increasing soil fertility led to larger mealybugs, which in turn resulted in a higher proportion of female *A. lopezi* and an enhanced biological control effect (Schulthess *et al.*, 1997).

While no insecticides are applied in Africa on cassava, insecticide drift from neighbouring fields sometimes affected *A. lopezi* and led to mealybug explosions. Such situations were observed where the pyrgomorphid grasshopper *Zonocerus variegatus* L. was treated, sometimes from the air, or where neighbouring cotton fields were heavily treated with insecticides.

As African agriculture is intensified and might in the future use more insecticides, such IPM situations that require taking into account environmental effects of insecticide use will become more frequent. Similarly, with soil nutrient and soil organic matter being steadily depleted under shortened fallow systems, the proportion of cassava fields susceptible to a mealybug attack despite the presence of *A. lopezi* will probably increase from its present level of about 5%. On mango, it was striking that highest infestations occurred in towns, and mainly at bus and taxi stops, where air pollution might have affected *G. tebygi*. Again, despite government efforts, air pollution is likely to increase in the near future, and with it the situations where high mango mealybug populations make shade trees unattractive.

## Conclusion

The inadvertent introduction of the cassava mealybug into Africa led to a unique alliance of institutions across three continents. The search for the original home proved long and arduous and, as in many other projects, the first introductions of natural enemies failed because of taxonomic confusion. Due to the huge damage done to a subsistence crop, donor support was maintained and eventually led to a great success. The prime natural enemy, *A. lopezi*, on first glance did not look like the best candidate and came from different ecological conditions from those encountered in Africa. It nevertheless adapted to the new conditions, competed against indigenous predators of mealybugs and permanently lowered *P. manihoti* to erratic small peak populations. In many areas, this re-established cassava cultivation and led to a good economic return. Along the way, new rearing methods, monitoring and impact assessment techniques, as well as evaluation by means of computer simulation models were developed so that the project became one of the best-researched biological control endeavours. The early inclusion of numerous African collaborators, their institutions and government agencies, extensive awareness building and training at all levels and material and technical support to African institutions constituted a new approach and had a beneficial effect on the acceptance of other biological control projects in Africa.

The next project done with the same collaborators concerned the equally successful, though less widespread, control of mango mealybug. Though the two mealybugs came from different continents, the scenarios of their invasion and biological control were highly similar. The largest biological difference consisted in the complementarity of the two parasitoids established on mango mealybug. By contrast, on cassava mealybug, a sole parasitoid, *A. lopezi*, kept the host populations low, thereby excluding another similar parasitoid with a different choice of host stages, as well as the indigenous predators, which needed higher host populations to stay in the field.

Both biological control projects had an institution building effect and served as a beacon for a new orientation in plant protection in Africa.

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