Review

Prospects for the biological control of the groundnut leaf miner, *Aproaerema modicella*, in Africa

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Abstract

The groundnut leaf miner, *Aproaerema modicella*, is a pest of groundnut and soybean in South and Southeast Asia that has recently invaded Africa. It was first found in Uganda in 1998 and is now recorded in Mozambique, Malawi, Democratic Republic of Congo and South Africa. In all African countries where *A. modicella* has been found, the pest has reached outbreak densities and severe yield losses have been observed on groundnut. In this paper, we review the natural enemies of *A. modicella* in Asia and evaluate their potential for biological control in Africa. The main natural enemies of *A. modicella* in Asia are parasitoids. Over 30 primary parasitoid species have been recorded with mean parasitism rates fluctuating between 20 and 50% and peak parasitism reaching 53–91%. The most often cited parasitoids belong to the genera *Goniozus* (Hym.: Bethylidae), *Apanteles*, *Bracon*, *Chelonus* and *Avga* (Hym.: Braconidae), *Brachymeria* (Hym.: Chalcididae), and *Stenomesius*, *Sympiesis* and *Tetrastichus* (Hym.: Eulophidae). Predators and pathogens have been poorly studied. *A. modicella* is a promising target for classical biological control using natural enemies from Asia. Damage levels are, on average, higher in Africa than in Asia, where parasitoids, and possibly predators and pathogens, probably play an important role in the natural control of the pest. However, surveys are needed in Asia to better study natural enemies of *A. modicella* before selecting the most suitable agents. Until now, most studies on natural enemies were carried out in India, where *A. modicella* is considered a serious pest. New surveys should focus on other regions, where the moth causes little damage and very little is known on its natural enemy complex.

Keywords: *Aproaerema modicella*, Groundnut leaf miner, Biological control, Natural enemies, Parasitoids, *Arachis hypogaea*, Groundnut

Review Methodology: CAB Abstracts was used to find publications using the following keyword terms: *Aproaerema modicella*, natural enemies, parasitoids. The CABI Crop Pest Compendium [1] and Internet were also consulted. Host-parasitoid interactions were searched in the interactive catalogues of Noyes [2] and Yu *et al*. [3]. In addition, we used the references from the articles obtained to check for additional relevant material. We also spoke to specialists of the groundnut leaf miner and other colleagues for grey literature and unpublished information.

Introduction

The groundnut leaf miner, *Aproaerema modicella* (Deventer) (Lep.: Gelechiidae) is a pest of groundnut (*Arachis hypogaea*), and soybean (*Glycine max*) in South and Southeast Asia. It occurs from Pakistan to China, the Philippines, and as far South as Indonesia and Sri Lanka [4–6]. Eggs are laid singly on the underside of the leaves of groundnut, soybean and other leguminous plants. Young larvae mine the leaves and later instars exit the mine to web together several leaflets. In general, larvae of *A. modicella* pass through five instars with the duration of larval development lasting between nine and 28 days. Pupation occurs in the webbed leaflets and is completed in three to ten days. The number of generations per crop is highly variable and may vary from two to seven generations depending on the crop, the season and the climate [6]. Damaged leaves become brownish, rolled and desiccated, which results in early defoliation and affects the growth and yield of the plants. *A. modicella* is recognised as a serious pest of groundnut in India, where it has been extensively studied and where yield losses of up to 30–50% are reported [6, 7]. In the other Asian countries where it occurs, reports of serious damage are much less frequent [8, 9]. Even in India, the pest is very sporadic with wide population fluctuations between generations and seasons.

Control methods in Asia rely mainly on chemical insecticides. However, in recent years numerous studies have suggested more integrated approaches involving other control methods to lower the use of chemical insecticides and minimise their negative effects on the environment and human health. These methods include intercropping, manipulation of planting dates, utilization of less susceptible crop genotypes, trap crops, botanical pesticides and *Bacillus thuringiensis* Berliner [1, 10]. Methods based on the conservation and enhancement of natural enemies have often been proposed, but have never been tested.

A. modicella has been recently discovered in various regions in Africa. First in 1998 in Uganda [11, 12], then in Malawi [13], South Africa [14], Mozambique [15] and Democratic Republic of Congo (DRC) [16]. The pest is spreading rapidly, causing serious damage to groundnut, particularly in Mozambique and Uganda. Most of the African groundnut production is considered at risk.

This paper reviews the knowledge on natural enemies of *A. modicella* in Asia and evaluates the potential for the classical biological control of the leaf miner in Africa through the introduction of natural enemies from Asia.

Pest Status and Natural Enemies in Africa

In all African countries where *A. modicella* has been found, the pest has reached outbreak densities and severe losses have been observed on groundnut. The pest was also found feeding on soybean, alfalfa, pigeon pea and other legumes [12–14]. Mozambique is particularly affected. *A. modicella* was first noticed in southern provinces in 1998. Surveys made in 2004–2005 showed that it is spreading further north and it now occurs in most provinces [15]. In Southern Mozambique, an average of 45–56 mines and 29–38 larvae per groundnut plant were found. Mean yield losses varied from 47 to 86% compared to sprayed plots. Such damage levels are very rarely found in Asia. For comparison, in India, insecticide treatments are advised when 5–10 larvae are found per plant [17]. Surveys in Northern Malawi showed that the pest was found in all farmers' fields that were visited [13]. In some fields, more than 5 larvae per leaflet were found. The pest is also well established in many districts of Eastern and Central Uganda [12]. Damage levels vary between regions but total crop losses are observed. In South Africa, the leaf miner is present over the entire groundnut production area in Free State, Northern Cape, North West and Mpumalanga Provinces, where it causes severe damage to crops [14].

Table 1 Hymenopteran parasitoids reared from *Aproaerema modicella* on groundnut in Uganda and the DRC [16]. Taxonomic status according to Noyes [2]

Parasitoid species	Country
Eulophidae	
Diglyphus sp.	Uganda
Stenomesius sp. (as *Euryscotolinx* sp.)	Uganda
Asecodes sp. (as *Teleopterus* sp.)	DRC
Pteromalidae	
Pteromalus sp.	DRC

In sub-Saharan Africa, groundnut is a basic staple crop, cultivated mainly by small-scale farmers both as subsistence and as a cash crop. It is an important source of protein and other nutrients for poor rural communities. Thus, the leaf miner represents not only a serious threat to groundnut production but also to food security. For the moment, the use of insecticides such as Cypermethrin or Dimethoate is the only available control method. Their effectiveness has been shown in both Uganda [12] and Mozambique [15]. However, insecticides are not affordable for most small-scale farmers and can have a serious impact on the environment and human health. Therefore, the development of sustainable management methods, including biological control, is highly recommended [12, 15].

Natural enemies have not yet been studied in detail in Africa. Parasitoids were reported on two occasions. Munyuli *et al.* [16] reared four larval parasitoids in Uganda and the DRC (Table 1). Parasitism rates varied from 1.4 to 4.5%. In Mozambique, Cugala *et al.* [15] observed several parasitoid species of the families Braconidae, Ichneumonidae, Chalcididae, Eulophidae and Bethylidae, with parasitism rates varying between 0 and 23.2%, but the parasitoids were not identified further.

Natural Enemies in Asia and Their Role in Population Dynamics

Predators

There are several reports of insects preying on *A. modicella* in India. However, nothing is known on predation rate and their impact on prey populations. Larvae of *Chlaenius* sp. (Col.: Carabidae) were found inside mines of *A. modicella* in groundnut and soybean leaves. *Chlaenius* larvae readily attacked and ate larvae of *A. modicella* in glass vials [18]. Srinivasan and Siva Rao [19] report predation by undetermined spiders and robber flies (Dipt.: Asilidae). Other predators reported for *A. modicella* include *Odynerus punctum* (F.) (Hym.: Eumenidae), *Cheilomenes sexmaculata* F. and *Coccinella septempunctata* L. (Col.: Coccinellidae) and *Chrysoperla carnea* Stephens (Neur.: Chrysopidae) [1]. The predatory bug *Rhynocoris marginatus* (F.) (Het.: Reduviidae) was tested on *A. modicella* in the laboratory and in field conditions [20, 21]. *A. modicella* was less preferred than two other groundnut pests. All the predators observed or tested on *A. modicella* in Asia are polyphagous species and, thus, would not be suitable for introduction into Africa.

Pathogens and Nematodes

Several diseases and nematodes have been recorded from *A. modicella* in India. Rajagopal *et al*. [22] showed that the bacterium *B. thuringiensis*, the fungus *Beauveria bassiana* (Bals.-Criv.) Vuill., and an unidentified virus, killed 5.6 to 36.4, 11.6 to 30.8 and 1.2 to 5.2% of larvae respectively. Shanower *et al*. [23] observed that viral and fungal pathogens killed up to 30% of larvae, but did not identify the species involved. Rao and Reddy [24] isolated the fungus *Metarhizium anisopliae* (Metschn.) Sorokīn from dead larvae and tested it successfully in the laboratory. They suggested that it could be used as a biological control agent.

Parasitoids

Although *A. modicella* is considered a pest in many countries in South and Southeast Asia, parasitoids have been studied almost exclusively in India and usually on groundnut. Data from other regions are usually unpublished, such as that of Phisitkul [9] who found 13 parasitoid species on groundnut in Northeast Thailand, or anecdotal (e.g. van der Laan and Ankersmit [25] in Indonesia). Yang and Liu [8] mention parasitism in China, but do not provide species or genus names. Two studies listed a total of seven parasitoids on soybean in India [26, 27]. The most complete study on parasitoids of *A. modicella* has been carried out in Andhra Pradesh by Shanower *et al.* [6, 23]. They also provided a literature review of other studies mentioning parasitoids of *A. modicella* up to 1991. Since then, parasitoid species have also been mentioned by Khan [28], Shetgar *et al*. [29], Kumar *et al*. [30] and Muthiah and Kareem [31]. Over 40 primary and secondary parasitoids belonging to 12 families have been reared from *A. modicella* (Table 2). However, only Bethylidae, Braconidae, Chalcididae and Eulophidae have been abundantly cited as primary parasitoids and will be discussed in detail in this review.

Many publications mention parasitism rates, a few assess the impact of parasitoids through life table studies (e.g. [30]). However, surprisingly little is known on the biology of these parasitoids. Furthermore, there is much uncertainty regarding the identity of these species. In many cases, only genera are mentioned and species names have to be taken with caution.

Bethylidae

Species of the genus *Goniozus* have been regularly cited as parasitoids of *A. modicella* in India. Muthiah [32] mentions a *Goniozus* sp. as the most important parasitoid in Tamil Nadu, with up to 30% parasitism rate. A later study in the same region [31] identified *Goniozus indicus* Ashmead as the third most abundant parasitoid, with a parasitism rate of 16%. In Maharashtra, *Goniozus stomopterycis* Ram and Subba Rao was found by Shetgar *et al.* [29]. *Goniozus* sp. was one of the three key parasitoids in Gujarat, with up to 50% parasitism [33] but was of low importance in Andhra Pradesh, where it was attacked by the hyperparasitoid *Elasmus anticles* Walker [23]. *Goniozus* sp. was also reared from soybean by Shetgar and Thombre [27].

Little is known of the biology of *Goniozus* spp. on *A. modicella*. In general, *Goniozus* spp. are idiobiont ectoparasitoids of concealed lepidopteran larvae. Several species have been used in biological control. For example *Goniozus legneri* Gordh, introduced against the pyralid *Amyelois transitella* (Walker) in California provided significant control of the moth [39] and *Goniozus nephantidis* (Muesebeck) is used as a biological control agent against the oecophorid coconut pest *Opisina arenosella* Walker [40, 41]. Bethylids tend to be rather polyphagous (e.g. [42]). However, some species are more host specific [43].

Braconidae

Four genera of braconid wasps have been frequently reared from *A. modicella*: *Apanteles* (including the closely related genus *Protapanteles* and their subgenera *Dolichogenidea* and *Glyptapanteles*), *Chelonus* (subgenus *Microchelonus*), *Bracon* (subgenus *Habrobracon*) and *Avga*. Their identity at the species level is not clear and since individual studies usually mention single species per genera, it is likely that different names may refer to a single species. In China, Yang and Liu [8] have observed an undetermined braconid species reaching 12–52% parasitism.

Apanteles and *Protapanteles* species are among the most frequently cited parasitoids of *A. modicella. Apanteles* sp. was considered as one of the three main parasitoids by Yadav *et al*. [33] in Gujarat, with up to 38% parasitism. In Tamil Nadu, Muthiah [32] mentioned a maximum parasitism rate of 18% by an *Apanteles* sp. Species names were cited by Kumar *et al*. [30] who reared *Protapanteles africanus* (Cameron) in Andhra Pradesh, Shetgar and Thombre [27] who cited *Apanteles litae* Nixon var. *operculellae* Nixon on soybean in Maharashtra, and Shanower *et al.* [6, 23] who mention *Apanteles javensis* Rohwer and *Apanteles singaporensis* Szépligeti in their reviews. In Java,

Table 2 Hymenopteran parasitoids reared from *A. modicella* on groundnut and soybean in Asia (sources [4, 6, 9, 19, 22, 23, 25–38]). Taxonomic status according to Noyes [2] and Yu *et al*. [3]

Parasitoid species[1]	Host stage parasitised[2]	Country	Host plant[4]
Bethylidae			
Goniozus sp. (syn. *Perisierola* sp.)	L	India	GN, SB
Goniozus indicus Ashmead	L	India	GN
Goniozus stomopterycis Ram & Subba Rao	L	India	GN
Braconidae			
Apanteles sp. (syn. *Dolichogenidea* sp.)	L	India, Indonesia, Thailand	GN, SB
Apanteles javensis Rohwer	L	India	GN
Apanteles litae Nixon	L	India	SB
Apanteles singaporensis Szépligeti	L	India	GN
Avga choaspes Nixon	L	India	GN
Avga nixoni Subba Rao and Sharma	L	India	GN
Bracon sp.	L	India, Thailand	GN
Bracon brevicornis Wesmael	L	India	GN
Bracon gelechiae Ashmead	L	India	GN, SB
Bracon (syn. *Microbracon*) *hebetor* (Say)	L	India	GN
Chelonus sp.	E-L	India	GN, SB
Chelonus blackburni Cameron	E-L	India	GN
Chelonus curvimaculatus Cameron	E-L	India	GN
Protapanteles (syn. *Glyptapanteles*) *africanus* (Cameron)	E-L	India	GN
Phanerotoma sp.	E-L	India	GN
Ceraphronidae			
Aphanogmus fijiensis (Ferrière)	hyp	India	GN
Ceraphron sp.	hyp	India	GN
Chalcididae			
Brachymeria sp.	L, P	India	GN
Brachymeria lasus (Walker)	L, P	Thailand	GN
Brachymeria marmonti (Girault) (syn. *wittei* Schmitz)	L	India	GN
Brachymeria minuta (L.)	P	Thailand	GN
Brachymeria phya (Walker) (syn. *plutellophaga* (Girault))	L, P	India	GN
Kriechbaumerella sp. (syn. *Eucepsis* sp.)	P	Thailand	GN
Encyrtidae			
Copidosoma sp.	L	India	GN
Homalotylus flaminius Dalman[1]	L	Thailand	
Eulophidae			
Elasmus sp.	L, hyp	India, Thailand	GN
Elasmus anticles Walker	hyp	India	GN
Elasmus brevicornis Gahan	L, hyp	India	SB
Oomyzus sp.	hyp	India	GN
Pediobius sp.	L, hyp	India	GN
Stenomesius sp.	L, hyp	India	GN
Stenomesius japonicus (Ashmead) (syn. *Stenomesioideus ashmeadi* Subba Rao and Sharma, syn. *Euryscotolinx coimbatorensis* Rohwer)	L	India, Thailand	GN, SB
Stenomesius modicellus Khan	L	India	GN
Sympiesis sp.	L	India	GN
Sympiesis dolichogaster Ashmead (syn. *Asympiesiella india* Girault)	L	India, Thailand	GN
Tetrastichus sp.	L, hyp	India, Thailand	GN
Eupelmidae			
Eupelmus sp.	L, P, hyp	India	GN
Eurytomidae			
Eurytoma sp.	L	India	GN
Plutarchia giraulti Subba Rao	L	Thailand	GN
Ichneumonidae			
Temelucha sp.	L	India	GN
Mymaridae			
Anagrus sp.[3]	L	India	GN

Table 2 (Cont.)

Parasitoid species[1]	Host stage parasitised[2]	Country	Host plant[4]
Pteromalidae			
Dibrachys sp.	L	Thailand	GN
Macromesus sp.[3]	L	Thailand	
Pteromalus (syn. *Habrocytus*) sp.	hyp	India	GN
Trichogrammatidae			
Trichogramma sp.	E	India	GN

[1]Names underlined have been cited in at least three different primary publications.
[2]Host stage parasitised as mentioned in the publications. E=egg parasitoid; E-L=egg-larval parasitoid: L=larval parasitoid; P=pupal parasitoid; hyp=mentioned at least once as hyperparasitoid.
[3]Probably a host or identification error.
[4]GN=groundnut; SB=soybean.

an *Apanteles* sp. was found to parasitise up to 60% of the larvae. An *Apanteles* sp. was also the most abundant parasitoid in the study of Phisitkul [9] in Northeast Thailand. *Apanteles* spp. are koinobiont endoparasitoids of Lepidoptera [44]. Many of them have a restricted host range and several species have been successfully used in biological control programmes, including against Gelechiidae, such as *Apanteles subandinus* Blanchard, which was released against the potato tuber moth, *Phthorimaea operculella* (Zeller) in South Africa [45].

Chelonus spp. have also been found in most studies on parasitoids of *A. modicella* in India. A *Chelonus* sp. was the most abundant parasitoid in Tamil Nadu, with a 26% parasitism rate [31]. *Chelonus curvimaculatus* Cameron and the exotic *Chelonus blackburni* Cameron, introduced to India to control various Lepidopteran pests, were apparently recovered from *A. modicella* by Khan and Raodeo [34] and Srinivasan and Siva Rao [19] respectively. A *Chelonus* sp. was also obtained from *A. modicella* on soybean [27], and Shanower *et al.* [23] reared three chalcid hyperparasitoids from *Chelonus* sp. All *Chelonus* spp. are solitary egg-larval koinobiont endoparasitoids of Lepidoptera, ovipositing into the host egg and killing the host larva just before pupation [44]. Many *Chelonus* spp. show a relatively high degree of specificity because of their high interaction with the host physiology, although some species such as *C. blackburni* or *C. curvimaculatus* have been reared from, and on several Lepidoptera [3]. Several species have already been used as biological control agents against Gelechiidae. For example, an African *Chelonus* sp. near *curvimaculatus* was released against the pink bollworm, *Pectinophora gossypiella* (Saunders), in the USA [46], and *Chelonus kellieae* Marsh was imported from Costa Rica to California to control *P. operculella* [47]. *C. blackburni*, from Hawaii, was used in inundative releases against *P. operculella* too [48].

Bracon species of the subgenus *Habrobracon* (which is often given full generic status, see Belshaw *et al.* [49]) are also often cited as parasitoids of *A. modicella*. Many studies mention *Bracon gelechiae* Ashmead, a polyphagous species of Nearctic origin introduced in India to control *P. operculella* [50]. Rajagopal *et al.* [22] cite *B. gelechiae* as the only parasitoid in Bangalore, with parasitism rates varying from 5.2 to 33.3%. *B. gelechiae* was also reared from the moth on soybean in India [26]. Other species records include the cosmopolitan and polyphagous *Bracon hebetor* (Say) and *Bracon brevicornis* Wesmael [23]. However, the taxonomy of the genus is very complicated and misidentifications are common. A *Bracon* sp. was also one of the common parasitoids reared from *A. modicella* in Thailand [9]. *Bracon* spp. are all idiobiont ectoparasitoids of concealed holometabolous insect larvae [44]. Several species have been used as biological control agents, including against gelechiid moths (e.g. *P. operculella* and *P. gossypiella*, see [50, 51]). However, their polyphagy has made them largely unsuitable for classical biological control in recent years.

Two species of *Avga* have been recorded exclusively from *A. modicella*. *Avga choaspes* Nixon has been mentioned in Andhra Pradesh [23, 30], Tamil Nadu [31] and Karnataka [35]. *Avga nixoni* Subba Rao and Sharma has been reported only once [36]. *Avga* is a small genus of the subfamily Hormiinae. Species are idiobiont or koinobiont ectoparasitoids of microlepidopteran larvae. *Avga* spp. are known only from Gelechiidae and Tortricidae [3] and may show a high degree of host specificity. They have never been used in biological control programmes.

Shanower *et al.* [23] reared two hyperparasitoids from cocoons of *Apanteles* sp., *Bracon* sp. and *Avga choaspes*: the eulophid *Oomyzus* sp. and the ceraphronid *Aphanogmus fijiensis* (Ferrière), but did not distinguish between the three braconid hosts.

Eulophidae

Several eulophid genera parasitise larvae of *A. modicella* in Asia. The most often cited species and one of the most abundant parasitoids of the moth is *Stenomesius japonicus* (Ashmead) (syn. *Stenomesioideus ashmeadi* Subba Rao and Sharma). It was the main parasitoid of the moth in Andhra Pradesh in the rainy season [23] and in Gujarat where it reached up to 79% parasitism [33]. It was also found on soybean in Maharashtra [27] and on groundnut in Thailand [9]. Secondary parasitoids developing on *S. japonicus* include two eulophids, *Oomyzus* sp. and interestingly, another *Stenomesius* sp. [23]. *S. japonicus* is known as a polyphagous and widely distributed species [2]. Another species, *Stenomesius modicellus* Khan, has been reared from *A. modicella*, which is its only known host [28].

Sympiesis dolichogaster Ashmead is another species frequently reared from *A. modicella*. Shanower *et al.* [23] found this species to be dominant in the post-rainy season in Andhra Pradesh and Shekharappa *et al.* [35] cite a *Sympiesis* sp. as one of the four dominant parasitoid species in Karnataka. *Asympiesiella india* Girault reared from *A. modicella* in Thailand by Phisitkul [9] probably refers to the same species. *S. dolichogaster* is a polyphagous species with a cosmopolitan distribution [2]. The genera *Stenomesius* and *Sympiesis* are usually idiobiont ectoparasitoids of leaf mining larvae and pupae of holometabolous insects [2].

Finally, several studies mention *Tetrastichus* sp. from *A. modicella* (e.g. [30, 31, 51]) but never as a major component of the parasitoid complex, with the exception of Phisitkul [9], who cite *Tetrastichus* sp. as one of the main parasitoids in Thailand. The other eulophids listed in Table 2 have been less frequently reared from *A. modicella*. Several of them are probably at least partially hyperparasitoids of other eulophids, braconids and bethylids [23].

Chalcididae

Several *Brachymeria* species have been recorded on *A. modicella*, but only occasionally as a main parasitoid. For example, Muthiah and Kareem [31] cited *Brachymeria marmonti* (Girault) (syn. *Brachymeria wittei* Schmitz) as the second most abundant parasitoid in Tamil Nadu, accounting for 20% of the parasitoids. However, there is confusion regarding which development stage is parasitised. Most, if not all, *Brachymeria* spp. are endoparasitoids of pupae of holometabolous insects [52]. In *A. modicella*, most records mention larvae as hosts (e.g. [30–32, 34]). In contrast, Yadav *et al.* [33] cite *Brachymeria* sp. as a pupal parasitoid. Similarly, Phisitkul [9] reared *Brachymeria lasus* (Walker), *Brachymeria minuta* (L.) and another encyrtid, *Kriechbaumerella* sp. (as *Eucepsis* sp.) from pupae in Thailand. The confusion between larval and pupal parasitoids is easily made in *A. modicella* because pupation occurs in the webbed leaflets constructed by the larva. If, as suspected, *Brachymeria* spp. parasitise *A. modicella* pupae, studies focusing mainly on larval parasitoids may have largely underestimated parasitism by *Brachymeria* spp.

Several *Brachymeria* species have been introduced as biological control agents against various Lepidoptera, without much success [51]. Augmentative releases of *Brachymeria nosatoi* Habu have been carried out successfully against the oecophorid coconut leaf-eating caterpillar, *O. arenosella* Walker [40].

Other parasitoids of interest

Many parasitoids belonging to other families have been occasionally mentioned from *A. modicella* (Table 2). Several of them are at least partly hyperparasitoids, developing on primary larval or pupal parasitoids, as shown by Shanower *et al.* [23]. In his review, Mohammad [4] also cites an encyrtid, *Copidosoma* sp., as a larval parasitoid of *A. modicella* in Andhra Pradesh. This is of interest because a congeneric species, *Copidosoma koehleri* Blanchard, has been successfully used in a biological control programme against *P. operculella* in Africa [45].

Egg parasitism has been poorly studied in *A. modicella*. A couple of publications mention a *Trichogramma* sp. as an egg parasitoid in India [4, 31]. It caused 10% egg mortality in Tamil Nadu [31]. Gelechiidae are particularly suitable hosts for *Trichogramma* spp. [2]. Many species are used as inundative biological control agents, but they are usually polyphagous and thus, not suitable for classical biological control programmes.

Impact of Parasitoids

Many publications mentioning larval and pupal parasitoids also provide parasitism rates. A comparison among studies and regions is difficult because the methods used to calculate parasitism rates are almost never mentioned. Calculation methods used to assess parasitism rates in leaf miners are numerous and may strongly influence the estimations [53]. Furthermore, sometimes only peak parasitism is given, whereas in other cases only means are provided. Nevertheless, two important conclusions can be drawn from these studies. Firstly, parasitism rates and the relative abundance of the parasitoids species vary strongly with location, season and generation [9, 23, 27, 31, 34]. But the reason for these variations is not clear. Secondly, parasitism rates are much higher in Asia than in Africa. In their native range, leaf miners are among the most parasitised insects [54]. In India, maximum parasitism rates of 53% [23], 83% [34], 89% [33] and 91% [35] were observed on groundnut and 84% on soybean [27]. In China, Yang and Liu [8] measured maximum parasitism rates of 60–98% depending on the generation. Estimations of mean parasitism rates tend to fluctuate between 20 and 50% [7, 23, 29, 30], except in a study in Tamil Nadu, where mean parasitism rates at various locations varied from 1 to 28% [31]. Parasitism rates were also lower in Thailand, varying between 0 and 12%, which, according to the investigator, was due to the intensive use of insecticides at the study sites [9]. Three studies of parasitism and other mortality factors over several generations [23, 29, 30] were assessed in parallel and all showed that parasitism is the main mortality factor for the moth. Parasitoids, and possibly predators and pathogens, undoubtedly play an important role in the wide population fluctuations observed between years and seasons [29, 30, 34]. However, the data presently available on parasitism and other natural enemies are insufficient to fully understand the complex population dynamics of the moth.

Conclusions – Potential for Classical Biological Control in Africa

From this literature survey, we believe that *A. modicella* is a promising target for biological control in Africa, using natural enemies from Asia. Damage levels recorded in countries such as Mozambique and Uganda are far above those commonly encountered in Asia. Although *A. modicella* has a wide distribution in Asia, it is recorded as a major pest only in India. Even there, population and damage levels strongly vary from year to year and the frequent collapses of pest populations are believed to be due to natural enemies. In other regions, the insect is well known but usually not recognised as a major pest, suggesting that natural enemies keep the insect under sufficient control. Several natural enemies attacking *A. modicella* in Asia could be considered for biological control. Parasitoids appear to be particularly important. They seem to play a key role in the natural control of the moth in Asia. Primary parasitoids could be even more important, would they not be attacked by a range of secondary parasitoids. Several parasitoids reared from *A. modicella* in Asia could be particularly suitable because many of them belong to genera (e.g. *Apanteles*, *Chelonus*, *Copidosoma*, *Avga*) that often have a narrow host range, reducing the likelihood for impact on non-target organisms in Africa. Furthermore, several congeneric species have been successfully used against other alien gelechiid moths, such as *P. operculella* controlled in South Africa with *A. subandinus* and *C. koehleri* [45].

However, despite a high number of publications listing parasitoids of *A. modicella* in India, too little is known on their identity, biology and ecology to presently select candidates for introduction into Africa. Thus a biological control programme against *A. modicella* in Africa should start with a broad study of the parasitoid complex of the moth in Asia. A particular emphasis should be put on a precise identification of the species, their specificity, life cycle, impact on moth populations, and climatic and ecological requirements. Since *A. modicella* is present in many different climatic regions in Africa, surveys for natural enemies should cover similarly wide climatic situations in Asia. Surveys for natural enemies should focus especially on regions where the moth seems to cause less damage and where virtually nothing is known on its natural enemy complex, e.g. Southeast Asia, China or Pakistan. Parallel studies should be carried out in Africa to monitor indigenous natural enemies that have adopted this new alien species and to identify empty ecological niches that could be filled by introduced natural enemies.

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