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CONTROL OF THE CASSAVA MEALYBUG IN AFRICA: LESSONS FROM A BIOLOGICAL CONTROL PROJECT

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ABSTRACT

During the Africa-wide Biological Control project, the neotropical parasitoid *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae) was established in 26 African countries, causing a satisfactory reduction in the population density of the cassava mealybug *Phenacoccus manihoti* Mat.-Ferr. (Homoptera: Pseudococcidae) in most farmers' fields. Four conclusions concerning the possible application of the research results to other biological control projects are discussed. (1) Foreign exploration was intensive and should be maintained at this level in other projects, if necessary at the cost of other activities. (2) In the controversy about the amount of research needed before the first releases are made, understanding the proper role of quarantine is essential. While quarantine (preferably outside the continent) guarantees non-noxiousness of natural enemies, only research in the experimental release sites can determine whether a given natural enemy will be efficient. The topic of how released exotic insects affect the diversity of the indigenous fauna is also addressed. Modalities used in this project for executing releases, always on request by and in collaboration with national programmes, are recommended for adoption in future projects. (3) Laboratory and field studies, sometimes leading to simulation models, established the scientific basis for quantifying the impact of the pest insect and its biological control. This was expressed as reduction in pest population levels and yield loss, as well as gain in revenue. Such studies are needed in order to attribute the observed effects to various causes and to advance the science of biological control. (4) It is concluded that biological control is the basis of IPM but cannot usually be manipulated by the farmer. Interventions such as cultural methods or the use of resistant varieties need to be compatible with biological control. This is usually so, unless resistances are very strong.

Key Words: **Biological control, *Epidinocarsis lopezi, Phenacoccus manihoti***

RÉSUMÉ

Ce projet a abouti à l'établissement du parasitoïde exotique *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae), d'origine néotropicale, dans 26 pays africains et à une réduction satisfaisante des populations de la cochenille farineuse du manioc, *Phenacoccus manihoti* Mat.-Ferr. (Homoptera: Pseudococcidae), dans la plupart des champs de paysans. Quatre conclusions concernant l'application des résultats de cette recherche à d'autres projets de lutte biologique sont discutées: (1) L'intensité de l'exploration à l'étranger a été considérable et devrait être maintenue à ce niveau dans d'autres projets, même si nécessaire au détriment d'autres activités. (2) Dans la controverse concernant l'intensité des recherches requises avant que les premiers lâchers ne soient entrepris, il est argumenté que la quarantaine (à l'extérieur du continent) doit garantir l'innocuité des ennemis naturels, tandis que seule la recherche dans les champs, dans des foyers de lâchers expérimentaux, peut évaluer l'efficacité d'un agent de lutte biologique. L'influence des lâchers d'insectes exotiques sur la diversité des organismes indigènes est discutée. Les modalités des lâchers

employés, toujours sur requête et en collaboration avec des programmes nationaux, sont justifiées et recommandées pour des projets futurs. (3) Des études scientifiques au laboratoire et aux champs, présentées aussi sous forme de modèles de simulation, ont jeté les bases d' une quantification de l'effet du ravageur et de son contrôle en termes de réduction des populations de la cochenille aussi bien que de pertes, exprimées en tubercules et en termes monétaires. De telles études sont nécessaires pour attribuer les effets observés et pour faire la science de la lutte biologique. (4) La lutte biologique occupe la place centrale dans l'IPM, progresser mais elle ne peut pas être manipulée par le paysan. Les mesures appliquées comme les méthodes culturales ou les variétés adaptées doivent être en accord avec la lutte biologique. Ceci est habituellement le cas, lorsque les résistances ne sont pas très fortes.

***Mots Clés*: *Epidinocarsis lopezi, Phenacoccus manihoti*, lutte biologique**

INTRODUCTION

The cassava mealybug, *Phenacoccus manihoti* Mat.-Ferr. (Homoptera: Pseudococcidae) was accidentally introduced into Africa from the New World in the early 1970s and became the most severe pest on cassava. It became the object of a large-scale biological control campaign by the International Institute of Tropical Agriculture (IITA) in collaboration with numerous national and international organisations. The solitary endophagous parasitoid *Epidinocarsis lopezi* (De Santis) (Hymenoptera: Encyrtidae) was introduced from South America, reared and released in Africa, and is now established in 26 African countries. Wherever country-wide studies on its impact have been made, its efficiency has been proven and biological control has been judged to be good in about 95% of all infested areas. Where the soil is very infertile, however, biological control has been shown to be unsatisfactory, unless complemented by soil-improvement practices. Numerous scientific studies, including exclusion experiments, population dynamic studies, and a simulation model, have demonstrated *E. lopezi*'s impact and how it is achieved. Finally, the economic return from this biological control project was estimated and proved to be excellent.

The research conducted in this project has been reviewed previously (Herren and Neuenschwander, 1991; Neuenschwander, 1993) and the rearing methodologies (Neuenschwander and Haug, 1992) and sampling techniques have been summarised and communicated to the national collaborators, who are supported and linked through an effective network (Herren, 1987, 1990; Neuenschwander and Zweigert, 1994). Training of national scientists has been given high priority and the project has been supported consistently by international donors.

Several studies are still underway and others need to be written up but the activities of the project have now shifted almost totally to implementation. However, several countries particularly in East Africa where the mealybug invaded only recently, are still actively pursuing biological control. Moreover, The International Institute of Tropical Agriculture (IITA) continues to maintain cultures of natural enemies to supply regions which may be invaded by *P. manihoti* in future, particularly Madagascar and other Indian Ocean islands, and Asia.

It has often been said that some of the research and support activities of the cassava mealybug project were not aimed directly at lowering population levels of the pest, but at improving the understanding of biological control in general. This laying of the foundations for other projects is the aspect that I would like to discuss critically here. The key questions are: what lessons can be drawn from the cassava project? In hindsight, what should have been done differently? How can the knowledge gained be applied in implementing IPM in cassava or other crops? These questions are considered under four headings.

MORE FOREIGN EXPLORATION AND IMPORTATION OR LESS?

Foreign exploration for potential natural enemies of the cassava mealybug for introduction into Africa was done by several organisations over much of South America. The results were: (1) - the discovery of a sibling species, *P. herreni* Cox and Williams (1981) in northern South America,

(2) - the discovery of a few localities where *P. manihoti* occurred, (3) - the listing of natural enemies of both mealybug species; and (4) - the collection of many of these natural enemies (sometimes under difficult conditions) which were sent for quarantine to the International Institute of Biological Control, CABI (IIBC) in Silwood Park, England (Löhr *et al.*, 1990). There the species were reared through a generation and then sent to IITA, first in Nigeria, then in Benin, for further study, mass-rearing, and release.

What these efforts did not include were studies on the population dynamics of the mealybug and its natural enemies in South America. We have often been criticised for not having done more. Thus, it has been claimed that the project did not find truly adapted natural enemies (e.g. Nénon and Fabres, 1991). Also, that the project should not have concentrated only on *E. lopezi* (Umeh, 1991) and that *E. lopezi* should have been imported from many sites in order to increase genetic diversity (Biassangama *et al.*, 1988).

In defence of the explorers, it must be noted that the geographical area they covered was impressively large and *P. manihoti* was discouragingly rare. The claim by Nénon & Fabres (1991) and others that *E. lopezi* was maladapted to *P. manihoti* was based on the observation of encapsulation of *E. lopezi* by this host to the extent of around 10% (Nénon *et al.*, 1988; Sullivan and Neuenschwander, 1988). Recent studies have, however, shown that the larvae of another unadapted parasitoid, *E. diversicornis* Howard, were less often encapsulated than those of *E. lopezi*, refuting the notion of encapsulation as a sign of incomplete adaptation (D. Kropf and P. Neuenschwander, unpubl. results). Moreover, the observation of melanisation may in fact have been due to the killing of supernumerary larvae through competition rather than the killing of larvae by encapsulation (Giordanengo and Nénon, 1990).

During the project, a total of four primary parasitoids of *E. lopezi* were imported into Africa and cultured. Three were subsequently released in different ecological zones. *Epidinocarsis lopezi* became dominant, *E. diversicornis* reproduced temporarily in many sites but then disappeared in most, and the third species was never found again. A thorough study of the two *Epidinocarsis* species later revealed small differences in their life histories which were not reflected in the intrinsic rate of natural increase (r_m) (Gutierrez *et al.*, 1993). There were, however, behavioural differences. *Epidinocarsis lopezi* was superior because it attacked earlier host instars, could produce more females on the early instars, and had a higher searching capacity. This led to the competitive exclusion of *E. diversiconis* whenever both species occurred together in Africa. It was speculated that, in South America, *E. diversicornis* persisted on other, larger hosts.

Four *Hyperaspis* species (Coleoptera: Coccinellidae) were also imported and released. *Hyperaspis notata* Mulsant became established in Zaire (highlands of Kivu), Burundi, and Mozambique. At present, *H. notata* from Colombia originally feeding on *P. herreni*, and from Brazil on *P. manihoti*, are available in culture. Both are being tested (B. Stäubli and P. Neuenschwander, unpubl. results), but the differences observed in life table and search parameters seem small.

Hyperaspis raynevali Mulsant, provisionally identified for IITA as *H. ?jucunda*, has been only recovered in a few specimens in Congo (A. Kiyindou, pers. comm.). It seems ill-adapted. The other two species also were not recovered. Another coccinellid, *Diomus hennesseyi* Fürsch, was released in numerous West, Central, East and southern African countries, but it established only in Kinshasa, Zaire (Hennessey and Muaka, 1987), Malawi (Neuenschwander *et al.*, 1991), Mozambique, and perhaps Congo. The predator *Sympherobius maculipennis* Kimmins (Neuroptera: Hemerobiidae) was released but never recovered in substantial numbers.

In summary, the record of introductions in this project corresponds to the success ratio for other biological control programmes from world-wide data (Waage and Greathead, 1988). A more careful matching of release zones with collection areas, often recommended and found to be successful (Messenger and van den Bosch, 1971), was not possible because of the limited distribution of *P. manihoti* in South America. In fact, the establishment and control achieved by *E. lopezi* in climatic zones of Africa as different as the Sahel and the equatorial rainforest is noteworthy. Overall, the South American gene pools of most of the natural-enemy species in culture at IITA are restricted. For most of them, insects from only two countries are available.

The relative dearth of information from the regions of origin is a recurrent problem in classical biological control. In the native habitat, studies of natural enemies are often difficult, particularly because of the rarity of their hosts. This rarity, however, makes for their successful use on other continents. In the past, funds for foreign exploration have been scarce; but it is hoped that, in a period of particular awareness of biodiversity issues (Wilson, 1988, 1992; Waage, 1991; Pimentel *et al.*, 1992; LaSalle and Gauld, 1993), funds for a thorough foreign exploration could be solicited under the 'catch' words of 'applied biodiversity'. After all, careful rearing in order to preserve genetic diversity (Mackauer, 1976) cannot make up for a lack of it because of the small numbers of insects originally available. Further studies in the neotropics are also justified because South America is rich in cassava-attacking arthropod species that have not yet reached Africa (Bellotti and van Schoonhoven, 1978; Bellotti *et al.*, 1994). With increasing international travel, future introductions of new pests into Africa seem inevitable.

For future biological control projects, we would therefore recommend giving priority to foreign exploration during the first few years, even though there is the danger of returning empty handed. So much depends on the quality of these natural enemies that all other considerations, like mass-rearing, laboratory studies on the biology, etc., should be of secondary importance.

STUDIES ON BIOLOGY, OR RELEASES?

The question is not whether one or the other should be done, but the relative importance of the two activities considering the limited resources available. There are different schools of thought on this topic.

A past head of the Inter-African Phytosanitary Council (IAPSC) took an extreme position advocating extensive studies of *E. lopezi* in simulated environments. Apart from the fact that the necessary temperature cabinets are costly and mostly unavailable in Africa, this position had scientific flaws. Observed performance in the insectary suggested that *S. maculipennis* should have been the most successful agent, whereas it was not. *Epidinocarsis lopezi*, by contrast, exhibited many laboratory traits, such as a relatively low r_m, that made it apparently inefficient. It had, in fact, been concluded that *E. lopezi* was not a good control agent (Odebiyi and Bokonon-Ganta, 1986; Fabres *et al.*, 1989; Umeh, 1991), though in a later study a much higher r_m was determined (Iziquel and Le Rü, 1992).

A comparative study of *E. lopezi* and *E. diversicornis* showed that both species had practically the same development parameters, but *E. lopezi*'s dominance was based on behavioural traits like choice of host instar and host searching capacity (Gutierrez *et al.*, 1993). Field experiments demonstrated that *E. lopezi*'s host finding and aggregation capacity surpassed those of all other imported and indigenous predators and parasitoids (Neuenschwander and Ajuonu, 1995). In olfactometer experiments, this remarkable host finding capacity of *E. lopezi* proved to be mediated by plant synomones (Nadel and van Alphen, 1987). By comparison, exotic coccinellids like *Diomus* sp. only reacted to odours of the mealybug itself, while indigenous predators did not respond to odours of the host at all (Hammond, 1988). Both local and exotic coccinellids were, however, arrested by *P. manihoti* and its remains (van den Meiraker *et al.*, 1990).

Most of these studies were done several years after *E. lopezi* had proven to be a successful biological control agent in the field, a judgement obtained from country-wide quantitative surveys and population dynamics studies (see below). It is now evident that life table studies in the laboratory might have led to the rejection of *E. lopezi* for release. This inability of laboratory studies to predict the efficiency of a potential control agent in the field has been noted before (Force, 1974), and it is a sobering thought that screening only led to the right answer after the performance in the new environment was known.

At the heart of the controversy about the amount of studies needed before release lies the notion of quarantine. The Inter-African Phytosanitary Council, originally sought a guarantee of efficiency to be obtained in the target country under quarantine conditions. As already pointed out, it seems impossible to predict efficiency in the field on the basis of laboratory studies. Field-like quarantine structures, on the other hand, are likely to 'leak' and it is therefore dangerous to dilute the quarantine concept by allowing insects into transitory quarantine inside target countries for efficiency studies.

In the IITA project, by contrast, biological control agents were released at experimental sites while concurrent detailed laboratory studies were made. The releases were invariably done in collaboration with colleagues from the national programmes. At the release sites, the establishment (defined as regular recovery one year after release) and the spread of the exotic natural enemies were monitored by sampling *P. manihoti* and other Pseudococcidae that could serve as alternative food sources.

This required the application of a strict quarantine that guarantees non-noxiousness. In the cassava mealybug project, this was done by IIBC in England. All insects were tested for innocuity to bees and silkworms, for freedom from pathogens, and for relative specificity. This last criterion would guard against the introduction of general natural enemies that could endanger indigenous plants and animals. For this project, it was particularly aimed at excluding hyperparasitoids, which are often found in the same families, even genera, as the primary parasitoids that are sought for introduction.

In view of the stabilising effect of hyperparasitoids on the population dynamics of the phytophagous host, it may be argued that even obligatory hyperparasitoids could be accepted for introduction. However, in some projects hyperparasitoids seemed to have prevented effective biological control. Quarantine rules, therefore, forbid the introduction of hyperparasitoids, a pragmatic decision that is generally accepted as sound (Luck *et al.*, 1981). Moreover, indigenous hyperparasitoids are ubiquitous. They readily found and attacked even the earliest colonies of *E. lopezi* (Neuenschwander *et al.*, 1987; Boussienguet *et al.*, 1991), but their impact on *E. lopezi*'s efficiency remained small (Neuenschwander and Hammond, 1988; Goergen and Neuenschwander, 1992).

Most, if not all, vertebrate and mollusc predators clearly do not fulfill the requirement of acceptable specificity and are no longer considered for possible introductions. Recently, even relatively polyphagous insect parasitoids and predators have come under attack as having been responsible for extinctions of rare local insects or plants (Howarth, 1991). Some examples given by Howarth (1991) are, however, not convincing and some claims have since been disproved by field data (Nafus, 1993). It appears that only a few cases of ill effects by classical biological control using arthropod natural enemies of a restricted arthropod prey spectrum have been documented (e.g. Garraway and Bailey, 1992). All the cases involved purely local island species.

In the cassava mealybug project, for example, the indigenous primary parasitoid *Anagyrus nyombae* Boussienguet (described in earler texts as *A.* nr. *bugandensis*) disappeared from cassava fields (Neuenschwander *et al.*, 1987), but was later discovered in adjacent forest (J. Noyes and P. Neuenschwander, unpubl. results). Similarly, numerous generalist mealybug predators were attracted to cassava following the invasion of *P. manihoti*. Some like the coccinellid *Hyperaspis pumila* Mulsant are now uncommon in cassava fields because they lack an abundant food source in this habitat. Their disappearance from cassava was caused by *E. lopezi*. This has, however, nothing to do with extermination. We would like to stress that the introduction of *E. lopezi* led to competitive displacement but *not* to extermination of indigenous parasitoids or predators in the countries where detailed studies were made.

Our project dealt with monophagous parasitoids and oligophagous predators that posed no quarantine problems. In other projects, polyphagous predators were imported. We are well aware that polyphagy in a Petri dish might be misleading, hiding factors in the field that effectively render such a control agent specific. Nevertheless, such predators, in our view, would need particularly careful screening and the costs of such screening need to be weighed against the potential benefits of introducing a polyphagous predator.

The influence of biological control agents on rare non-target organisms was debated by an FAO panel in Rome in 1993 which produced draft guidelines that will form the basis for national biological control legislation. The conclusion was that biological control remains the most rewarding and sustainable pest control practice wherever it can be implemented successfully. The natural enemies have to be screened carefully and professionally. It is in the nature of biological control against weeds that testing different hosts, including crops, takes a larger effort than usually needed in projects against arthropod pests.

The outcome of the world-wide controversy between biological control practitioners and wildlife conservationists (see e.g. Carruthers and Onsager, 1993; Lockwood, 1993) could determine the way biological control is implemented in the future. It behoves us, however, to remember that both sides have similar goals, namely to balance preservation and exploitation, for the sake of future generations, of natural resources, of which biodiversity might in fact be the most important. We also have to weigh the known extermination of a species against the unknown number of exterminations occurring because of habitat destruction if a particular biological control project against an exotic invader cannot be implemented.

We should therefore advocate the continuation of biological control, as is presently being done in the case of the cassava mealybug. In summary, the main features of this project were: (1) screening for non-noxiousness in a quarantine facility *outside* the ecological zone targeted for release; (2) importation of biological control agents only with formal government approval (request for action, import permit) and under the auspices of the IAPSC; (3) releases of exotic species only in collaboration with the national programmes concerned and only on their national territory; and (4) extensive follow-up studies which are discussed below.

WHAT USE ARE STUDIES ON EFFICIENCY?

After the release of an exotic beneficial, there is little entomologists can do to improve its efficiency. In some cases, adding food sources (e.g. growing flowering plants for honey or spraying artificial honeydew) or using arrestants (Hagen *et al.*, 1970; Hagen, 1986) improve the chances for the released insect to remain *in situ*. This, in turn, prevents early dispersal and assures mating of the members of the next generation, whose numbers in practice are often low. Generally, however, direct benefits to the farmer are assured with a properly executed release.

Why, then, did we make such an effort to assess the impact of *E. lopezi*? It is our contention that a biological control project cannot be judged without quantitative assessment of the impact, even if pest populations seem to drop precipitously after the release. In order to obtain the necessary data, surveys that are based on a regular, non-biased, choice of fields and random samples within each field are needed. Unfortunately, the required number of shoot tip samples to be collected in a field, as calculated from sampling plans (Schulthess *et al.*, 1989), is high and at the limit of what is feasible.

Based on such sampling plans, surveys were executed in many African countries. Some of the results await publication including the one for the Congo (W. N. O. Hammond, H. D. Nsiama She, J. Boussienguet, T. Ganga and G. Reyd, unpubl. results). Invariably, a large reduction in mealybug populations or, if the surveys had been done years after the establishment of *E. lopezi*, low pest populations were documented. Low mealybug numbers led to corresponding increases in yield and sometimes in the area of cassava grown.

Successful biological control was, however, not evident to all. In Ghana, for example, farmers in those areas where *E. lopezi* had been present for more than one year, recognised that populations of *P. manihoti* had declined, but invariably attributed this effect to the weather. However, farmers in areas where *E. lopezi* had invaded only recently saw no decline, despite similar weather conditions (Neuenschwander *et al.*, 1989).

In south western Nigeria, farmers experimented with new, mostly local, cassava varieties during the mealybug outbreak. After 1986, the practice of changing varieties to combat mealybug ceased almost completely (P. Ay, 1991, unpubl. report). We take this as recognition by the farmers that the problem no longer preoccupied them. It has been claimed that increased use of mealybug-tolerant varieties was partly responsible (Umeh. 1991), but the observations by the farmers corresponded well with the spread and impact of *E. lopezi* on *P. manihoti* in this area as documented by Neuenschwander and Hammond (1988). In fact, IITA varieties tolerant to *P. manihoti* accounted at the time for only a small part of planted cassava (Akoroda *et al.*, 1989) and the alleged spread of tolerant local varieties was not substantiated by data.

In Malawi, some farmers claimed falsely that their fields were devastated by cassava mealybug because they hoped to prolong food aid by these means (Neuenschwander *et al.*, 1991). Moreover, these claims were accepted in a sociological study (Pelletier and Msukwa, 1990).

The impact of biological control is often slow. In Zambia, infestations and damage by *P. manihoti* actually increased after the first releases. In any one area, they only declined in the second year. Because of further spread of *E. lopezi* to new areas, the decline became significant at the country level only in the fourth year (Chakupurakal *et al.*, 1994). Similar observations were made in Malawi (Neuenschwander *et al.*, 1991). So, understandably, ministry officials and extension agents were at first worried and sceptical. In Nigeria, for example, it took many years before entomologists would acknowledge that *E. lopezi* did more than just spread extremely fast.

During regional conferences in Mombasa, Kenya in 1992 and Bujumbura, Burundi in 1993, however, all countries of central and southern Africa that had been infested by *E. lopezi* for some years reported good biological control and vastly reduced population levels of *P. manihoti*. Consequently, the insect was relegated to minor pest status (Allard *et al.*, 1994). Without monitoring, neither the countries' extension agents and plant protection officials, nor the entomologists at IITA would have known this. Conversely, without the consent of the majority of affected countries, IITA could not have scaled back its cassava mealybug operations, as it has done now.

Surveys were complemented by studies on population dynamics. Frequent long-term monitoring (for more than a year and at short intervals) was reported only from Nigeria (Hammond and Neuenschwander, 1990) and Ghana (Cudjoe, 1990), but several other studies remain to be published. All show predominance of *E. lopezi* among the natural enemies and generally low mealybug populations. These findings were supported by the results of exclusion experiments in Nigeria and Ghana (Neuenschwander *et al.*, 1987; Cudjoe *et al.*, 1992). In some restricted areas, however, *P. manihoti* populations remained unacceptably high (Neuenschwander *et al.*, 1990; Le Rü *et al.*, 1991).

Apart from documenting mealybug population levels, field studies furthered understanding of the interactions between parasitoids, phytophagous insects and plants, as described in a simulation model (Gutierrez *et al.*, 1988a, b). Further experiments on tri-trophic relations showed that adding nutrients or mulch to very infertile sandy soils measurably improved plant health. Stronger plants allowed the mealybugs to become larger in size which, in turn, affected the sex ratio of *E. lopezi* and improved biological control (F. Schulthess, P. Neuenschwander and S. Gounou, unpubl. results). Such sex ratio shifts relative to the available host instars had been demonstrated previously for *E. lopezi* (van Dijken *et al.*, 1991).

In view of this tri-trophic relationship and the demonstrated density-dependence of *E. lopezi* (Hammond and Neuenschwander, 1990), the often expressed desire to release additional *E. lopezi* into remaining foci of mealybug infestations, i.e, to make 'supporting releases', is not justified scientifically. Reducing mealybug populations in residual foci is best achieved by improving plant conditions by mulching (cited above), a technique that was further studied in agronomic experiments (Okeke, 1990; Ohiri and Ezumah, 1990; Ehui *et al.*, 1991). When additional releases are made - and IITA sometimes participated in such actions - they must be clearly understood as being a political palliative, serving for information and publicity only.

In summary, studies concerning the efficiency of an exotic biological control agent in comparison to its indigenous enemies and competitors and in relation to the growth of the host plant, are essential to guide a project. This involves primarily questions of when and where to release agents once the experimental releases have led to successful establishment and when to stop releasing. These studies also apportion the contribution to the pest population reductions and yield increases among the released agents and other factors. In addition to just describing the pest population levels, we also tried to elucidate the underlying mechanisms responsible for the observed success in biological control, but this is tricky (Murdoch, 1993). The cassava mealybug project is one of few in which many of these questions have been addressed and partially answered. Since reviews on biological control often lament the lack of such studies it seems to be time that the scientific impact of the project is recognised.

BIOLOGICAL CONTROL OR IPM?

By destroying existing, sometimes unrecognised, natural enemies, all insecticide treatments run the risk of necessitating more treatments:- the dreaded "pesticide tread mill" (van den Bosch, 1978; Gips, 1987). In order to minimise insecticide use, the IPM concept was formalised (Stern *et al.*, 1959). It relies heavily on the recognition of threshold population levels, which in practice increase as the season progresses (Hueth and Regev, 1974). Though selective use of insecticides is possible (Pickett, 1988; Greathead, 1989), the record on safety and efficiency in their use by smallholders is generally poor (Andrews and Bentley, 1990). Moreover, frequent state subsidies for pesticides in developing countries are incompatible with IPM (Goodell, 1984). However, change is possible if the will to change is mustered, as in the Philippines. Rice production in Asia is only now recovering from the pesticide tread mill (Fox, 1991; Kenmore, 1991).

The unease with an often misused IPM concept, combined with occasional misdirected resistance breeding (van Emden, 1991), has gradually led to the development of a more holistic approach (Huffaker, 1979; Croft *et al.*, 1984). This development culminated in the definition of systems management, which puts emphasis on prevention by repairing agricultural ecosystems, rather than by relying only on what is still present (Delucchi, 1987, 1989). In this concept, sustainability of the resource basis becomes as important as production (Rabbinge, 1993) and the degradation of these resources is recognised as being ultimately an economic, social and political problem (Jones, 1993).

In developing the cassava mealybug project, the above ideas were adapted to the conditions of the African farmer and insecticide use was deliberately excluded (Herren, 1987; 1990). It is only now, after the successful implementation of the classical biological control project, that insecticides sometimes are seen to do damage. Thus, on several occasions, local outbreaks of *P. manihoti* were observed, e.g., in Ghana, Benin, and Nigeria, where *E. lopezi* had been killed by drift of insecticides from cotton fields and those applied against the variegated grasshopper, *Zonocerus variegatus* L. (Orthoptera: Pyrgomorphidae) (see also Modder, 1994). To meet these eventualities, IPM decisions are now required on how best to apply insecticides without harming natural enemies. Since these insecticide-induced pest resurgences occur only occasionally, the Asian model of IPM in rice mentioned above applies only marginally to African subsistence farming.

The influence of soil conditions on the cassava mealybug was recognised early on (Fabres, 1981), but effective cultural control became feasible and effective only under the umbrella of biological control (Neuenschwander *et al.*, 1990).

From the beginning, IITA relied on research on host plant resistance (HPR) and biological control to give long-term sustainable solutions. Owing to past successes by the international centres in HPR (Bosque-Perez and Buddenhagen, 1992), HPR was given equal if not higher priority than biological control. In fact, HPR was always core-funded, whereas biological control was 'only' a special project.

Some IITA cassava varieties, derived from parents which originated in East Africa (Beck, 1980; Jennings, 1994), proved to be less attacked by *P. manihoti* than other varieties, particularly local Nigerian ones (Hahn *et al.*, 1989). This reduced susceptibility was attributed to the hairiness of the young leaves. By lowering the rate of settlement of crawlers, hairiness imparts some antixenosis to such varieties. Cyanide content could not be linked definitively with cassava mealybug population levels. Thus, antibiosis could not be demonstrated (Schulthess *et al.*, 1987). In fact, recent studies indicate that cyanide may even be beneficial to the development of *P. manihoti* (Le Rü, 1994). Detailed studies on the physiology of cassava of different growth types, in relation to pest insects, revealed that some IITA varieties excelled by having a superoptimal leaf area index (LAI) (F. Schulthess, unpubl. results). By the sheer vigour of the canopy they could sustain more mealybug damage than some local varieties, i.e, they exhibited tolerance.

After much controversy between resistance breeders and biological control specialists at IITA, there is now general agreement that the cassava mealybug was reduced mainly by *E. lopezi*, but that the level of control achieved differs among varieties. Breeding efforts are no longer directed at finding varieties resistant to *P. manihoti*, but care is taken not to select inadvertently a particularly susceptible variety.

It is concluded that, in the future, classical biological control should be given priority when new exotic pests are to be combatted. Favouring biological control would save costs since breeding, selecting, and disseminating new resistant varieties takes a long period of time in the order of ten years.

The resistances to *P. manihoti* discovered in some cassava varieties were rather weak (Hahn *et al.*, 1989). Such resistance can slow down the development of a phytophagous insect, thereby exposing the pest for a longer time to predation and parasitism (Panda, 1979). In such cases, the assumed synergy between biological control and resistance breeding is probably correct.

When resistance is strong, however, the population dynamics of all the organisms involved have to be considered. Thus, Thomas and Waage (1994) modelled the interactions between different types of resistance in plants, the different life styles in phytophagous insects and the different response of predators and parasitoids to their host. The model takes into account that a reduction in pests will decrease the efficiency of natural enemies because of their density-dependence. If compensation is complete, this does not seem, at first glance, to pose any disadvantage. This conclusion is, however, wrong. If most of the reduction in pest populations is achieved by breeding alone, there is strong selection pressure for the phytophagous insect to overcome this resistance. In fact, break-down of resistance has been observed frequently (Georghiou, 1990). Single gene or vertical resistance has often been overcome, requiring new breeding efforts within a few years (Heinrichs, 1992). Horizontal resistance, involving many genes, provides more stability, but has not been widely deployed against insects (Robinson, 1991; Simmonds, 1991; Thomas and Waage, 1994). In this 'race' between host plant and phytophagous insect, the breeder's selection is opposed by the pest insect. Therefore, the system is not stable and is certainly not self-renewing. It would have been better to have the same population reduction achieved by biological control, which pits insect against insect and leads to a stable equilibrium.

The counterpart to resistance break-down, the much dreaded 'resurgence', understood here as a permanent increase in host populations following successful biological control, on the other hand, has never been observed in practice. Theoretical reasons have been proposed for why it should occur (Pimentel, 1961). They involve a hypothetical 'agreement' between host and parasitoid by which both populations would stay at a high level. This hypothesis does not take into account other competing predators. For example, *E. lopezi* is adapted to low host populations; it has an extremely high searching capacity and, despite the fact that it is time-limited (Hammond *et al.*, 1995), low fecundity. With this combination of characters, it occupies a niche on its own by excluding coccinellids. Coccinellids are adapted to high host populations, being oligophagous and having relatively low search capacities but high egg loads.

Apart from a (total) compensation by the density-dependent reaction of the natural enemy, there exist other scenarios where resistance breeding and biological control are not additive. The much-touted hairiness of leaves can have many different and contradictory effects (Obrycki, 1986). Far from being a deterrent, some hairs facilitate settling of homopteran crawlers by satisfying their thigmotactic response. Other types of hairs, particularly those with glandular secretions, can strongly inhibit natural enemies (Rabb and Bradley, 1968; Hulspas and van Lenteren, 1978). In addition, breeding might produce cassava plants lacking chemical components that act as synomones for attracting parasitoids, as with *E. lopezi* (Nadel and van Alphen, 1987).

These examples, some taken from different crops, demonstrate why entomologists have a more important role when they collaborate with breeders than merely producing insects for homogeneous infestations, or developing scoring scales for the evaluation of breeding lines. It is for these reasons that in 1992 the Host Plant Resistance Programme was created within the Plant Health Management Division of IITA.

In summary, we suggest that there are situations where biological control should be given priority over resistance breeding. Biological control can give a sustainable solution to pest problems that HPR cannot match, particularly where pests have been newly introduced and where breeding and biological control efforts are not additive, but are either compensatory or outright antagonistic. With hindsight, it is clear that in the cassava mealybug project the two groups would have collaborated better if they had taken into account each other's results. Retaining an IPM concept that was not adapted to the local conditions and thinking that all possible options in IPM must be pursued, were a mistake that was made also in many national programmes and by other institutions.

As to the question 'biological control or IPM?', we can now conclude that, in the implementation of IPM, biological control is the foundation upon which rest other approaches that need continuous human intervention. Host plant resistance requires continuous efforts by researchers in breeding, and cultural control practices must be applied regularly by the farmers. In the implementation of IPM, lack of communication often remains the single most important stumbling block (Escalada and Heong, 1993). Even for those techniques that do not need to be brought to the farmers by the extension services, like biological control, there are numerous steps between donors and their governments, international institutions, national research institutions, universities, and extension services, and - as a feedback - the press, where human relations play a prime role. These relationships have been reviewed (Neuenschwander, 1993), but to foster them needs a conference such as the one that led to this proceedings volume.

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