Biological Control **21,** 214–229 (2001)
doi:10.1006/bcon.2001.0937, available online at http://www.idealibrary.com on IDEAL®

Biological Control of the Cassava Mealybug in Africa: A Review

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Received March 15, 2001; accepted March 20, 2001

Among several natural enemies introduced to combat the cassava mealybug, *Phenacoccus manihoti* (Homoptera: Pseudococcidae), the neotropical parasitoid *Apoanagyrus (Epidinocarsis) lopezi* (Hymenoptera: Encyrtidae) was the most successful. It established in 26 African countries, causing a satisfactory reduction in the population density of *P. manihoti* 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 results needed before first releases are made, an understanding of the proper role of quarantine is essential. Whereas quarantine (preferably outside the continent) guarantees nonnoxiousness of natural enemies, only research in the experimental release sites can determine whether a given natural enemy will be efficient. It was confirmed that the released exotic insects did not affect the diversity of the indigenous fauna. Modalities used in this project for the execution of releases, i.e., always on request by and in collaboration with national programs, are recommended for adoption in future projects. (3) Laboratory and field studies established the scientific basis for quantifying the impact of the pest insect and its control by *A. lopezi*. This was expressed as reduction in pest population levels and yield loss and gain in revenue. Behavior of adult females in searching and choosing hosts was identified as a better predictor of efficiency of a species in the field than life table studies under controlled temperatures. (4) It is concluded that biological control is the basis for integrated pest management. Other interventions, such as cultural methods or the use of resistant varieties, need to be in harmony with biological control because the impact of natural enemies cannot usually be manipulated by the farmer. To achieve sustainability, the aim is to optimize tritrophic interactions among the plant, the phytophagous pest organisms, and their natural enemies, rather than to maximize the effect of a single intervention. © 2001 **Academic Press**

***Key Words: Apoanagyrus lopezi;* cassava mealybug; *Phenacoccus manihoti;* biological control; IPM; Africa.**

INTRODUCTION

The cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae), was accidentally introduced into Africa from South America in the early 1970s, becoming the most severe pest on cassava. A large-scale biological control campaign by the International Institute of Tropical Agriculture (IITA) in collaboration with numerous national and international organizations led to the successful control of *P. manihoti*. Numerous scientific studies demonstrated important interactions among cassava, the mealybug, and exotic and indigenous natural enemies and quantified the impact by *Apoanagyrus (Epidinocarsis) lopezi* De Santis (Hymenoptera: Encyrtidae) on cassava mealybug, tuber yield, and farmers' revenue. This research has been reviewed (Herren and Neuenschwander, 1991; Neuenschwander, 1993) and the rearing methodologies (Neuenschwander and Haug, 1992) and sampling techniques have been summarized and communicated to the national collaborators, who are supported and linked through an effective network with high priority on training of national scientists (Herren, 1990; Neuenschwander and Zweigert, 1994). The project has been supported consistently by international donors.

Many of the scientific studies have now been published. Some additional implementation is still planned, particularly in eastern and southern Africa. IITA continues to maintain cultures of natural enemies to supply regions which may be invaded by *P. manihoti* in the future, particularly Madagascar, other Indian Ocean islands, and Asia. It is therefore opportune to draw lessons from this project, which in 1996 cumulated in the award of the prestigious World Food Price to the former director of IITA's Plant Health Management Division, Dr. H. R. Herren. This paper expands at

1049-9644/01 $35.00

length on some material previously presented earlier in the program (Neuenschwander, 1994). It gives an update and focuses on questions of particular interest in view of recent controversies concerning classical biological control.

FOREIGN EXPLORATION AND IMPORTATION OF EXOTIC SPECIES

Foreign exploration for potential natural enemies of the cassava mealybug for introduction into Africa was done by several organizations in much of Central and South America, starting in the late 1970s. The results of this vast search were: (1) A bisexual species, *Phenacoccus herreni* Cox and Williams (1981) was discovered in northern South America, but its parasitoids did not accept *P. manihoti* as a host. (2). *P. manihoti*, a parthenogenetic species, was discovered in 1981 in a few localities, first in Paraguay by the Centro Internacional de Agricultura Tropical (CIAT) and later in nearby parts of Brazil by explorers from the Gesellschaft für technische Zusammenarbeit (GTZ) and IITA. (3) An inventory of natural enemies of both mealybug species was established (Löhr *et al.*, 1990). As in other biological control projects, it was difficult to study natural enemies in their native habitat because of the rarity of their host. (4) All natural enemies of *P. manihoti* destined for introduction in Africa were sent for quarantine to the International Institute of Biological Control CABI (IIBC) in Silwood Park, England. To guarantee nonnoxiousness, the insects were reared through one generation and tested for innocuity to bees and silkworms, absence of pathogens, and 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 exclusion of hyperparasitoids. Since hyperparasitoids have sometimes prevented effective biological control, quarantine rules forbid their introduction (FAO, 1996). From quarantine, primary parasitoids and oligophagous predators were sent to IITA, first in Nigeria and then in Benin, for further study, mass-rearing, and release. To increase genetic diversity (Mackauer, 1976), most beneficial insects were imported several times from both Paraguay and Brazil.

The ultimate success of this biological control project hinged on thorough foreign exploration. Though huge areas were covered, *P. manihoti* was found in a very restricted area only. For future biological control projects, we would again 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, such as mass-rearing, laboratory studies on the biology, etc., should be of secondary importance. 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; LaSalle and Gauld, 1993; Pimentel *et al.*, 1992), funds for thorough foreign exploration could be solicited under the catch word of "applied biodiversity."

Further studies in the Neotropics are 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, new introductions of other pests into Africa seem inevitable.

RELEASE, ESTABLISHMENT, AND SPREAD OF EXOTIC NATURAL ENEMIES

To test their capability to establish in the new environment, biological control agents that had successfully passed quarantine were released at experimental sites while concurrent detailed laboratory studies were made. The releases were invariably done in collaboration with colleagues from the national programs. At the release sites, the establishment (defined as regular recovery 1 year after release) and the spread of the exotic natural enemies were monitored by the sampling of *P. manihoti* and other Pseudococcidae that could serve as alternate food sources. *A. lopezi* was imported in 1981 and released for the first time the same year. Since it quickly became the dominant species and on the basis of studies demonstrating its efficiency (see below), many releases followed. Table 1 for the first time gives a comprehensive list of the releases made in Africa by IITA and its national collaborators, from 1981 to 1995. No releases have been made since 1994.

Two other primary parasitoids of *P. manihoti* were caught in South America in sufficient numbers to make it through quarantine. *Apoanagyrus (Epidinocarsis) diversicornis* Howard (Hymenoptera: Encyrtidae) was released in different ecological zones (Table 1), where it reproduced temporarily, but disappeared from most sites. Today, it seems to persist perhaps in Rwanda and in coastal Kenya (G. Goergen and H. R. Herren, pers. comm.). *Allotropa* sp. (Hymenoptera: Platygasteridae) was released on many occasions, but disappeared from all release sites.

Four *Hyperaspis* species (Coleoptera: Coccinellidae) were also imported and released (Table 1). *Hyperaspis notata* Mulsant (Coleoptera: Coccinellidae) became established in Zaire (highlands of Kivu), Burundi, and Mozambique. At present, *H. notata* from Colombia, originally feeding on *P. herreni*, and from Brazil, originally feeding on *P. manihoti*, are available in culture.

H. raynevali Mulsant, provisionally identified for IITA as *H. ?jucunda*, had been recovered in Congo (A. Kiyindou, pers. comm.), but seemed ill adapted. Another two *Hyperaspis* species were released, but were

TABLE 1

Complete List of Releases of Exotic Parasitoids and Predators against the Cassava Mealybug, by IITA and Its Collaborators, in Africa from 1981 to 1995

Country	Locality[a]	Date[b]	Species	Number[c]
Burundi	Kabonga, Nyanza	1/88	*A. lopezi*	9610
			H. notata	750
			D. hennesseyi	1960
			Hyperaspis sp.	743
			Allotropa sp.	1780
		7/88	*A. lopezi*	4000
			H. notata	50
			D. hennesseyi	600
	Magara, Ruziba, Rumorge	7/89	*A. lopezi*	16650
			H. notata	150
			D. hennesseyi	500
			A. diversicornis	500
			Allotropa sp.	150
	Limbo	11/89	*A. lopezi*	16600
	Bubanza	2/90	*A. lopezi*	5800
			A. diversicornis	2750
Central African Republic	Boda, M'Baïki	3/88	*A. lopezi*	18000
			H. notata	750
			D. hennesseyi	4000
			A. diversicornis	800
			Hyperaspis sp.	450
			Allotropa sp.	2600
	Dombé II, Bogoula, Bakère (Badissi, Bogamangon Berberati, Ndyoh, Bolitoua Boda, Bossembélé, Sibut)	4/88	*A. lopezi*	97800
			H. notata	1250
			D. hennesseyi	85600
			A. diversicornis	3400
			Hyperaspis sp.	100
			Allotropa sp.	1000
	Bangassou, Bambari (Kaga Bandoro Bangui, Ouango)	5/88	*A. lopezi*	40600
			D. hennesseyi	3800
			A. diversicornis	1000
			Hyperaspis sp.	300
			Allotropa sp.	1600
Congo	Brazzaville	9/82	*H. jucunda*	400
	Brazzaville, Mantsoumba	6/82–10/83	*A. lopezi*	3000[d]
	Mbè	10/83–9/84	*A. lopezi*	—[d]
Côte d'Ivoire	Toumodi	4/86	*A. lopezi*	7700
			D. hennesseyi	9000
		5/86	*A. lopezi*	20400
			H. notata	1400
			D. hennesseyi	2000
			H. jucunda	300
			Allotropa sp.	2200
	Abidjan	3/87	*A. lopezi*	3000
			D. hennesseyi	3000
			Hyperaspis sp.	1000
	Bingerville	4/87	*A. lopezi*	6350
			D. hennesseyi	1600
			Hyperaspis sp.	1200
Equitorial Guinea	Annobon	6/90	*A. lopezi*	2750
			H. notata	150
			D. hennesseyi	100
			A. diversicornis	200
Gabon	Libreville, Moujla	2/86	*A. lopezi*	1200[d]
			Allotropa sp.	400
	Mouila	9/86	*A. lopezi*	500[d]
Gambia	Jambanjali	3/84	*A. lopezi*	250
		3/85	*A. lopezi*	4000
Ghana	Pokoase, Sege	3/84	*A. lopezi*	1800

TABLE 1—*Continued*

Country	Locality[a]	Date[b]	Species	Number[c]
			H. notata	100
			D. hennesseyi	2200
	Accra		*H. jucunda*	100
	Koforidua	11/84	*A. lopezi*	2600
			H. notata	100
			D. hennesseyi	2000
			H. jucunda	100
			S. maculipennis	1400
	Kumasi, Bimbila	3/85	*A. lopezi*	24000
	Ejura	4/89	*A. lopezi*	11400
			H. notata	330
			D. hennesseyi	180
			Hyperaspis sp.	30
Guinea Bissau	Bissau	1/84	*A. lopezi*	1500
		2/85	*A. lopezi*	1700
			S. maculipennis	3500
			D. hennesseyi	500
Guinea Conakry	Telimele, Kindia	4/89	*A. lopezi*	10000
			H. notata	210
			D. hennesseyi	550
			Hyperaspis sp.	90
	Pita	6/89	*A. lopezi*	9590
			H. notata	719
			D. hennesseyi	119
	Telimele, Kindia	5/90	*A. lopezi*	7650
			H. notata	520
			D. hennesseyi	250
			A. diversicornis	2600
		6/90	*A. lopezi*	4575
			H. notata	400
			D. hennesseyi	300
Kenya	Migori, Muhuru	7/90	*A. lopezi*	20100
	Kisumu	8/90	*A. lopezi*	22350
			H. notata	600
			D. hennesseyi	250
			A. diversicornis	1000
			Allotropa sp.	1000
	Giribe, Kisumu	11/90	*A. lopezi*	1500
Malawi	Nkhata Bay	11/85	*A. lopezi*	6500
			H. notata	200
			D. hennesseyi	2200
			H. jucunda	100
	Thekero, Lwezga, Chisumulo (Kaporo, Salima, Monkey Bay Nkhata Bay, Nkhotakota)	3/86	*A. lopezi*	7000
			D. hennesseyi	1600
	Chintheche, Chilumba	7/86	*A. lopezi*	6000
			D. hennesseyi	4200
			Allotropa sp.	1600
	Chintheche, Chilumba	8/86	*A. lopezi*	1200
			D. hennesseyi	1000
	Mgorozera, Chihami, Thowolo	10/86	*Allotropa* sp.	3080
	Balaka, Nkhata Bay	6/87	*A. lopezi*	23200
			D. hennesseyi	1800[d]
			A. diversicornis	600
			Allotropa sp.	2400
	Karonga, Nkhotakota	8/87	*A. lopezi*	4900
			D. hennesseyi	1900
			A. diversicornis	270
			Allotropa sp.	1330
		9/87	*A. lopezi*	14580
			H. notata	50
			D. hennesseyi	4000
			A. diversicornis	300
			Hyperaspis sp.	100

TABLE 1—*Continued*

Country	Locality[a]	Date[b]	Species	Number[c]
			Allotropa sp.	2600
	Mangochi	8/88	*A. lopezi*	10900
			H. notata	100
			D. hennesseyi	800[d]
			Hyperaspis sp.	50
	Mulanje	10/89	*A. lopezi*	5750
Mozambique	Maputo	7/88	*A. lopezi*	20000
			H. notata	500
			D. hennesseyi	4100
	Catembe	8/88	*A. lopezi*	9000
			D. hennesseyi	2900
			Allotropa sp.	400
	Xai-Xai, Lichinga, Inhambane	9/89	*A. lopezi*	22924
			H. notata	1250
			D. hennesseyi	100
			A. diversicornis	800
			Hyperaspis sp.	100
			Allotropa sp.	1200
	Beira, Inhambane, Xai Xai	9/90	*A. lopezi*	14800
			H. notata	450
			D. hennesseyi	200
			A. diversicornis	300
	Maputo	6/93	*A. lopezi*	3000
Nigeria	Abeokuta	12/80	*H. jucunda*	1200
	Ibadan, Ilora	11/81–1/82	*A. lopezi*	1850
	Ibadan		*D. hennesseyi*	2200
	Aguleri-Otu	10/82	*A. lopezi*	1500
	Abeokuta	10–11/82	*D. hennesseyi*	1500
		11–12/82	*A. lopezi*	2050
	Ibadan	3/83	*S. maculipennis*	10
	Onne	5/83	*A. lopezi*	420
	Abeokuta		*D. hennesseyi*	471
	Enugu	12/83	*A. lopezi*	2000
	Olokoro		*A. lopezi*	5000
	Etiti		*A. lopezi*	5200
	Ibere		*A. lopezi*	1200
	Igbariam	2/84	*A. lopezi*	500
	Otobi	3/84	*A. lopezi*	300
	Ibadan	10/84	*S. maculipennis*	200
	Moniya, Ibadan	11/84	*D. hennesseyi*	1000
	Ibadan		*S. maculipennis*	2330
		4/85	*S. maculipennis*	700
		5/85	*S. maculipennis*	2365
	Abeokuta		*Allotropa* sp.	1500
	Ibadan	11/85	*Allotropa* sp.	600
	Abeokuta, lgbo Ora	1/86	*Hyperaspis* sp.	150
			Allotropa sp.	670
	Ibadan	2/86	*A. lopezi*	7200
			D. hennesseyi	7200
	Abeokuta		*Hyperaspis* sp.	100
	Ibadan		*Allotropa* sp.	636
	Abeokuta, Ibadan	3/86	*Allotropa* sp.	620
	Ibadan	4/86	*Allotropa* sp.	2128
		5/86	*A. lopezi*	2000
			Allotropa sp.	1600
		8/86	*A. diversicornis*	100
	Abeokuta	11/86	*Allotropa* sp.	1200
		12/86	*A. lopezi*	70
			A. diversicornis	70
	Abeokuta, Ibadan	1/87	*H. notata*	400
			D. hennesseyi	2000
			A. diversicornis	150
			Hyperaspis sp.	250
			Allotropa sp.	3130

TABLE 1—*Continued*

Country	Locality[a]	Date[b]	Species	Number[c]
	Ibadan	3/87	*A. diversicornis*	650
		4/87	*A. diversicornis*	1500
		6/87	*A. diversicornis*	200
	Ibadan, Umudike	11/87	*Allotropa* sp.	2000
			A. diversicornis	930
	Umudike	12/87	*A. diversicornis*	3100
		1/88	*A. diversicornis*	1600
Rwanda	Gisenyi, Byahi	1–6/85	*A. lopezi*	4800
			H. notata	100
			H. jucunda	100
		10/85	*H. notata*	850
			D. hennesseyi	2240
			H. jucunda	300
		9/86	*A. lopezi*	4320
			Allotropa sp.	1200
	Kibuye	6/87	*A. lopezi*	10000
			Allotropa sp.	4000
		8/87	*A. lopezi*	10800
			H. notata	100
			D. hennesseyi	1200
			Allotropa sp.	2800
	Gitarama	2/90	*A. lopezi*	25800
			H. notata	170
			D. hennesseyi	250
			A. diversicornis	6870
			Hyperaspis sp.	81
	Kigali, Gitarama	3/90	*A. lopezi*	20000
			H. notata	980
			D. hennesseyi	50
			A. diversicornis	3650
		7/91	*A. lopezi*	5500
		11/91	*A. lopezi*	4300
Senegal	Thiès	2/84	*A. lopezi*	250
	Tivaouane		*A. lopezi*	112
			H. notata	150
		3/84	*D. hennesseyi*	4400
	Tivaouane	2/85	*S. maculipennis*	3600
	Dakar	5/85	*A. lopezi*	9700
	Bayakh	1/92	*H. notata*	300
			D. hennesseyi	500
	Moussa Mbougane		*A. diversicornis*	1000
			Hyperaspis sp.	200
			Allotropa sp.	100
Sierra Leone	Freetown, Newton	12/85	*A. lopezi*	3500
			H. jucunda	200
			Allotropa sp.	2000
	Makeni, Freetown, Lunghi, Newton	3/87	*A. lopezi*	5200
			Allotropa sp.	1200
	Makeni, Freetown	5/87	*A. lopezi*	4400
			H. notata	700
			D. hennesseyi	4000
			Hyperaspis sp.	1700
			Allotropa sp.	2000
	Freetown, Lunghi	4/88	*A. lopezi*	5000
	Port Loko	4/89	*A. lopezi*	17000
			H. notata	120
			A. diversicornis	200
Tanzania including Zanzibar	Dar-es-Salaam	2/88	*A. lopezi*	4000
	Sanze, Mzenga	6/88	*A. lopezi*	10000
	Zanzibar, Mbamba Bay, (Kigoma, Matema, Mbeya)	9/88	*A. lopezi*	49600
	Ngulakula, Kisiju	10/88	*A. lopezi*	38000
	Pemba	7/89	*A. lopezi*	17200∼
	Musoma, Nachingwea	8/89	*A. lopezi*	34200
	Mwanza	9/89	*A. lopezi*	14050

TABLE 1—*Continued*

Country	Locality[a]	Date[b]	Species	Number[c]
		10/89	*A. lopezi*	35750
	Mwanza, Morogoro	11/89	*A. lopezi*	21550
		1–2/90	*A. lopezi*	1015
	Mtwara, Lindi	8/90	*A. lopezi*	22000
	Mafia Isl.	9/90	*A. lopezi*	14150
	Musoma, Mwanza	10/90	*A. lopezi*	105000
	Tabora, Migori, Ukerewe Island	11/90	*A. lopezi*	143650
	Kibaha	11/94	*H. notata*	900[d]
	Kibaha, Bunda, Mara	7/95	*H. notata*	490
Togo	Glidji, Bokokopè, Togoville (Kamina, Sokodè)	3/84	*A. lopezi*	2500
			D. hennesseyi	2700
	Aného	3/87	*A. lopezi*	5500
			H. notata	200
			D. hennesseyi	2000
			Hyperaspis sp.	300
			H. jucunda	200
			Allotropa sp.	50
	Aného, Lac Togo	3/88	*D. hennesseyi*	1000
			A. diversicornis	580
			Allotropa sp.	800
Uganda	Tororo, Lumino, West Budama	5/92	*A. lopezi*	5800
	Tororo	6/92	*A. lopezi*	6700
			H. notata	500
		9/92	*A. lopezi*	12750
			H. notata	160
	Masindi	9/92	*A. lopezi*	17600
			H. notata	500
			D. hennesseyi	300
	Arua	7/93	*A. lopezi*	6600
			H. notata	1890
			D. hennesseyi	700
Zaire	Kinshasa	7/82	*A. lopezi*	200
	M'Vuazi		*A. lopezi*	800
	Likasi	7/83	*A. lopezi*	325
			H. notata	19
			D. hennesseyi	2250
	Lubumbashi	3/84	*A. lopezi*	400
			D. hennesseyi	200
	Kikwit, Mosango	5/84	*A. lopezi*	500
	Kazenze	10/84	*A. lopezi*	605
	Bunkeya, Malemba-Nkulu (Goma, Museka)	8/85	*A. lopezi*	6300
			H. notata	410
			D. hennesseyi	540
			H. jucunda	225
			Allotropa sp.	150
			S. maculipennis	200
	Kinshasa	6/86	*Allotropa* sp.	3000
	Kinkondja	8/87	*A. lopezi*	4550
			Allotropa sp.	2000
	Moba, Kisangani	11/87	*A. lopezi*	39200
			H. notata	300
			D. hennesseyi	8800
			Hyperaspis sp.	1100
			Allotropa sp.	4200
	Kinshasa	5/88	*A. lopezi*	600
	Goma, Kisangani	8/88	*A. lopezi*	4000
			H. notata	50
			D. hennesseyi	1200
			A. diversicornis	100
			Allotropa sp.	600
	Luberizi, Saké, Uvira	8/90	*A. lopezi*	12450
	Goma		*H. notata*	500
			A. diversicornis	1000
	Uvira	9/92	*A. lopezi*	7800

TABLE 1—*Continued*

Country	Locality[a]	Date[b]	Species	Number[c]
Zambia	Mansa, Mwense	10/84	*A. lopezi*	3360
			H. notata	150
			D. hennesseyi	2370
			H. jucunda	150
			S. maculipennis	950
		1/85	*A. lopezi*	660
			S. maculipennis	200
	Mansa, Samfiya	7/85	*A. lopezi*	2400
	Chilubi, Nsombo, Mununga, Lubwe (Kaputa, Mpulungu)	8/86	*A. lopezi*	16910
			D. hennesseyi	5440
			Allotropa sp.	8600
	Luanshya, Mufulira, Solwezi (Mwinilunga)	9/86	*A. lopezi*	28600
			H. notata	200
			D. hennesseyi	4920
	Manyinga, Samfiya, Serenje	9/86	*A. lopezi*	19940
			H. notata	390
			D. hennesseyi	950
			H. jucunda	50
			Allotropa sp.	6300
	Chinsali, Mukupa-Katandula	7/87	*A. lopezi*	35750
			D. hennesseyi	1330
			Hyperaspis sp.	300
			Allotropa sp.	2100
	Mpika, Mongu	8/87	*A. lopezi*	24300
			H. notata	450
			D. hennesseyi	3020
			Allotropa sp.	5300
	Lukulu, Zambezi	9/87	*A. lopezi*	44650
			H. notata	1155
			D. hennesseyi	6670
			Allotropa sp.	9600
	Solwezi, Mwinilunga, Kabompo	10/87	*A. lopezi*	24800
			H. notata	500
			D. hennesseyi	8000
			Hyperaspis sp.	200
			Allotropa sp.	7000
	Mbala	8/88	*A. lopezi*	10900
			D. hennesseyi	2090
	Chambeshi, Chingola	10/88	*A. lopezi*	24450
	Kabwe	11/88	*A. lopezi*	18330
	Mongu, Kaoma, Senanga	9/89	*A. lopezi*	21256
			H. notata	1400
			D. hennesseyi	400
			Allotropa sp.	1000
	Kabompo, Kasama, Mporokoso (Isoka, Kapenga)	10/89	*A. lopezi*	27430
			H. notata	1680
			A. diversicornis	300
	Lusaka	10/90	*A. lopezi*	1000

[a] Sometimes only the main locality is indicated. Localities in parentheses refer to the line above. Names are not repeated on the next line if identical.
[b] Dates are not repeated on the next line if identical.
[c] Wherever prerelease mortalities were known, the numbers represent live insects.
[d] Partially from local insectaries. Not all figures are known.

never recovered. *Diomus hennesseyi* Fürsch (Coleoptera: Coccinellidae) was released in numerous African countries (Table 1), but was established only in Kinshasa, Zaire (Hennessey and Muaka, 1987), Malawi (Neuenschwander *et al.*, 1991; Borowka, 1996), Mozambique, and perhaps Congo. The predator *Sympherobius maculipennis* Kimmins (Neuroptera: Hemerobiidae) was released, but never recovered in substantial numbers. In the insectary, however, it outcompeted all other exotic natural enemies.

The record of introductions in this project seems to correspond to the success ratio for other biological control programs as observed in a worldwide data set (Waage and Greathead, 1988). A more careful matching of release zones with collection areas, often a successful tool (Messenger and van den Bosch, 1971), was not possible because of the limited distribution of *P. manihoti* in South America. In fact, the establishment by *A. lopezi* in climatic zones of Africa as different as the sahel and the equatorial rainforest is noteworthy.

DETERMINING THE QUALITY OF NATURAL ENEMIES

From life table studies of indigenous and exotic coccinellids held under different constant temperatures, the niche of each species was described. The exotic *H. raynevali* thereby showed no distinctive advantages over indigenous African species (Nsiama She *et al.*, 1984; Fabres and Kiyindou, 1985; Kiyindou and Fabres, 1987; Kanika-Kiamfu *et al.*, 1992).

H. notata, from Colombian highlands and Brazilian lowlands, crossed freely and reproduced on several mealybugs that are common on cassava, but not on other homopterans that can also be found on the same plant host (Stäubli Dreyer *et al.*, 1997a). *H. notata* showed a remarkable capacity to survive and reproduce, though slowly, on minimal amounts of food (Stäubli Dreyer, 1997a), but this trait was not compared with that trait in indigenous coccinellids. At all temperatures tested, the differences between beetles of the two origins in life table and search parameters and functional responses of the adults were small (Stäubli Dreyer, 1994; Stäubli Dreyer *et al.*, 1997b). It was concluded that introduction of a specially adapted strain of *H. notata* was an attractive idea, but the results indicated no particular benefits for implementation.

On the basis of laboratory studies, it had been concluded earlier that *A. 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 rate of increase was determined (Iziquel and Le Rü, 1992).

Such life table data were then used in a simulation model and the potential impact of *A. lopezi* and coccinellids on *P. manihoti* was estimated (Gutierrez *et al.*, 1988a,b). In the absence of information on searching capacity and prey consumption for local African coccinellids, data from other species were used. The resulting simulations, which were in line with independently obtained field data, predicted a 10-fold reduction due to *A. lopezi* and an additional 25% reduction attributable to coccinellids. This model was later integrated into a more general tritrophic model (Gutierrez *et al.*, 1994).

A comparative study of *A. lopezi* and *A. diversicornis* clarified the mechanisms by which *A. lopezi* was efficient, as shown by its performance in the field. Both species indeed had practically the same developmental parameters, but *A. lopezi's* dominance was based on behavioral traits such as choice of host instar and host searching capacity, which are not reflected in the intrinsic rate of natural increase (Gutierrez *et al.*, 1993). The key lay in the following behavioral differences (van Alphen *et al.*, 1989; Neuenschwander and Ajuonu, 1995; Pijls *et al.*, 1995, 1996): *A. lopezi* was superior because it attacked earlier host instars, could produce more females on the early instars, had an advantage in mixed infestations inside the same host, and had a higher search capacity. This led to the competitive exclusion of *A. diversicornis* whenever both species occurred together in Africa. It was speculated that, in South America, *A. diversicornis* persisted on other, larger hosts. It is interesting to note that in southern Brazil this species had been collected from plants artificially infested with *P. manihoti*.

Contrary to expectations, the apparent lack of adaptation of *A. diversicornis* was not associated with a higher degree of encapsulation of its eggs within *P. manihoti*. In fact, encapsulation was lower in *A. diversicornis* than in *A. lopezi* (D. Kropf and P. Neuenschwander, unpublished results). In the latter species, a 10% encapsulation rate had been found repeatedly, which had sometimes been interpreted as a sign of maladaptation (Nénon *et al.*, 1988; Sullivan and Neuenschwander, 1988; Giordanengo and Nénon, 1990).

Field experiments demonstrated that *A. 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 *A. lopezi* proved to be mediated by plant synomones (Nadel and van Alphen, 1987). By comparison, exotic coccinellids, such as *Diomus* sp., reacted only to odors of the mealybug itself, whereas indigenous predators did not respond to odors 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 years after *A. lopezi* had proven to be a successful biological control agent in the field, a judgement obtained from countrywide 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 *A. 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 led to the right answer only after the performance in the new environment was known.

DOCUMENTING IMPACT ON CASSAVA MEALYBUG AND YIELD

Techniques for evaluating the efficacy and ultimate impact of biological control agents released against *P.*

manihoti and two other exotic homopterans have recently been compared and reviewed (Neuenschwander, 1996). The best technique to quantify impact on a large scale was based on surveys with a regular, nonbiased choice of fields and random samples within each field, based on sampling plans (Schulthess *et al.*, 1989). Such surveys were executed by IITA in collaboration with national programs in many African countries. To the best of our knowledge, no comparable surveys were done by other institutions. Invariably, a large reduction in mealybug populations or, if the surveys had been done years after the establishment of *A. lopezi*, low pest populations were documented. Where relatively high infestation levels were reported (locally in Nigeria, Congo, etc.) this was from limited areas only (5% of randomly chosen fields). Low mealybug numbers led to correspondingly higher yields and sometimes expanded cassava cultivation.

The success of biological control was, however, not evident to all. In Ghana, for example, farmers recognized that populations of *P. manihoti* had declined, but attributed this effect to weather. In contrast, no decline was reported from areas with similar weather conditions, but without long term presence of *A. lopezi* (Neuenschwander *et al.*, 1989).

In southwestern Nigeria, the formerly common practice of changing varieties to combat mealybug ceased almost completely after 1986 (P. Ay, 1991, unpublished report), i.e., after the establishment of *A. lopezi*. We take this as recognition by the farmers that the problem no longer preoccupied them. Though cassava varieties tolerant to *P. manihoti* had been developed by IITA and the national program, they accounted for only a small proportion of all cassava grown (Akoroda *et al.*, 1989) at the time of the collapse of the *P. manihoti* infestations. Today, tolerant varieties cover vast areas and mean mealybug numbers are lower than on susceptible varieties.

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). These claims were accepted as facts 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 declined only in the second year. Because of further spread 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 worried and sceptical.

In these surveys all over Africa, no ecologies were ever found, in which *A. lopezi* was unable to establish itself. On the northern fringe of distribution of cassava, *P. manihoti* populations wax and wane. *A. lopezi* might loose contact with its host populations locally and therefore not exert sufficient control. In the vast body of the cassava belt, however, such phenomena of dissociation have never been observed.

During regional conferences in Mombasa, Kenya in 1992 and in Bujumbura, Burundi in 1993, all countries of central and southern Africa that had been infested by *A. lopezi* for some years reported good biological control with vastly reduced population levels of *P. manihoti*, and the insect was relegated to minor pest status (Allard *et al.*, 1994). Since then, the situation has remained essentially the same. In vast national surveys based on equal-area sampling grids and nonbiased choice of fields in Ghana, Benin, Nigeria, and Cameroon (Yaninek *et al.*, 1994) this was later confirmed.

IMPACT ON NONTARGET SPECIES

Introductions of relatively polyphagous parasitoids and predators in classical biological control campaigns have recently been claimed to be responsible for extinctions of rare local species (Howarth, 1991). Examples are, however, often not convincing and some claims have since been disproven by field data (Nafus, 1993). It appears that only a few cases of ill effects by classical biological control with arthropod natural enemies of a restricted arthropod prey spectrum have been documented (e.g., Garraway and Bailey, 1992). All cases involved local island species.

In the cassava mealybug project, the indigenous primary parasitoid *Anagyrus nyombae* Boussienguet (described in earlier texts as *A.* nr. *bugandensis)* disappeared from cassava fields (Neuenschwander *et al.*, 1987). It was later caught in yellow pans in adjacent forests where it attacked its yet unknown mealybug host (J. Noyes and P. Neuenschwander, unpublished results). Other *Anagyrus* spp. rarely reproduced on the newly arrived *P. manihoti*.

A rich species complex of indigenous hyperparasitoids of these primary parasitoids, however, profited from the introduction of *A. lopezi*. Hyperparasitoids proved to be ubiquitous, readily finding and attacking even the earliest colonies of *A. lopezi* (Neuenschwander *et al.*, 1987; Boussienguet *et al.*, 1991). Because of their density-dependent reaction to *A. lopezi* populations, they reached high levels at the beginning of the campaign and in remaining foci of infestations of *P. manihoti*, but not in low-density equilibrium situations. In large cage experiments, hyperparasitoids did not stop *A. lopezi* from controlling *P. manihoti* (Goergen and Neuenschwander, 1992). Similarly, *A. lopezi's* documented suppression of mealybug populations in the field was achieved in the presence of hyperparasitoids (Neuenschwander and Hammond, 1988), whose biologies have meanwhile been studied in detail (Goergen and Neuenschwander, 1990, 1994). How *A. lopezi* would fare in the field without hyperparasitoids can, however, not be inferred from the data.

Similarly, numerous generalist mealybug predators were attracted to cassava because of the invasion of *P. manihoti*. Some, such as the coccinellid *Hyperaspis pumila* Mulsant, are now uncommon in cassava fields because they lack an abundant food source in this habitat. It is concluded that the introduction of *A. lopezi* led to some competitive displacement, but not to extermination of indigenous parasitoids or predators. Though the influence of biological control agents on rare nontarget organisms, as stipulated in the new FAQ guidelines (FAQ, 1996), was not specifically tested in this project at the time of introduction, the introduced organisms would probably fulfill the modern safety requirements.

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

UNDERSTANDING IMPACT

To better understand how impact was achieved by biological control, surveys were complemented by studies on population dynamics. Frequent long-term monitoring (for more than 1 year and at short intervals) was reported only from Nigeria (Hammond and Neuenschwander, 1990) and Ghana (Cudjoe, 1990). Both show predominance of *A. lopezi* among the natural enemies throughout the year and low equilibrium levels of mealybug populations.

In some restricted areas (about 5%), marked by extremely poor soils with low water retention capacity, however, *P. manihoti* populations remained unacceptably high despite the presence of *A. lopezi* (Le Rü *et al.*, 1991; Neuenschwander *et al.*, 1990). Further experiments on tritrophic relations showed that the addition of nutrients or mulch to such infertile sandy soils measurably improved plant health. Stronger plants allowed the mealybugs to become larger in size which, in turn, increased the ratio of female *A. lopezi* and improved biological control (Schulthess *et al.*, 1997). Such sex ratio shifts relative to the available host sizes had been demonstrated for *A. lopezi* before (van Dijken *et al.*, 1991). They depend on the ability of the female to determine the sex of their offspring (and the degree of superparasitism) (van Dijken *et al.*, 1993).

In view of this tritrophic relationship and the demonstrated density dependence of *A. lopezi* (Hammond and Neuenschwander, 1990), the often expressed desire to release additional *A. lopezi* into remaining foci of mealybug infestations, that is, to make “supporting releases,” is not justified scientifically. Reduction of mealybug populations in residual foci is best achieved by a good choice of tolerant cassava varieties and by improvement of plant conditions by mulching (cited above), a technique that had been tested 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.

The much dreaded “resurgence,” understood here as a permanent increase in host populations following successful biological control, has not been observed with the cassava mealybug. Neither has it been observed in other biological control projects unless new introductions of other pest races occurred. Theoretical reasons have been given to explain why populations of a parasitoid and its host would stay at a high level (Pimentel, 1961). This hypothesis does not take into account other competing predators. For example, *A. lopezi* is adapted to low host populations; it has an extremely high searching capacity and, despite the fact that it is time limited, a low fecundity (Hammond, 1988). With this combination of characters, it occupies a niche on its own. *A. lopezi* thereby excludes oligophagous coccinellids, which—with relatively low search capacities, but high egg loads—are adapted to high host populations.

INTEGRATION INTO AN INTEGRATED PEST MANAGEMENT (IPM) CONCEPT

By destroying existing, sometimes unrecognized, natural enemies, unchecked insecticide treatments lead to the dreaded “pesticide tread mill” (van den Bosch, 1978; Gips, 1987). To minimize insecticide use, the original IPM concept, which relies heavily on the recognition of threshold population levels, was formulated (Stern *et al.*, 1959). In practice, intervention thresholds 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 in developing countries are incompatible with good IPM (Goodell, 1984). Change is possible only where the will to change is mustered. This was the case for example in the Philippines, where rice production is now recovering from this pesticide syndrome (Kenmore, 1991; Fox, 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 the deficiencies in agroecosystems (Delucchi, 1987). In this concept, sustainability of the resource basis becomes as important as production (Rabbinge, 1993) and the degradation of these resources is recognized as being ultimately an economic, social, and political problem (Jones, 1993).

In combating the cassava mealybug, plant health management had to be adapted to Africa, where small-scale and resource-poor farmers produce a diversity of locally adapted crops by using few resources other than their labor (Herren, 1994). In most conditions, insecticide use was no option and biological control was therefore especially indicated. It is only now, after the successful implementation of the classical biological control project, that insecticides sometimes are seen to play a role. Thus, on several occasions, local outbreaks of *P. manihoti* were observed, where *A. lopezi* had been killed by drift of insecticides from cotton fields or by those applied against the variegated grasshopper, *Zonocerus variegatus* L. (Orthoptera: Pyrgomorphidae). To meet these eventualities, IPM decisions are now required on how best to apply insecticides on adjacent crops without harming *A. lopezi*. 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 recognized early on (Fabres, 1981), but effective cultural control became feasible only under the umbrella of biological control (Neuenschwander *et al.*, 1990).

From the beginning, IITA relied on research on host plant resistance and biological control to give long-term sustainable solutions. Some cassava varieties proved to be little attacked by *P. manihoti* and other pests (Beck, 1980; Hahn *et al.*, 1989). The reduced susceptibility to *P. manihoti* was attributed to pubescence of young leaves. Hairiness of leaves can, however, 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-Jordaan and van Lenteren, 1978).

Cyanide content of cassava was sometimes assumed to be the factor responsible for antibiosis, though tests could not link it with lower cassava mealybug population levels (Schulthess *et al.*, 1987). In fact, cyanide may even be beneficial to the development of *P. manihoti* (Le Rü and Calatayud, 1994). Detailed studies on the physiology of cassava of different growth types, in relation to pest insects, revealed that some varieties excelled by the sheer vigor of the canopy, allowing them to sustain more mealybug damage than some local varieties (Schulthess and Saka, 1992).

As concerns cassava mealybug control, there is now general agreement that this pest was reduced mainly by *A. 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 specially susceptible varieties. This requires a breeding effort, in collaboration with biological control specialists, which aims at optimizing these tritrophic interactions.

Recent models quantifying the interactions between different types of resistance in plants and the different response of predators and parasitoids to their host demonstrated that host plant resistance and biological control are most often compatible (Thomas and Waage, 1996). Where resistances are moderate, breakdown of resistance, observed particularly with strong single-gene or vertical resistance (Georghiou, 1990), is reduced and systems become more sustainable. Horizontal resistance, involving many genes, provides more stability, but has not been widely deployed against insects (Robinson, 1991; Simmonds, 1991; Thomas and Waage, 1996). Moderate resistance can slow down the development of a phytophagous insect and expose the pest for a longer time to predation and parasitism (Panda, 1979).

All plant protection interventions on cassava are now sought to be integrated in an ecologically sustainable manner, adapted to the different ecological and socioeconomic conditions (Yaninek and Schulthess, 1993). In this IPM concept, biological control is the foundation upon which other approaches that need continuous human intervention rest. For successful implementation, communication with and among farmers and researchers, between donors and international and national institutions, and as a feedback from the press are needed (Escalada and Heong, 1993; Neuenschwander, 1993; Yaninek *et al.*, 1994).

ACKNOWLEDGMENTS

The cassava mealybug project was financed mainly by the aid agencies of Austria, Belgium, Canada (IDRC), Denmark, Germany (BMZ-GTZ), Italy, the Netherlands, Norway, and Switzerland and by the African Development Bank, the European Economic Community, the International Fund for Agricultural Development, and the UNDP. I specially thank my colleagues at IITA for stimulating discussions.

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