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# Biological Control of *Helicoverpa armigera* in Africa

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## Introduction – the African Bollworm as a Pest

The African bollworm, *Helicoverpa armigera* (*Heliothis armigera*) (Hübner) (Lepidoptera, Noctuidae), is an indigenous species considered to be a major constraint to food, fibre and horticultural crop production in Africa. Its perception as a particularly serious pest derives from its polyphagy, high fecundity and short generation time (often being multivoltine), high mobility, preference for the harvestable fruiting parts of its host plant, and its propensity to develop resistance to chemical insecticides. The severity of *H. armigera* attack varies not only between crops and regions, but also on a temporal scale. Moreover, due also to its dispersive and migrational attributes, incidence of *H. armigera* is unpredictable. Four heliothine species are reported as of economic importance in Africa: *Helicoverpa armigera*, *Helicoverpa assulta afra* (Hardwick), *Helicoverpa fletcheri* (Hardwick) and *Helicoverpa peltigera* (Schiffermüller), but *H. armigera* is the only species of major economic importance and the published literature is overwhelmingly concerned with this species (Greathead and Girling, 1989). This chapter confines itself to *H. armigera* and we focus attention principally on the two best studied areas, southern and East Africa.

Greathead and Girling (1989) list 35 crop hosts of *H. armigera* plus 25 wild host plants in eastern and southern Africa. In East Africa it attacks various crops including cotton, legumes, maize, sorghum, sunflower, tobacco and tomato. In South Africa crops attacked include peas, beans, wheat, cotton, maize, grain sorghum, oats, barley, sunflower, tobacco, citrus, cucurbits, potato, tomato, lucerne, sunnhemp, cape gooseberry, chickpea and groundnuts (Annecke and Moran, 1982). To this list may be added a large variety of garden ornamentals and wild host plants. In South Africa it is regarded as one of the most serious citrus pests (Bedford, 1968) and is the key pest on cotton (van Hamburg and Guest, 1997).

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Low economic damage thresholds in high value crops like cotton, tomato, pulses and tobacco require a high level of control that leads to reliance on heavy and frequent use of synthetic insecticides. However, regional and even relatively local differences in host preference can give rise to differences in pest status on particular crops (*Crop Protection Compendium*, 2001), and may also lead to exaggerated perceptions of the species as a pest. Integrated control programmes exist for *H. armigera* that seek to minimize pesticide inputs and maximize the impact of natural enemies, but a major constraint to their development, particularly on cotton, has been the need to deal with a complex of pests where control needs may conflict (e.g. Kuklinski and Borgemeister, 2002; Mensah, 2002).

## Indigenous Natural Enemy Complexes

Most studies on the natural enemies of the African bollworm have been carried out in East and southern Africa and have focused on parasitoids that attack bollworm eggs and larvae, often in cotton cropping systems. Predators and naturally occurring pathogens have been less well studied. Natural enemy data are largely restricted to records only, with few studies providing quantitative information on percentage parasitism or infection. Data on impact in the context of pest life tables were generally lacking until recent studies in East Africa by van den Berg and Cock (1993a,b, 1995a,b), and van den Berg *et al.* (1993, 1997).

### *Parasitoids*

The natural enemies of *H. armigera* in Africa have been reviewed and catalogued by van den Berg *et al.* (1988). A total of 83 identified and 93 partially identified species of parasitoids, some of which are important biological control agents, have been recorded from *H. armigera* (van den Berg *et al.* 1988). Most records are from southern and East Africa and concern larval parasitoids in the families Ichneumonidae, Braconidae and Tachinidae.

Most parasitoids recorded from *H. armigera* in Africa attack a range of host species. A minority of parasitoids recorded are host specific, notably five members of the braconid genus *Cardiochiles* that have only been recorded from the African bollworm. Among egg parasitoids, the scelionid wasp *Telenomus ullyetti* Nixon (Hymenoptera, Scelionidae) is specific to African bollworm whereas trichogrammatid wasp species will parasitize a wide range of lepidopteran eggs in a specific habitat.

Records suggest that geographical and temporal distribution of parasitoids and their importance within the local natural enemy complex vary considerably within and between East and southern Africa. For example in Kenya, van den Berg *et al.* (1993) found that in smallholder crops (sunflower, maize, sorghum and cotton) in several agroecological zones, occurrence of parasitoids varied greatly between seasons and sites. *Trichogrammatoidea* spp. (Hymenoptera, Trichogrammatidae) egg parasitoids, and *Linnaemya longirostris* (Macquart)

(Diptera, Tachinidae), a late-larval parasitoid, were the most common parasitoid species, but mean percentage parasitism was generally rather low (<5%), even though egg parasitism by *Trichogramma* spp. and late larval parasitism by *L. longirostris* occasionally reached up to 20%. Levels of parasitism were lower and species diversity poorer during this Kenyan study than in a similar study in western Tanzania (Nyambo, 1990).

One of the few quantitative studies of parasitism of *H. armigera* in East Africa was conducted in the western cotton growing area of Tanzania over the period 1981–1985 (Nyambo, 1990) on five major crops; cotton, tomato, chickpea, sorghum and maize, and one weed *Cleome* sp. (*Capparidaceae*). The study found variation within and between seasons, and between crops in the levels of both mortality factors. Twelve parasitoid species are listed belonging to the families Braconidae, Ichneumonidae and Tachinidae. Peak parasitism levels were much greater on the weed host *Cleome* sp. than on any of the crops. Except in sorghum, disease caused more mortality than parasitism, and mean peak parasitism did not exceed 24.5% in any of the five crops. Across all seasons and all crops, however, mean percentage parasitism did not rise above 2% for any of the 12 parasitoid species listed.

In East Africa in general, hymenopteran larval parasitoids are the most commonly recorded parasitoids, whereas in southern Africa dipterans are more frequently recorded (van den Berg, 1993). The braconid *Apanteles diparopsidis* Lyle is an important parasitoid of *H. armigera* in Tanzania, where parasitism of up to 26% has been recorded. In southern Africa, the same parasitoid is only found on the red bollworm *Diparopsis castanea* Hampson (Lepidoptera, Noctuidae) and spiny bollworms *Earias* spp. (Lepidoptera, Noctuidae). Records show high levels of egg parasitism in southern Africa with figures of up to 60–70% in the field in maize, cotton and other crops. In eastern Africa, egg parasitoid records are rare and in sunflower, maize and sorghum egg parasitism was between 0% and 22% (van den Berg and Cock, 1993b), while in Malagasy cotton, Kuklinski and Borgemeister (2002) recorded a peak of 32% egg parasitism by *Trichogramma evanescens* Westwood. In a 3-year study in sunflowers in South Africa, von Maltitz (E.F. von Maltitz, 1992, Grahamstown, unpublished results) recorded an average of 19% egg parasitism and 27% larval parasitism. The most abundant parasitoid was *Palexorista laxa* (Curran) (Diptera, Tachinidae), which emerged from 44% of parasitized larvae. Also in South Africa, *Paradrino halli* Curran (Diptera, Tachinidae) was recorded as the first tachinid species to emerge in spring and was responsible for up to 24.8% parasitism in citrus (Parry-Jones, 1938). Only three species of parasitoids are important in both areas: the braconid *Chelonus curvimaculatus* Cameron and the tachinids *P. laxa* and *P. halli*. All other species are important in only one of the areas, although they may be present in both.

Parry-Jones (1937) noted temporal variation in the bionomics of two egg parasitoids in citrus in Zimbabwe: *Trichogrammatoidea lutea* Girault was most active during the summer months (December–March) when *H. armigera* was most abundant on alternative host plants, whereas *T. ullyetti* was more abundant in the spring months. Similarly, Parsons and Ullyett (1934, 1936) showed that in South Africa, *T. ullyetti* was abundant in winter on irrigated vegetable crops and citrus and became scarce in summer. On the other hand, *T. lutea* was inactive during winter, but from spring until the end of summer, it predominated on rain grown cotton, maize and other summer crops (Parsons, 1940).

One of the most interesting findings in African studies on bollworm natural enemies is the huge variation in occurrence and impact in different host-plant associations. This is especially relevant for African smallholder farmers who typically cultivate a mixture of different crops within a small area. For example in western Tanzania, a parasitoid guild comprising the tachinid fly *P. laxa,* and the braconids *C. curvimaculatus* and *A. diparopsidis*, inflicts heavy parasitism on *H. armigera* in sorghum (van den Berg *et al.* 1990), but not to a significant degree on other crops. In contrast, *Cardiochiles* spp. were associated with cotton and cleome, and were rare on sorghum and maize (Nyambo, 1986). The ichneumonid *Charops* sp. was the only parasitoid species to occur on all crops and was the most frequent species found. *A. diparopsidis* was frequent on sorghum in two seasons, and *Cardiochiles* spp. were the dominant parasitoids in each season on cleome (Nyambo, 1986). Cleome itself was associated with a more diverse population of parasitoids than any of the other host plants (Nyambo, 1990). In the few studies that have compared natural enemy numbers in different crops, sorghum and maize seem to attract more predators and parasitoids as bollworm moths prefer to lay their eggs on these plants. Caution is required with crop-specific interpretations since parasitoids tend to have habitat-specific, rather than crop-specific host searching behaviour. Furthermore, inter-variety variation in crop plants also plays a role, and hairiness of plants in particular has been associated with natural enemy-mediated differences in pest incidence (Bottrell *et al.*, 1998).

## *Predators*

van den Berg *et al.* (1988) list predator records from Africa available at that time including Anthocoridae (five or more species), Reduviidae (eight species), Carabidae (four species), Staphylinidae (one species), Coccinellidae (two species), Asilidae (one species), Vespidae (one species), Eumenidae (two species), Sphecidae (two species), and Formicidae (four species). However, as subsequent studies in Kenya have shown (e.g. van den Berg and Cock, 1993a), this list just scratches the surface of the generalist predators associated with *H. armigera* in different crops. More recent studies in cotton fields in South Africa considerably expand this list of predators and show even the mouse *Mastomys natalensis* (Smith) to be an important predator of *H. armigera* pupae (Watmough, 1991; Watmough and Kfir, 1995; van Hamburg and Guest, 1997).

The impact of predation in the field is more difficult to assess than that of parasitism. An extensive investigation conducted in western, central and coastal Kenya over the period 1987–1991 focused on the impact of indigenous predators, as well as parasitoids and pathogens, in the population dynamics of *H. armigera* in smallholder crops, including cotton and sunflower, that suffer yield loss from *H. armigera*, and secondary crops, including maize and sorghum, that generally tolerate *H. armigera* infestation. Studies were also carried out on several important local crops known to be attacked by *H. armigera*, although detailed studies subsequently focused on sunflower and cotton. The incidence of *H. armigera* and natural enemies was monitored over several seasons (van den Berg *et al.*, 1993). Throughout the study period, the incidence of *H. armigera* on unsprayed experimental crops was low.

Accumulated data were used to construct partial life tables for each crop and each season (van den Berg and Cock 1993b). These showed that mortality due to parasitoids and diseases was not significant, but that mortality due to unknown factors including predation was very large. Thus, partial lifetables showed that mortality was highest on maize, where between the egg stage and the second larval stage more than 95% died. On cotton, sunflower and sorghum, this figure was 78–85%. In the latter crops, second- to sixth-instar larvae showed high mortality. Total mortality until the sixth instar was around 99% on maize, sorghum and cotton, and 95% on sunflower. The most important mortality factors were predation and/or unknown mortality, which includes disappearence due to abiotic factors, during the egg and young larval stages, respectively.

Data from regular sampling of the experimental plots were used to examine the degree of temporal overlap among the common groups of predators known to attack *H. armigera* (van den Berg *et al.*, 1993). The data were further analysed by location within the plant of both *H. armigera* and the major groups of predators, to establish the degree of spatial overlap between the predators and their potential prey (van den Berg and Cock, 1995b).

Of the large complex of predators recorded in the same crops in several agroecological zones across Kenya, only anthocorids (*Orius* spp. (Heteroptera, Anthocoridae)) and ants (predominantly *Pheidole* spp., *Myrmicaria* spp. and *Camponotus* spp. (Hymenoptera, Formicidae)) were sufficiently common and widespread to be of importance in suppressing *H. armigera* (van den Berg *et al.*, 1993; van den Berg and Cock, 1993b, 1995a).

The presence of anthocorids was associated with high mortality of *H. armigera* eggs, which suggests that anthocorids can suppress *H. armigera* when they are common concurrently with the egg stage. However, correlative field data on predators and prey demonstrated in the Kenyan study that anthocorids were generally poorly associated with eggs on sunflower and sorghum. This may explain the relative high survival of young stages on sunflower. On maize, the association of anthocorids with eggs and larvae of *H. armigera* was stronger.

Ants showed differences in behaviour between crops. For instance, *Myrmicaria* spp., a common predacious ant in western Kenya, visited sunflower plants more often than maize or sorghum, even though it was equally common in pitfall traps in the three crops. Ant foraging activity in the canopy may be directed by the availability of alternative food sources, such as plant exudates or honeydew-producing Homoptera. *Myrmicaria* spp. was often found feeding on exudates on sunflower (van den Berg *et al.*, 1997). The degree to which ants visit vegetation may have important implications for the role of ants in suppressing *H. armigera*, particularly in sunflower, where ants may have contributed to the relatively high late-larval mortality. Furthermore, ants were most common on the sunflower plants with the highest number of larvae, indicating new recruitment of workers in response to *H. armigera* density (van den Berg and Cock, 1995b).

Subsequent experiments on cotton and sunflower were aimed at assessing the relative importance of these two main groups of predators. Manipulative experiments in which crawling predators, dominated by *Pheidole* spp. ants, were excluded from sunflower plots showed the role of ants to vary considerably. In one location, *H. armigera* levels were almost seven times greater in the absence of ants than in control plots where predators were not excluded (van den Berg *et al.*, 1997). Exclusion of flying predators, dominated by anthocorids, had little impact on *H. armigera*. Exclusion trials conducted on cotton and sunflower showed no irreplaceable mortality by predation in either crop. In sunflower, this was attributable to the lack of predators during the trial; in cotton, an extremely high background mortality had masked the effect of predation (van den Berg and Cock, 1995a; van den Berg *et al.*, 1997).

The combined effect of predators and parasitoids was measured using a cage exclusion experiment with artificially enhanced prey density on cotton (van den Berg and Cock, 1993c). The results clearly indicated the ability of natural enemies to reduce pest numbers; in the absence of natural enemies, *H. armigera* were four to six times as numerous and there was a corresponding increase in damaged plant parts. Background mortality was again high, but egg numbers at inoculation were sufficient to measure significant differences in larval numbers.

The effectiveness of anthocorids as predators of eggs was studied in a separate experiment where cohorts of eggs of *H. armigera* were laid on experimental plants in the field and monitored for 48 h. The fate of the eggs (present, disappeared, sucked) was recorded, showing that the percentage of predation by sucking increased from 12% early in the season to 65% late in the season, contributing 23–83% of the total recorded mortality. Other mortalities included 15% eggs that were lost and 6% that were parasitized.

A field experiment on natural populations of *H. armigera* attempted to distinguish the different categories of predation and their effect upon the *H. armigera* population on cotton (van den Berg and Cock, 1995a) by excluding either walking predators or all natural enemies. Although the incidence of *H. armigera* was low, there were strong indications of an effect due to predators. When anthocorids and ants were both present, there were 71% fewer *H. armigera*. When crawling predators (i.e. ants) were excluded, but not flying predators such as anthocorids, there were again 71% fewer *H. armigera*. The implication being that in this experiment nearly all the mortality was due to anthocorids, and not due to ants. A parallel experiment exposing eggs on cotton plants showed 20% were sucked by anthocorids over 96 h.

Thus, although it was demonstrated that predators are the most important group of natural enemies, no generalizations could be made about the impact of predation on field populations of *H. armigera* in Kenya (van den Berg, 1993). The variable mortality due to predation could be obscured by other, larger mortality factors. In some instances, high background mortality suppressed the pest, in other instances survival was better and the role of predation became more obvious. For example, where anthocorid bugs are common *H. armigera* populations are always low; where anthocorid populations are low *H. armigera* populations are sometimes low and sometimes high. This shows that anthocorids are generally poorly associated with the pest, mainly because they arrive too late in the season.

Because populations of *H. armigera* almost never reached economically damaging levels during this study, it is difficult to say what effect these natural enemies might have had on a high incidence of *H. armigera*. The implication is that they would have contributed substantial mortality, which would have been easily disrupted by the use of broad spectrum insecticides. It is thus important that any IPM strategy for cotton in this region should take this natural mortality due to predators into consideration, and any control strategies should be based on conserving and encouraging these predators.

### Enhancement of indigenous natural enemies

*H. armigera* has a large array of indigenous natural enemies that are not always able to prevent the pest from causing economic damage. Apart from augmentative and inundative releases of indigenous natural enemies to enhance the efficacy, there have been considerable advances in the understanding of tritrophic natural enemy–pest–crop interactions and there is evidence that environmental manipulations can improve the contribution of natural enemies to *H. armigera* control. Ecological theory predicts that pests find plants more easily if concentrated in a monoculture than plants grown in a polyculture (Root, 1973) and increasing crop diversity often reduces pest infestation (Risch, 1983; Andow, 1991). An increased abundance and action of natural enemies in polycultures may be responsible for reduced pest levels (Russell, 1989). Environmental manipulation to enhance natural enemies is intimately associated with cultural control techniques. Greathead and Girling (1989) concluded that improvements to the cultural controls employed in traditional farming to conserve and enhance the impact of natural enemies represents the best prospect for biological control of *H. armigera* in Africa. Data from East Africa suggest that there are prospects to improve the impact of anthocorids, ants and parasitoids (van den Berg *et al.*, 1990, 1997; van den Berg and Cock, 1995b) through intercropping or adjacent planting of susceptible host crops with crops that are attractive to these natural enemies. For example, the BioRe project in Tanzania successfully uses sunflowers as a trap crop in and around organic cotton fields. Cannibalism and predation by ants (*Pheidole* spp.) on these sunflowers induce high mortality among *H. armigera* larvae (Saro Ratter, Consultant, Germany, 2002, personal communication).

With the advent of readily available broad-spectrum pesticides, it became the norm in South Africa for farmers to spray cotton against *H. armigera*, mainly for preventative control purposes with up to 15 treatments per season (van Hamburg and Guest, 1997). As a result, the pest populations became resistant to a number of insecticides, which led to more frequent spraying and ever escalating costs (Whitlock, 1973; Anon., 1992). Since 1975, a spray programme against *H. armigera,* based on scouting for eggs, was developed. This led to a reduction in the average number of insecticide applications, from 15 for preventative control to eight, when sprayed according to egg density counts (van Hamburg and Kfir, 1982). Later it was learned that the egg population was a poor indicator of the damaging larval populations, due to loss from parasitism and predation (van Hamburg, 1981). A new scouting method based on larval counts was developed, whereby an average of only two to three sprays per season were required, without substantial decline in yield (Kfir and van Hamburg, 1983). This new system resulted in a 60% reduction in pest control costs for cotton growers. Since the importance of natural enemies is now better appreciated, to protect and conserve them restrictions were imposed on the use of certain harmful insecticides including a ban on the use of synthetic pyrethroids on cotton less than 12 weeks old (Charleston *et al.*, 2003). This approach has favoured more sustainable biological control in cotton. Despite the recent arrival and rapid expansion of the area under transgenic *Bt* cotton, this system is still relevant today.

## Classical, Inundative and Augmentative Biological Control

The apparent variation in geographical and temporal distribution of indigenous natural enemies, as well as in host-plant association, offers the possibility of natural enemy introduction or redistribution. Gaps in parasitoids guilds indicate which groups of species may be of value to particular ecological niches.

### *Egg parasitoids*

In 1930, Parsons and Ullyett (1936) were the first to consider inundative biological control against *H. armigera* in South Africa and undertook investigations on the mass production and releases of *T. lutea.* Up to 1 million parasitoids day$^{-1}$ were produced and released on maize, cotton, and citrus crops. Although releases of up to 10,000 parasitoids acre$^{-1}$ week$^{-1}$ were made with egg parasitism ranging from 21% to 82%, no reduction in the larval pest population was achieved.

Attempts at classical biological control with egg parasitoids were made in South Africa in the 1970s and 1980s, when *Trichogramma chilonis* Ishii (from Columbia and Taiwan), *Trichogramma perkinsi* Girault and *Trichogramma semifumatum* Perkins (from Columbia), *Trichogramma pretiosum* Riley (from the USA), *Trichogramma ostrinia* Pang and Chen (from Taiwan) and *Trichogrammatoidea brasiliensis* (Ashmead) (from Colombia and France) were released in cotton and maize fields, but did not become permanently established (van Hamburg, 1980; Kfir, 1981, 1982, 1994).

Classical biocontrol attempts with egg parasitoids are also reported from elsewhere in Africa. Bournier and Peyrelongue (1973) were able to control *H. armigera* in Madagascar with regular inundative releases of *T. brasiliensis.* Two million adults were released in 2 ha of cotton over a 2-month period. This schedule permitted a delay in the start of insecticide treatments and a reduction by five in the number of treatments from the usual ten to 12. In the Sudan, augmentative releases of *T. pretiosum* on cotton were reported to be promising (Abdelrahman and Munir, 1989). In 1986 and 1987, *T. chilonis* was released in rather small numbers on the island of Santiago, Cape Verde and is reported to be possibly established, but there is no discussion of impact (van Harten *et al.*, 1990).

## *Larval parasitoids*

In western Kenya, parasitoids of young *H. armigera* larvae were almost absent from experimental sites (van den Berg *et al.*, 1993), yet outside of Africa parasitoids of young larvae such as *Campoletis chlorideae* Uchida (in India), *Hyposoter didymator* (Thunberg) (Hymenoptera, Ichneumonidae) (a European species with a wide host range), *Glabromicroplitis croceipes* (Cresson) (a North American species) and *Cotesia kazak* Telenga (Hyenoptera, Braconidae) (a European species), often have a substantial impact on *H. armigera* or related Heliothinae (Messenger, 1974; King *et al.*, 1985; Carl, 1989; Mohyuddin, 1989). Greathead and Girling (1982) proposed that the introduction of exotic larval parasitoids into East Africa might improve the overall level and reliability of biological control. It is, however, worth noting that in India, where *H. armigera* causes substantial crop losses, the many introductions of exotic egg, egg-larval and larval parasitoids have met with limited success only (Romeis and Shanower, 1996).

There have been several attempts at classical and augmentative biological control with larval parasitoids of *H. armigera* in South Africa. Taylor (1932) experimented with the indigenous parasitoid *Habrobracon brevicornis* (Wesmael) (Hymenoptera, Braconidae). Ullyett (1933) and Parsons and Ullyett (1934) also worked with the parasitoid, but discontinued when no practical results were obtained. Between 1944 and 1949 another attempt to control *H. armigera* was made in South Africa, when *Chelonus texanus* Cresson (Hymenoptera, Braconidae) was imported from the USA (originally against the Karoo caterpillar *Loxostege frustralis* Zeller (Lepidoptera, Pyralidae)). Altogether 1.4 million parasitoids were released on vegetables and citrus, but no subsequent recoveries were made (Bedford, 1954). In the 1980s, the braconid *C. kazak* was introduced from New Zealand to cotton fields in South Africa (Anon., 1992) but, like the egg parasitoids, did not became permanently established. *C. kazak* was also introduced to Cape Verde between 1983 and 1987 (van Harten *et al.*, 1990) along with *H. didymator* and *Cotesia ruficrus* (Haliday). However, none of these three species were subsequently recovered from the field.

Classical, inundative and augmentative releases of exotic and indigenous egg parasitoids can lead to high levels of parasitism and serve to reduce or avoid early-season insecticide applications, but while this approach has been widely employed, it has not worked everywhere. Furthermore, against the background of very high early natural mortality, the significance of even high levels of egg parasitism is unclear. Attempts at biological control of *H. armigera* through introduction and augmentation of exotic and indigenous larval parasitoids were not successful in South Africa. The recommendation to introduce exotic larval parasitoids to East Africa (Greathead and Girling, 1982) appears not to have been followed, while results from elsewhere are mixed.

There are no records of introductions of exotic predators of *H. armigera* to Africa. Moreover, as predators are not normally host specific, the increasing difficulty of introducing exotic species that have a wide host range could constrain any such introductions in the future. From the examples given above the potential value of classical or inoculative and augmentative biological control to the integrated management of *H. armigera* appears to be limited. Indeed, Greathead and Girling (1989), in an apparent revision of their earlier proposal, concluded that since *H. armigera* is highly polyphagous, moves between crops and weeds as they flower, and is capable of migrating long distances, it does not seem to be a promising target for classical biological control.

## Experiences with Microbial Control

Of the four major groups of entomopathogens, viruses and bacteria have been most used against *H. armigera* in Africa. While fungi and protozoa have been isolated on many occasions, they have received little attention. Although the most extensive literature relates to the use of baculoviruses against *H. armigera*, in practical control terms *Bacillus thuringiensis* Berliner (*Bt*) has undoubtedly been more widely used.

*H. armigera* is possibly the most widely targeted of African field crop pests for control by viruses; it is susceptible to its homologous nucleopolyhedrovirus (*Ha*NPV) (*Baculoviridae*) (Plate 61a,b) and to those of *Mamestra brassicae* (L.) and *Helicoverpa zea* (Boddie) (Lepidoptera, Noctuidae). A granulovirus (GV) (*Baculoviridae*) of *H. armigera* is known from South Africa, but may not be suitable for field control because of its effect on larval maturation. Use of baculoviruses against *H. armigera* in Africa was reviewed by Kunjeku *et al.* (1998). A cypovirus (CPV) (*Reoviridae*) is also known from *H. armigera* in Africa, but has not been seriously considered as a pest management option.

Although the NPV of *H. armigera* is widespread, natural control by the virus is usually inadequate. For example, of the diseases infecting *H. armigera* in Tanzania on maize, sorghum, cotton, chickpea, tomato and cleome, NPV was the most frequent, particularly on maize and cleome, but it was not able to prevent the pest from causing economic damage on the crops (Nyambo, 1990). von Maltitz (E.F. von Maltitz, 1992, Grahamstown, unpublished results) recorded up to 40% larval mortality from a polyhedral virus in sunflower in South Africa. Epizootics of baculoviruses in insect pests of short-term crops are rather rare; pest populations are not normally allowed to reach critical thresholds, rates of transmission remain low, and the reservoir of virus does not accumulate.

The experimental use of baculoviruses against *H. armigera* has been most extensive on cotton and dates back to the late 1950s, when Coaker (1958) tested the efficacy of a local isolate of *Ha*NPV against *H. armigera* on cotton in Uganda. While the virus was capable of killing larvae on treated foliage in cages, it was not recommended for use in Uganda where *H. armigera* populations were low and the virus endemic. The greatest concentration of experimental use of baculoviruses against *H. armigera* on cotton has been in West and Central Africa. Over the period spanning the 1960s to the 1980s, numerous trials conducted in Cameroon, Togo, Côte d'Ivoire and Chad focused on the use of indigenous isolates of *H. armigera* NPV and two imported species *M. brassicae* NPV and *H. zea* NPV (as the commercial formulations Biotrol VHF from Nutrilite Products Inc., Viron-H from International Minerals Corp. and Elcar from Sandoz). All three viruses were tested either alone or in combination with reduced doses of chemical insecticides or *Bt*. Results have been variable, but indigenous isolates of *H. armigera* NPV generally performed better than imported *H. zea* NPV (Atger, 1969; Angelini and Couilloud, 1972). Use of *M. brassicae* NPV against *H. armigera* has the advantage of also controlling *Diparopsis watersi* (Rothschild) (Lepidoptera, Noctuidae). Yields with *H. armigera* NPV and *M. brassicae* NPV have matched those achieved with standard chemical insecticides, but high dose rates of up to $1 \times 10^{13}$ occlusion bodies (OB) $ha^{-1}$ are usually required. Additionally, in combination with chemical insecticides at reduced dose and a phagostimulant, all three baculoviruses have given control that is often as good as control achieved with chemical insecticides alone (Angelini and Couilloud, 1972; Cadou and Soubrier, 1974; Montaldo, 1991; Silvie *et al.*, 1993; Vaissayre *et al.*, 1995).

On other crops, baculoviruses have had mixed success. In Botswana, Roome (1971) reported promising results with *Ha*NPV on sorghum, cowpeas and maize. In later trials in sorghum, neither *Hz*NPV nor *Bt* were as effective as a local *Ha*NPV, which itself could be as effective as the chemical standard if used at high doses. According to Kunjeku *et al.* (1998), *H. armigera* control with NPV on sorghum has been exceptionally successful and should be pressed forward. In Cape Verde, Elcar (*H. zea* NPV) was used successfully in tomatoes as part of an IPM programme. Withdrawal of Elcar from the market led to substitution with *Bt* that was reported to be less efficient (van Harten and Viereck, 1986). Lutwama and Matanmi (1988) used Elcar at 1 and $2 \times 10^{12}$ OB $ha^{-1}$ and *Bt* against *H. armigera* on tomatoes in southern Nigeria. At these rates, Elcar was not significantly better than *Bt* or Carbaryl.

Despite extensive testing in Africa, there is no evidence that baculoviruses have ever been used on anything other than an experimental scale and nothing to indicate that they are being widely used today. At least two foreign companies have, at one time or another, invested in either the development and/or testing of baculoviruses against *H. armigera* in West Africa. Regrettably, progress was inadequate, investment was halted and today neither company is present on the ground. Two particular problems with NPV for control of *H. armigera* in Africa are highlighted by Kunjeku *et al.* (1998). The first is the need for better formulations and the use of frequent application of fairly low doses, seen in North America as one of the main keys to successful *H. zea* control. The taxonomic diversity of cotton bollworm species in Africa is the second problem faced by the use of highly specific baculoviruses.

*B. thuringiensis* is widely used against lepidopteran pests in Africa and several subspecies/serovars are effective against *H. armigera* (Glare and O'Callaghan, 2000). Although *Bt* has been tested against *H. armigera* for many years and was included alongside NPV in many of the trials mentioned above in cotton, literature on the use of *Bt* against *H. armigera* in Africa is scant. In the coastal countries of West Africa, *H. armigera* is an important pest of vegetables and *Bt* has become one of the most important insecticides used against lepidopteran larvae in peri-urban vegetable crops. This has been more in response to farmer concern over chemical insecticide efficacy than any concern for the environment (A. Cherry, Cotonou, 2002, unpublished observations).

## Conclusions

There are rich and varied indigenous natural enemy complexes attacking *H. armigera* in both East and southern Africa. These natural enemies vary geographically, temporally and in their host-plant associations. Generalist predators tend to be more important than parasitoids and this makes the situation more difficult to grasp, since their effectiveness depends on the presence of other concurrent food sources. The combined impact of indigenous natural enemies is not negligible, they can cause major mortality and contribute to pest suppression. Yet, they have no clear cut role and the consensus of opinion is that alone they do not always prevent economic damage. This seems more true in high-value crops with their low economic-damage thresholds. The absence of consistent effect dictates the need for locally adapted pest control strategies that take account of regional variation.

Nevertheless, the potential to enhance the impact of natural enemies exists through a variety of mechanisms. Classical biological control exchanges between regions, the use of new associations, and augmentative and inoculative releases of indigenous and exotic natural enemies have been tested. These options have, however, generally failed to achieve substantial or permanent gains in control, and it seems that particularly with high-value crops, these approaches alone will not solve the *H. armigera* problem.

Manipulation and diversification of the crop environment through cultural techniques to conserve and enhance indigenous natural enemy impact may hold a key role, and was seen by Greathead and Girling (1989) as among the best prospects for biological control in Africa. In this regard, Africa already has an advantage in that much of Africa's agriculture is practised in smallholdings where a diversity of crops are grown in relatively small plots and where pesticide inputs are relatively low. This mosaic, which on the one hand provides a continuous supply of food for *H. armigera*, on the other hand conserves or even promotes natural enemies.

Farmers' pesticide spraying practices can negatively affect natural enemy populations, particularly when applied early in the season. Natural enemies that might otherwise have built up and suppressed the pest are killed and more insecticides are required. Reductions in the use of hazardous insecticides and early season substitution of broad spectrum insecticides with softer biological alternatives such as *Bt*, NPV and botanical insecticides may permit early establishment of natural enemies and contribute to pest suppression. However, as Landis *et al.* (2000) notes, while eliminating a pesticide treatment within a field may permit the establishment or persistence of a natural enemy population, if viable meta-populations do not exist at the landscape level to provide immigrants, the within-field effort may be ineffective.

Use of microbial control agents against *H. armigera* was rejected by Greathead and Girling (1989) because of high costs, short shelf-life and the difficulty of finding suitable formulations. Increased availability and improvements to the formulations of commercially available products, together with increasing resistance to chemical insecticides will make microbials a more favourable option. Nevertheless, the specificity of some microbials, and the frequent occurrence of *H. armigera* as part of a pest complex, means that there will continue to be a need for chemical pesticides.

Effective mating disruption by pheromones has been demonstrated in small plots outside Africa (Kehat *et al.*, 1998; Chamberlain *et al.*, 2000), although it is unlikely that this approach will provide cost-effective control because of the mobility and polyphagy of the pest. In Africa, use of the pheromone has been very limited. Pheromone traps were used for monitoring *H. armigera* as well as the other bollworms on cotton throughout Egypt during the 1980s and 1990s (Critchley, 1991). Lures have been provided to Kenya, Tanzania, Malawi, Sudan and Zimbabwe for evaluation. Synthetic sex pheromone traps for *H. armigera* were also tested in South Africa with the idea of establishing economic threshold levels for chemical control of the pest. The study was terminated because no correlation was found between larval infestations in the field and moth catches. Bourdouxhe (1982) reported use of pheromone traps for monitoring the flight periods of *H. armigera* in Senegal and Nyambo (1989) reported similar work in Tanzania.

Progress in biological control and IPM of *H. armigera* requires that situation-adapted strategies employing combinations of the options discussed above be adopted by farmers on a regional scale. Few examples exist and even though the results of the research conducted in Kenya (van den Berg, 1993) had important implications for the way farmers grow and manage their crops, the results remain unutilized at the field level. Recent developments in participatory IPM and action research in the region suggest ways in which research findings can be adopted and expanded by farmer communities in a process which is continuous and which includes direct stakeholders as well as researchers (Bruin and Meerman, 2001).

One way forward was exemplified by the cotton IPM programme in South Africa, driven not by a demand for biological control, but by the need to reduce pest management costs that had escalated as a result of the increasing frequency of pesticide applications. An example of how this approach might be extended can be seen in Australia. There, high cotton yields are maintained by intensive synthetic insecticide dependence, but in one study indigenous predators were used as the basic component of an IPM programme supported by interplanting with lucerne, the use of supplementary food sprays, biopesticides based on *Bt* and NPV, and judicious use of synthetic insecticides. The project demonstrated yields and economic returns that are equivalent to, or better than, the conventional system (Mensah, 2002).

The advent of *Bt*-transgenic plant varieties to Africa offers the promise of reduced insecticide inputs and the knock-on effect of conserved natural enemies. *Bt*-transgenic cotton and several *Bt*-transgenic maize hybrids are now commercially available in South Africa. During the 1998/1999 growing season, approximately 50,000 ha of irrigated land was planted with *Bt*-transgenic maize hybrids. In 2001, about 70% of cotton planted in South Africa was *Bt* cotton, but in some regions the figure was above 80%. South African legislation requires cotton farmers to plant at least 20% of each field with non-transgenic varieties as refugia to slow the potential for accelerated development of resistance to *Bt*. Only the smooth-leaved *Bt* cotton variety is available and, although very efficient against *H. armigera* and other bollworms, it is susceptible to leafhoppers (Cicadellidae). As a consequence, transgenic cotton usually still has to be sprayed against jassids. However, two recent reports show that both *Bt* cotton and *Bt* maize do enhance biodiversity through reduced insecticide application (Carpenter *et al.*, 2002; Gianessi *et al.*, 2002).

Finally, prospects for improved implementation of biological control and IPM in the future could be driven by external factors such as changes to market structure, consumer requirements and pest management economics. For instance, increasingly strict pesticide residue tolerance limits imposed by foreign markets on export products will fuel the demand for pest management approaches with reduced synthetic pesticide inputs. Such developments are already visible among those countries with a significant horticultural export sector. In the domestic market, increasing consumer awareness of pesticide residue hazards will drive a demand for improved control of residue limits, and an extension of this is the development and expansion of the organic products market whose consumers are willing to pay a green premium for pesticide-free products. The propensity of *H. armigera* to develop resistance will continue to escalate the costs of conventional insecticide-dependent pest management. At the same time, it will fuel the search for more economic and environmentally sound alternatives, but also alter the cost–benefit ratio of currently uneconomic or unattractive options.

## References

Abdelrahman, A.A. and Munir, B. (1989) Sudanese experience in integrated pest management of cotton. *Insect Science and its Application* 10, 787–794.

Andow, D.A. (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36, 561–586.

Angelini, A. and Couilloud, R. (1972) Les moyens de lutte biologique contre certains ravageurs du cotonnier et une perspective sur la lutte intégrée en Côte d'Ivoire. *Coton et Fibres Tropicales* 27, 283–289.

Annecke, D.P. and Moran, V.C. (1982) *Insects and Mites of Cultivated Plants in South Africa*. Butterworths, Pretoria, South Africa.

Anonymous (1992) Integrated pest management of cotton pests: a compromise between biological and chemical control. *Plant Protection News*, Bulletin of the Plant Protection Research Institute, Pretoria, South Africa, 29, 6–7.

Atger, P. (1969) Observations sur la polyhedrose nucléaire d'*Heliothis armigera* (Hbn.) au Tchad. *Coton et Fibres Tropicales* 24, 243–244.

Bedford, E.C.G. (1954) Summary of the biological control of insect pests in South Africa 1895–1953. Department of Agriculture and Technical Services, Pretoria, South Africa. Special Report 2/53–54.

Bedford, E.C.G. (1968) Biological and chemical control of citrus pests in the Western Transvaal. An integrated spray programme. *South African Citrus Journal* 417, 21–28.

Bottrell, D.G., Barbosa, P. and Gould, F. (1998) Manipulating natural enemies by plant variety selection and modification: a realistic strategy? *Annual Review of Entomology* 43, 347–367.

Bournier, J.P. and Peyrelongue, J.Y. (1973) Introduction, rearing and releases of *Trichogramma brasiliensis* Ashm. (Hym. Chalcididae) with a view to controlling *Heliothis armigera* Hbn. (Lep. Noctuidae) in Madagascar. *Coton et Fibres Tropicales* 28, 231–237.

Bourdouxhe, L. (1982) Comparaison de deux types de pièges pour le piégeage sexuel de *Heliothis armigera* au Sénégal. *Plant Protection Bulletin FAO* 30, 131–136.

Bruin, G.C.A. and Meerman, F. (2001) *New Ways of Developing Agricultural Technologies: the Zanzibar Experience with Participatory Integrated Pest Management*. Co-publication Wageningen University and Research Centre and CTA (CTA number 1047), Wageningen, The Netherlands.

Cadou, J. and Soubrier, G. (1974) Utilisation d'une polyédrose nucléaire dans la lutte contre *Heliothis armigera* (Hb.) (Lep. Noct.) en culture cotonnière au Tchad. *Coton et Fibres Tropicales* 29, 357–365.

Carl, K.P. (1989) Attributes of effective natural enemies, including identification of natural enemies for introduction purposes. In: King, E.G. and Jackson, R.D. (eds) *Proceedings of the Workshop on Biological Control of* Heliothis*: Increasing the Effectiveness of Natural Enemies. November 11–15, 1985, New Delhi, India*. Far Eastern Regional Research Office, U.S. Department of Agriculture, New Delhi, India, pp. 351–361.

Carpenter, J., Felsot, A., Goode, T., Hamig, M., Onstad, D. and Sankula, S. (2002) *Comparative Environmental Impacts of Biotechnology-derived and Traditional Soybean, Corn and Cotton Crops*. Council for Agricultural Science and Technology, Ames, Iowa, USA. www.cast-science.org

Chamberlain, D.J., Brown, N.J., Jones, O.T. and Casagrande, E. (2000) Field evaluation of a slow release pheromone formulation to control the American bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae) in Pakistan. *Bulletin of Entomological Research* 90, 183–190.

Charleston, D.S., Kfir, R., van Rensburg, N.J., Barnes, B.N., Hattingh, V., Conlong, D.E., Visser, D. and Prinsloo, G.J. (2003) Integrated pest management in South Africa. In: Maredia, K., Dakouo, D. and Mota-Sanchez, D. (eds) *Integrated Pest Management in the Global Arena*. CAB International, Wallingford, UK.

Coaker, T.H. (1958) Experiments with a virus disease of the cotton bollworm *Heliothis armigera* (Hbn). *Annals of Applied Biology* 46, 536–541.

Critchley, B.R. (1991) Commercial use of pink bollworm pheromone formulations in Egyptian cotton pest management. *Pesticide Outlook* 2, 9–13.

*Crop Protection Compendium* (2001) CD ROM. CAB International, Wallingford, UK.

Gianessi, L.P., Silvers, C.S., Sankula, S. and Carpenter, J.E. (2002) *Plant Biotechnology: Current and Potential Impact for Improving Pest Management in US Agriculture*. National Centre for Food and Agricultural Policy. www.ncfap.org

Glare, T.R. and O'Callaghan, M. (2000) *Bacillus thuringiensis: Biology, Ecology and Safety*. John Wiley & Sons, Chichester, UK.

Greathead, D.J. and Girling, D.J. (1982) Possibilities for natural enemies in *Heliothis* management and the contribution of the Commonwealth Institute of Biological Control. In: *Proceedings of the International Workshop on* Heliothis *Management,* November 15–20, 1981, Patancheru, A.P., India. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India, pp. 147–158.

Greathead, D.J. and Girling, D.J. (1989) Distribution and economic importance of *Heliothis* and of their natural enemies and host plants in southern and eastern Africa. In: King, E.G. and Jackson, R.D. (eds) *Proceedings of the Workshop on Biological Control of* Heliothis*: Increasing the Effectiveness of Natural Enemies.* November 11–15, 1985, New Delhi, India. Far Eastern Regional Research Office, United States Department of Agriculture, New Delhi, India, pp. 329–345.

Kehat, M., Anshelevich, L., Gordon, D., Harel, M. and Dunkelblum, E. (1998) Evaluation of Shin-Etsu twist-tie rope dispensers by the mating table technique for disrupting mating of the cotton bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae), and the pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). *Bulletin of Entomological Research* 88, 141–148.

Kfir, R. (1981) Effect of host and parasite density on the egg parasite *Trichogramma pretiosum* (Hym.: Trichogrammatidae). *Entomophaga* 26, 445–451.

Kfir, R. (1982) Reproduction characteristics of *Trichogramma brasiliensis* and *T. lutea*, parasitising eggs of *Heliothis armigera. Entomologia Experimentalis et Applicata* 32, 249–255.

Kfir, R. (1994) Attempts at biological control of the stem borer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in South Africa. *African Entomology* 2, 67–68.

Kfir, R. and van Hamburg, H. (1983) Further tests of threshold levels for control of cotton bollworms (mainly *Heliothis armigera*). *Journal of the Entomological Society of Southern Africa* 46, 49–58.

King, E.G., Powell, J.E. and Coleman, R. (1985) A high incidence of parasitism of *Heliothis* spp. (Lepidoptera: Noctuidae) larvae in cotton in southeastern Arkansas. *Entomophaga* 30, 419–426.

Kuklinski, F. and Borgemeister, C. (2002) Cotton pests and their natural enemies in Madagascar. *Journal of Applied Entomology* 126, 55–65.

Kunjeku, E., Jones, K.A. and Moawad, G.M. (1998) Africa, the Near and Middle East. In: Hunter Fujita, F.R., Entwistle, P.F., Evans, H.F. and Crook, N.E. (eds) *Insect Viruses and Pest Management*. John Wiley & Sons, Chichester, UK, pp. 280–302.

Landis, D.A., Wratten, S.D. and Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45, 175–201.

Lutwama, J.J. and Matanmi, B.A. (1988) Efficacy of *Bacillus thuringiensis* subsp. *kurstaki* and *Baculovirus heliothis* foliar applications for suppression of *Heliothis armigera* (Hübner). *Bulletin of Entomological Research* 78, 173–179.

Mensah, R.K. (2002) Development of an integrated pest management programme for cotton. Part 2: Integration of a lucerne/cotton interplant system, food supplement sprays with biological and synthetic insecticides. *International Journal of Pest Management* 48, 95–105.

Messenger, P.S. (1974) Procedures for conducting a biological control programme against *Heliothis armigera*. *Plant Protection Service Technical Bulletin,* Department of Agriculture, Thailand 19.

Mohyuddin, A.I. (1989) Distribution and economic importance of *Heliothis* spp. in Pakistan and their natural enemies and host plants. In: King, E.G. and Jackson, R.D. (eds) *Proceedings of the Workshop on Biological Control of* Heliothis*: Increasing the Effectiveness of Natural Enemies.* November 11–15, 1985, New Delhi, India. Far Eastern Regional Research Office, United States Department of Agriculture, New Delhi, India, pp. 229–240.

Montaldo, T. (1991) Microbial control in cotton crops in North Cameroon: overview of experiments conducted from 1979 to 1988. *Coton et Fibres Tropicales* 46, 230–240.

Nyambo, B.T. (1986) Studies in the bollworm, *Heliothis armigera* Hübner, the key cotton pest in Tanzania, as a basis for improved integrated pest management. PhD thesis, University of London, UK.

Nyambo, B.T. (1989) Assessment of pheromone traps for monitoring and early warning of *Heliothis armigera* Hübner (Lepidoptera, Noctuidae) in the western cotton-growing areas of Tanzania. *Crop Protection* 8, 188–192.

Nyambo, B.T. (1990) Effect of natural enemies on the cotton bollworm, *Heliothis armigera* Hübner (Lepidoptera: Noctuidae) in Western Tanzania. *Tropical Pest Management* 36, 50–58.

Parry-Jones, E. (1937) The egg parasites of the cotton bollworm, *Heliothis armigera* Hübner (*obsuleta* Fabr.), in southern Rhodesia. *Publication, Mazoe Citrus Experimental Station* 6, 37–105.

Parry-Jones, E. (1938) The biology of a tachinid parasite (*Sturmia rhodesiensis*, sp. n.) of the cotton bollworm (*Heliothis armigera* Hübner) in southern Rhodesia. *Publication, Mazoe Citrus Experimental Station* 7, 11–34.

Parsons, F.S. (1940) Investigations on the cotton bollworm *Heliothis armigera* Hübn. (*obsoleta* Fabr.). Part II. The incidence of parasites in quantitative relation to bollworm populations in South Africa. *Bulletin of Entomological Research* 31, 89–109.

Parsons, F.S. and Ullyett, G.C. (1934) Investigations on the control of the American and red bollworms of cotton in South Africa. *Bulletin of Entomological Research* 25, 349–381.

Parsons, F.S. and Ullyett, G.C. (1936) Investigations of *Trichogramma lutea*, Gir., as a parasite of the cotton bollworm, *Heliothis obsoleta* Fabr. *Bulletin of Entomological Research* 27, 219–235.

Risch, S.J. (1983) Intercropping as cultural pest control: prospects and limitations. *Environmental Management* 7, 9–14.

Romeis, J. and Shanower, T.G. (1996) Arthropod natural enemies of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) in India. *Biocontrol Science and Technology* 6, 481–508.

Roome, R.E. (1971) A note on the use of biological insecticides against *Heliothis armigera* (Hbn.) in Botswana. *Proceedings of the Cotton Insect Control Conference*, Blantyre, Malawi, pp. 221–238.

Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43, 95–124.

Russell, E.P. (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology* 18, 590–599.

Silvie, P., Le Gall, P. and Sognigbé, B. (1993) Evaluation of a virus-insecticide combination for cotton pest control in Togo. *Crop Protection* 12, 591–596.

Taylor, J.S. (1932) Report on cotton insect and disease investigations part II. Notes on the American bollworm (*Heliothis obsoleta* Fabr.) on cotton, and its parasite, *Microbracon brevicornis* Wesm. *Science Bulletin,* Department of Agriculture, Union of South Africa 113, 1–18.

Ullyett, G.C. (1933) The mass-rearing of *Bracon brevicornis* Wesm. *South African Journal of Science* 30, 426–432.

Vaissayre, M., Cauquil, J. and Sylvie, P. (1995) Protection phytosanitaire du cotonnier en Afrique tropicale. *Agriculture et Développement* 8, 3–23.

van den Berg, H. (1993) Natural control of *Helicoverpa armigera* in smallholder crops in East Africa. PhD thesis, Wageningen University, The Netherlands.

van den Berg, H. and Cock, M.J.W. (1993a) *African Bollworm and its Natural Enemies in Kenya*. CAB International, Wallingford, UK.

van den Berg, H. and Cock, M.J.W. (1993b) Stage-specific mortality of *Helicoverpa armigera* in three smallholder crops in Kenya. *Journal of Applied Ecology* 30, 640–653.

van den Berg, H. and Cock, M.J.W. (1993c) Exclusion cage studies on the impact of predation on *Helicoverpa armigera* in cotton. *Biocontrol Science and Technology* 3, 491–497.

van den Berg, H. and Cock, M.J.W. (1995a) Natural control of *Helicoverpa armigera* in cotton: assessment of the role of predation. *Biocontrol Science and Technology* 5, 453–463.

van den Berg, H. and Cock, M.J.W. (1995b) Spatial association between *Helicoverpa armigera* and its predators in smallholder crops in Kenya. *Journal of Applied Ecology* 32, 242–252.

van den Berg, H., Waage, J.K. and Cock, M.J.W. (1988) *Natural Enemies of* Helicoverpa armigera *in Africa: a Review.* CAB International and Institute of Biological Control, Ascot, UK.

van den Berg, H., Nyambo, B.T. and Waage, J.K. (1990) Parasitism of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in Tanzania: analysis of parasitoid-crop associations. *Environmental Entomology* 19, 1141–1145.

van den Berg, H., Cock, M.J.W., Oduor, G.I. and Onsongo, E.K. (1993) Incidence of *Helicoverpa armigera* (Lepidoptera: Noctuidae) and its natural enemies on smallholder crops in Kenya. *Bulletin of Entomological Research* 83, 321–328.

van den Berg, H., Cock, M.J.W. and Oduor, G.I. (1997) Natural control of *Helicoverpa armigera* in sunflower: assessment of the role of predation. *Biocontrol Science and Technology* 7, 613–629.

van Hamburg, H. (1980) Biological control efforts of *Heliothis armigera* in South Africa. In: *Workshop on Biological Control of* Heliothis *spp*. Queensland Department of Primary Industries, 25 September 1980. Toowomba, Australia.

van Hamburg, H. (1981) The inadequacy of egg counts as indicator of threshold levels for control of *Heliothis armigera* on cotton. *Journal of the Entomological Society of Southern Africa* 44, 289–295.

van Hamburg, H. and Kfir, R. (1982) Tests of threshold levels based on larval counts for chemical control of cotton bollworms. *Journal of the Entomological Society of Southern Africa* 45, 109–121.

van Hamburg, H. and Guest, P.J. (1997) The impact of insecticides on beneficial arthropods in cotton agroecosystems in South Africa. *Archives of Environmental Contamination and Toxicology* 32, 63–68.

van Harten, A. and Viereck, A. (1986) Umweltfreudlichere Schädlingsbekämpfung durch integrierten Pflanzenschutz in Kapverden. *Entwicklung and Ländlicher Raum* 4, 22–24

van Harten, A., Neves, A.M. and Brito, J.M. (1990) Importaçáo, criaçáo, libertaçáo e recuperaçáo de parasitas e predatores de pragas em Cabo Verde no período Abril 1983 – Dezembro 1987. *Investigaçáo agrária (INIA) Cabo Verde* 3, 39–49.

Watmough, R.H. (1991) Predation, an important cause of mortality in the pupae of the American bollworm. *Plant Protection News,* Bulletin of the Plant Protection Research Institute, Pretoria, South Africa, 26, 4.

Watmough, R.H. and Kfir, R. (1995) Predation on pupae of *Helicoverpa armigera* Hbn. (Lep., Noctuidae) and its relation to stem borer numbers in summer grain crops. *Journal of Applied Entomology* 119, 679–688.

Whitlock, V.H. (1973) Studies on insecticidal resistance in the bollworm *Heliothis armigera* Hübner (Lepidoptera: Noctuidae). *Phytophylactica* 5, 71–74.