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Review Article

Biological control of *Rastrococcus invadens*

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Abstract
Rastrococcus invadens became a serious pest of (especially) mango and citrus in West Africa in the 1980s. Economic losses were high, with mango yields often reduced by 50–90%, and pest infestations also caused social and cultural problems. Surveys for natural enemies were conducted in India and Malaysia, following taxonomic work which identified the likely origin of the pest. Work in India resulted in the provision of two primary encyrtid parasitoids, *Gyranusoidea tebygi* and *Anagyrus mangicola*. *Gyranusoidea tebygi* was released in Togo in 1987–88, rapidly controlled the mealybug in most areas, and spread at around 100 km/year. *Anagyrus mangicola* was introduced after laboratory studies indicated that it was unlikely to reduce control by *G. tebygi* and was likely to supplement it in certain situations. Both parasitoids were subjected to high levels of indigenous hyperparasitism, which did not interfere markedly with the control exerted. The mealybug remains under good control; the benefits to African farmers amount to many multiples of research and implementation costs and the project also resulted in the amelioration of many social problems caused by the mealybugs.

Keywords
Rastrococcus invadens
Gyranusoidea tebygi
Anagyrus mangicola
mealybugs
parasitoids
biological control
mango
citrus
fruit trees

1. Introduction

In 1982 an exotic mealybug was observed in the coastal regions of the West African states of Ghana, Togo and Benin where it rapidly became a serious pest especially of mango *(Mangifera indica)* and citrus *(Citrus* spp). Taxonomic research showed that the insect was an unknown species which was described as *Rastrococcus invadens* Williams (Hom., Pseudococcidae) [1]. Agounké *et al.* [2] investigated the distribution, food plants and indigenous natural enemies of *R. invadens* in Benin and Togo. Although the species is polyphagous, mango, citrus, breadfruit (*Artocarpus altilis*), banana (*Musa* spp.), frangipani (*Plumeria alba*) and species of *Ficus* were among the most attacked hosts. They assessed the damage caused to mango, and the intensity of attack on about 20 plants (classified as forest trees, vegetables, shade trees, fruit trees and ornamental plants) but also reported occurrence on 45 plant species of 22 families [2]. Biassangama *et al.* [3] presented a similar list of 23 food plants supporting *R. invadens* in the Congo. Agounké *et al.* [2] also listed 14 species of indigenous predators (Coleoptera, Lepidoptera and a chrysopid) and one parasitoid (a species of *Anagyrus*). These natural enemies had little impact on the populations of the mealybug which consequently reached very high levels.

The mealybugs occurred in vast numbers on the leaves and fruit of hosts; they weakened plants by puncturing the tissues and consuming sap but the major damage was caused by the production of large amounts of honeydew upon which saprophytic fungi developed. The resultant thick black layer of sooty mould caused a drastic reduction in the photosynthetic activity in the plants, worsened by the premature drop of mature leaves. In some areas the flowers were also destroyed by the mealybugs. Fruit production was greatly reduced by severe infestations. In addition to its agricultural importance the infestations had an adverse social impact, especially on rural life in West Africa [4]. The pest spread rapidly and was soon present in Sierra Leone, Côte d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Gabon, Congo and the Democratic Republic of Congo [5, 6]. Its continued spread threatened fruit production in the neighbouring countries.

Infestation of fruit caused a significant reduction in the weight and size of fresh mango fruit, reflected in significant reductions in the ash content, crude fibre and reducing sugar levels of both ripe and unripe fruit [7] and protein, fat and carbohydrate levels [8]. The sooty mould *Capnodium mangiferum* Cooke & Broome (Capnodiaceae) was found to raise the leaf temperature of infected mango seedlings.

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In Nigeria the spread of *R. invadens* was greatest in the humid southwest [9]. *Rastrococcus invadens* was found on over 20 species of host plants belonging to 12 plant families ranging from fruit crops (which constituted 42.8% of the crop species attacked) to food crops (14.28%) and to shade trees and ornamentals (42.85%). The severity of attack, based on the number and area of foliage, inflorescence and fruit attacked by *R. invadens* alone or together with sooty mould, was highest in mango, citrus, breadfruit, guava (*Psidium guajava*) and ornamentals including oleander (*Nerium oleander*), frangipani and roses (*Rosa* spp.). The frequency with which infested plants were being felled, burnt or sprayed with synthetic chemicals showed that the presence of *Rastrococcus invadens* caused a degree of panic in growers, a feature noted by Agounké *et al.* [2] and Vögele *et al.* [4].

The range of effects of *R. invadens* include the sociological impact of the pest [4]. Yields of mango and citrus plummeted, effectively to nothing in areas with longest exposure to the insect. These crops provided the most freely available fruit energy and vitamin A and C sources, especially valuable for children in a part of the world where up to 20% of infants die before the age of five. In a fragile economy where people relied heavily on mango and citrus fruit for income supplements, the economic impact was devastating.

However, the mealybug's significance went beyond economics. In Togo, and many other West African countries, village life is centred around particular trees. They are the central meeting points for rest, debate, judgement and community action and training. Forebears planted many trees which consequently were the last links with parents or grandparents and animists believed that gods were incarnate within the trees. These trees, with leaves dropping sticky honeydew below, attracting clouds of flies or denuded of leaves and so providing little shade, were unable to fulfil their social functions [4]. The mango tree also has medicinal uses, for curing fevers and other ailments.

2. Biocontrol Project

The Food and Agriculture Organization of the United Nations (FAO) provided assistance to the Government of Togo for the biological control of the mealybug, tentatively identified as *Rastrococcus spinosus* (Robinson), through a project beginning in April 1986. Within the framework of the project, CABI Bioscience (then the International Institute of Biological Control) was contracted to search for suitable natural enemies, to assess their effectiveness if found, and to make them available for release in Togo. This work was conducted in conjunction with scientists of the Service de la Protection des Végétaux (SPV), Togo and the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ). Through the project activities two suitable primary parasitoids were identified and released in collaboration with the International Institute of Tropical Agriculture (IITA) in Cotonou (Benin), and SPV, Benin who proceeded to conduct extensive scientific and practical work on the pest problem and its biological control by both primary parasitoids.

2.1. Taxonomy

At the start of the project it became obvious that not only was the taxonomic status of the pest mealybug uncertain, so was its distribution. Identification [1] allowed confirmation of the origin of the mealybug as the Oriental Region, where it was known from a wide area, but always mistaken for *R. spinosus*, a closely related species.

Studies of available *Rastrococcus* spp. material at the Natural History Museum, London (UK) indicated Malaysia and perhaps India as the area of original distribution of *R. invadens* [1]. Serious outbreaks on mango in some areas of the Oriental Region suggested recent introductions also, although records from other parts of the Oriental Region were as early as 1900. Using the taxonomy as a guide, surveys and preliminary studies were carried out by scientists from CABI centres in Malaysia and India, beginning in mid 1986.

Williams [10] later revised the genus *Rastrococcus* to include 22 species, five of them new. He gave detailed descriptions and illustrations of all the species, together with the distribution of the genus throughout Australia and southern Asia and host-plant data.

Field diagnostic characters to differentiate between adults of three species of *Rastrococcus*, including *R. invadens* and *Rastrococcus mangiferae* (Green), and between immature stages of *R. invadens* and *R. mangiferae* were described and illustrated [11]. The most important field character to separate the species, the number of waxy tassels, corresponded to a key microscopic character, the number of cerarii, and hence was reliable.

Distribution maps, supporting references and codes for the extent or status of *R. invadens* are available [12].

Other than *R. invadens,* which received attention because of its pest status, *Rastrococcus iceryoides* (Green) is probably the best-known of the genus. A distribution map giving its geographical distribution notes it as a pest of cocoa (*Theobroma cacao*), mango, cotton (*Gossypium* spp.), *Albizia lebbeck* and *Samanea saman* in Africa and Asia [13]. The morphologies of different instars of both sexes of *R. iceryoides* were described by [14], along with those of five other species of mealybugs.

2.2. Work in India and Malaysia

Surveys for *Rastrococcus* spp. and their natural enemies were initiated in India in July 1986. Four species of *Rastrococcus* were collected: *R. iceryoides,* a polyphagous oviparous species that was recorded as a minor pest on mango, and three ovoviviparous species that produce eggs which develop and hatch within the mother, *R. mangiferae*, *R. invadens* and *Rastrococcus ornatus* (Green) [=*Lankacoccus ornatus* [10]] [15]. The last species was easily differentiated as it occurred only on wild jasmines (*Jasmimum* spp.), was oval in shape and had a markedly different colour from *R. mangiferae* and *R. invadens.* A field diagnostic key was developed to differentiate between the ovoviviparous species and between the immature stages of *R. invadens* and *R. mangiferae.*

The studies in India resulted in a number of natural enemies of the *Rastrococcus* complex being recorded [15]. Three parasitoid species that showed direct parasitism of *R. invadens* were found and between 1986 and 1988 two of these species of primary parasitoids were supplied to CABI Bioscience for further study in UK. Both were new species, identified and described by Noyes [16, 17]. The third, a *Coccophagus* sp. was not considered for use because, while the female is a primary parasitoid, the male is probably a hyperparasitoid, developing only on *R. invadens* hosts that are already parasitized.

Predators were also recorded. However, although there are exceptions such as the coccinellid *Cryptolaemus montrouzieri* Mulsant, predators are rarely as successful in biological control of mealybugs as hymenopterous parasitoids [18]. Hyperparasitoids of the primary parasitoids were also studied [15].

Overall the surveys in India demonstrated that although *Rastrococcus* spp. were widely distributed they were never of anything other than local importance and even then of only short duration. The complex of natural enemies appeared capable of maintaining good control over the mealybugs, probably in conjunction with other factors such as mango cultivar and prevailing weather conditions [15]. Further biological studies, on spatial distribution and movement of the mealybug species were carried out by Narasimham & Chacko [19].

Gyranusoidea tebygi Noyes (Hym., Encyrtidae) was sent to the UK in 1986 and proved easy to rear on mango and citrus seedlings. In contrast, *Anagyrus mangicola* Noyes (Hym., Encyrtidae) initially proved difficult to rear and around 1500 individuals were sent from India before the culture became established. Three further shipments of *A. mangicola* (about 180 adults) reared from field-collected *R. invadens* on mango were sent to the UK during 1990 with a view to rejuvenating the colonies held in quarantine. The insects appeared to adapt to the rearing conditions as, after many generations of poor production, significant improvements in production occurred with no apparent changes in conditions. The same feature was noted at IITA in Benin, where many generations of poor production were suddenly followed by good and continued production. The reasons for this adaptation were not discovered.

Studies in India indicated that parasitoids were equally active when populations were markedly different. Analysis also indicated that the parasitoid most successfully (efficiently) parasitized on leaves with 31 to 40 mealybugs. This probably represents the population level at which the parasitoid can find significant numbers of hosts of a suitable stage without having to spend much time searching. Above this density, the parasitoid was disturbed by excess wax on the leaves and the defensive strategies of the mealybugs which included violent movements of the body that could physically dislodge the parasitoid from both mealybug and leaf.

Despite extensive searches in Malaysia, where historical records suggested *R. invadens* occurred, it was not found, although *R. spinosus* and *Rastrococcus rubellus* Williams were. The most common species in peninsular Malaysia was *R. spinosus* which was easily bred on healthy mango seedlings but could not complete its development on pumpkins. *Rastrococcus spinosus* could complete a generation in about 6 weeks under laboratory conditions. Females reached the adult stage after the third instar moult and did not appear to be parthenogenetic. Males would spin a silk puparium at the end of the second instar after which they would moult.

The second species of *Rastrococcus* was a relatively uncommon species, *R. rubellus,* which closely resembled *R. invadens.* It was found on mango, *Citrus sinensis* and *Citrus microcarpa.*

3. Biology of Host and Parasitoids

3.1. Rastrococcus invadens

Early studies of *R. invadens* were carried out by Willink & Moore [20] who described the life cycle in controlled temperature rooms and in a quarantine glasshouse. Later authors found variations, often explained by temperature, host plant, etc. First-instar *R. invadens* are yellow crawlers which spend the first hours of life under the body of the mother. This stage takes about 11 days at 25°C (main range 7–12 days) to develop to the second instar. The second stage lasts about 10 days. The sexes cannot be distinguished in the first two instars, but the morphology changes after the second moult. The third-instar female maintains its shape and takes about 8 days to become adult. Consequently, the adult female has a juvenile period of an average of 29 days. Adult females live, on average, 89 days (range 51–110), and produce about 160 crawlers (range 54–282) during a period of about 67 days (range 31–84). The third-instar male covers itself in wax forming a cocoon in which it undergoes another moult to form the ‘pupa’ from which the adult male emerges after about 10 days. Thus the female has three moults and the male four. Soon after emergence, the alate male searches for a young female and copulation occurs.

Nymphal development is around 28–30 days for both males and females [20] although Boavida & Neuenschwander [21] found female development significantly quicker than male development. The proportion of males to females in laboratory cultures is usually about 85:15. General mortality is around

40% (the final number of adult males and females compared with the number of crawlers originally produced). The crawlers tend to stay on the leaf that they were born on and only a few colonize other leaves.

Boavida & Neuenschwander [22] produced detailed life tables for *R. invadens* (and *G. tebygi*) from field data gathered in southern Benin and from laboratory studies. The relatively minor differences in most results compared with Willink & Moore [20] can probably be explained by environmental differences. Field populations of *R. invadens* showed a very variable sex ratio compared with laboratory cultures, although the reasons for this are not known. This finding is of great practical significance, however, as a high proportion of males results in less damage in the present generation and fewer offspring for subsequent generations.

Development time of *R. invadens* was influenced by host plant (mango, *Ficus* sp., frangipani and *Citrus* spp.). Mango-fed nymphs exhibited the highest survival and the shortest developmental period (21 and 24 days for female and male, respectively) while the development of *Citrus*-fed nymphs was the longest (26 and 24 days). Based on the development and the intrinsic rate of increase, mango is the most preferred host for *R. invadens* [23].

In India *R. invadens* can complete eight generations in a year [24]. The female and male nymphs complete development in 35 ± 5.4 and 38 ± 4.0 days, respectively, during the winter at 15–21°C and 25 ± 3.3 to 33 ± 2.7 days and 28 ± 3.2 to 36 ± 9.6 days at 18–33°C, respectively. The male and female ratio ranged from 2.1:1 to 3.3:1. The maximum pre-reproductive period and oviposition period and minimum fecundity were 20–29 days, 34–45 days and 165 (145–175) nymphs, respectively. Minimum pre-reproductive period and maximum fecundity were 14–18 days and 204 (180–235) nymphs, respectively, and the minimum oviposition period ranged between 28 and 35 days [24].

All stages of *R. invadens* stretch out the abdomen from the leaf surface at a right angle when exposed to bright sunlight [25]. In the laboratory, the degree of lifting was found to be related to temperature. The reaction started at about 34°C and reached a maximum at 37°C. Temperatures measured in the field on leaves exposed to bright sunlight were 34.5–41.1°C, indicating that the reaction of the mealybug to high temperature may be a heat-regulating mechanism. Similar behaviour is seen when mealybugs are exposed to parasitoids, so it may be a general distress feature.

Differences between mango cultivars in *R. invadens* infestation levels were investigated in Gabon in 1988–92 [26]. Cultivars Alphonse, Amelioree du Cameroon and Schmith were the most infested, and Cambogeana, Julie, Lippen and Kent were the least.

The spatial dispersion pattern and intra-canopy distribution of *R. invadens* were assessed between 1988 and 1990 in a small mango plantation in southern Benin, in order to develop sampling plans and facilitate sampling in mango trees [27]. Because of an almost total overlap of generations, the number of females corresponded closely to that of the total population (the use of female numbers to estimate relative populations was originally used by Agricola *et al.* [28]). To analyse the dispersion pattern of the mealybug, Taylor's power law was applied to the sampling data. The index of aggregation did not change significantly with season. On this basis, a common index of aggregation was calculated, which was incorporated into Wilson & Room's and Karandino's equations to develop enumerative and binomial sampling plans [27].

The population dynamics of *R. invadens* were studied in the Congo [29] on mango and frangipani. The population dynamics of *R. invadens*, which was very different on the two host plants, seemed to be linked more to the physiological and phenological characteristics of the host plant than to climatic factors.

In the field, the mealybug's populations were not markedly checked by biotic factors. Agounké *et al.* [2, 30] identified several indigenous natural enemies in Togo, but their ability to regulate the populations of *R. invadens* was very low. The most important among the predators were the coccinellids *Chilocorus nigrita* (F.), *Exochomus promtus* Weise and *Exochomus troberti* Mulsant and the lycaenids *Spalgis pilos* Druce and *Spalgis lemolea* Druce. An indigenous encyrtid parasitoid, *Anagyrus* sp. ?nr *aurantifrons* Compère, became adapted to the pest, but caused only low levels of control.

Fernández-García *et al.* [31] described a new species of entomopathogenic fungus, *Hirsutella cryptosclerotium* Fernández-García, H. C. Evans & Samson (Clavicipitaceae), which had been obtained from cadavers of *R. invadens* from Togo. The potential of this fungus for biological control of mealybugs has never been fully explored [32]. The fungus grew on a variety of simple defined media and produced both conidia and sclerotia. Laboratory trials showed a high level of mortality of *R. invadens* following inoculation with fragmented mycelia; treated populations declined rapidly and subsequent populations also became infected by the fungus. It was later shown that dispersal of spores and mycelia by raindrops could be a factor in spreading disease within (and, it was hypothesised, between) tree canopies [33].

The other fungus associated with *R. invadens* was reported by Keller [34]. Mealybugs infected with Entomophthorales from West Africa were examined and the fungus identified as *Neozygites fumosa* (Speare) Remaudiere & Keller.

3.2. Gyranusoidea tebygi

Gyranusoidea tebygi is a solitary endoparasitoid [20]. Generally the female is bigger than the male (0.83–1.11 mm *vs* 0.70–0.92 mm), but size can vary greatly. The adults live around 20 days. They generally mate after emerging, and can begin parasitizing 48 hours after emergence. Each female can parasitize between 70 and 90 mealybugs during its life. The parasitoid prefers the first and second instars of the mealybug and will not parasitize the adult female nor the male cocoon and adult.

The parasitoid is endoparasitic, developing inside the mealybug; mummification occurs 14–17 days after oviposition and it takes another 10 days for the adult to emerge. The proportion of sexes produced is usually about 3:1 biased towards the female, but when a female has not been fertilized she produces only males.

In an unparasitized culture, approximately 9% of crawlers could be expected to become adult females, taking sex ratio and mortality data into consideration. Less than 4% of the original crawlers become females when parasitoids are present. This halving (at least) of the potential reproductive female population obviously has significant effects on the species' population dynamics.

The parasitoid was tested against the pseudococcid mealybugs *Planococcus citri* (Risso), *Pseudococcus affinis* (Maskell) [= *Pseudococcus viburni* (Signoret)] both on citrus and *Phenacoccus manihoti* Matile-Ferrero on cassava (*Manihot esculenta*). No evidence of parasitization of species other than *R. invadens* was obtained. *Rastrococcus invadens* cultures maintained on rough lemon and lime (*Citrus* spp.), oleander and mango were all susceptible to attack by *G. tebygi*, and the choice of host plant had no noticeable effect on the parasitoid.

Gyranusoidea tebygi was shown to parasitize first- to third-instar nymphs of *R. invadens* by Boavida & Neuenschwander [21] in contrast to Willink & Moore [20] who considered that only the first two instars were attacked, and that the wasps generally avoided hosts that were already parasitized. Host feeding was occasionally observed. Uncrowded wasps produced a very female-biased sex ratio, whereas the sex ratio of groups of wasps foraging under crowded conditions varied from male-biased in smaller hosts to female-biased in larger hosts. Females had longer development times than males, developed faster in larger mealybugs than in smaller ones and were always larger than males emerging from the same host instar. Female size increased with the instar of the host at oviposition. About 90% of all ovipositions in second- and third-instar nymphs resulted from an attack with multiple stings, starting usually with a sting in the head. The function of these head stings may have been either to assess the quality of the host or to subdue it prior to oviposition. Encounter rates, number of attacks and number of stings during one attack increased, while number of ovipositions decreased, with host instar. Time investment per oviposition and time spent preening increased with increasing host age because older hosts defended themselves more vigorously than younger ones. Thus, while the fitness of the parasitoid increased with host size, fitness returns per time decreased.

After detailed biological studies under quarantine in the UK, *G. tebygi* was introduced into Togo in October 1987. The parasitoid was first released in November 1987 and by May 1988 parasitism was recorded in the field up to 15 km from the release sites and the mealybug was effectively controlled in the immediate area of the release. The parasitoid was also released and established in four other experimental sites.

Agricola & Fischer [35] studied hyperparasitism in two newly introduced parasitoids of two exotic mealybug plant pests in Togo. Associated with *R. invadens* and *G. tebygi* were two unidentified species of the signiphorid *Chartocerus,* the encyrtids *Prochiloneurus insolitus* (Alam) and *Prochiloneurus aegyptiacus* Mercet, the eulophid *Tetrastichus* sp. and the aphelinid *Marietta leopardina* Motschulsky. Hyperparasitism ranged from 56% to 86%, with one species of *Chartocerus* being the most important. Multiple parasitism was observed on several occasions. The efficacy of biological control seemed undiminished despite generally high hyperparasitism. Interestingly the same complex of hyperparasitoids (with only one *Chartocerus* species) was recorded on the cassava pest *Phenacoccus manihoti* and its introduced primary parasitoid *Epidinocarsis lopezi* De Santis (Hym., Encyrtidae).

The interaction between two natural enemies of *R. invadens*, *G. tebygi* and the fungal pathogen *H. cryptosclerotium*, was studied in the laboratory [36]. Levels of parasitism by *G. tebygi* were reduced in the presence of the pathogen, but overall mortality of *R. invadens* was greater when both agents were acting together.

3.3. Anagyrus mangicola

Studies on *A. mangicola*, under controlled conditions at 27°C and 75% RH [37] gave results similar to Bokonon-Ganta *et al.* [38] (see Table 1). *Anagyrus mangicola* is a solitary endoparasitoid which attacks second instar nymphs, but prefers third instars and female fourth instars. Its preference for the later stages means that there is a greater impact on female mealybug numbers as second stage mealybugs may develop into either males or females, but the majority develop into males. Males were mainly produced from the smaller (younger) hosts and females from the larger. Adult females emerged from 95% of parasitized fourth-instar hosts and only 35% of parasitized second-instar hosts. Development time from oviposition to emergence was 18–20 days, significantly less than for *R. invadens.*

All host instars of *R. invadens* were parasitized by *A. mangicola* [37]. First-instar nymphs were less often encountered, and seldom stung and parasitized, but were preferred for host feeding. Handling time per host decreased with increasing host size. Female parasitoids were able to recognize previously-parasitized hosts and, in cases where they attacked them, did not oviposit in them. The proportion of males was lowest when mature adult female *R. invadens* were parasitized and increased with decreasing host size, from young adult females to first-instar nymphs. Female wasps emerging from any size of host were always larger than the corresponding males. Male

Table 1. A comparison of biological attributes of *Gyranusoidea tebygi* and *Anagyrus mangicola*.

Attribute	*G. tebygi*	*A. mangicola*	Comments
Host stages	1st and 2nd instars, males	2nd and 3rd instars, adults	*G. tebygi* has the larger number of potential female hosts but *A. mangicola* kills only females when attacking 3rd instars and adult hosts
Host feeding	1st instars	1st instars	Significant mortality (10%?) of 1st instars by host feeding and probing by *G. tebygi*; host feeding by *A. mangicola* on 1st instars in Benin [51]
Sex ratio	40–47% female	23–34% female	Exact sex ratios vary. Usually *G. tebygi* has a more female biased ratio than *A. mangicola*.
Development time (oviposition to emergence of female)	27–29 days	20–22 days	*A. mangicola* has potential for more generations throughout the year
Adult longevity	20 days	?	
Female fecundity	70–90 hosts?	?	Fecundity of *G. tebygi* appears higher than that of *A. mangicola*
Superparasitism	Yes	Yes	Only one adult parasitoid emerges
Multiple parasitism	Yes	Yes	Larval *A. mangicola* are superior competitors to *G. tebygi*
Hyperparasitoids	At least 8 species recorded from West Africa	Attacked by at least 3 species that attack *G. tebygi*.	*A. mangicola* appears to be more severely attacked than *G. tebygi*

size increased with that of the host, while female size was independent of host instar at oviposition. *Anagyrus mangicola* was regarded as a complementary natural enemy to *G. tebygi* for the biological control of *R. invadens*.

Overall, levels of control were very similar whether the parasitoids acted alone or together. There was no evidence that the introduction of *A. mangicola* would reduce the level of control exerted by G. *tebygi* although the laboratory evidence suggested that *G. tebygi* may be the superior in terms of hosts killed even if an inferior competitor under some circumstances [39].

4. Biocontrol Programme in West Africa

Gyranusoidea tebygi was shipped to Togo in October 1987 where it was mass reared. In November 1987 and during 1988 the parasitoid was released in a number of different ecological zones in Togo. Within 12 months the parasitoid had spread 100 km from the initial release point where *R. invadens* was under control [28, 40, 41].

Boavida & Neuenschwander [21] obtained life table data for *R. invadens* and *G. tebygi* in the field and in the laboratory, substantiating release for biocontrol. The ability of *G. tebygi* to control *R. invadens* was assessed in mango trees in Benin in 1989–90 using paired sleeve cages [42]. In sleeve cages left open to allow parasitoid attack, *G. tebygi* reduced *R. invadens* numbers 2.7-fold within 1.5 host generations compared with the closed-sleeve treatment where there was no parasitoid attack. A parasitism index of 34.4% was measured in the open-sleeve treatment whereas on leaves without sleeves, the parasitism index was two-fold higher, and the *R. invadens* population was two times less than in the open-sleeve treatment. The lower levels of *R. invadens* found on uncaged leaves were attributed to higher mortality caused both by parasitism and by abiotic factors such as rain and wind. From this it was assumed that the potential of *G. tebygi* to reduce *R. invadens* populations was even higher than the paired sleeve experiments suggested.

Gyranusoidea tebygi and *A. mangicola* were mass-reared in Cotonou, Benin, and released against *R. invadens* [43]. *Gyranusoidea tebygi* was released in Benin, Gabon, Ghana, Nigeria, Sierra Leone and the Democratic Republic of Congo (formerly Zaire). In addition, it established itself without previous release in Congo and Côte d'Ivoire. *Anagyrus mangicola* was released from 1991 onwards.

Post-release surveys which started in 1987, across all the ecological zones of Benin and less than 1 year after the first release of *G. tebygi,* showed that within 3 years *G. tebygi* had colonized the entire area of infestation, and was found on practically all infested mango trees as well as other infested host plants [44]. By 1991, the incidence of *R. invadens* on the secondary host plants had declined significantly. The percentage of infested mango trees declined from 31% in 1989 to 17.5% in 1991.

Life tables constructed for *R. invadens* and *G. tebygi* from data from the field and laboratory [21] showed that the mealybug population's potential rate of increase ranged from 0.066/day to 0.078/day, around half of that of the parasitoid. Seasonal fluctuations in abundance of *R. invadens* from 1988 to 1992 on mango trees in southern Benin showed that the population density decreased during the rainy seasons and peaked during the dry seasons. Mealybug field sex ratios were extremely variable. *Gyranusoidea tebygi*, introduced into Benin in 1988, had populations synchronized with the host populations. The spatial patterns of parasitism in relation to the host population density were either independent or directly density-dependent, depending on the type of analysis, both at the tree level and for larger zones. Both relationships can result in stable population regulation. The successful biocontrol exerted appeared to result from local patch extinction of the mealybug rather than from persistence of *G. tebygi* at low host densities. The debate between local extinction or host density may come down to the area of a local extinction (leaf, tree or orchard?) and interpretations of metapopulations.

Six species of hyperparasitoids attacked mealybugs parasitized by *G. tebygi*, with four developing high populations [21]. In the two mango orchards studied, mealybug populations eventually collapsed and disappeared. This was interpreted as an indication that the biological control of the mango mealybug by *G. tebygi* was achieved by non-equilibrium local dynamics, and should be evaluated from a metapopulation perspective [21].

Biassangama *et al.* [3] found that in the Congo *G. tebygi* was also attacked by a range of hymenopteran hyperparasitoids: *Chartocerus* sp., *Tetrastichus* sp., *Prochiloneurus aegyptiacus*, *P. insolitus, Cheiloneurus cyanonotus* Waterston (Encyrtidae), *Pachyneuron* sp. and *Marietta javensis* (Howard) [= *M. leopardina*].

The rate of parasitism of *R. invadens* 3–4 months after the introduction of *G. tebygi* was 50–90%, a level which significantly affected the population dynamics of the mealybug [29]. After 8–9 months, low densities of the pest confirmed that the parasitoid had successfully adapted to the environment and was controlling the mealybug. Mortality of *G. tebygi* (50–60%) attributable to eight species of a hyperparasitoid complex did not influence its effectiveness as an efficient parasitoid.

A mango orchard was producing no fruit in 1990 before *G. tebygi* was introduced; by 1998 the fruit yield was restored [8]. During that time the population density of *G. tebygi* was found to be negatively correlated with *R. invadens* populations and positively correlated with mango fruit yield. Parasitism was highly correlated with mealybug populations and yield.

The occurrence of *R. invadens* was investigated and compared in the absence (in 1988–89) and presence (1990–92) of *G. tebygi* [26]. Before the introduction of the parasitoid, *R. invadens* was very polyphagous, with at least 38 species of food plant. After the introduction of the parasitoid, reduced population densities resulted in a reduction in the range of the food plants used by the pest. In this situation, mango, citrus, *Ficus* spp. and frangipani remained as significant hosts.

There has been debate in biological control over the relative merits of single or multiple introductions of natural enemies to control exotic pests. Sometimes the debate is purely theoretical as often only one parasitoid is available for introduction at any one time and if reasonably successful no other introductions are made. In the present situation the first introduction, G. *tebygi*, was very successful and the concern with a second parasitoid was that theoretical studies suggested that control could be reduced [45].

Age-structured host–parasitoid population models with overlapping generations were developed to investigate the interactions of *R. invadens* and two potential parasitoids, *G. tebygi* and *A. mangicola* [45]. The models predicted that *G. tebygi* would cause a greater decrease in mealybug density than *A. mangicola*. The robustness of this prediction was tested by sensitivity analysis. The models predicted that the addition of *A. mangicola* to a system already containing *G. tebygi* would lead to little improvement in host depression.

Hyperparasitoids emerging from mummies of *R. invadens* collected from mangoes in Togo and Benin were identified and competition experiments were carried out with the primary parasitoids *G. tebygi* and *A. mangicola* in the laboratory at 25°C and 80–90% RH [39]. Both primary parasitoids were capable of eliminating the host, but on occasions they went extinct before the mealybug. Four hyperparasitoid species emerged from mummies of *G. tebygi* and three of these also attacked *A. mangicola*. The latter species was more heavily parasitized than the former, especially by *Chartocerus hyalipennis* Hayat. In competition experiments, the presence of hyperparasitoids slightly slowed the speed of extinction of either *R. invadens* or the primary parasitoid, which may add stability to the system. *Anagyrus mangicola* was heavily parasitized by *C. hyalipennis* and went extinct while many suitable mealybug hosts were available. It was concluded that the introduction of *A. mangicola* was unlikely to lessen the control being exerted in West Africa by *G. tebygi*.

As yet there are no satisfactory methods of predicting the consequences of multiple introductions. In the present instance the two parasitoids coexist in the field in India and contribute to a very good level of control of *R. invadens*. Laboratory studies demonstrated that both parasitoids appeared capable of controlling mealybug populations and that under differing circumstances one or the other would prove superior [39]. One weakness of predictions from laboratory studies is that only a very restricted range of conditions can be tested; minor variations in aspects such as temperature may completely alter the competitive ability of a parasitoid. It is quite likely that if a number of parasitoids establish after introduction (and many do not), their relative success may vary according to specific, and perhaps very localized, environmental conditions. For example, the outcome of competition between parasitoids may be determined by the temperature at which experiments are conducted [46].

Even after introduction it may be difficult to resolve the issue. The introduction of *A. mangicola* could theoretically lead to a rise in the overall numbers of *R. invadens* in some areas, but if this were to be against a background of more regular population levels, it could be preferable to the occasional outbreak that occurs despite G. *tebygi* being widespread. A minor reduction of control in some areas would probably be of no practical significance and, if accompanied by increased control in other areas, may be acceptable.

During laboratory based competition studies between *G. tebygi* and *A. mangicola* [47], no significant differences were found in the way each parasitoid species examined, attacked, stung and oviposited in hosts, unparasitized or previously parasitized by the other species. This suggests that neither species discriminates against the other. The total number of parasitoids of either species emerging did not significantly differ between competition experiments. When *A. mangicola* was the first parasitoid to attack a host, it had no significant advantage over *G. tebygi*. However, when *A. mangicola* followed *G. tebygi* by either 4 or 24 h, it clearly 'won'. Overall, *A. mangicola* won the competition in 70.9% of all cases. The level of the competition, at either the egg or larval stages, and factors responsible for the elimination of older larvae by younger ones could not be assessed in these experiments. The results suggested that the coexistence of the two parasitoids would be complementary for the biological control of *R. invadens*.

5. Success of the Biocontrol Programme

5.1. Biological

Monitoring the impact of *G. tebygi* on *R. invadens* in Nigeria started in 1991, which was about 2 years after the first release in Ibadan [48]. By 1997–98, *G. tebygi* was found to have crossed all agroecological barriers to colonize the entire area of mealybug infestation nationwide on mango as well as other host plants. As a consequence, populations of *R. invadens* were greatly decreased from between 11.0 and 98.0 mealybugs per mango leaf in 1991 to between 0.0 and 18.2 mealybugs per leaf in 1998.

Effects of host plant on biological control were demonstrated [22]. Life history characteristics of *R. invadens* infesting two neighbouring mango trees were compared in Benin in 1992–94. On the heavily infested tree (possibly cv. 'Quinte') *R. invadens* survival was high because of good feeding conditions and low escape. In addition the pre-reproductive period of *R. invadens* on the heavily infested tree was shorter and total offspring production greater than on the slightly infested tree (cv. 'Gouverneur'). This significantly affected the intrinsic rate of natural increase and explained the observed differences in population densities between the trees. Results obtained from juvenile clones of the same two mango varieties, in which environmental factors were uniform, supported the field findings.

By 1991 the incidence of *R. invadens* on secondary host plants had declined significantly [44]. The percentage of infested mango trees declined from 31% in 1989 to 17.5% in 1991, with the largest remaining populations being found in coastal savanna. Average mealybug densities declined by 30% between 1989 and 1991. Multiple regression analyses, based on 23 meteorological, agronomic and plant variables, showed that the duration of the parasitoid's presence was the major factor, reducing mealybug population densities and sooty mould incidence and subsequently leading to increased production of new leaves.

5.2. Financial and Social

Rastrococus invadens is now kept at low population densities by *G. tebygi* and *A. mangicola*. The population density of *G. tebygi* was found to be negatively and significantly correlated with *R. invadens* populations and consequently parasitism was considered a major factor in the control of the pest and the subsequent increase in mango fruit yield [8].

Neuenschwander [49] described techniques for evaluating biological control of *Phenacoccus manihoti, R. invadens* and *Aleurodicus dispersus* Russell (Hom., Aleyrodidae) in tropical Africa. In each case, two exotic hymenopterous parasitoids were introduced, which controlled the pest species, with indigenous and exotic coccinellids playing a minor role. Control was achieved in large areas where the exotic parasitoid(s) had been present for more than 2–4 years. The impact was documented by (a) exclusion experiments, (b) long-term population dynamics studies, (c) laboratory and field experiments contributing to simulation models, and (d) quantitative results from large-scale surveys. In many countries, the main introduced parasitoid proved to be the most important factor contributing to the decline of pest populations and the recovery of plant growth and yields. Nontarget species were only affected through reduction in their food sources. The impact was scale-neutral, benefiting subsistence and commercial farmers alike. The population reduction remained stable (in the order of ten-fold over outbreak levels). In economic terms, both the *P. manihoti* and *R. invadens* projects returned benefits to African farmers that amounted to a multiple of the research and implementation costs.

The first attempt at an economic analysis was by Vögele *et al.* [4] who also noted important social effects of the pest. The value of citrus and mango production in Togo was estimated at US$3.9 million per annum and the original project cost around $175000. The mealybug had reduced yields by at least 50%, and some estimates put losses at more than 80%; this loss was mostly reversed within 3 years of introducing *G. tebygi*. Consequently, in Togo alone the value of products saved far outweighed the cost of the programme. It was estimated that with a minimal saving of 20% of the yield loss (a percentage which was greatly exceeded) savings of $370/ha were realised by farmers of grafted trees.

This analysis was confirmed by more detailed studies [50]. Additional work by IITA and SPV in Benin, and throughout the region had raised the total cost of control to $3.66 million. Yield loss due to infestation by *R. invadens* was estimated at 89%. Production of local varieties increased four-fold after control and almost ten-fold with grafted varieties after control. The authors state "The present value of accrued benefits is estimated at $532 million over a period of 20 years". This is for Benin alone and is a benefit–cost ratio of 145:1. If the value of protected crops from the remainder of the afflicted countries was similarly estimated the benefit–cost ratio would be much greater.

6. Conclusions

The biological control of *R. invadens* is one of the most successful examples of the last 20 years. Cost–benefit analysis shows that it was highly economic and the savings in a very poor part of the world greatly exceeded costs [3, 8, 50]. The project demonstrated very excellent cooperation between organizations and countries, and has produced some very good science to support the concept of classical biological control. Of special significance is the scientific output of IITA, largely based on the field situation in Africa; too many projects are unable to monitor introduced species and post-release study is usually very limited.

One of the ironies of the project was that it was completed very rapidly, so the true scale of the pest outbreak and the damage caused was only fully appreciated in the affected countries. Consequently this programme is not recognized for the outstanding success that it undoubtedly was.

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