STEMBORER PARASITISM BY *COTESIA SESAMIAE* AND *STURMIOPSIS PARASITICA* AND AN ASSESSMENT OF THE NEED TO INTRODUCE *COTESIA FLAVIPES* INTO ZIMBABWE

BY

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DECLARATIONS

It is hereby declared this thesis is my original work and has not been presented for a degree in any other university or any other award.

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We as Kenyatta University and ICIPE's supervisors confirm that the work reported in this thesis was carried out by the candidate under our supervision. The thesis was examined and we approved for its final submission.

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DEDICATION

To my wife, **Rumbidzai**,

whose love, care, encouragement and support saw me through;

and *my daughter*, **Rukudzo**,

whose unspoken love I will always cherish.

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ABSTRACT

Stemborers are major pests of maize and sorghum in Zimbabwe. An analysis of the research work on cereal stemborers in the country revealed several gaps for which information is required. Thus, as a way of bridging the identified information gaps, the studies reported in this thesis were conducted mainly to provide information on the distribution, abundance and seasonal occurrence of stemborers and their natural enemies, parasitoid seasonal carryover mechanisms and parasitoid biology, and to assess the need for the introduction of the exotic larval endoparasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae).

The seasonal occurrence of cereal stemborers and their natural enemies was studied for three seasons (1999-2000, 2000-01 and 2001-02) within the highveld (> 1200 m), middleveld (600-1200 m) and lowveld (< 600 m) ecological zones of Zimbabwe. Three species of stemborers were recorded, namely, *Busseola fusca* Fuller (Lepidoptera: Noctuidae), *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) and *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae). *Chilo partellus* was the most abundant and widely distributed species, occurring at all sites, but predominantly in the lowveld and middleveld. *Busseola fusca* was the second most abundant species but predominated only in the highveld. *Sesamia calamistis*, on the other hand, appeared to be an uneconomic pest due to its overall low frequency of occurrence.

Stemborer natural enemies recorded included the larval parasitoids, *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae) and *Sturmiopsis parasitica* (Curran) (Diptera: Tachinidae), the egg-larval parasitoid, *Chelonus curvimaculatus* Cameron (Hymenoptera: Braconidae), the pupal parasitoids, *Procerochasmias nigromaculatus* Cameron, *Dentichasmias busseolae* Heinrich (both Hymenoptera: Ichneumonidae) and *Pediobius*

furvus Gahan (Hymenoptera: Eulophidae), and an entomogenous nematode, *Hexamermis* sp. (Mermithidae). While *C. sesamiae* had a much wider distribution and host range, *S. parasitica* occurred only within the highveld (Harare area) where it parasitized *B. fusca*. Outside the highveld, *C. sesamiae* was, however, not recovered at Muzarabani (lowveld) and also appeared to be scarce at Bushu (middleveld).

In the Harare area, *S. parasitica* parasitism predominated for about half of the season (December-February) and attained a peak (10.9-60.2%) between the end of January and mid-February. Thereafter, parasitism declined sharply and by the end of March, recoveries of *S. parasitica* had all but ceased. In contrast, *C. sesamiae* parasitism generally fluctuated below that of *S. parasitica* for the period December-February, attaining a peak (14.5-37.5%) between mid-February and end of February, and thereafter fluctuated between 0 and 20% for the remainder of the season. *Sturmiopsis parasitica* overwintered in diapausing larvae from which it emerged in October-December when host diapause was terminated. In contrast, the seasonal carryover mechanism of *C. sesamiae* could not be identified.

Laboratory experiments were conducted to evaluate *B. fusca*, *S. calamistis* and *C. partellus* for their acceptability and suitability as hosts to a highveld and a lowveld *C. sesamiae* population. Both *C. sesamiae* populations preferred the noctuids to *C. partellus* for oviposition, possibly reflecting differences in evolutionary history. However, the three hosts showed differential suitability for the development of the two *C. sesamiae* populations. While all were suitable for the development of the highveld *C. sesamiae*, *B. fusca* was a partially suitable host to the lowveld population. Crosses between the highveld and lowveld *C. sesamiae* adults were compatible, producing mixed sex progenies. Based on the results of the host suitability and mating compatibility studies and a knowledge of the maize growth cycles within the different ecological zones, it is postulated that one probable *C. sesamiae* seasonal

carryover mechanism in Zimbabwe could be a yearly net outward migration of the parasitoid from lowveld "ecological islands" to niches where populations die out each year due to a long dry season and the consequent diapause-induced host unavailability. On its own, however, sustenance of *C. sesamiae* in such "ecological islands" is not a satisfactory carryover mechanism thus other possible mechanisms need to be investigated.

The development and levels of parasitism of *S. parasitica* on *B. fusca*, *S. calamistis* and *C. partellus* were studied in the laboratory. Parasitoid puparia recoveries were much higher on *B. fusca* (83.3% parasitism) than on *C. partellus* (15% parasitism). No development occurred on *S. calamistis* due to maggot encapsulation. At 25 ± 0.5°C, parasitoid larval developmental period on non-diapause *B. fusca* larvae averaged 14.2 days and the pupal period ranged from 13.7 days (males) to 15.8 days (females). Maggots were first observed at 6 days after mating and their numbers peaked (537-848 per female) after a 10-16 day gestation. Inoculation of diapausing *B. fusca* larvae resulted in a greatly extended larval period. Thus, the observed seasonal carryover mechanism of *S. parasitica* is simply a reflection of host hormonal influences on the parasitoid's larval developmental duration in diapausing as opposed to non-diapausing host larvae.

The suitability of *B. fusca* and *C. partellus* for development of the exotic parasitoid, *C. flavipes*, was investigated in Zimbabwe. Although *C. flavipes* accepted both stemborer species for oviposition, development was only completed on *C. partellus*. *Busseola fusca* was an unsuitable host due to egg encapsulation. While this result confirms the suitability of *C. partellus* for development of the exotic parasitoid, the apparent absence or very low impact of the indigenous *C. sesamiae* at some of the *C. partellus* "hotspots" further highlight the need to release *C. flavipes* in the country.

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CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 INTRODUCTION

Maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* [L.] Moench) are the staple food crops in many parts of sub-Saharan Africa (FAO and ICRISAT, 1996; Pingali, 2001). In Zimbabwe, maize is the single most important crop grown in the smallholder communal area sector. For the 1985/86 to 1988/89 seasons, the area under maize and sorghum production in Zimbabwe in the communal area sector represented 45 and 10%, respectively, of the total cropped area (Anderson *et al.*, 1993). However, maize yields are quite variable, depending on farming sector. In the communal area sector, yields are reported to have increased from about 402 kg/hectare during the 1969/70 season to 1,100 kg/hectare during the 1989/90 season (Anderson *et al.*, 1993). On the other hand, average yields of about 4,702 kg/hectare have been reported in the large scale-commercial sector (Central Statistical Office, 2000).

Lepidopteran stemborers, especially *Busseola fusca* Fuller, *Chilo partellus* (Swinhoe) and *Sesamia calamistis* Hampson, are among some of the most important insect pests that attack maize and sorghum in Africa (Polaszek, 1998). Although each stemborer species has a characteristic life history, the life cycle and damage of all species is very similar. Plant damage is caused by the larval stages, which, for a greater part of their life, feed cryptically within the stems. Reported yield losses due to stemborers in Africa vary widely, depending on species, region, crop, season and farming sector (Kfir *et al.*, 2002).

Chemical control of stemborers, although widely used, is too expensive and thus unsustainable, particularly at the smallholder level. Although various cultural practices are

known to reduce stemborer incidence (Lawani, 1982; van den Berg *et al.*, 1998), farmers only adopt them if they fit into their crop production systems. As our knowledge of stemborer ecology improves, in addition to increased awareness of the adverse effects of chemical control upon the biodiversity of beneficial arthropods, there is now general understanding that stemborer natural enemies, particularly insect parasitoids, need to be harnessed and placed at the core of integrated pest management (IPM) strategies targeted at the pests.

The list of stemborer natural enemies recorded in Africa is quite impressive (Polaszek, 1998). However, their ability to suppress stemborers and maintain their populations at below injurious levels is doubtful (Overholt, 1998). The introduction of the Asian borer, *C. partellus*, onto the continent has only exacerbated the situation. In many parts of eastern and southern Africa, the invasive species has proved to be a highly competitive colonizer, gradually displacing native species and becoming the most injurious stemborer (Kfir *et al.*, 2002). Although most of the indigenous stemborer parasitoids have also expanded their host range to include the invasive borer species, the level of *C. partellus* control by natural enemies is not satisfactory hence justifying the introduction of exotic parasitoids (Overholt, 1998).

In Zimbabwe, stemborer damage on the staple crops maize and sorghum has been ascribed mainly to the species *B. fusca*, *C. partellus* and *S. calamistis* (Sithole, 1995; Chinwada *et al.*, 2001). Chinwada *et al.* (2001) analysed the status of stemborer research activities in the country and reported information gaps on several important aspects. For example, the major focus of pre-1980 work seemed to be on studying stemborer life histories but, however, only *B. fusca* was covered (Smithers, 1960a; Rose, 1962; Blair, 1971). Although the first mention of the tachinid larval parasitoid *Sturmiopsis parasitica* (Curran)

being a major *B. fusca* natural mortality factor in the Harare area came from the life history studies by Smithers (1960a), no follow-up attempts were made to study the parasitoid's biology. Sithole (1995) studied the incidence, relative abundance and distribution patterns of stemborers in the country but ignored the association of the pests with natural enemies. Furthermore, his work only dealt with sorghum leaving out maize which is by far the most important and widely-grown crop.

Surveys by Chinwada and Overholt (2001) gave the first comprehensive insight into the interaction of stemborers and their natural enemies in Zimbabwe. However, as this work covered only the Harare area and some parts of the central and northern highveld region, they recommended an extension of the surveys to the lowveld where Sithole (1995) had earlier reported *C. partellus* to be the dominant stemborer species. Chinwada and Overholt (2001) also indicated the need for more detailed studies on the bioecology of *S. parasitica* as its apparent confinement to the Harare area was puzzling given the wider distribution of its principal host, *B. fusca*. In general, as well as assisting to fill in the current information gaps on stemborers and their natural enemies in Zimbabwe, studies on stemborer distribution, abundance and incidence, their seasonal occurrence and interaction with natural enemies and general parasitoid biology are essential as the information generated forms part of the decision-making tools in IPM.

1.2 LITERATURE REVIEW

1.2.1 Major Stemborer Species in Africa and Their Distribution

Lepidopteran stemborers of the families Noctuidae, Crambidae and Pyralidae are among some of the most important insect pests that attack gramineous crops on mainland Africa and the outlying Indian Ocean Islands (Holloway, 1998; Maes, 1998). Kfir *et al.* (2002) reviewed the biology and management of the economically important species. Among the noctuids, *Busseola fusca* Fuller, *Sesamia calamistis* Hampson, *Sesamia cretica* Lederer and *Sesamia nonagrioides botanephaga* Tams & Bowden are the most economically important (Holloway, 1998). Crambid species that have been recorded in Africa include *Chilo partellus* (Swinhoe), *Chilo orichalcociliellus* (Strand), *Chilo aleniellus* (Strand), *Chilo sacchariphagus* (Boyer), *Chilo zacconius* Bleszynski, *Chilo agememnon* Bleszynski, *Chilo diffusilineus* (de Joannis), *Coniesta ignefusalis* (Hampson) and *Scirpophaga* spp. (Maes, 1998). In the Pyralidae family, only *Eldana saccharina* (Walker) and *Maliarpha separatella* (Ragonot) have been recorded as pests in Africa.

The African maize stalk borer, *Busseola fusca*, is a major pest in Africa south of the Sahara. It is a serious pest in southern Africa (Zimbabwe, Zambia, Malawi, Mozambique and South Africa), eastern Africa (Kenya, Uganda and Tanzania) and parts of West Africa (Nigeria, Ghana and Côte d'Ivoire) where its main cereal hosts are maize and sorghum (Harris and Nwanze, 1992; Kfir *et al.*, 2002). In east and southern Africa, *B. fusca* is primarily a pest at high altitude (> 600 m), but in West Africa, it occurs from sea level to greater than 2000 metres (Kfir *et al.*, 2002). Of the *Sesamia* species, *S. calamistis* is the most important and widely distributed. Although widespread in sub-Saharan Africa, attacking

mainly maize, sorghum, rice, millet and sugarcane (Holloway, 1998), *S. calamistis* seems to be a serious pest of cultivated cereals only in West Africa (Bosque-Pérez and Mareck, 1990).

Of the *Chilo* species, only *C. partellus* and *C. sacchariphagus* are not indigenous to Africa. Commonly known as the spotted stemborer, *C. partellus* is native to Asia and is thought to have been introduced before 1930 when it was first recorded in Malawi (Tams, 1932). It is now widely distributed in eastern and southern Africa where it is now the dominant stemborer species at below 900 metres, attacking maize and sorghum (Sithole, 1990; Kfir *et al.*, 2002). Apparently, *C. partellus* appears to have been so successful in colonizing new habitats that in both east and southern Africa, there is evidence of a competitive displacement of native stemborer species (Kfir *et al.*, 2002). However, the displacement may not lead to extirpation of the native species as differential development and/or preference for various cultivated (Kfir, 1997a) and wild hosts (Ofomata *et al.*, 2000) appear to have resulted in some form of mutual coexistence.

Chilo orichalcociliellus is mainly known as a stemborer of maize and sorghum along coastal areas of East Africa. Another introduced species, *C. sacchariphagus*, is a serious pest of sugarcane in the Indian Ocean Islands and recently, has been reported attacking sugarcane in Mozambique (Kfir *et al.*, 2002). *Chilo sacchariphagus* is thought to have been introduced into Madagascar, Réunion and Mauritius either from Sri Lanka or Java with the introduction of sugarcane. *Coniesta ignefusalis* is widely distributed in Sahelian West Africa where its main cereal host is pearl millet. Four species in the genus *Scirpophaga* have been recorded in various African countries attacking mainly rice but none is of any real economic importance on the continent at the moment (Maes, 1998).

Eldana saccharina occurs throughout sub-Saharan Africa where it is mainly a pest of sugarcane. In West Africa, however, the borer is also an economic pest of maize and rice

(Harris, 1962; Bosque-Pérez and Mareck, 1991; Kfir *et al.*, 2002). *Maliarpha separatella*, the only other pyralid stemborer of economic importance in Africa, occurs primarily in West Africa where it mainly attacks rice (Heinrichs, 1998). Other records of the species are from the Indian Ocean Islands (Kfir *et al.*, 2002).

1.2.2 Life History, Biology and Behaviour

Although each species of stemborer has a characteristic life history, the general life cycle of cereal stemborers is the same (Smith *et al.*, 1993). The dull-coloured moths emerge from pupae during late afternoon and early evening and are active at night. During the day they rest on plants and plant debris and are seldom seen unless disturbed, when they fly briefly. For the first few hours after emergence, females remain near the site of emergence and release a pheromone to attract males. Mating occurs shortly afterwards. Females begin to oviposit on the night following emergence and most of the eggs are laid by the third night. Adults die within a week after emergence. Eggs are laid singly or in batches on the underside of leaves, leaf sheaths and stems (Harris and Nwanze, 1992; Shanower *et al.*, 1993) or between dead leaves or sheaths (Atkinson, 1980).

After hatching, first generation larvae either tunnel directly into the stem or migrate to the whorls inside which they feed for some time before boring into the stems. Older larvae are almost exclusively cryptic stem-feeders. Pupation takes place in the stem in a chamber prepared by the mature larva. The pupal chamber is excavated slightly larger than the feeding tunnel and access to the feeding tunnel is blocked with frass and lightly lined with silken threads. To facilitate emergence of the adult from the stem, the mature larva constructs an exit tunnel from the pupal chamber to the outside of the stem. The outer layer of epidermis on the outside of the stem is left intact and forms a conspicuous "window" on the green stem

(Smith *et al.*, 1993). In cold and/or dry conditions, larvae of some species enter a resting stage (diapause) in stems, stubble, and other crop debris, where they may spend up to six months before resuming development and pupating at the return of favourable conditions (Scheltes, 1978; Harris and Nwanze, 1992). Other species have a facultative diapause and under favourable climatic conditions which permit the growing of crops throughout the year, continue to develop without a resting stage (Ingram, 1958; Girling, 1978; Kfir, 1991).

1.2.2.1 *Chilo partellus*

Harris (1990) reviewed published information on the biology and ecology of *C. partellus*. Females mate soon after emergence and lay eggs on two to three consecutive nights, laying 200-600 eggs in overlapping batches of 10-80 on the underside of leaves (Bate *et al.*, 1990; Päts and Ekbom, 1994). On older plants, however, some egg batches have also been found to be located on the upper leaf surfaces and on the stem (Bonhof, 2000). Eggs hatch 4-8 days after oviposition. Young larvae migrate to the leaf whorl where they start to feed. Some may leave the plant on which eggs were laid and "balloon" to nearby plants on silken threads, or by crawling when leaf contact allows (Berger, 1992). Older larvae tunnel into stems where they feed for 2-3 weeks before pupating. Adults emerge 5-12 days after pupation. In the wetter part of the season, the life cycle is completed in 25-50 days. In a single season, five or more generations may develop. However, when there are breaks between consecutive growing seasons, larvae enter into a diapause state lasting for up to six months (Scheltes, 1978; Kfir, 1991).

1.2.2.2 *Busseola fusca*

The biology and ecology of *B. fusca* has been studied by various workers (Ingram, 1958; Smithers, 1960a; Harris, 1962; van Rensburg *et al.*, 1987) and reviewed recently by Harris and Nwanze (1992). At the beginning of the season, plants are attractive as sites for oviposition between three and five weeks after crop emergence (van Rensburg *et al.*, 1987). Each female lays a total of about 200 eggs (Plate 1) in batches of 30-100 under the inner surfaces of the leaf sheaths and the outer ear husks. These hatch about one week later. Initially, newly hatched larvae remain in clusters under the leaf sheath but disperse later on and can be found crawling over the plant. Later, they congregate in the whorls and begin to feed on the young leaves. On subsequent nights, some larvae may migrate to nearby plants. As they feed, larvae (Plate 2) gradually penetrate deeper into the whorl and finally penetrate into the stem where they feed for 3-5 weeks, producing extensive tunnels. Larvae normally pass through six instars before pupating and adults (Plate 3) emerge 9-14 days later. The life cycle is of variable length but during the wet part of the season, egg-adult development is completed in 7-9 weeks. There are usually three generations in one season, the third being the diapause generation (Smithers, 1960a; Harris, 1962).

1.2.2.3 *Sesamia calamistis*

The biology of *S. calamistis* was studied by Harris (1962) and Shanower *et al.* (1993). Infestations often commence two to three weeks after planting and can lead to entire crop destruction due to 'deadhearts'. Each female lays about 300 eggs in batches of up to 100 and inserted between the lower leaf sheaths and stems. Under field conditions, eggs hatch in 5-7 days. Most larvae (Plate 4) bore directly into the stem shortly after hatching or after feeding

Plate 1. *Busseola fusca* egg mass

Plate 2. Fully-grown *Busseola fusca* larva

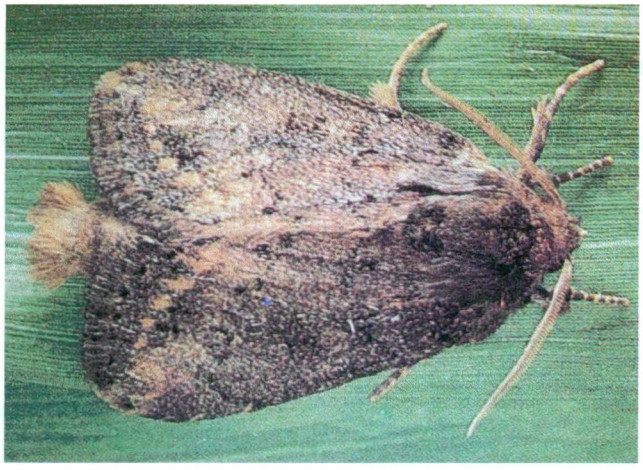


Plate 3. ***Busseola fusca*** **male moth**

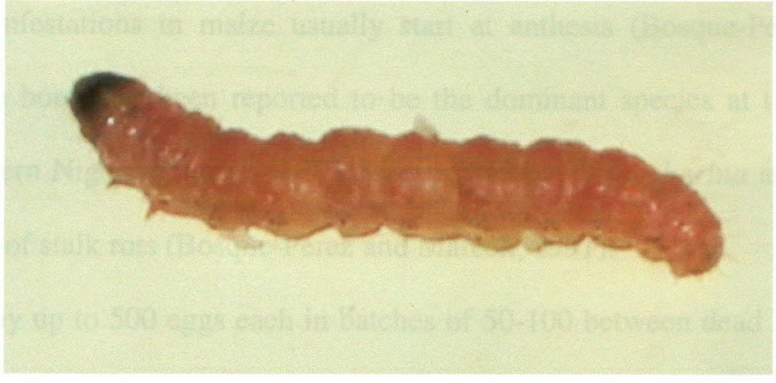


Plate 4. ***Sesamia calamistis*** **larva**

on the leaf sheath for some time. They do not congregate in the whorls like *B. fusca*. After passing through five to six instars in 4-6 weeks, most larvae pupate inside the tunnels but some vacate the galleries and pupate between the stem and leaf sheath. Pupae are secured in position by loose silken threads. Adults emerge 9-13 days after pupation. Under tropical conditions and provided host plants are continuously available, *S. calamistis* breeds throughout the year with no resting stage (diapause).

1.2.2.4 *Eldana saccharina*

The available literature on *E. saccharina* is quite extensive and comes from West Africa (Bosque-Pérez and Mareck, 1991; Shanower *et al.*, 1993), East Africa (Girling, 1978) and Southern Africa (Atkinson, 1980). Atkinson (1980) studied the biology of *E. saccharina* and reported its distribution and host plant range in South Africa. Unlike other stemborer species, *E. saccharina* infestations in maize usually start at anthesis (Bosque-Pérez and Mareck, 1991) hence the borer has been reported to be the dominant species at the time of maize harvest in southern Nigeria (Harris, 1962). Infestations by *E. saccharina* are also associated with high levels of stalk rots (Bosque-Pérez and Mareck, 1991).

Females lay up to 500 eggs each in batches of 50-100 between dead leaves or sheaths, on curled edges of dead leaves or sheaths, between the base of the stem and soil, or under dead leaves on soil (Girling, 1978; Atkinson, 1980). Eggs hatch after about 6-7 days and the young larvae feed externally on leaf sheath tissue before boring into stems. Some degree of larval migration between plants also occurs (Girling, 1978). The larval period is variable, but at 25-30°C, is completed within 20-22 days (Atkinson, 1980). In Uganda, Girling (1978) reported a larval period of about 28 days. Pupation takes place at least partially outside the stem. The larva spins a tough cocoon that partially protrudes through the moth exit hole.

Adults emerge after a pupal period lasting about 10 days. There is no diapause and up to six generations may develop in a year.

1.2.3 Wild Host Plants

Most African cereal stemborers are generally polyphagous and have several cultivated and wild host plants. Undoubtedly, the domestication of crops and subsequent cultivation in large tracts of land as monocrops has helped to elevate stemborers to their current economic status. Stemborer wild host plants are found in the Graminae, Cyperaceae and Typhaceae families. In the Graminae, Polaszek and Khan (1998) listed four *Hyparrhenia* spp., two *Panicum* spp., four *Pennisetum* spp., two *Setaria* spp., three *Sorghum* spp. and two *Sporobolus* spp. as hosts of *C. partellus*, *B. fusca*, *S. calamistis* and *E. saccharina* in Kenya. In the Cyperaceae family, Atkinson (1980) reported at least six *Cyperus* spp. which are known to be hosts of *E. saccharina* in South Africa. Van den Berg *et al.* (2001) also reported 12 wild plant species as hosts of *B. fusca*, *C. partellus* and *S. calamistis* in the northern part of South Africa.

Since the presence of wild and/or alternative host plants in the vicinity of fields predisposes crops to greater damage by serving as stemborer reservoirs, their destruction or removal is a standard cultural control recommendation (Lawani, 1982). However, recent studies have highlighted the benefits stemborer wild host plants may have in the sustenance of natural enemy populations through the provision of refugia as well as being sources of pollen and nectar. In Kenya, Napier grass (*Pennisetum purpureum* Schumach.) and Sudan grass (*Sorghum vulgare sudanense* Stapf.) planted around a maize field have been shown to trap stemborer populations that are repelled from the crop by molasses grass (*Melinis minutiflora* Beauv.) and silver leaf (*Desmodium* spp.) intercrops (Khan *et al.*, 2001). Although oviposition occurs on the trap crops, most of the larvae die due to antibiosis

properties of the plants (Khan *et al.*, 2001; van den Berg *et al.*, 2001). This stimulo-deterrent diversionary strategy, termed "push-pull", reportedly increases stemborer parasitism by attracting *Cotesia* spp. to molasses grass (Khan *et al.*, 2001).

1.2.4 Damage and Larval Behaviour

Damage to cereal crops by stemborers and larval behaviour has been studied and reviewed by various authors (Smithers, 1960a; Harris, 1962; Bernays *et al.*, 1983; van Rensburg *et al.*, 1987; Bosque-Pérez and Mareck, 1990; Berger, 1992; Smith *et al.*, 1993). Soon after hatching, larvae crawl over the plant, congregate in the funnel and feed for some time on the rolled leaves before penetrating into the stem. Some of the larvae migrate to nearby plants soon after hatching. As the plant grows and the leaves in the funnel unroll, a characteristic pattern of holes ('shot-holes') and 'window panes' (Plate 5) can be seen. On young plants, larval feeding on the growing point results in the apical meristem dying, becoming brown, creating a 'deadheart' condition (Plate 6). Maize is particularly susceptible to deadhearts because of its non-tillering growth habit. Other crops such as sorghum, millets and rice compensate for deadhearts by tillering. Where newly hatched larvae penetrate the stems of young plants directly soon after hatching, severe stunting, in addition to deadhearts, has been observed.

Tunnelling by larvae in stems restricts translocation of water and nutrients and weakens the stem leading to lodging. Apart from primary damage caused directly by the feeding habits of larvae, secondary damage can also result. Extensive larval tunnelling in the stem increases the incidence and severity of stalk rots (Bosque-Pérez and Mareck, 1991) while cob damage facilitates the entry of cob-rotting fungi. In sorghum, larval tunnelling in the stem supporting the head leads to peduncle breakage and development of 'chaffy' panicles.

Plate 5. "Window-paning" on maize leaves

Plate 6. Maize "deadheart"

Plate 7. *Chilo partellus* larva (diapause stage)

1.2.5 Larval Diapause

The most frequently used criterion for larval diapause in Lepidoptera is the failure of the mature larva to pupate within the normal time required for pupation after cessation of feeding (Scheltes, 1978). When in diapause, many of the tropical stemborer species are distinguishable from non-diapause larvae by the loss of the cuticular pigmentation of the pinnaculi (Plate 7), transforming them into an unspotted morph (Harris, 1962; Usua, 1974; Scheltes, 1978). Although the onset of diapause has been linked to the state of maturity of the host plant (Usua, 1973; Scheltes, 1978), moisture content (Smithers, 1960b; Okuda, 1988, 1990), and temperature (Kfir, 1991), the factors inducing and terminating diapause are not very clear. However, the clear influence of juvenile hormones has been demonstrated (Scheltes, 1978). Both Usua (1970) and van Rensburg *et al.* (1987) reported the presence of diapausing larvae throughout the year irrespective of the condition of the plant and environmental conditions, suggesting that induction of diapause may be under genetic control.

Busseola fusca has an obligatory diapause throughout its distribution whereas diapause in *C. partellus* is facultative (Kfir, 1991). Diapause is normally terminated as rainfall increases during the subsequent season (Harris and Nwanze, 1992). This termination of diapause is thought to occur as a result of rehydration of larvae through active water uptake (Harris, 1962), contact with water in the vapour state (i.e., higher relative humidity) (Adesiyum, 1983) and mere contact of larvae with water (Okuda, 1988, 1990). However, it is likely that water contact through rain or higher relative humidity simply hastens diapause termination rather than trigger its termination as larvae have been observed pupating even when they have not been exposed to water (Kfir, 1991).

1.2.6 Yield Losses

Reported crop yield losses due to stemborers in Africa vary widely among ecological zones, regions and seasons and depend on crop, cultivar, crop age at the time of infestation and stemborer density. For the most part, these are unreliable owing to the multiplicity and non-standardization of the methodologies used.

Extensive reviews on yield losses from West, Central, East and Southern Africa due to the stemborers *B. fusca*, *C. partellus*, *S. calamistis* and *E. saccharina* are available (Bosque-Pérez and Schulthess, 1998; Seshu Reddy, 1998; Kfir *et al.* 2002). In West Africa, studies on maize yield losses due to *E. saccharina* showed a depression of 15-28% (Bosque-Pérez and Mareck, 1991). In the guinea savannahs of Ghana, yield losses on maize due to *Sesamia* spp. were reported to range between 14 and 27% (Bosque-Pérez and Schulthess, 1998). In Kenya, grain yield losses of about 18% in maize due to *C. partellus* and *C. orichalcociliellus* have been reported (Warui and Kuria, 1983). On sorghum, Seshu Reddy (1998) reported losses of 2-88% due to *C. partellus*. In a study on the relationships between stemborer damage and plant physical conditions in Kenya, Songa *et al.* (2001) reported that damage by a single stemborer larva could result in a potential yield reduction of 8-10% in maize.

In Southern Africa, variable yield losses have been reported (Kfir *et al.*, 2002). In South Africa, losses of 10-100% due to stemborers have been reported. More than 50% grain yield losses due to *C. partellus* have been reported in the southern parts of Mozambique. In Zimbabwe, yield losses on sorghum by *C. partellus* were reported to range between 50 and 60% (Kfir *et al.*, 2002).

1.2.7 Control Methods

Various methods are used to control stemborers in Africa. With maybe only a few exceptions, the choice of control method is dependent on farm size, resources available and crop age. The main stemborer control methods currently in use in Africa include cultural practices, chemical control, host-plant resistance and biological control.

1.2.7.1 Cultural control

Cultural control practices for the management of cereal stemborers have been reviewed by various authors (Lawani, 1982; van den Berg *et al.*, 1998). Essentially, these methods involve the deliberate manipulation of aspects of crop agronomy to make it less favourable for the pests or more favourable for their natural enemies. The most common stemborer cultural control practices include appropriate crop residue management, tillage practices, intercropping, crop rotation, manipulation of planting dates and removal of alternative and volunteer host plants. The adoption or non-adoption of each or a combination of these practices depends on local weather conditions and how well they fit into an individual farmer's or community's crop production systems.

1.2.7.1.1 Crop residue management

Crop residues left in the field are an important source of infestation as they harbour diapausing larvae. As such, their disposal has been recommended as a way of minimizing infestations in subsequent crops. In South Africa, Kfir (1990) reported that destruction of maize and sorghum stems by slashing destroyed 70% of the stemborer population. Discing

and ploughing the slashed stems reduced the population by a further 24%. In Nigeria, one *B. fusca* control recommendation was to burn the stalks completely after harvest (Harris, 1962). However, as the stalks are sometimes used for building, fencing and fuel, Adesiyum and Ajayi (1980) showed that partial burning of the stalks could kill 95% of *B. fusca* larvae while at the same time curing the stalks and making them more suitable for firewood and construction purposes. Usua (1967) reported that felling stalks resulted in 89% mortality of diapausing larvae thus making the practice of destroying crop residues by removal, burying or burning largely unnecessary. Although not deliberately adopted as a stemborer control measure, the practice of using maize residues for composting purposes by smallholder farmers in Zimbabwe is also thought to result in a significant reduction in stemborer infestation levels in a subsequent maize crop (Chinwada *et al.*, 2001).

1.2.7.1.2 Tillage practices

Soil tillage may reduce stemborer populations through mechanical destruction of overwintering larvae, burying crop residues so deep that moth emergence is hindered, or by bringing them to the surface where they are exposed to adverse weather factors, birds and other natural enemies (Lawani, 1982; van den Berg *et al.*, 1998). Tillage also destroys volunteer plants and weeds that may provide food and breeding sites for the pests. However, despite the noted success of conventional tillage in reducing pest and disease incidence, most highly mechanized large-scale commercial farming enterprises are opting for zero or minimum tillage. According to Kfir (1990), this shift towards zero tillage will result in increased stemborer incidence which in turn will increase usage of insecticides.

1.2.7.1.3 Intercropping

Controlling insect pests by increasing the diversity of agroecosystems through intercropping is the most widespread traditional cropping system practised by subsistence farmers in many tropical countries. However, while there are often benefits in terms of reduced damage by monophagous pests, no benefits are apparent in the level of damage caused by highly polyphagous species (Glen, 2000). Thus, it is important that the right diversity is established in order to obtain the desired result (Lawani, 1982).

Work in Kenya by Amoako-Atta and Omolo (1983) indicated that maize-cowpea-sorghum intercropping systems gave the highest grain yields/cob from plants attacked by stemborers. In Nigeria, Adesiyum (1983) showed that interplanting pearl millet with sorghum in alternate stands within the same row reduces *B. fusca* infestation as a result of the inability of female moths to utilize millet for oviposition. On the other hand, the millet stemborer, *C. ignefusalis* showed preference for millet and infestation did not seem to be influenced by intercropping with either maize or sorghum. In an intercropping system, stemborer control could be achieved by wasted oviposition on non-host plants and a reduction in larval migrations. Ampong-Nyarko *et al.* (1995) reported that 30% of *C. partellus* oviposition in a maize-sorghum-cowpea intercropping system was on cowpea and that the number of larvae reaching host plants from cowpea plants decreased with distance. In general, although intercropping reduces pest incidence as a result of increased crop diversity, the need to manage several different crops simultaneously makes it unattractive as a pest management option (Mumford and Baliddawa, 1983).

1.2.7.1.4 Crop rotation

Any crop rotation system that interrupts the successive cultivation of one crop on the same piece of land may help to reduce pest numbers by making it difficult for specialist herbivores to sustain their populations (Glen, 2000). However, its effectiveness as a stemborer management technique is doubtful in smallholder farming systems where farmers make independent decisions on their cropping patterns and there is a greater likelihood of invasions by moths from elsewhere (Harris and Nwanze, 1992).

1.2.7.1.5 Manipulation of planting dates

The manipulation of planting dates as a stemborer control measure works on the principle that crops are planted at a time when the pest population is still low or when fewer borers are in the ovipositing (moth) stage. However, the effectiveness of the technique depends on the season and population dynamics of stemborers within a locality. In semi-arid parts of Africa, rainfall is a limiting factor and farmers almost always plant with the first rains so as to get their crops established much earlier and lessen the adverse impact of likely erratic rains later on in the season (van den Berg *et al.*, 1998).

Studies on the effects of early or late planting on stemborer incidence have produced mixed results. In Kenya, Warui and Kuria (1983) found lower incidence of *C. partellus* and *C. orichalcociliellus* on maize planted at the onset of rains and much higher incidence on crops planted 3-8 weeks later. Lower incidence of stemborer infestations on early-planted crops were also reported in Ethiopia (Gebre-Amlak *et al.*, 1989) and Zimbabwe (Sithole, 1987). In Tanzania, however, Swaine (1957) reported higher *B. fusca* infestation levels on

maize planted with the first rains as a result of oviposition of moths arising from the diapause generation of larvae. Chinwada *et al.* (2001) also reported high *B. fusca* infestation levels on early-planted (September/October) irrigated maize crops on the highveld of Zimbabwe. Van Rensburg *et al.* (1987) clarified the conflicting observations by showing that differences in infestation levels between maize planted at different times in a season were simply a reflection of the seasonal moth flight patterns and their interactions with the phenological stage of the crop. Thus, an early- or a late-planted crop could show higher stemborer infestation levels if it was at the right phenological stage at the time of peak moth flight of a particular generation. In other words, "early-" or "late-planting" as a means of escaping stemborer infestation should ideally be defined in the context of the moth flight pattern of the locality and for a particular season.

1.2.7.1.6 Removal of alternative and volunteer host plants

Many wild Graminae and Cyperaceae are hosts to some of the economically important species of stemborers (Atkinson, 1980; Polaszek and Khan, 1998) and studies by Khan *et al.* (2001) and van den Berg *et al.* (2001) have demonstrated how some of these common wild plant hosts can be harnessed to manage stemborers. However, when not being used to deliberately control stemborers, wild grass hosts and volunteer plants are potential sources of infestation. As such, their removal from the field and the vicinity is recommended (Lawani, 1982).

1.2.7.2 Chemical control

A review of stemborer chemical control and its economics was outlined by van den Berg and Nur (1998). In Africa, although chemical control of stemborers by smallholder farmers is generally uneconomical, their use is widespread. On the other hand, at a commercial farming level, chemical control forms the basis of pest control. In general, all stemborer chemical control strategies are targeted at the larval stage. Unfortunately, larvae are largely cryptic-feeders and for chemical control to be effective and economical, a good understanding of the bioecology of the pests is required (van den Berg and Nur, 1998). Thus, economic threshold levels (ETL) need to be defined. Although some stemborer ETLs based on the number of larvae/plant were determined (Sharma and Sharma, 1987; Seshu Reddy and Sum, 1992), van den Berg *et al.* (1997) pointed out that a more practical approach would be to define the ETL in terms of a non-destructive method such as the incidence of plants with visible damage. In South Africa, the ETL for the control of *B. fusca* in the large-scale commercial farming sector is reached when 10% of plants in a field show whorl-damage symptoms (van Rensburg *et al.*, 1988a).

The earliest use of insecticides for the control of stemborers in Zimbabwe dates back to the 1920s when whorl applications of carbolic and arsenic cattle dips were recommended for *B. fusca* control in maize (Arnold, 1928). With the rapid advances in chemical production technologies, several insecticides, formulated mainly as whorl-applied granules, foliar sprays and soil-applied systemics, are now available for use in stemborer control operations. However, whorl-applied granular insecticides are the most widely used at the smallholder level due to their low cost, ease of application and lack of requirement for special application equipment.

The most common insecticides used for stemborer control include carbaryl, endosulfan, trichlorforn, sythetic pyrethroids and carbofuran. The effectiveness of these for the control of various stemborer species in Africa has been demonstrated. In South Africa, Drinkwater *et al.* (1979) reported that a 0.2 g a.i. per metre application of carbofuran to the planting furrow gave superior control of *B. fusca* and maize streak virus leaf hopper (*Cicadulina* spp.) vectors. Granular application of trichlorforn in maize and sorghum whorls were reported to be effective in controlling stemborers in Kenya and Zimbabwe (Sithole and Makombe, 1989; Seshu Reddy and Sum, 1992). Studies which showed the effectiveness of foliar applications of insecticides against stemborers have also been conducted (van den Berg and van Rensburg, 1992). Unlike whorl-applied granules, foliar sprays can be directed at the whorls to kill larvae feeding inside and other parts of the plant against later infestations which occur post-anthesis.

1.2.7.3 Host plant resistance

Breeding for resistance to stemborers is one of the most promising and cost-effective ways of reducing crop damage and subsequent yield losses. As Maxwell (1985) put it, "....the very foundation of any IPM programme should begin with the variety to be grown". Initially, cereal breeding programmes in Africa were targeted at improving yield. However, in recent years, there has been increased collaboration between national agricultural research programmes and international agricultural research centres such as the International Centre of Insect Physiology and Ecology (ICIPE), the International Institute of Tropical Agriculture (IITA), the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and the International Maize and Wheat Improvement Centre (CIMMYT) in the screening of crop germplasm and development of stemborer-resistant cultivars. Although some of the

techniques and methodologies employed in breeding crops for insect resistance and determine mechanisms and bases of resistance have been outlined (Davis, 1985), a major handicap in the breeding for stemborer resistance has been the lack of efficient screening techniques (Harris and Nwanze, 1992). Singh *et al.* (1983) assessed stemborer resistance reaction using several parameters and suggested that the number of holes/plant or internode was a good indicator of percent stem tunnelling and thus could be used to evaluate sorghum for *C. partellus* resistance.

Several studies in Kenya have shown good levels of resistance to stemborers in maize and sorghum lines that could be utilized in breeding programmes against *Chilo* spp. and *B. fusca* (Seshu Reddy, 1985; Omolo and Seshu Reddy, 1985; Ampofo *et al.*, 1986; Kumar, 1992; Kumar and Saxena, 1992; Kumar, 1993; Kumar *et al.*, 1993). Work in Kenya also demonstrated the potential of combining traits for shootfly and stemborer resistance in a single grain sorghum line (Elbadawi *et al.*, 1997). In Zimbabwe, Sithole and Mtisi (1987) reported high levels of stemborer tolerance in six out of 25 sorghum lines from ICRISAT and moderate tolerance in ten others. Although the mechanisms of resistance were not elucidated in some studies, several mechanisms, including non-preference for oviposition, reduced larval feeding, reduced tunnelling, tolerance of plants to leaf damage, deadheart and stem tunnelling, and antibiosis, have been implicated (Kumar and Saxena, 1985; Kumar, 1992, 1993; Kumar *et al.*, 1993).

In general, although traditional breeding techniques have identified some stemborer-resistant maize and sorghum lines that are now being used in breeding programmes, they look set to be eclipsed by the rapid technological advances in biotechnology which have seen the production of hybrids that have been genetically modified to express insecticidal crystal proteins or δ-endotoxins derived from the Gram-positive spore-forming bacterium, *Bacillus*

thuringiensis Berliner (*Bt*). The '*Bt*' maize' hybrids were first introduced in the USA in 1996 in order to control the European Corn Borer (ECB), *Ostrinia nubilalis* Hübner (Cannon, 2000). These transgenic hybrids have demonstrated good control of ECB as well as other species, such as *Diatraea grandiosella* Dyar (Bergvinson *et al.*, 1997). In Africa, CIMMYT is currently involved in a project in which it aims to incorporate *Bt* genes into maize varieties that already have multigenic pest resistance in order to enhance the levels and durability of resistance to maize pests including stemborers (Mugo *et al.*, 2001).

Although transgenic plants fit in well with integrated strategies for pest management, there is a likelihood of resistance development in target pests due to single gene expression. Indeed, van Emden (1999) questioned the advantages of single toxin transgenic plant resistance over traditional breeding. The effects of *Bt* crops on non-target invertebrates, not to mention human health and safety concerns, also need to be addressed. So far, although adverse effects of *Bt* maize on the biodiversity of beneficial insects appear not to have been detected (Cannon, 2000), possible adverse effects on stemborer parasitoids have been reported with other transgenic gramineous crops. In the USA, Sétamou *et al.* (2002) reported that while transgenic sugarcane expressing snowdrop lectin had no adverse effects on the development of the sugarcane borer, *Diatraea saccharalis* (F.), a number of biological and fitness components of its introduced larval parasitoid, *Cotesia flavipes* Cameron were affected.

In general, whether insect resistance is obtained through traditional breeding or transgenic modification of crops, the greatest potential of host plant resistance lies in its many beneficial interactions with biological control, as plant resistance mechanisms that disrupt normal behaviour patterns of the target insect pests may expose them more readily to natural enemies (Maxwell, 1985).

1.2.7.4 Biological control

A complex of natural enemies, including insect parasitoids, predators and pathogens, has been recorded attacking cereal stemborers in Africa. Polaszek (1998) reviewed the bioecology of the stemborer species, associated natural enemies, taxonomy and control methods.

1.2.7.4.1 Parasitoids

Several species of native parasitoids have been recorded attacking stemborer eggs, larvae and pupae in Africa. Stemborer egg parasitoids recorded in Africa belong to the genera *Trichogramma*, *Trichogrammatoidea* and *Telenomus* (Polaszek, 1998). Their impact on stemborers in various parts of Africa is, however, reportedly variable. In Kenya, Skovgård and Päts (1996) recorded 19-71% parasitism of *Chilo* spp. and *S. calamistis* eggs by *Trichogramma* sp. in a maize monocrop and 31-76% in maize intercropped with cowpea. Also in Kenya, Bonhof (2000) recorded *Chilo* spp. egg mortality of 18-78% with *Trichogramma* parasitism being the most important factor. In South Africa, Kfir (1997b) reported that although they were recovered from stemborer eggs, the egg parasitoids *Telenomus busseolae* Gahan and *Trichogrammatoidea lutea* Girault were rare. Schulthess *et al.* (1997) reported cumulative parasitism of *S. calamistis* eggs of over 90% by *T. busseolae* and *Telenomus isis* Polaszek in Benin. In Côte d'Ivoire, Moyal (1998) reported 72% parasitism of *B. fusca* eggs by *T. busseolae*. Considering the scarcity of *T. isis* in Eastern and Southern Africa and its abundance in West Africa, Schulthess *et al.* (1997) felt that the parasitoid should be considered for introduction into East Africa against *B. fusca*. Based on life table, host suitability and discrimination studies, Agboka *et al.* (2002) concluded that *T.*

isis could establish in the mid altitude ecological zones of East Africa. However, egg parasitoids may not make a significant impact to stemborer egg mortality as non-parasitism mortality levels and density-dependence mortalities are already above 90% (van Hamburg and Hassel, 1984).

Stemborer larval parasitoids indigenous to Africa are mainly parasitic Hymenoptera of which the majority belong to the Braconidae family. *Cotesia sesamiae* (Cameron) is the most commonly recovered braconid larval parasitoid of stemborer species in sub-Saharan Africa (Overholt, 1998). In east and southern Africa, it is the most important parasitoid attacking the stemborers *B. fusca*, *C. partellus*, *C. orichalcociliellus* and *S. calamistis* (Overholt, 1998; Kfir, 1998). In West Africa, however, *C. sesamiae* is scarce (Schulthess *et al.*, 1997). Besides *C. sesamiae*, other notable stemborer larval parasitoids recorded in Africa include the tachinid, *Sturmiopsis parasitica* (Curran) (Harris, 1998; Chinwada and Overholt, 2001), and the braconids, *Bracon sesamiae* Cameron and *Chelonus curvimaculatus* Cameron (egg-larval) (Bonhof *et al.*, 1997). Variable parasitism rates due to these parasitoids have been reported in different parts of Africa. In South Africa, Kfir (1998) reported rearing *C. sesamiae* from at least 80% of parasitized larvae. Chinwada and Overholt (2001) reported *S. parasitica* parasitism on *B. fusca* on the highveld of Zimbabwe reaching a peak of 18.5% in January 1997. In earlier studies conducted in Zimbabwe during the growing season in 1956 and 1957, Smithers (1960a) reported *S. parasitica* parasitism levels of between 3-35%. In Kenya, as high as 20% parasitism on *Chilo* spp. and *S. calamistis* by *C. sesamiae* was reported in maize intercropped with cowpea (Skovgård and Päts, 1996). In the same study in Kenya, parasitism by *C. curvimaculatus* ranged between 1 and 9%.

Stemborer pupal parasitism recorded in Africa has been mainly due to the ichneumonids, *Procerochasmias nigromaculatus* (Cameron) and *Dentichasmias busseolae*

Heinrich, and the eulophid, *Pediobius furvus* Gahan (Polaszek, 1998). In South Africa, *B. fusca* pupal parasitism levels by *P. nigromaculatus* of up to 100% and 80% during February-March and November, respectively, have been reported (Kfir, 1998; Kfir, 2000). These parasitism levels coincided with the periods when pupae from the first larval generation and the diapause-generation where abundant. On the other hand, parasitism levels of almost 100% on *C. partellus* pupae by *D. busseolae* were recorded during the second part of January and the beginning of February (Kfir, 1992). In Kenya, Skovgård and Päts (1996) reported combined parasitism of *Chilo* spp. and *S. calamistis* pupae by *P. furvus* of up to 11.8%.

1.2.7.4.2 Predators

Predation of stemborers in Africa has been ascribed to several arthropod species, notably ants (*Pheidole* spp., *Camponotus* spp., *Dorylus* spp.), spiders, earwigs (*Diaperasticus erythrocephala* [Olivier] and *Forficula* spp.) and ladybirds (*Cheilomenes* spp.) (Mohyuddin and Greathead, 1970; Oloo, 1989; Harris and Nwanze, 1992; Bonhof, 2000). Most of these prey on eggs and first-instar larvae. Although some stemborer predation studies have been conducted (Leslie, 1988; Bonhof, 2000), the overall impact of predators on stemborer populations is still poorly understood.

1.2.7.4.3 Pathogens

Poinar and Polaszek (1998) summarized the available information on pathogens associated with cereal stemborers in Africa. These pathogens fall into five different classes; namely, bacteria, fungi, nematodes, viruses, and protozoa. However, there have been very few serious

efforts to determine their usefulness in regulating stemborer populations in the field. Among the bacteria, *Bacillus thuringiensis* Berliner has been the most frequently recorded (Bonhof *et al.*, 1997; Hoekstra and Kfir, 1997; Kfir, 2000). Entomopathogenic fungi which have been implicated in stemborer mortality include *Beauveria bassiana* (Balsamo) Vuillemin, *Aspergillus* spp. and *Metarhizium* spp. Among the nematodes, the genera *Hexamermis* Steiner (Plate 8) and *Steinernema* Travassos are the most commonly recorded (Odindo *et al.*, 1989; Poinar and Polaszek, 1998). Of the protozoans, only the genus *Nosema* has been frequently recorded from stemborers (Hoekstra and Kfir, 1997; Polaszek, 1998).

In South Africa, microbial pathogens recorded on *B. fusca* and *C. partellus* include *B. bassiana*, the microsporidian *Nosema partelli* Walters & Kfir, nuclear polyhedrosis viruses (NPV), granulosis virus, cytoplasmic polyhedrosis virus, *Entomophthora* sp., *B. thuringiensis*, *Serratia marcescens*, Entomopox virus, *Aspergillus* sp. and *Streptococcus* sp. (van Rensburg *et al.*, 1988b; Hoekstra and Kfir, 1997). The nuclear polyhedrosis virus occurred throughout the growing season and was also abundant in diapausing *B. fusca* larvae in dry maize stalks (Hoekstra and Kfir, 1997). In Kenya, preliminary field trials with *B. bassiana* and *Metarhizium anisopliae* (Metschnikoff) Sorokin showed that significant reductions in stemborer larval populations can be obtained by using entomopathogenic fungi (Maniania *et al.*, 1994).

In general, although pathogens have been recorded as stemborer natural mortality factors in many situations, they do not appear to be of great value in regulating populations of the pest in the field as the feeding behaviour of larvae permits only very little contact between them and thus does not create conditions conducive for the development of epizootics (Harris and Nwanze, 1992).

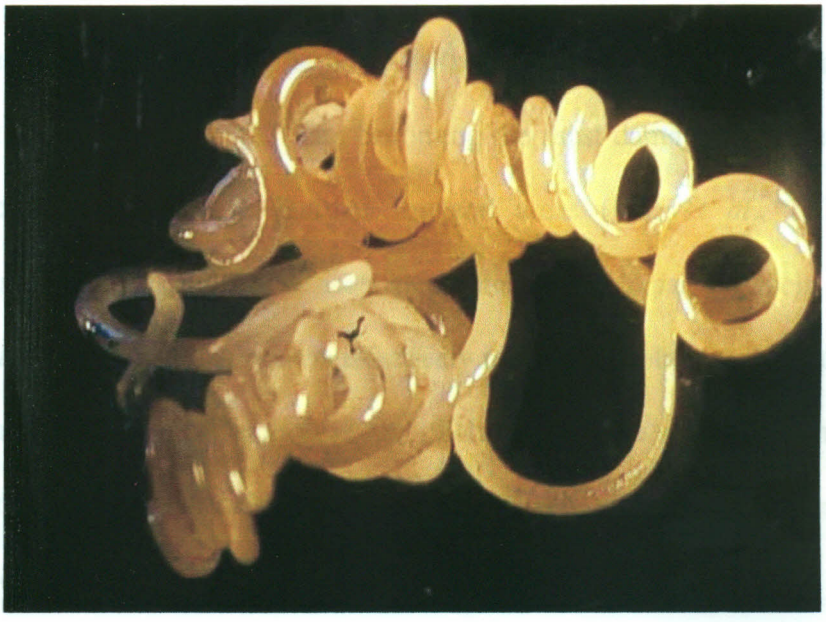


Plate 8. Entomogenous nematode, *Hexamermis* sp.

1.2.7.4.4 Classical biological control

With the exception of *C. partellus*, all stemborer species attacking cereal crops in Africa are thought to be indigenous (Kfir *et al.*, 2002). *Chilo partellus* invaded Africa from Asia sometime before 1930 when it was first recorded in Malawi (Tams, 1932). Since arriving on the continent, *C. partellus* has proved to be an aggressive colonizer and has spread to nearly all countries in east and southern Africa, often becoming the most damaging species ahead of the indigenous species, particularly in warmer lowland areas (Kfir *et al.*, 2002). Although indigenous parasitoids attacking the African stemborers have expanded their host range to include *C. partellus*, they do not appear to effectively regulate stemborer populations at below economically damaging levels (Overholt *et. al.* 1994a). Thus, due to its economic importance and status as an introduced species, *C. partellus* has been the target of biological control attempts in both east (Overholt *et al.*, 1997) and southern Africa (Kfir, 1994).

Kfir *et al.* (2002) reviewed attempts that have been made over the past sixty years to introduce exotic parasitoids for biological control of stemborers on mainland Africa and the outlying Indian Ocean Islands. Apparently, there have been many more successful establishments on the islands than on the mainland. On the mainland, only *C. flavipes* has established. Various reasons have been proposed to explain the differential rate of establishment of exotic natural enemies of pests on the Indian Ocean Islands and on mainland Africa. One major reason put forward is the theory of island biogeography (Overholt, 1998). Unlike on mainlands, species are not packed as tightly on islands and thus, specialist parasitoids colonizing islands encounter less interspecific competition. For the same reason, exotic pests are more likely to establish on islands thus becoming obvious targets for classical biological control. Another potentially influential factor that probably explains the differential establishment on the

islands as opposed to the mainland is ecosystem stability. The major emphasis of the stemborer biological control activities on the Indian Ocean Islands was against *C. sacchariphagus* in a sugarcane ecosystem. On the mainland, work was divided between maize, rice and sugarcane. Sugarcane is grown throughout the year and thus provides a fairly stable habitat. The maize ecosystem is unstable as it provides habitat for stemborers and their parasitoids for only a few months each year.

In East Africa, the Commonwealth Institute of Biological Control (CIBC) (now International Institute of Biological Control) conducted releases of *C. flavipes* over a five year period starting from 1968 (Overholt, 1998). Despite initial recoveries, there was no evidence that these releases resulted in successful establishment. In 1991, ICIPE initiated another stemborer classical biological control programme in East Africa and released *C. flavipes* in the southern coastal area of Kenya in 1993. Two years later, establishment was confirmed (Overholt *et al.*, 1997).

In a study on the spatial-temporal population dynamics of *C. flavipes* in Kenya, Zhou and Overholt (2001) reported an increase in *C. flavipes*-occupied sites from 60% during the first growing season of 1995 to about 80% in 1999. They also reported a maximum density of 30 parasitoids per 20 plants in the second growing season of 1997 at one site, clearly showing that the population density of the parasitoid had increased. Although Zhou *et al.* (2001) credited a 52% reduction in *C. partellus* density observed at a southern coastal site of Kenya by 1999 to *C. flavipes* parasitism, there is yet no evidence that the parasitoid has reached an equilibrium density (Kfir *et al.*, 2002).

Following the successful introduction of *C. flavipes* in Kenya, other releases were made in Mozambique, Uganda, Somalia, Zimbabwe, Zambia, Malawi and Zanzibar between 1996 and 1999. From these releases, establishment has only been confirmed in Uganda (Matama-

Kauma *et al.*, 2001), Mozambique (Cugala and Omwega, 2001) and Malawi (Omwega, C.O., personal communication). In Ethiopia, *C. flavipes* which now accounts for about two-thirds of total stemborer parasitism (Getu *et al.* 2001), was never released in the country. Overholt (1998) speculated that the parasitoid could have invaded Ethiopia from Somalia where it was released in 1997. In Tanzania, Omwega *et al.* (1997) reported recovering *C. flavipes* in two northern districts during surveys conducted in 1995. These districts border an area of southwestern Kenya where the parasitoid is known to have established earlier (Omwega *et al.*, 1995). During the 1995 surveys, no *C. flavipes* recoveries were made in areas where the CIBC had conducted releases in 1970. Omwega *et al.* (1997) consequently concluded that the parasitoid had spread into northern Tanzania from a founding population that could have been inadvertently released from the Mbita Point Field Station of ICIPE in 1991. Similarly, it is believed that the establishment of *C. flavipes* which has been confirmed in a north-eastern region of Tanzania bordering Kenya could also have occurred due to invasion from the coastal zone of Kenya where the parasitoid had earlier on been released and became established (Nsami *et al.*, 2001).

Although *C. flavipes* releases on mainland Africa were conducted against an old-association host, *C. partellus*, the number of failures of establishment is particularly surprising, especially when considered in light of the success that has been achieved in the neotropics against the new-association host, *D. saccharalis* (Kfir *et al.*, 2002). Hypotheses put forward to explain the failure of *C. flavipes* establishment in Africa include competition with the indigenous *C. sesamiae*, host unsuitability (Ngi-Song *et al.*, 1995) and climatic incompatibility (Skoroszewski and van Hamburg, 1987). Overholt (1998), however, pointed out that there is a possibility that *C. flavipes* could have successfully established on some mainland locations where failure was reported but due to inadequate sampling, this establishment was not recognised. Unlike islands, the geographic area with suitable habitats over which the parasitoid

disperses on the mainland is usually too large, thus it takes much longer for the population to reach a characteristic density. Failure to recognize the establishment of *C. flavipes* could also have been due to an inability to distinguish between the species and *C. sesamiae* (Overholt, 1998). *Cotesia flavipes* and *C. sesamiae* are morphologically quite similar and features previously used to distinguish between the two, for example adult colouration and cocoon (Plate 9) differences (Mohyuddin, 1971), are unreliable.

1.2.8 The Parasitoids *Cotesia sesamiae* and *Sturmiopsis parasitica*

1.2.8.1 Identification

Taxonomic descriptions, diagnosis and keys for identification of *C. sesamiae* were outlined by van Achterberg and Walker (1998). The adult body is black or dark brown with forewing of about 1.8 mm long. Antennae are robust (females) or slender (males) and less than body size in females or 1.4 times as long as body size in males. The basal half of antenna is usually completely yellowish brown. Legs are yellowish; hind coxae blackish basally and usually largely yellowish. Cocoons of *C. sesamiae* are grouped loosely and thus to some extent can be distinguished from those of *C. flavipes* which are closely packed (Mohyuddin, 1971).

Harris (1998) outlined taxonomic keys, diagnostic and identification characters of the main Afrotropical tachinid species, including *S. parasitica*. *Sturmiopsis parasitica* is a medium-sized tachinid, about 8 mm long, basically black but with lighter grey to white pollinosity, especially dorsally on the thorax and in wide bands across the abdominal tergites. Females (Plate 10) are easily recognized by the whitish frons (smoky-grey in males, Plate 11) and the presence of a pair of proclinate orbital setae, which are absent in males.

Plate 9. *Cotesia* **cocoon mass**

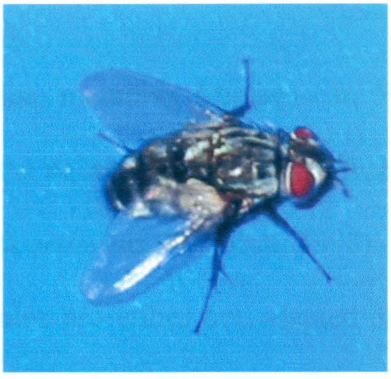


Plate 10. *Sturmiopsis parasitica* **adult female**

Plate 11. *Sturmiopsis parasitica* **adult male**

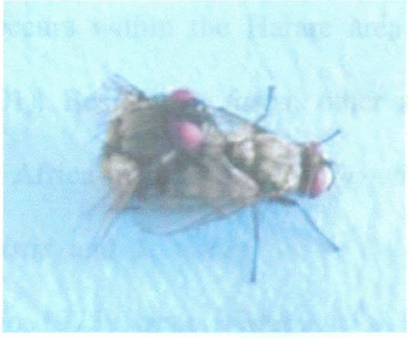


Plate 12. *Sturmiopsis parasitica* **mating pair**

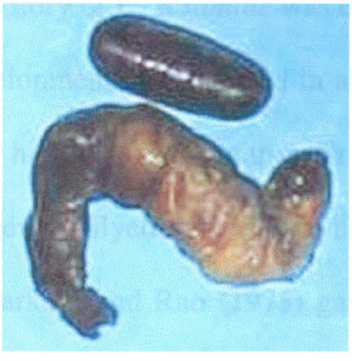


Plate 13. *Sturmiopsis parasitica* **puparium besides the remains of a** *Busseola fusca* **larva**

Plate 14. Ovipositing adult *Cotesia* **female**

1.2.8.2 Distribution and host range

Cotesia sesamiae occurs throughout sub-Saharan Africa, including Madagascar, Mauritius and Réunion. Its natural host range in Africa includes the noctuid stemborers *B. fusca* and *S. calamistis*, and the crambids *C. partellus* and *C. orichalcociliellus* (Overholt, 1998). It is rare in West Africa probably suggesting that the local strains are either not adapted or do not breed successfully on the stemborer species found in the region (Hailemichael *et al.*, 1997; Schulthess *et al.*, 1997).

Sturmiopsis parasitica is widespread in West, East and Southern Africa. Described from Zimbabwe (Crosskey, 1980), *S. parasitica* occurs within the Harare area where it parasitizes *B. fusca* (Chinwada and Overholt, 2001). Besides *B. fusca*, other stemborer species on which the tachinid has been recorded in Africa include *C. orichalcociliellus*, *C. partellus*, *C. ignefusalis*, *E. saccharina*, *S. calamistis* and *S. nonagrioides botanephaga* (Mohyuddin and Greathead, 1970; Nagarkatti and Rao, 1975; Harris, 1998).

1.2.8.3 Biology and host attack strategies

The life history of *C. sesamiae* was described by Ullyett (1935) and Mohyuddin (1971). Egg-adult development is completed in about 18.5 days at 30°C and 21.4 days at 21-26.5°C. The species is highly fecund, with each parasitized host larva capable of producing up to 100 adult progeny (Ullyett, 1935; Mohyuddin, 1971).

Nagarkatti and Rao (1975) gave an account of the life history of *S. parasitica*. Each mated adult female (Plate 12) produced 500-900 maggots after a gestation period of 18-19 days. At 26°C, the larval period was 12-14 days (occasionally up to 35 days), and the prepupal and pupal periods 12 hours and 12-19 days, respectively. In Zimbabwe, Chinwada

and Overholt (2001) recovered *S. parasitica* puparia mainly singly or in groups of up to six from a single *B. fusca* larva (Plate 13).

The host attack strategies of *C. sesamiae* and *S. parasitica* are different. While females of both parasitoids use cues such as odour from frass and host tunnel to guide them to the immediate vicinity of the host, *C. sesamiae* actually enters the tunnel to sting (Plate 14) host larvae (ingress-and-sting) (Smith *et al.*, 1993). *Sturmiopsis parasitica*, on the other hand, deposits mobile first instar maggots (planidia) on moist frass at stemborer tunnel entrances. The moistened frass packed in tunnels then assists in the conveyance of the maggots throughout the tunnel. Once host larvae are located, the maggots penetrate the integument to feed internally (planidial ingress) (Smith *et al.*, 1993).

1.3 JUSTIFICATION AND RATIONALE OF THE STUDY

Attacks by the stemborers *B. fusca*, *C. partellus* and *S. calamistis* are considered to be the most important biotic constraint limiting potentially harvestable yields of the staple crops maize and sorghum in Zimbabwe. Although local research work conducted so far on stemborers has produced some useful information, a lot of gaps have been identified. These are in the following areas: i) stemborer abundance and distribution patterns in the country, (ii) stemborer incidence and damage on the staple crops maize and sorghum, (iii) the range, seasonal occurrence and carryover of the most important parasitoids, (iv) the impact of indigenous parasitoid species in ecological zones where the invasive borer *C. partellus* is predominant, and (v) parasitoid biology.

In the Harare area of Zimbabwe, Chinwada and Overholt (2001) identified the larval parasitoids *C. sesamiae* and *S. parasitica* to be the most important on *B. fusca*. They reported *S. parasitica* parasitism levels of 18.5, 9.6, 1.3, 3.3 and 1.3% during the months of January to May 1997. During the same period, *C. sesamiae* parasitism levels were 4.9, 9.6, 20.5, 25.8 and 13.8%, respectively. Chinwada and Overholt (2001) also reported *S. parasitica* emerging between October and December from second generation larvae originally collected between March and May during the 1994/95 to 1997/98 seasons. They then concluded that the deferred emergence of *S. parasitica* from these larvae until diapause termination several months later was actually an overwintering mechanism utilised by the parasitoid. However, they recommended more exhaustive studies on *C. sesamiae* and *S. parasitica*, particularly their seasonal fluctuations in parasitism, seasonal carryover mechanisms and distribution in the country. Considering that the Harare area of Zimbabwe is the type locality of *S. parasitica* (Crosskey, 1980), and that the only published record on the biology of the species

comes from a population that was collected in Ghana (Nagarkatti and Rao, 1975), Chinwada and Overholt (2001) also stressed the need to study the parasitoid's biology in the country. It was particularly important to determine why *S. parasitica* seemed to be confined only to the Harare area while its host, *B. fusca*, had a much wider distribution in the country. When provided, such information would make it easier to assess the overall value of the indigenous parasitoid species as biological control agents.

Ullyett (1935) and Mohyuddin (1971) reported cocoon quiescence as a possible *C. sesamiae* overwintering mechanism in regions where its stemborer hosts diapause in response to dry conditions. In addition, Mohyuddin (1971) mentioned the possibility of *C. sesamiae* overwintering inside its hosts as immature larvae. In India, Subba Rao *et al.* (1969) reported that part of the *C. flavipes* population near Delhi hibernated as second instar larvae inside diapausing *C. partellus* larvae. However, although both overwintering mechanisms have not been proven by field studies anywhere in Africa, it is probable that *C. sesamiae* could indeed utilise one or both, particularly in unimodal rainfall regions where host stemborers enter into a resting stage (diapause) lasting for about six months (Kfir, 1991). Although, Mbapila and Overholt (1997) did not notice significant differences in the development of *C. sesamiae* in non- and aestivating *C. partellus* larvae, it is unlikely that the parasitoid remains active throughout the dry season on dry crop residues as larvae diapausing inside do not elicit the necessary host-finding cues (Smith *et al.*, 1993). In the frost-prone highvelds of Zimbabwe and South Africa, most potential wild grass hosts of stemborers also dry out during the dry season so there is little likelihood of a part of the stemborer population moving onto the wild hosts together with *C. sesamiae*. Thus, one of the major aims of the current study was to provide information on the seasonal carryover mechanism of *C. sesamiae*. As well as helping in explaining why the performance of *C. sesamiae* seems to be different from region to

region, for example, West and East Africa (Schulthess *et al.*, 1997), information on carryover mechanisms could be critical in the identification of superior strains of the parasitoid that are ideal candidates for redistribution. For example, a *C. sesamiae* strain from a bi-modal rainfall region that does not have a mechanism by which it can survive the typical long dry season of unimodal rainfall zones would not be ideal for introduction into a semi-arid area.

In collaboration with national agricultural research institutions in eastern and southern Africa, the International Centre of Insect Physiology and Ecology (ICIPE) has embarked on a classical biological control programme which has seen the introduction of *C. flavipes* into several countries of Eastern and Southern Africa as part of a broad *C. partellus* IPM strategy. This programme follows the successful introduction and establishment of the parasitoid in Kenya. *Cotesia flavipes* is native to Asia where it attacks *Chilo* spp. (Overholt, 1998). In Zimbabwe, *C. partellus* is the predominant stemborer species at medium and low elevation areas (below 1200 m) (Chinwada *et al.*, 2001). Although the invasive borer is attacked by several parasitoid species in the country, including *C. sesamiae*, their distribution is generally unknown and their impact considered unsatisfactory hence the need to try classical biological control. However, the first step in any classical biological control programme is to conduct host suitability tests as the introduction of an exotic natural enemy into an environment in which the target pest is unsuitable for its development would be an unnecessary waste of resources. Thus, the last major objective of this study was to determine if the main cereal stemborer species in Zimbabwe were suitable hosts for *C. flavipes*.

1.4 OBJECTIVES

1.4.1 General Objective

To determine the seasonal occurrence and levels of stemborer parasitism by *Cotesia sesamiae* and *Sturmiopsis parasitica* and to assess the establishment of *Cotesia flavipes* after its release in Zimbabwe.

1.4.2 Specific Objectives

a. To determine the abundance, distribution patterns and seasonal occurrence of cereal stemborers and their natural enemies in the highveld (> 1200 m), middleveld (600-1200 m) and lowveld (< 600 m) ecological zones of Zimbabwe;

b. To determine seasonal fluctuations in *C. sesamiae* and *S. parasitica* parasitism patterns and their seasonal carryover mechanisms.

c. To determine the relative acceptability and suitability of different stemborer species for development of *C. sesamiae* populations occurring in the highveld and lowveld ecological zones.

d. To determine the mating compatibility of the highveld and lowveld *C. sesamiae* populations.

e. To determine the life history of *S. parasitica* and the relative suitability of different stemborer species for its development.

f. To determine the relative acceptability and suitability of local populations of *B. fusca* and *C. partellus* for the development of *C. flavipes*.

1.5 HYPOTHESES

(i) There exists different stemborer species in the country.

(ii) There is an association between agroecological region and stemborer species.

(iii) The different stemborer species do not occur in equal proportions within the different ecological zones.

(iv) *Cotesia sesamiae* occurs throughout the country.

(v) *Sturmiopsis parasitica* occurs in the Harare area only.

(vi) Stemborer larval parasitism by *S. parasitica* attains a peak early in the season while parasitism by *C. sesamiae* peaks towards the end of the season.

(vii) *Sturmiopsis parasitica* and *C. sesamiae* have similar seasonal carryover mechanisms.

(viii) *Busseola fusca*, *C. partellus* and *S. calamistis* are equally acceptable to oviposition by a highveld or lowveld population of *C. sesamiae*.

(ix) For each *C. sesamiae* population, there are differences among the stemborer hosts *B. fusca*, *C. partellus* and *S. calamistis* in larval development periods, brood sizes and sex ratios of emerged parasitoid progeny.

(x) There are differences in larval development periods, brood sizes and sex ratios between progeny from reciprocal crosses of highveld and lowveld *C. sesamiae* populations.

(xi) The development of *S. parasitica* is different in *B. fusca*, *C. partellus* and *S. calamistis.*

(xii) The duration of *S. parasitica* larval development in non-diapause *B. fusca* larvae is different from that in diapausing larvae.

(xiii) *Busseola fusca* and *C. partellus* in Zimbabwe are neither equally acceptable nor suitable for development of *C. flavipes*.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 REARING PROCEDURES FOR STEMBORERS

Stemborer larvae were reared on artificial diet (Ochieng *et al.*, 1985; Onyango and Ochieng'-Odero, 1994) and on natural diet (maize or sorghum stems). Where natural diet was used, stems were first washed in running tap water and then surface-sterilized using cotton wool soaked in 70% alcohol.

2.2 REARING PROCEDURES FOR PARASITOIDS

2.2.1 *Cotesia* species

Emerged parasitoid cocoons were collected in vials (2.5 cm dia. x 7.5 cm high) and held at room temperature (18-26°C) or 25 ± 0.5°C, 65-80 % relative humidity and 12:12 (L:D) hour photoperiod. Adults were fed on 20% honey/water solution and left to mate inside the vials or Perspex® cages for about 24 hours before females were offered 4th instar larvae for oviposition using a hand-stinging procedure described by Overholt *et al.* (1994b). After exposure, larvae were placed individually or in pairs on artificial diet inside vials and incubated. While *C. flavipes* was reared only on *C. partellus*, *C. sesamiae* was reared on *B. fusca*, *C. partellus* or *S. calamistis* depending on the borer species from which the parasitoid population was recovered in the field.

2.2.2 *Sturmiopsis parasitica*

The rearing procedures for *S. parasitica* were adapted from Nagarkatti and Rao (1975). Laboratory colonies were initiated from pupariating maggots emerging from *B. fusca* larvae or pupae collected in the Harare area of Zimbabwe. Subsequent rearing was then conducted at ICIPE in Kenya.

2.3 FIELD SAMPLING

The optimal number of plants to be sampled in order to arrive at a reliable estimate of the percentage of plants infested (binomial sampling) and stemborer density per plant (enumerative sampling) was arrived at after taking preliminary samples of 20 plants each from maize and sorghum plots at two study sites: Henderson Research Station and Chisumbanje Experiment Station.

For binomial sampling, the desired number of plants to be sampled was estimated using the formula:

$$N = q/(p \times D^2)$$

Where N = the number of samples

q = the proportion of plants not infested from the preliminary sample

p = the proportion of plants infested (i.e., 1-q)

D = the desired precision level

For enumerative sampling, the desired number of plants to be sampled was estimated using the formula,

$$N = s^2/(m \times D)^2$$

Where s^2 = sample variance

m = sample mean

D = precision level

The results of preliminary sampling at the two sites and the estimated sample sizes, N (based on a precision level of 0.2*), for each crop are shown in Table 2.1. From the calculations, it was clear that far fewer plants needed to be sampled at Chisumbanje where stemborer infestation levels by *C. partellus* were very high. At Henderson, infestation levels by *B. fusca* were very low at the beginning of the season, hence the N-values were very high. As more reliable information was needed on stemborer densities per plant, the N-values selected were based on enumerative sampling only. At Chisumbanje, the N-values for enumerative sampling under maize and sorghum gave a mean of about 16 plants, i.e., (13+18)÷2. From a practical point of view, the values obtained from sampling at Chisumbanje could not be adopted as there was no guarantee that such high levels of stemborer infestation were going to be obtainable at every location each season. Thus, in order to get a standard N-value that could be relied upon throughout the study and would apply to all the different locations, it was decided to consider only the results from the Henderson samplings. At Henderson, a mean N of 325, i.e., (500+149)÷2, was obtained under enumerative sampling.

* In pest management sampling, it is usually desirable to have the standard error of our estimate to be within 20-30% of the true mean (i.e., a precision of 0.2-0.3).

Table 2.1. Stemborer infestation levels, larval density and estimations of sample sizes from preliminary sampling.

Site	Parameter	Crop	
		maize	Sorghum
Henderson	Infestation level	0.25	0.05
	Mean no. of larvae/plant	0.15	0.2
	Sample variance, s^2	0.1342	0.8
	Sample size, N, binomial sampling	75	475
	Sample size, N, enumerative sampling	149	500
Chisumbanje	Infestation level	0.75	0.85
	Mean no. of larvae/plant	3	4.4
	Sample variance, s^2	6.31579	9.7263
	Sample size, N, binomial sampling	8	4
	Sample size, N, enumerative sampling	18	13

Thus, this was the sample size adopted at all locations throughout the study. However, as it was felt to be difficult to adhere to an absolute number during the general surveys, the real sample size fell within the range 250-350 plants.

CHAPTER 3

Seasonal Occurrence of Cereal Stemborers and their Natural Enemies in Three Ecological Zones of Zimbabwe

3.1 INTRODUCTION

Busseola fusca Fuller and *Chilo partellus* (Swinhoe) are the most important stemborer species that attack maize and sorghum in Zimbabwe (Chinwada *et al.*, 2001). In the central northern highveld region, Chinwada and Overholt (2001) recorded several stemborer parasitoid species and discussed their role in the regulation of *B. fusca* populations. Outside the highveld, *C. partellus* is the predominant species (Sithole, 1995; Chinwada *et al.*, 2001), but its natural enemies have not yet been documented.

In an analysis of the status of stemborer research activities in Zimbabwe, Chinwada *et al.* (2001) found information gaps on several aspects and on which exhaustive studies were necessary. These included provision of bioecological information on other stemborer species besides *B. fusca*, stemborer incidence and distribution patterns, yield losses, host plants, control, and the role of natural enemies, particularly outside the highveld. In general, information on seasonal occurrence of pests and their natural enemies is important as it helps in identifying key natural pest mortality factors as well as deciding when in the crop growth cycle one might need to adopt chemical control in order to bring down an increasing pest population to a level where natural enemies alone can regulate it below the economic injury level. This study was aimed at providing information on: i) the stemborer species composition and incidence in different ecological zones of Zimbabwe, (ii) the range of

natural enemies and their impact, and (iii) the seasonal fluctuations in parasitism by the larval parasitoids *Cotesia sesamiae* (Cameron) and *Sturmiopsis parasitica* (Curran).

3.2 MATERIALS AND METHODS

3.2.1 Sites and field layout

The occurrence, composition and abundance of cereal stemborers and their natural enemies in Zimbabwe were studied at various sites in the highveld, middleveld and lowveld during the 1999-2000, 2000-2001 and 2001-2002 cropping seasons. Henderson Research Station (31°58' E 17°35' S, altitude 1292 m) in the highveld (Harare area), and Chisumbanje Experiment Station (32°15' E 20°48' S, altitude 421 m) in the lowveld, were chosen as the principal study sites. Studies were also conducted at other locations within the Harare area and outside the highveld but these were treated as general survey sites (Table 3.1; Appendix 1). At Henderson, adjacent fields (each 40 x 15 m) (Appendix 2) of maize (SC 701 or SC 627 medium to late maturing hybrids) and sorghum (variety SV1 or SV2) were planted at the beginning (November/December) of each season (November-May). The planting dates for the first crops varied from season to season depending on the onset of the rains. For the three seasons, the first crops were planted on 18 October 1999, 30 November 2000 and 4 December 2001, respectively. Second plantings were conducted on 29 November 1999, 21 December 2000 and 24 January 2002. When necessary, rainfall was supplemented by overhead sprinkler irrigation. At Chisumbanje, fields of maize (SC 405 short-season hybrid) and sorghum (variety SV1 or SV2), each of size 40 x 36 m, were established (Appendix 3). There was only one planting date for

Table 3.1. Sites at which studies were conducted during the 1999-2000 to 2001-2002 cropping seasons.

Ecological zone	Site	Coordinates	Elevation
Highveld (>1200m)	Harare		
	Henderson Research Station	30°58' E 17°35' S	1292 m
	Harare Research Station	31°03' E 17°49' S	1506 m
	Kutsaga Research Station	31°05' E 17°56' S	1463 m
	Gwebi Variety Testing Centre	30°52' E 17°41' E	1448 m
	ART‡ Farm	31°03' E 17°42' S	1524 m
Middleveld	Mushandike	30°43' E 20°13' S	878 m
(600-1200 m)	Bindura	31° 17' E 17°18' S	1097 m
	Bushu	31°36' E 17°09' S	866 m
Lowveld (< 600m)	Chisumbanje Experiment Station	32°15' E 20°48' S	421 m
	Birchenough Bridge	32°20' E 19°50' S	525 m
	Musikavanhu	32°18' E 20°27' S	430 m
	Muzarabani	31°00' E 16°23' S	441 m

‡ Agricultural Research Trust

each crop per season. For the three seasons, the planting dates were 30 December 1999, 22 December 2000 and 30 November 2001, respectively. Rainfall was supplemented by surface/flood irrigation.

3.2.2 Sampling

To facilitate sampling, fields at Henderson were divided into 16 sub-plots, each of size 10 x 4 m. Starting at 6 weeks after crop emergence and thereafter at two-weekly intervals until harvestable maturity, 20 plants (320 per plot) (refer to Chapter 2, section 2.3) were sampled in each sub-plot. At Chisumbanje, fields were subdivided into 8 equal sub-plots, each measuring 20 x 9 m. Owing to long distance and other logistical problems, no proper sampling schedule could be followed at Chisumbanje. However, at each sampling interval, 250-350 plants were sampled from each field. At general survey locations outside Harare, 5-10 farmers' fields were randomly selected for sampling at each location and at least 250 plants were sampled. Within the Harare area, sampling was conducted at research stations and a large-scale commercial farm. At each of these locations, sampling was only conducted in one or two fields.

Plants were sampled along two or more diagonal transects in a field and selecting a plant, or the nearest infested plant (Overholt *et al.* 1994c), every five steps. Selected plants were examined for stemborer feeding symptoms (`shot-holes', leaf scarification, cob-feeding or stem-tunnelling) and categorised as either "infested" or "uninfested". Only infested plants were removed from the field. Excised plants were dissected and assessed for the presence of stemborers (larvae and pupae) and parasitoid pupae inside stemborer tunnels. All stemborer larvae and pupae were identified to species.

Early instar larval stages feeding inside whorls, or on developing tassels or cobs, were reared in groups of 10-20 on rolled-up leaves and developing cobs inside 350 ml plastic jars. Stem-boring larval instars were placed individually in plastic vials (4 cm dia. x 10 cm high) and provided with small pieces of maize stems as food and then incubated in the laboratory at 24-27°C and 55-80% relative humidity. Stems were dissected every two days to check for stemborer mortality, pupation or parasitoid emergence. Stemborer and parasitoid pupal stages were held individually in vials plugged with cotton wool and monitored for emergence of adult stages. Emerged adult parasitoids were identified using taxonomic keys outlined by Polaszek (1998) and voucher specimens deposited at the Biosystematics Unit at ICIPE.

Percentage parasitism was determined for each stemborer life stage and species collected from a particular location during a sampling visit. After at least 8 weeks of rearing, all larvae that had not pupated and had lost the cuticular pigmentation of the pinnaculi (Harris, 1962; Scheltes, 1978) were assumed to be in diapause. Stems in which such larvae were feeding were allowed to dry and held at room temperature in plastic vials that were plugged with cotton wool. Although vials were examined for emerged moths or parasitoid adults once every week, the stems were not dissected until mid-October by which time larvae had resumed development and were pupating (as evidenced by the development of pupation windows on the dry stems). Thereafter, all stems were dissected and examined for larval mortality, pupation and parasitoid emergence. Larvae that were still alive were then supplied with fresh green stems obtained from early-planted irrigated maize and monitored as before.

3.2.3 Data analysis

Seasonal stemborer count data obtained from both general and intensive surveys were pooled to obtain totals for each ecological zone and subjected to chi-square tests (PROC FREQ, SAS Institute, 1990a) to determine likely associations between ecological zone and species. Pooled *B. fusca* larval parasitism levels by *C. sesamiae* and *S. parasitica* within the Harare area at the beginning (1^{st}-10^{th}), middle (11^{th}-20^{th}) and end (21^{st}-31^{st}) of each month from December to May each season were plotted against time to show how parasitism by each species fluctuated throughout the season.

3.3 RESULTS

3.3.1 Stemborer distribution, composition and abundance

A highly significant ($P < 0.01$) association between species and ecological zone was obtained for the three seasons (Table 3.2). *Busseola fusca* was dominant in the highveld (> 1200 m) where it comprised between 81 and 99% of all the larvae sampled on maize and sorghum during each season (Table 3.3). On the other hand, *C. partellus* accounted for 0.9 to 9.5% of the borers in the highveld. However, in both the middleveld (600-1200 m) and lowveld (< 600 m), *C. partellus* was the dominant species, comprising 67.4-99.7% and 83.3-100%, respectively, of the sampled larvae. Although *S. calamistis* was relatively more abundant in the highveld (1-9.1%) compared to the middleveld (0.2-1.4%) or lowveld (0-0.5%), there did not seem to be any significant difference in its abundance among the three ecological zones (Table 3.3).

Table 3.2. Chi-square tests for association between stemborer species and ecological zone†.

Season	Combined number of larvae and pupae									Chi-square value	Prob.
	Busseola fusca			*Chilo partellus*			*Sesamia calamistis*				
	HV	MV	LV	HV	MV	LV	HV	MV	LV		
1999-2000	1269	193	4	38	394	4673	35	4	13	5589.94	<0.01
2000-2001	1483	15	14	37	684	1175	33	3	0	3134.06	<0.01
2001-2002	1338	9	16	10	411	3357	19	2	12	4955.63	<0.01

† HV, highveld; MV, middleveld; LV, lowveld

Table 3.3. Distribution, composition and abundance of stemborer larvae collected from different ecological zones.

Season	Ecological zone	Site[a]	Crop[b]	N	% composition of larvae by species[c] (mean no. of larvae/plant in parentheses)		
					BF	*SC*	*CP*
1999-2000	Highveld	HRE	Mz	925	98.1 (0.25)	1.0 (0.002)	0.9 (0.002)
			Sg	285	81.4 (0.009)	9.1 (0.01)	9.5 (0.01)
	Middleveld	MUS	Mz	577	31.9 (0.46)	0.7 (0.01)	67.4 (0.97)
	Lowveld	BIR	Mz	278	--[d]	--	100 (1.11)
		CHS	Sg	2510	0.2 (0.005)	0.3 (0.01)	99.5 (3.12)
		MUZ	Mz	1571	--	0.3 (0.01)	99.7 (3.13)
2000-2001	Highveld	HRE	Mz	962	95.4 (0.39)	1.5 (0.006)	3.1 (0.01)
			Sg	459	94.6 (0.15)	4.1 (0.007)	1.3 (0.002)
	Middleveld	BIN	Mz	222	4.5 (0.04)	0.9 (0.008)	94.6 (0.84)
		BUS	Mz	404	1.2 (0.006)	0.2 (0.001)	98.5 (0.50)
	Lowveld	CHS	Mz	42	16.7 (0.04)	--	83.3 (0.18)
			Sg	892	--	--	100 (2.23)
2001-2002	Highveld	HRE	Mz	909	96.9 (0.26)	2.0 (0.005)	1.1 (0.003)
			Sg	104	99.0 (0.08)	1.0 (0.008)	--
	Middleveld	BUS	Mz	316	--	0.3 (0.001)	99.7 (0.39)
		MUS	Mz	73	8.2 (0.06)	1.4 (0.01)	90.4 (0.66)
	Lowveld	BIR	Mz	30	--	--	100 (0.12)
		CHS	Mz	2032	--	0.5 (0.01)	99.5 (2.47)
			Sg	573	--	--	100 (1.64)
		MSK	Mz	394	3.6 (0.02)	0.5 (0.003)	95.9 (0.47)

[a] HRE, Harare; CHS, Chisumbanje; BIR, Birchenough; BIN, Bindura; MUS, Mushandike; BS, Bushu; MSK, Musikavanhu; MUZ, Muzarabani.

[b] Mz, maize; Sg, sorghum

[c] *BF*, *Busseola fusca*; *SC*, *Sesamia calamistis*; *CP*, *Chilo partellus*

[d] Respective species not recorded

Except for the trial plots established at Henderson and Chisumbanje, sorghum was not widely grown, hence almost all sampling was conducted on maize. In the Harare area, the mean number of *B. fusca* larvae recorded on maize during the three seasons averaged 0.25-0.39 per plant (Table 3.3). On sorghum, far lower numbers of stemborer larvae were recorded. At Chisumbanje, mean *C. partellus* larval densities on maize and sorghum were in the ranges 0.18-2.47 and 1.64-3.12 per plant, respectively. At Muzarabani, *C. partellus*, which comprised 99.7% of the sampled stemborers, had a density of 3.13 larvae/plant during the 1999-2000 season. The remaining lowveld and middleveld general survey locations had *C. partellus* larval densities ranging between 0.39 and 0.97 larvae/plant.

3.3.2 Diversity of stemborer parasitoids and entomogenous nematodes

The parasitoids reared from stemborer larvae included *Cotesia sesamiae* (Cameron), *Chelonus curvimaculatus* Cameron, *Amyosoma nyanzaense* (Quicke & Wharton) (Hymenoptera: Braconidae), *Sturmiopsis parasitica* (Curran) (Diptera: Tachinidae) and an undetermined Muscidae species (Table 3.4). Pupal parasitoids included *Procerochasmias nigromaculatus* Cameron, *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae) and *Pediobius furvus* Gahan (Hymenoptera: Eulophidae). Stemborer larval mortalities due to *Hexamermis* sp., an entomogenous nematode, were also recorded. Two hyperparasitoids were recorded, namely, *Aphanogmus fijiensis* (Ferrière) (Hymenoptera: Ceraphronidae) and *Dendrocerus rodhaini* (Bequaert) (Hymenoptera: Megaspilidae). These were recovered from *C. sesamiae* cocoons and *S. parasitica* puparia, respectively.

Table 3.4. Stemborer parasitoids, hyperparasitoids and entomogenous nematodes recorded during the 1999-2000 to 2001-2002 seasons in Zimbabwe.

Species[a]	Recovery location[b] and host[c]	Status[d]
PARASITOIDS		
HYMENOPTERA		
Braconidae		
Cotesia sesamiae (L)	HRE (*Bf*, *Sc*, *Cp*), BIN (*Bf*, *Cp*), BUS (*Cp*), CHS (*Sc*, *Cp*), MUS (*Bf*, *Cp*), MSK (*Sc*, *Cp*), BIR (*Cp*)	major
Chelonus curvimaculatus (E-L)	HRE (*Bf*), CHS (*Cp*), BIR (*Cp*), MUZ (*Cp*), MUS (*Cp*), MSK (*Cp*)	major
Amyosoma nyanzaense (L)	CHS (*Cp*)	minor
Ichneumonidae		
Dentichasmias busseolae (P)	CHS (*Cp*), BIR (*Cp*), BUS (*Cp*), MSK (*Cp*)	major
Procerochasmias nigromaculatus (P)	HRE (*Bf*)	major
Eulophidae		
Pediobius furvus (P)	HRE (*Bf*), BIR (*Cp*)	minor
DIPTERA		
Tachinidae		
Sturmiopsis parasitica (L)	HRE (*Bf*)	major
Muscidae		
Unidentified sp. (?*Phaonia* sp.)	HRE (*Bf*), MUZ (*Cp*)	minor
HYPERPARASITOIDS		
HYMENOPTERA		
Ceraphronidae		
Aphanogmus fijiensis (P)	HRE (*Cse*), CHS (*Cse*), MSK (*Cse*)	minor
Megaspilidae		
Dendrocerus rodhaini (P)	HRE (*Spa*)	minor
PATHOGENS		
Nematoda: Mermithidae		
Hexamermis sp.	HRE (*Bf*, *Sc*), MUZ (*Cp*)	major

[a] Parasitoid guild: L, larval; E-L, egg-larval; L-P, larval-pupal; P, pupal

[b] HRE, Harare; CHS, Chisumbanje; BIR, Birchenough; BIN, Bindura; MUS, Mushandike; MSK, Musikavanhu; BUS, Bushu; MUZ, Muzarabani

[c] *Bf*, *Busseola fusca*; *Sc*, *Sesamia calamistis*; *Cp*, *Chilo partellus;* *Cse*, *Cotesia sesamiae*; *Spa*, *Sturmiopsis parasitica*

[d] major – reared from at least 5 hosts; minor – reared from less than 5 hosts.

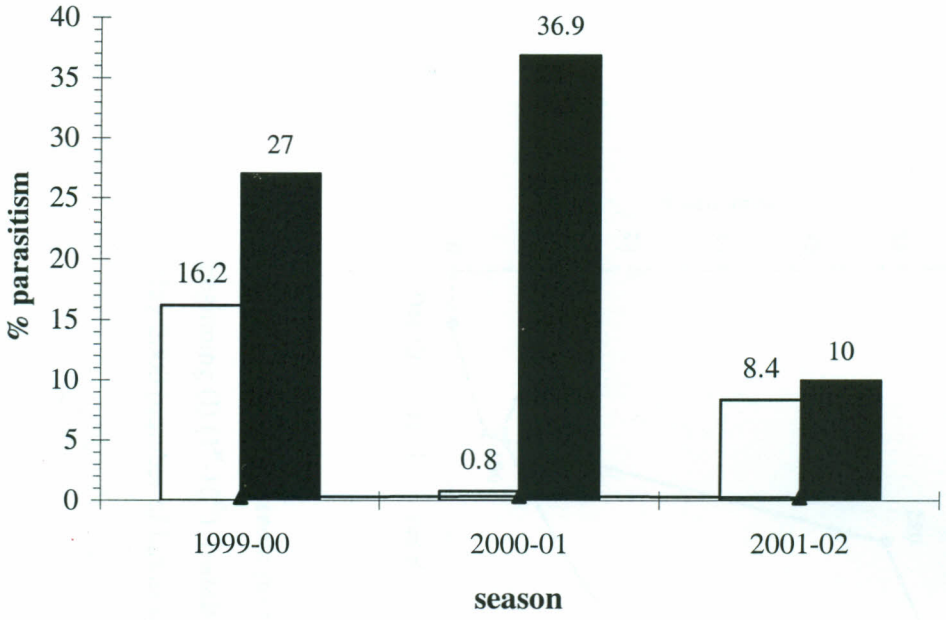
3.3.3 Seasonal occurrence of *S. parasitica* and *C. sesamiae* in the Harare area

Cotesia sesamiae parasitism on *B. fusca* on maize was 16.2, 0.8 and 8.4% during the 1999-2000, 2000-2001 and 2001-2002 seasons, respectively (Fig. 3.1). In contrast, for the three seasons and on maize, parasitism levels by *S. parasitica* were 27, 36.9 and 10%, respectively. On sorghum, stemborer parasitism levels by *C. sesamiae* were below 2% each season. Except for the 1999-2000 season when *S. parasitica* parasitized 12.1% of the sampled *B. fusca* larvae, parasitism levels by the tachinid on sorghum during the 2000-2001 and 2001-2002 seasons were also below 2%.

Although *S. parasitica* parasitized more larvae than *C. sesamiae* each season, parasitism by the tachinid did not extend beyond mid-March. From zero at the end of December 1999, parasitism by *S. parasitica* rose sharply to about 48% in mid-January 2000, and finally attained a peak of 54% at the end of January (Fig. 3.2). At the beginning of February, parasitism was below 20%, but by mid-February, had risen to 52%. From then onwards, *S. parasitica* was not recovered from all the sampled larvae. In contrast, *C. sesamiae* was active throughout the period December 1999 to May 2000 but the level of parasitism generally remained below that of *S. parasitica* until after mid-February when field recoveries of the latter ceased. By mid-May 2000, when sampling was terminated, *C. sesamiae* parasitism was about 14%.

During the 2000-2001 season, *C. sesamiae* parasitism was very low and fluctuated between zero and 3% (Fig. 3.3). Starting at about 8% at the end of December 2000, the percentage of larvae parasitized by *S. parasitica* rose to attain a peak of about 60% at the end of January 2001. By mid-February, parasitism had declined to 25% and then zero by mid-March. Although *C. sesamiae* parasitism was generally above that of *S. parasitica* throughout the

(a) maize



(b) sorghum

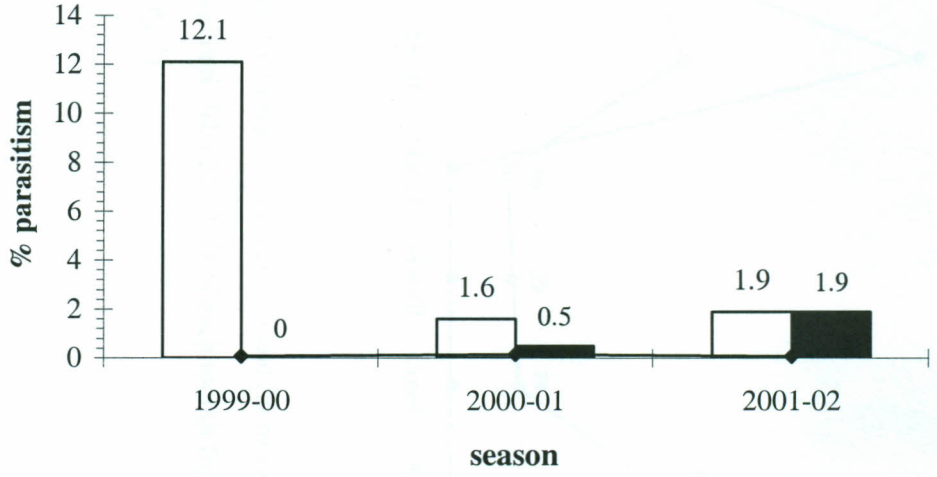


Fig. 3.1. Average seasonal *Busseola fusca* parasitism levels by *Cotesia sesamiae* (□) and *Sturmiopsis parasitica* (■) on (a) maize and (b) sorghum in the Harare area.

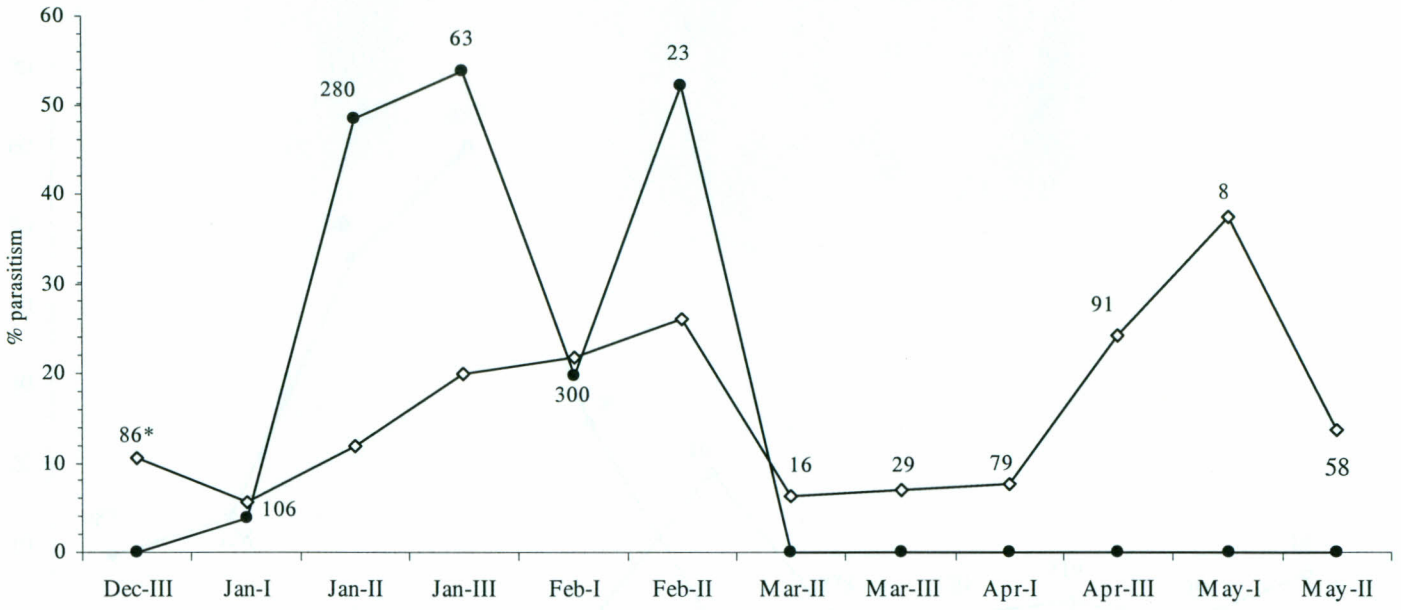


Fig. 3.2. Pooled *Busseola fusca* larval parasitism by *Cotesia sesamiae* (◇) and *Sturmiopsis parasitica* (●) at the beginning (I) (1^{st}-10^{th}), middle (II) (11^{th}-20^{th}) and end (III) (21^{st}-31^{st}) of each month from December 1999 to May 2000 (number of larvae sampled denoted by *).

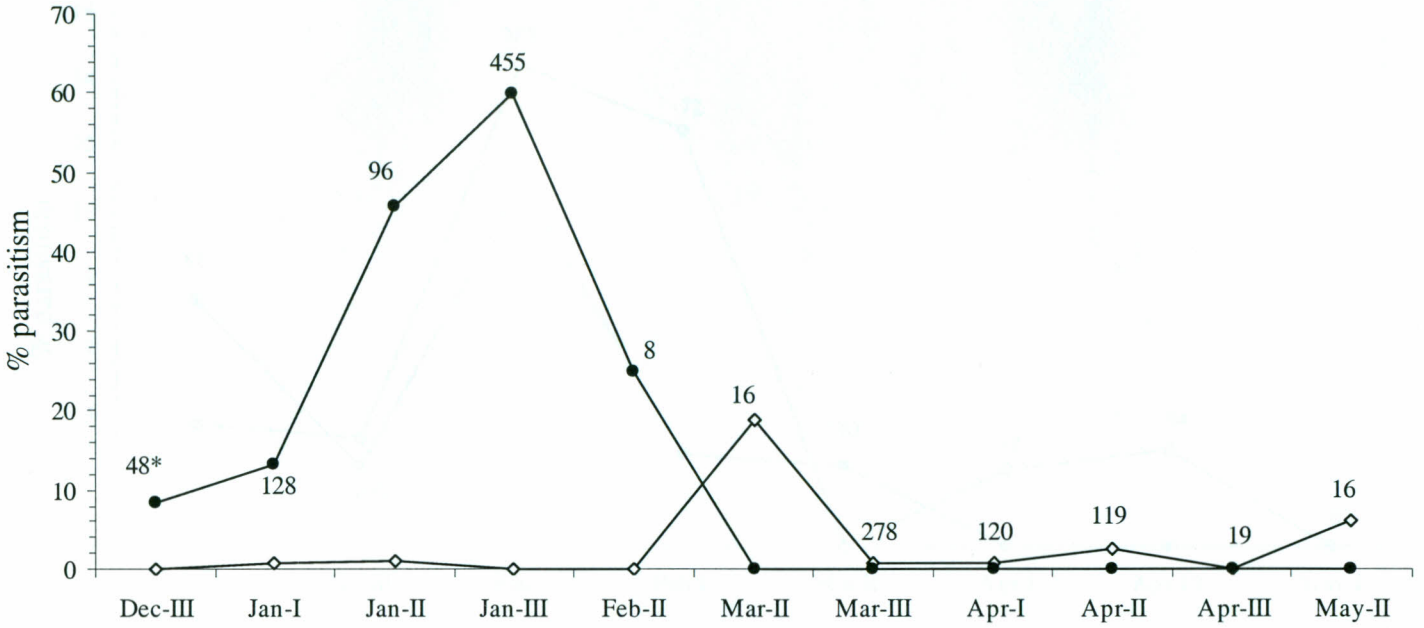


Fig. 3.3. Pooled *Busseola fusca* larval parasitism by *Cotesia sesamiae* (◇) and *Sturmiopsis parasitica* (●) at the beginning (I) (1^{st}-10^{th}), middle (II) (11^{th}-20^{th}) and end (III) (21^{st}-31^{st}) of each month from December 2000 to May 2001 (number of larvae sampled denoted by *).

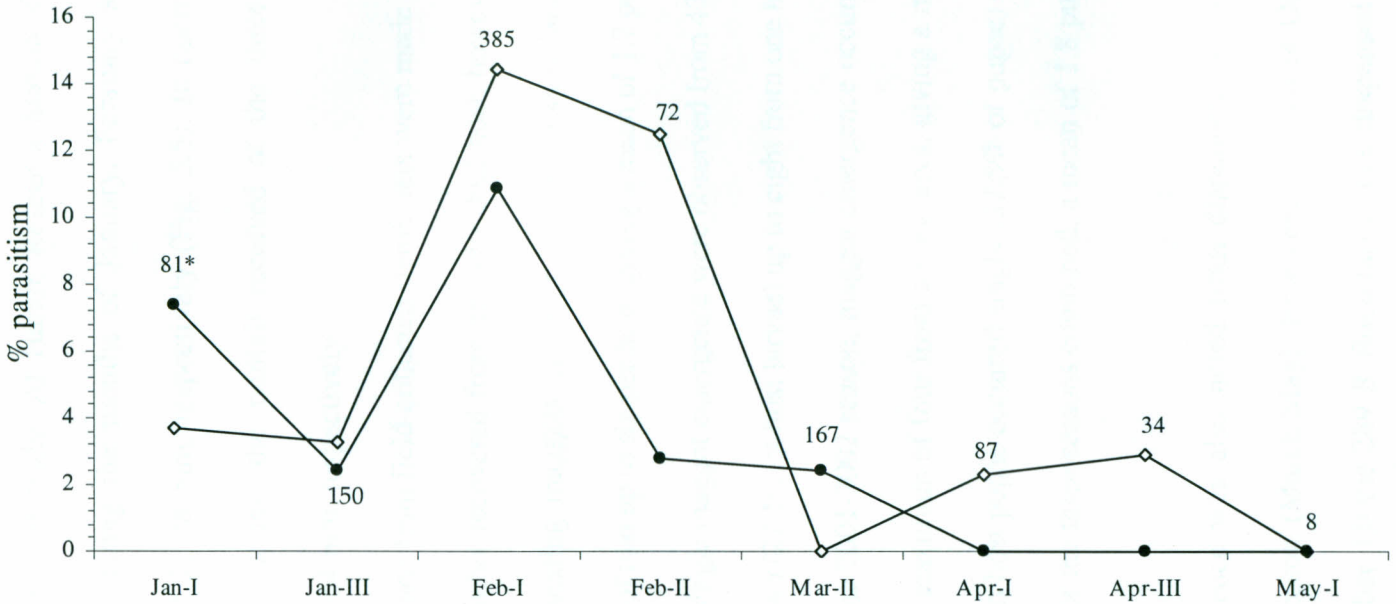


Fig. 3.4. Pooled *Busseola fusca* larval parasitism by *Cotesia sesamiae* (◇) and *Sturmiopsis* parasitica (●) at the beginning (I) (1^{st}-10^{th}), middle (II) (11^{th}-20^{th}) and end (III) (21^{st}-31^{st}) of each month from December 2001 to May 2002 (number of larvae sampled denoted by *).

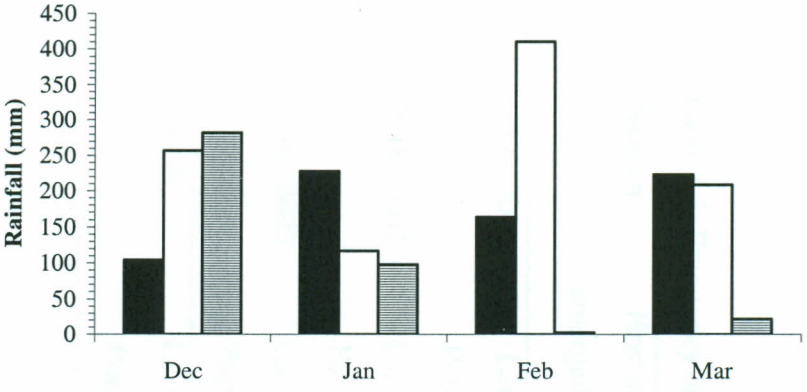
2001-2002 season, parasitism by the tachinid followed a pattern similar to the preceding two seasons (Fig. 3.4). A peak (about 11%) was attained at the beginning of February 2002 and thereafter parasitism declined to end at 2.4% by mid-March.

Rainfall received at three Harare area locations where *S. parasitica* was recovered was quite variable during the three seasons of study. At Harare Research Station, Gwebi and Kutsaga, rainfall received in 2002 during the months of January, February and March averaged between 80-110, 1-70 and 21-28 mm, respectively (Fig. 3.5). In contrast, in the wetter 1999-2000 and 2000-2001 seasons, the rainfall received at the three locations averaged 42-285, 345-420 and 210-264 mm, respectively.

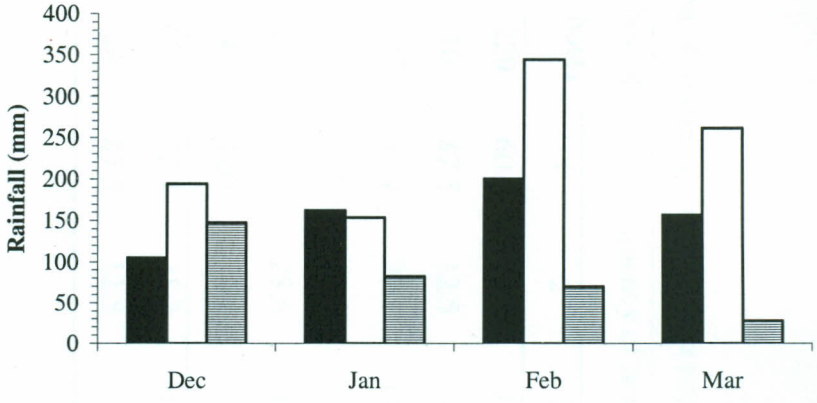
Recoveries of *S. parasitica* puparia from field-collected stemborers were made at both the host larval and pupal stages. The number recovered from an individual host, however, varied. During the 1999-2000 season, pupariating maggots emerged from stemborer larvae mainly singly (60.7% of larvae) or in groups of two up to six per host, giving a mean of 1.7 puparia/host (Table 3.5). In the following season, single maggot emergence were observed from 43.7% of the host larvae and the rest in groups of two (27.1% of host larvae) up to eight from one host, giving a mean of 2.1 puparia/host. During the 2001-2002 season, maggot emergence occurred mainly singly (63.1% of host larvae) up to a maximum of four from a host larva, giving a mean of 1.5 puparia/host. Maggot emergence from host pupae occurred singly (87.5% of pupae) or in twos, giving a mean of 1.1 puparia/host. For the three seasons combined, a mean of 1.8 puparia were recovered per host larva.

Sturmiopsis parasitica emergence was also noted from diapausing *B. fusca* larvae collected towards the end of the season (March-May). Emergence started in October and lasted until the beginning of December. Of the 289 *B. fusca* larvae that diapaused at the end of the 1999-2000 season, 25.3% were parasitized by *S. parasitica* (Table 3.6). During the

(a) Harare Research Station



(b) Gwebi



(c) Kutsaga

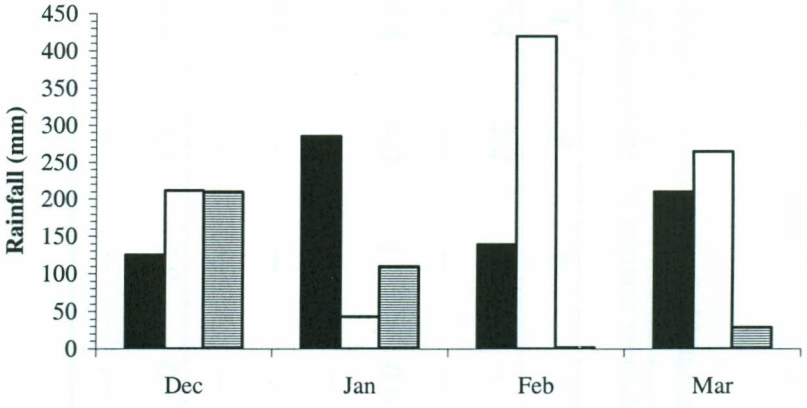


Fig. 3.5. December-March rainfall totals at (a) Harare Research Station, (b) Gwebi and (c) Kutsaga Research Station during the 1999-2000 (■), 2000-2001 (□) and 2001-2002 (▤) seasons.

Table 3.5. Frequency distribution of *Sturmiopsis parasitica* puparia per host recovered from field-sampled *Busseola fusca.*

Season	Host stage emerged from	No. of hosts	% frequency of hosts with given number of puparia recovered/host								Mean no. of puparia/host
			1	2	3	4	5	6	7	8	
1999-2000	Larva	229	60.7	21.4	7.9	7.4	2.2	0.4	--	--	1.7
	Pupa	16	87.5	12.5	--	--	--	--	--	--	1.1
2000-2001	Larva	339	43.7	27.1	14.7	7.4	5.0	1.2	0.6	0.3	2.1
	Pupa	2	50.0	50.0	--	--	--	--	--	--	1.5
2001-2002	Larva	84	63.1	28.6	3.6	4.8	--	--	--	--	1.5
	Pupa	6	100	--	--	--	--	--	--	--	1.0
Totals	Larva	652	52.1	25.3	10.9	7.1	3.4	0.8	0.3	0.2	1.8
	Pupa	24	87.5	12.5	--	--	--	--	--	--	1.1

Table 3.6. *Busseola fusca* seasonal parasitism by *Sturmiopsis parasitica* adjusted for the latent percentage "carried-over" in diapausing larvae.

Season	Tot. no. of larvae and pupae collected during the season (Dec-May)	Pooled % seasonal parasitism	No. of larvae going into diapause	% parasitism on diapausing larvae (Oct-Dec)	Adjusted % seasonal parasitism
1999-2000	1140	21.5	289	25.3	27.9
2000-2001	1352	25.2	153	33.3	29.0

2000-2001 season, *S. parasitica* parasitism on diapause-generation larvae was 33.3%. When the overall 1999-2000 seasonal *S. parasitica* parasitism was adjusted for this parasitization that had been latent until diapause termination, *B. fusca* parasitism in the Harare area rose to 27.9% up from 21.5%. A similar adjustment during the 2000-2001 season resulted in an elevation of *S. parasitica* parasitism from 25.2% to 29%.

3.3.4 Larval parasitism outside the highveld

Outside the highveld, larval parasitism was mainly due to *C. sesamiae* and *C. curvimaculatus* (Table 3.7). *Cotesia sesamiae* was recorded at all locations with the exception of Muzarabani. Although reared from a numerically large number of *C. partellus* larvae at Chisumbanje (23-179) during the three seasons, parasitism by *C. sesamiae* did not exceed 7%. At the middleveld sites of Mushandike and Bindura, *C. sesamiae* parasitism on *B. fusca* and *C. partellus* averaged 16.3-20.0 and 4.5-23.3%, respectively. At Bushu, however, *C. sesamiae* was only recorded during the 2000-2001 season when two (0.5%) *C. partellus* larvae were parasitized. During the 2001-2002 season, none of the 315 *C. partellus* larvae sampled at Bushu were parasitized.

Although reared from both *B. fusca* and *C. partellus*, parasitism by *C. curvimaculatus* was a major larval mortality factor only at Mushandike and Muzarabani. At the latter location, 24 *C. partellus* larvae (1.5%) were parasitized during the 1999-2000 season.

3.3.5 Pupal parasitism

The solitary ichneumonids, *P. nigromaculatus* and *D. busseolae* and the gregarious eulophid, *P. furvus*, were reared from stemborer pupae. While *P. nigromaculatus* was confined to the

Table 3.7. Parasitism levels by *Cotesia sesamiae* and *Chelonus curvimaculatus* on *Busseola fusca* and *Chilo partellus* outside the highveld.

Season	Ecological zone	Location	crop	Borer sp.[a]	% parasitism	
					Cotesia sesamiae	*Chelonus curvimaculatus*
1999-2000	middleveld	Mushandike	maize	Bf	16.3 (30)[b]	--[c]
				Cp	11.8 (46)	1.3 (5)
	lowveld	Birchenough	maize	Cp	17.6 (49)	--
		Chisumbanje	sorghum	Cp	6.9 (173)	0.04 (1)
		Muzarabani	maize	Cp	--	1.5 (24)
2000-2001	middleveld	Bindura	maize	Bf	20.0 (2)	--
				Cp	23.3 (49)	--
		Bushu	maize	Cp	0.5 (2)	--
	lowveld	Chisumbanje	maize	Cp	--	--
			sorghum	Cp	5.4 (48)	--
2001-2002	middleveld	Mushandike	maize	Bf	16.7 (1)	--
				Cp	4.5 (3)	3.0 (2)
		Bushu	maize	Cp	--	--
	lowveld	Chisumbanje	maize	Cp	3.4 (69)	0.05 (1)
			sorghum	Cp	4.0 (23)	--
		Birchenough	maize	Cp	20.0 (6)	--
		Musikavanhu	maize	Cp	6.3 (4)	0.3 (1)

[a] Bf, *Busseola fusca*; Cp, *Chilo partellus*

[b] Number of parasitized larvae in parentheses

[c] not recorded

Harare area where it parasitized *B. fusca* pupae, *D. busseolae* was recovered from *C. partellus* at all middleveld and lowveld locations with the exception of Mushandike and Muzarabani. In the Harare area, pupal parasitism by *P. nigromaculatus* was recorded from mid-January to mid-February. This period coincided with the pupation of most first-generation *B. fusca* larvae. At Henderson, parasitism in January and February 2000 averaged 2.9-25% (Table 3.8). In February 2002, *P. nigromaculatus* parasitized between 15 and 24% of the *B. fusca* pupae sampled at ART Farm, Kutsaga and Gwebi. *Pediobius furvus* was recorded at Kutsaga and ART Farm where it parasitized a combined total of two pupae.

In the lowveld, *D. busseolae* pupal parasitism was recorded during the period December to mid-February and averaged 4.2-35.3% for the three seasons (Table 3.9). At Bushu in the middleveld, *D. busseolae* was only recorded during the 2001-2002 season where it parasitized one (8.3%) of the 12 *C. partellus* pupae collected on 25 January 2002. At Birchenough in the lowveld, *P. furvus* was reared from one of the 24 *C. partellus* pupae collected on 30 December 1999 (Table 3.9).

3.3.6 Incidence of entomogenous nematodes

Apart from insect parasitoids, stemborer larval mortalities at Henderson and Muzarabani were also due to a mermithid nematode, *Hexamermis* sp. At Muzarabani, the nematode was recovered from one *C. partellus* larva sampled during the 2000-2001 season. In the Harare area, 12 *B. fusca* (1.1%) and two (5.7%) *S. calamistis* larvae sampled during the 1999-2000 season, were parasitized. In the following season, four (0.3%) *B. fusca* larvae and three (9.1%) *S. calamistis* larvae died due to parasitism by the nematode. In most cases, nematode

Table 3.8. *Procerochasmias nigromaculatus* parasitism levels on *Busseola fusca* pupae within the Harare area.

Season	Location	Sampling date	No. of pupae	% parasitism
1999-2000	Henderson Res. Stn	17 Jan 2000	22	13.6
	Henderson Res. Stn	20 Jan 2000	34	2.9
	Henderson Res. Stn	31 Jan 2000	21	9.5
	Henderson Res. Stn	14 Feb 2000	12	25.0
2000-2001	Harare Res. Stn	18 Jan 2001	19	10.5
	ART Farm	30 Jan 2001	61	4.9
	Harare Res. Stn	31 Jan 2001	45	2.2
2001-2002	ART Farm	6 Feb 2002	146	15.8
	Kutsaga Res. Stn	7 Feb 2002	88	15.9
	Gwebi	14 Feb 2002	17	23.5
	ART Farm	18 Feb 2002	98	16.3

Table 3.9. *Dentichasmias busseolae* parasitism levels on *Chilo partellus* pupae at various middleveld and lowveld locations.

Season	Location	Sampling date	No. of pupae	% parasitism
1999-2000	Birchenough	30 Dec 1999	24	4.2
2000-2001	Bushu	25 Jan 2001	12	8.3
2001-2002	Birchenough	18 Dec 2001	8	25.0
	Chisumbanje	16 Jan 2002	152	3.9
		1 Feb 2002	77	11.7
	Musikavanhu	17 Jan 2002	53	1.9
		31 Jan 2002	17	35.3

juveniles emerged singly from a larva but four juveniles emerged from a *S. calamistis* larva sampled at Harare Research Station on 18 January 2001.

3.3.7 Hyperparasitism

The ceraphronid, *A. fijiensis* was reared from three *C. sesamiae* cocoon masses collected at Henderson on 8 February 2000 and one cocoon mass collected at ART Farm on 6 February 2002. Outside the highveld, the hyperparasitoid was reared from one cocoon mass collected at Musikavanhu on 31 January 2002. Between 15 and 25 *A. fijiensis* adults emerged from each cocoon mass. The megaspilid, *D. rodhaini*, was reared from two *S. parasitica* puparia collected at Henderson on 14 February 2000 and one puparium collected at ART Farm on 6 February 2002. A total of 20-30 *D. rodhaini* adults emerged from each *S. parasitica* puparium.

3.4 DISCUSSION

Busseola fusca, *S. calamistis* and *C. partellus* were the only stemborer species recorded attacking maize and sorghum. A highly significant association between species and ecological zone was obtained each season indicating that there were different ecological zone preferences by the three species. While *B. fusca* was the dominant species at high elevation (highveld), *C. partellus* predominated at both medium (middleveld) and low elevation (lowveld). *Sesamia calamistis* showed a preference for the highveld, but its frequency of occurrence was very low overall indicating that it is not of economic importance. These results corroborate earlier findings by Sithole (1995) which also showed a high association between stemborer species and ecological zone. However, unlike in the present study, Sithole

(1995) reported that the relative compositions of *B. fusca* and *C. partellus* in the middleveld were almost similar and that *S. calamistis* had the middleveld as its preferred ecological zone.

Parasitism by the larval parasitoids *C. sesamiae*, *S. parasitica* and the egg-larval parasitoid *C. curvimaculatus* was an important stemborer mortality factor. With the exception of Muzarabani, *C. sesamiae* was recorded at every site. An almost complete absence of the parasitoid was also observed at Bushu where, despite collecting a combined total of over 700 stemborer larvae during the 2000-2001 and 2001-2002 seasons, *C. sesamiae* was only reared from two larvae.

In the Harare area, stemborer larval parasitism was almost entirely due to *S. parasitica* and *C. sesamiae*. For the three seasons, there was a clear difference in the pattern of parasitism by each species. While parasitism by either or both species started being detected at the end of December, *S. parasitica* predominated for about half of the season (December-February), with peak parasitism being attained between the end of January and mid-February. Thereafter, a steep decline in parasitism was observed such that by the end of February or mid-March, parasitism was generally zero. In contrast, *C. sesamiae* parasitism either rose gradually to attain a peak soon after *S. parasitica* parasitism had declined, fluctuating below 20% throughout much of the season, but with occasional sub-peaks as the season progressed.

Chinwada and Overholt (2001) speculated that the observed seasonal patterns of parasitism by *C. sesamiae* and *S. parasitica* could indicate that the two species have a putative niche partitioning mechanism through which they minimize interspecific competition and by so doing make their effects complementary. However, since *S. parasitica* utilizes diapausing *B. fusca* larvae for its seasonal "carry-over" (Chinwada and Overholt, 2001; refer to Chapter 5), it is clear that the rapid decline in parasitism from March onwards

was largely due to the presence of second-generation host larvae, most of which do not pupate until the beginning of the rainy season (October/November) (Smithers, 1960a; Blair, 1971). Similarly, the generally lower *S. parasitica* parasitism recorded on sorghum was due to the fact that stemborer infestation recorded on the crop was mainly due to second-generation larvae. Thus, due to the deferred emergence of *S. parasitica* until after diapause termination, then this low parasitism was to be expected. In the case of *C. sesamiae*, its low parasitism early in the season may indicate that the parasitoid is largely absent, or only present in very low densities at that time. This finding appears to support the hypothesis that one of the seasonal carryover mechanisms of *C. sesamiae* in Zimbabwe could be a yearly sustenance on non-diapause *C. partellus* larvae in some lowveld locations ("ecological islands") from which it disperses to re-occupy niches (such as the highveld) where the parasitoid dies out at the end of each cropping season (refer to Chapter 4).

Weather patterns, particularly December-March rainfall, could also have had a significant influence on the observed patterns of *S. parasitica* parasitism. When *S. parasitica* parasitism patterns and the December-March rainfall totals for each of the three seasons were examined, it appeared as if the low levels of parasitism recorded during the 2001-2002 season corresponded to a drop in rainfall in the same season. Unlike in the first two seasons when *S. parasitica* parasitism was above that of *C. sesamiae* during the period January to mid-February, the reverse happened during the 2001-2002 season. Hardly any rains fell during the months January to March 2002 due to a severe drought. Thus, as much as high moisture level within stemborer tunnels could enhance movement of planidia (Chinwada and Overholt, 2001), microclimatic conditions outside the tunnel might also have a significant influence on *S. parasitica* parasitism levels. The tachinid, which utilizes the planidial-ingress host attack strategy (Smith *et al.*, 1993), may have been adversely affected by prolonged dry

conditions which resulted in the rapid drying of the frass at borer tunnel entrances. This, in turn, could have resulted in the desiccation of most maggots shortly after their deposition. The ingress-and-sting host attack strategy of *C. sesamiae* (Smith *et al.*, 1993) ensures that its performance is less influenced by weather fluctuations. In fact, sustained dry conditions may enhance its parasitism due to the absence of wet and sticky frass that might hinder tunnel exploration (Chinwada and Overholt, 2001).

It is important to recognize that even if weather factors influence parasitoid activity, there is a time lag in their effects. In a study on the influence of weather patterns on seasonal fluctuations in *C. flavipes* parasitism levels in India, Srikanth *et al.* (1999) found that they could amplify some relationships better by correlating monthly parasitism rates with weather data of the previous month. Probably, since the life cycle of *C. flavipes* is known, they could have further improved on their correlations by factoring into the models only weather data of specific time periods within the previous month rather than for the whole month. In the present study, the time period from host inoculation to emergence of pupariating *S. parasitica* maggots on non-diapause larvae is about 14 days (range 11-20 days) (refer to Chapter 5), so a similar study on the effect of, for example, rainfall on *S. parasitica* parasitism patterns, would only consider rainfall received 11-20 days prior to the date of parasitoid emergence.

Unlike *S. parasitica*, the physiological state (diapause/non-diapause) of host larvae does not affect the development of *C. sesamiae* (Mbapila and Overholt, 1997) hence parasitism by the braconid was recorded right up to the end of the season. However, no particular seasonal mechanism was observed for *C. sesamiae*. Although *C. sesamiae* has been reported to remain active throughout the year (Kfir, 1988), its occurrence on winter-grown crops has not been investigated in Zimbabwe.

The megaspilid hyperparasitoid, *D. rodhaini*, was reared from *S. parasitica* puparia. Its occurrence, particularly at the end of January and the beginning of February when many puparia were present in stem tunnels was, however, very low. First reported in Zimbabwe by Polaszek and Chinwada (2000), their record was the first in Africa on any other host beside the tsetse fly, *Glossina palpalis* (Robineau-Desvoidy) (Dessart, 1978, 1982). Throughout sub-Saharan Africa, the most common and widely occurring hyperparasitoid associated with tachinid parasitoids is the encyrtid, *Exoristobia dipterae* (Risbec) (Polaszek *et al.*, 1998).

Besides larval parasitoids, pupal parasitism by *P. nigromaculatus* and *D. busseolae* accounted for a significant proportion of the total stemborer parasitism in both the highveld and lowveld. In the Harare area, parasitism levels on *B. fusca* pupae by *P. nigromaculatus* were quite high. Predictably, parasitism by *P. nigromaculatus* was mostly confined to the period mid-January to mid-February in every season when most first-generation larvae were pupating. This result differed from observations in the highveld in South Africa where Kfir (2000) reported two peaks of *B. fusca* pupal parasitism by *P. nigromaculatus*; the first occurring in October and November shortly after larvae terminate diapause (Kfir, 1998; Kfir, 2000) and the second during the months of February and March (Kfir, 1998).

In conclusion, this study depicted the occurrence and impact of some of the natural enemies associated with cereal stemborers in Zimbabwe. Cumulative stemborer mortality by parasitoids, although significant, did not seem to be effective in reducing stemborer populations, particularly in the lowveld where *C. partellus* is the predominant species. There were also variations in the performance of *C. sesamiae*, particularly within the different middleveld and lowveld locations. The apparent absence of *C. sesamiae* from Muzarabani — if not simply a result of inadequate sampling — and the scarcity of larval parasitoids at Bushu, seem to point to the need to seriously consider introducing *C. flavipes* into

Zimbabwe. The result from Muzarabani might even suggest that if introduced and successfully established, *C. flavipes* would probably exploit the entire niche without significant competition in the same trophic level.

In the Harare area, combined parasitism by *C. sesamiae*, *S. parasitica* and *P. nigromaculatus* appears to play a significant regulatory role on *B. fusca* populations. However, the work needs to be expanded further with a view of devising ways in which the activity of the three parasitoids could be enhanced. For *S. parasitica*, its seasonal carryover mechanism places it in a position whereby it can, right from the onset of the rainy season, regulate populations of *B. fusca*. Unfortunately, it is likely that most of the populations of *S. parasitica* that emerge much earlier (October) when there are very few crops to sustain its host die out. Nonetheless, considering the high parasitism levels by *S. parasitica* in the Harare area and its seasonal carryover mechanism, it would be interesting to see if it is possible to successfully redistribute the parasitoid to other parts of the highveld, especially at irrigation schemes where the earliest planting date of maize is September.

CHAPTER 4

Host Suitability and Mating Compatibility Between Two *Cotesia sesamiae* Populations and Implications for Stemborer Control

4.1 INTRODUCTION

The conceptual model of successful parasitism is divided into the hierarchical processes of host habitat location, host location, host acceptance and host suitability (Godfray, 1994). The last process is usually the most critical and has been cited as one of the main reasons for failure of establishment of the exotic stemborer parasitoid *Cotesia flavipes* Cameron in mainland Africa (Kfir *et al.*, 2002). In recognition of the apparent differences in the impact of the indigenous stemborer parasitoids among different regions of Africa, Schulthess *et al.* (1997) proposed the introduction from West to East Africa of the egg parasitoid *Telenomus isis* Polaszek and *C. sesamiae* from East to West Africa.

One of the main factors currently limiting the introduction of *C. sesamiae* into other parts of the world and within Africa itself is lack of knowledge of the intraspecific variations that exist within different populations of the species (Schulthess *et al.*, 1997). In Kenya, evidence of a variable ability of different populations of *C. sesamiae* to develop in *B. fusca* has been reported (Ngi-Song *et al.*, 1995; 1998; Mochiah *et al.*, 2001). Ngi-Song *et al.* (1998) showed partial reproductive incompatibility between an inland and a coastal population of *C. sesamiae,* which they attributed to infection of the latter population by *Wolbachia. Wolbachia*, a bacterium that induces cytoplasmic incompatibility and other effects, has been reported in many insect species (Werren, 1997).

In Zimbabwe, the extent of variation in host specificity and reproductive compatibility between the *C. sesamiae* populations that mainly utilize *B. fusca* as a host in the highveld and those parasitizing *C. partellus* in the lowveld are not known. In order to enhance the effectiveness of *C. sesamiae* and thus improve overall stemborer control in Zimbabwe, it is imperative to understand the physiological compatibility between the parasitoid and its hosts. The objectives of the current study were two-fold: i) to determine whether *C. sesamiae* populations found in the highveld and lowveld differ significantly in their ability to parasitize and develop in *B. fusca*, *S. calamistis* and *C. partellus*; and ii) to determine the mating compatibility between the two *C. sesamiae* populations and the implications for stemborer control in the two agroecological regions.

4.2 MATERIALS AND METHODS

4.2.1 Insects

Fourth instar larvae of *B. fusca*, *C. partellus* and *S. calamistis* were used in all the experiments. These were reared on artificial diet (Ochieng *et al.*, 1985; Onyango and Ochieng'-Odero, 1994). Colonies of *C. sesamiae* were initiated with parasitoids reared from *B. fusca* sampled at Harare Research Station (highveld population) and *C. partellus* sampled at Chisumbanje Experiment Station (lowveld population) (Appendix 1). For each population, adults of the founder population were obtained from 80 mated females that emerged from twenty cocoon masses. Subsequent rearing was then conducted at the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya (Overholt *et al.*, 1994b), with each population being reared on the stemborer species from which it was recovered in the field. Emerged parasitoid cocoons were collected in vials (2.5 cm x 7.5 cm) stopped with cotton wool.

Adult parasitoids were provided a 20% honey/water solution and left to mate for 24 hours in Perspex® cages prior to host exposure (Overholt *et al.*, 1994b). After host exposure, stemborer larvae were maintained on artificial diet at 25 ± 0.5°C, 65-80% RH and 12:12 (L:D) hour photoperiod.

4.2.2 Host acceptability studies

Busseola fusca, *C. partellus* and *S. calamistis* larvae were individually exposed to naive, mated female parasitoids of highveld and lowveld *C. sesamiae* using the method described by Ngi-Song *et al.* (1995). Prior to exposure, larvae were removed from the artificial diet and fed on maize stems for 24 hours. A one-day old mated female parasitoid was introduced into an inverted vial (2.5 x 7.5 cm) placed on a flat surface, and allowed to climb to the top (bottom of the vial). Once the parasitoid had reached the top, the vial was placed over a larva and the time it took to descend and sting the host was recorded. An observation was terminated when the parasitoid stung the larva, or after five minutes. Individual parasitoids and larvae were used only once. Ten larvae of each species replicated four times, were exposed to females of each *C. sesamiae* population. For each stemborer species, the percentage of larvae stung was calculated and reported as acceptance.

4.2.3 Host suitability studies

The suitability of the three stemborer species for the development of each of the two *C. sesamiae* populations was assessed by hand-stinging stemborer larvae using 24 hour-old mated female parasitoids. Hand-stinging involves exposure of stemborer larvae held with soft forceps to female parasitoids in a Perspex® cage. Females readily oviposit in a few seconds

and then the larvae are removed from the cage and placed on artificial diet (Overholt *et al.* 1994b). Larvae stung during the host acceptance tests plus additional ones hand-stung to have a total of 80 for each species, were reared on artificial diet at 25 ± 0.5°C. Three days after exposure, five larvae of each species were randomly selected and dissected to check for encapsulated eggs. Exposed larvae were inspected daily for mortality, pupation or parasitoid emergence. Ten days after exposure, larvae were removed from the diet and placed individually in clean vials so that parasitoid emergence would not occur inside the diet media where it would have been difficult to account for all emerged parasitoid larvae. Each stemborer larva rested on a piece of tissue paper that had been placed at the bottom of the vial. One day after parasitoid emergence, the tissue paper was removed. The proportion of stung larvae that produced cocoons, parasitoid development time (egg-adult), proportion of stung larvae that pupated or died prior to parasitoid emergence, the brood size and sex ratio, the number of parasitoid larvae that exited the host but failed to pupate and the number of parasitoids that died inside cocoons were recorded.

Data for each *C. sesamiae* population were subjected to analysis of variance (ANOVA) (PROC GLM, SAS Institute, 1990b), followed by Student-Newman-Keul's (SNK) multiple range test when the F-ratio was significant ($P < 0.05$). Insect counts and proportions were log-transformed and arcsine square root-transformed, respectively, before being subjected to analysis (Sokal and Rohlf, 1981; Fowler *et al.*, 2000).

4.2.4 Mating compatibility studies

Adult parasitoids from the two *C. sesamiae* populations were cross-mated using the procedure outlined by Ngi-Song *et al.* (1998). In brief, adults were allowed to emerge singly from cocoons

by separating single dark cocoons from each cocoon mass. Mating pairs were then formed as follows: (i) highveld males x lowveld females and (ii) lowveld males x highveld females.. After mating, females were offered fourth instar larvae of *S. calamistis* for oviposition. Stung larvae were then reared on artificial diet at 25 ± 0.5°C and observed daily for mortality, pupation or parasitoid emergence. The proportion of hosts which produced cocoons, developmental time, clutch size, sex ratio, the number of emerged parasitoids that failed to pupate and the number that died inside cocoons were recorded.

Data were subjected to t-test (PROC TEST, SAS Institute, 1990b). Insect counts and proportions were log-transformed and arcsine square root-transformed, respectively, before being subjected to analysis (Sokal and Rohlf, 1981; Fowler *et al.*, 2000).

4.3 RESULTS

4.3.1 Host acceptability

Only one (2.5%) *C. partellus* larva was accepted for oviposition by mated females of the highveld *C. sesamiae* population compared to 80.6% and 96.3% of *B. fusca* and *S. calamistis* larvae, respectively (Table 4.1). None of the females of the lowveld *C. sesamiae* population stung *C. partellus*. Compared to the highveld population, only seven (17.7%) of the offered *B. fusca* larvae were stung by lowveld *C. sesamiae* females. Acceptance of *S. calamistis* by the lowveld *C. sesamiae* was also low, with only 55.8% of the larvae being stung within the allotted 5-minute period.

Table 4.1. Acceptability of *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* for oviposition by highveld (Hv) and lowveld (Lv) *Cotesia sesamiae* populations.

Host sp.	n	Mean % (± SE) of larvae stung	
		Hv *C. sesamiae*†	Lv *C. sesamiae*‡
B. fusca	40	80.6 ± 7.1 a	17.7 ± 8.8 b
S. calamistis	40	96.3 ± 16.2 a	55.8 ± 10.0 a
C. partellus	40	2.5 ± 2.5 b	0.0 ± 0.0 b

Means within a column followed by the same letter are not significantly different (SNK)
† $F = 29.96$; df = 2,6; $P = 0.0008$
‡ $F = 14.27$; df = 2,6; $P = 0.0052$

Table 4.2. Percentage (mean ± SE) of hosts successfully parasitized or pupating after exposure to *Cotesia sesamiae*.

Host sp.	n	% hosts producing parasitoid cocoons	% hosts pupating
		Highveld *C. sesamiae*[a]	
B. fusca	80	74.1 ± 5.5 a	18.8 ± 3.8 a
S. calamistis	80	95.4 ± 10.6 a	2.5 ± 1.4 b
C. partellus	78	92.2 ± 13.3 a	1.4 ± 1.4 b
		Lowveld *C. sesamiae*[b]	
B. fusca	77	35.1 ± 2.3 b	55.8 ± 1.9 a
S. calamistis	79	77.1 ± 9.8 a	3.8 ± 2.4 c
C. partellus	80	86.3 ± 2.6 a	11.3 ± 2.4 b

Means within a column followed by the same letter are not significantly different (SNK)
[a] Percentage hosts producing cocoons: $F = 4.63$; $df = 2,6$; $P = 0.0608$
Percentage hosts pupating: $F = 16.17$; $df = 2,6$; $P = 0.0038$
[b] Percentage hosts producing cocoons: $F = 36.44$; $df = 2,6$; $P = 0.0004$
Percentage hosts pupating: $F = 199.95$; $df = 2,6$; $P < 0.0001$

Table 4.3. Developmental time (days ± SE) of *Cotesia sesamiae* on *Busseola fusca*, *Sesamia calamistis* and *Chilo partellus* at 25 ± 0.5°C.

Host sp.	n	Highveld *C. sesamiae*[a]	n	Lowveld *C. sesamiae*[b]
B. fusca	59	20.7 ± 0.2 b	27	19.9 ± 0.3 ab
S. calamistis	75	20.0 ± 0.1 c	60	19.4 ± 0.1 b
C. partellus	70	21.3 ± 0.2 a	69	20.3 ± 0.2 a

Means within a column followed by the same letter are not significantly different (SNK)
[a]$F = 18.18$; $df = 2,198$; $P = 0.0001$
[b]$F = 8.73$; $df = 2,150$; $P = 0.0003$

Table 4.4. Brood sizes, percentage adult emergence and percentage female progeny of highveld *Cotesia sesamiae* produced on different stemborer hosts.

Host sp.	n	Mean brood size[a]	n	% adult emergence[b]	n	% female progeny[c]
B. fusca	60	44.9 ± 0.1 b	60	89.3 ± 4.7 a	59	66.9 ± 5.0 a
S. calamistis	75	74.7 ± 0.1 a	75	93.9 ± 3.2 a	75	69.2 ± 3.7 a
C. partellus	75	12.3 ± 0.2 c	75	64.4 ± 6.2 b	75	61.0 ± 5.3 a

Means within a column followed by the same letter are not significantly different (SNK)
[a]$F = 60.86$; $df = 2,204$; $P < 0.0001$
[b]$F = 37.59$; $df = 2,204$; $P < 0.0001$
[c]$F = 1.40$; $df = 2,203$; $P = 0.25$

4.3.2 Percentage of hosts successfully parasitized

The percentage of hosts successfully parasitized by the *C. sesamiae* population from the highveld was high, with 74.1, 95.4 and 92.2% of the *B. fusca*, *S. calamistis* and *C. partellus* larvae, respectively, producing cocoons (Table 4.2). When exposed to lowveld *C. sesamiae*, the percentage of *B. fusca* larvae that produced cocoons (35.1%) was significantly lower ($P < 0.001$) than for *S. calamistis* (77.1%) or *C. partellus* (86.3%). Of the *B. fusca* larvae exposed, 55.8% pupated. Larval dissections 3 days after exposure did not show any evidence of egg encapsulation by any of the three borer hosts.

4.3.3 Developmental time

On average, egg-adult development took 19-21 days. However, there were significant differences ($P < 0.001$) in the parasitoid developmental time among the three host species. Development of either of the two *C. sesamiae* populations was shortest on *S. calamistis*, intermediate on *B. fusca* and longest on *C. partellus* (Table 4.3).

4.3.4 Brood sizes, percentage adult emergence and sex ratios

Compared to either *B. fusca* (44.9 adults) or *S. calamistis* (74.7 adults), the highveld *C. sesamiae* population produced the smallest adult progeny broods on *C. partellus* (12.3 adults) (Table 4.4). Percentage adult emergence of the highveld *C. sesamiae* population was also significantly lower on *C. partellus* than on the other two hosts. On the other hand, when exposed to the lowveld *C. sesamiae* population, the three hosts did not differ in parasitoid brood sizes, percentage adult emergence or sex ratios (Table 4.5).

Table 4.5. Brood sizes, percentage adult emergence and percentage adult progeny of lowveld *Cotesia sesamiae* produced on different stemborer hosts.

Host sp.	n	Mean brood size[a]	n	% adult emergence[b]	n	% female progeny[c]
B. fusca	27	42.3 ± 0.3a	27	92.9 ± 7.8 a	27	71.3 ± 8.1 a
S. calamistis	60	41.7 ± 0.1 a	60	93.4 ± 4.6 a	59	76.6 ± 4.8 a
C. partellus	69	26.6 ± 0.1 a	69	86.7 ± 4.6 a	66	76.0 ± 4.8 a

Means within a column followed by the same letter are not significantly different (SNK)
[a]$F = 3.46$; $df = 2,150$; $P = 0.0341$
[b]$F = 3.24$; $df = 2,150$; $P = 0.0418$
[c]$F = 0.34$; $df = 2,146$; $P = 0.7154$

Table 4.6. Mortality of immature parasitoids after emergence from different stemborer hosts.

Host sp.	No. of emerged parasitoids failing to pupate				No. of parasitoids dying inside Cocoons			
	n	Hv *C. sesamiae*[a]	n	Lv *C. sesamiae*[b]	n	Hv *C. sesamiae*[c]	n	Lv *C. sesamiae*[d]
B. fusca	60	1.7± 0.1 b	27	0.4 ± 0.1 b	60	4.1 ± 0.2 a	27	2.7 ± 0.2 a
S. calamistis	75	0.8 ± 0.1 c	60	0.6 ± 0.1 b	75	4.2 ± 0.1 a	60	2.6 ± 0.1 a
C. partellus	75	3.1 ± 0.1 a	69	1.9 ± 0.1 a	75	6.2 ± 0.2 a	69	3.8 ± 0.1 a

Means within a column followed by the same letter are not significantly different (SNK)
[a]$F = 22.63$; $df = 2,204$; $P < 0.0001$
[b]$F = 13.72$; $df = 2,150$; $P < 0.0001$
[c]$F = 2.38$; $df = 2,204$; $P = 0.0951$
[d]$F = 1.54$; $df = 2, 150$; $P = 0.2186$

Table 4.7. Developmental time, brood sizes, percentage adult emergence and sexes of highveld and lowveld *Cotesia sesamiae* crosses on *Sesamia calamistis*.

Cross	Statistical parameters	n	Developmental time [days] (mean ± SE)	n	Brood size (mean ± SE)	n	% adult emergence (mean ± SE)	n	% female progeny (mean ± SE)
Hv♂ x Lv♀		49	19.5 ± 0.1 a	49	62.5 ± 1.1 a	49	96.6 ± 3.2 a	49	64.7 ± 7.2 a
Lv♂ x Hv♀		49	19.4 ± 0.2 a	46	39.2 ± 2.3 b	46	92.3 ± 4.6 b	46	70.8 ± 4.7 a
	t		0.3129		3.1083		2.4553		0.9675
	df		96		93		93		93
	P		0.7550		0.0025		0.0159		0.3358

Means within a column followed by the same letter are not significantly different (t-test, $P \geq 0.05$).

Table 4.8. Mortality of immature parasitoid progeny from highveld and lowveld *Cotesia sesamiae* crosses.

Cross	Statistical parameters	n	Mean no. of emerged parasitoids failing to pupate	Mean no. of parasitoids dying inside cocoons
CsHv♂ x CsLv♀		49	0.3 ± 0.06 b	2.0 ± 0.12 a
CsLv♂ x CsHv♀		46	0.7 ± 0.11 a	2.7 ± 0.13 a
	t		2.1056	1.1494
	df		93	93
	P		0.0379	0.2533

Means within a column followed by the same letter are not significantly different (t-test, $P \geq 0.05$)

4.3.5 Mortality of immature parasitoids

Although there were significant differences ($P < 0.01$) among the three host species in the number of emerged parasitoids that failed to pupate, mortalities were quite low (Table 4.6). For hosts exposed to highveld *C. sesamiae*, the mean number of parasitoid larvae that emerged but died without pupating was highest (3.1) on *C. partellus* and lowest (0.8) on *S. calamistis*. For lowveld *C. sesamiae*, the number of emerged parasitoid larvae that died without pupating ranged from 0.4 (ex *B. fusca*) to 1.9 (ex *C. partellus*). Similarly, the number of parasitoids that died inside cocoons was quite low, with no significant differences ($P > 0.05$) observed among the three stemborer hosts. For highveld *C. sesamiae*, the mean number of emerged parasitoids that died inside cocoons ranged from 4.1 to 6.2 per borer. In comparison, parasitoid mortalities inside cocoons for lowveld *C. sesamiae* ranged from 2.7 to 3.8 per borer.

4.3.6 Mating compatibility

Egg-adult development durations of progeny from the two crosses were not significantly different from each other (Table 4.7). There was a significant difference ($P < 0.05$) between the two crosses in brood size. The highveld ♂ x lowveld ♀ cross resulted in 62.5 adults emerging per borer, whereas the reciprocal cross resulted in 39.2 adults emerging per oviposition. For both crosses, parasitoid mortalities inside cocoons were very low, with adult emergence from either cross being above 90% (Tables 4.7 and 4.8). There was no significant difference ($P > 0.05$) between the two crosses in adult progeny sex ratios. For the highveld ♂ x lowveld ♀ cross, 64.7% of the adults in each brood were females while 70.8% of the adults in broods arising from the lowveld ♂ x highveld ♀ cross were females.

4.4 DISCUSSION

The lowveld *C. sesamiae* population was more discriminatory in host acceptance than its highveld counterpart. While there was high acceptance for *B. fusca* and *S. calamistis* by highveld *C. sesamiae*, the lowveld population accepted far fewer larvae of the two noctuid species. Neither population, on the other hand, accepted *C. partellus*, even though the lowveld population used in the study had been recovered from this borer in the field. The poor acceptance of *C. partellus* for oviposition was quite evident in the host suitability studies where, in most cases, successful hand-stinging of *C. partellus* larvae could only be achieved after dipping caterpillars in *S. calamistis* frass, probably suggesting that host acceptance in this case required olfactory stimuli from both the host plant (Ngi-Song *et al.*, 2000) and the stemborer. This acceptance of *C. partellus* only when dipped in frass produced by *S. calamistis* differs from Ngi-Song and Overholt's (1997) results in Kenya which showed no significant differences in *C. sesamiae* attraction to frass volatiles produced by any particular stemborer species.

The three stemborer species showed differential suitability for the development of highveld and lowveld *C. sesamiae*. While *S. calamistis* was suitable for the development of both *C. sesamiae* populations, each population, however, showed some degree of physiological incompatibility to the stemborer species (*B. fusca* or *C. partellus*) with which it was not normally associated in its ecological zone. Thus, highveld *C. sesamiae* in whose ecological zone *C. partellus* has a low frequency of occurrence showed partial suitability to the borer by way of depressed progeny broods. Similarly, lowveld *C. sesamiae* in whose zone *B. fusca* is almost completely absent showed some degree of physiological incompatibility with the borer by way of a low percentage of stung larvae producing cocoons (35%) and having about 55% of the stung larvae developing to the pupal stage. Going by this argument, it might be possible to infer

that the poor parasitization of *C. partellus* noted at Bushu (refer to Chapter 3) — a middleveld site some 100 km northeast of Harare — could be because this location falls within the area of occurrence of the highveld *C. sesamiae* population.

In general, while physiological incompatibility between *C. partellus* and *C. sesamiae* has not been reported before, the differential suitability of *B. fusca* as a host to various populations of the parasitoid has, however, been noted in other parts of Africa. In Kenya, Ngi-Song *et al.* (1995) reported that a *C. sesamiae* population originating from the coast where *B. fusca* does not occur could not complete development in the noctuid due to egg encapsulation. However, in the present study, there was no evidence of parasitoid egg encapsulation by either *B. fusca* or *C. partellus*. Thus, other host immune responses could have been responsible.

Crosses between highveld and lowveld *C. sesamiae* adults were compatible, producing progeny of mixed sexes. However, compared to the highveld ♂ x lowveld ♀ cross, the reciprocal cross appeared to result in depressed brood sizes. In Kenya, Ngi-Song *et al.* (1998) reported the production of male-only broods when coastal *C. sesamiae* males were mated with females from an inland population. On the reciprocal cross, the resultant broods produced adults of nearly 1:1 sex ratios. Ngi-Song *et al.* (1998) attributed this unidirectional incompatibility to *Wolbachia* bacterial infection present only in adults from the coastal population. While significant differences in host acceptability and suitability shown by the two *C. sesamiae* populations strongly suggest genetic differences between them, the fact that both populations are infected by *Wolbachia* (Ngi-Song and Mochiah, 2001) probably permits reproductive compatibility. *Sesamia calamistis* was the only host used in the mating compatibility studies because it had been shown to be the most suitable for development of both highveld and lowveld *C. sesamiae* populations. The use of either *B. fusca* or *C. partellus* could have

confounded the results because these two species had earlier shown differential suitability for development of the two populations.

Since *C. sesamiae* does not seem to have a seasonal carryover mechanism similar to that of the tachinid larval parasitoid *S. parasitica* (Chinwada and Overholt, 2001; refer to Chapter 3), the results of the present study could, to some extent, point to a simple seasonal carryover mechanism of the parasitoid in Zimbabwe. Firstly, the mating compatibility between lowveld and highveld *C. sesamiae* populations could suggest that the two may belong to one parent population. The advent of the Asian stemborer, *C. partellus*, in the lowveld and the consequent displacement of the native *B. fusca* could then have led to some behavioural and physiological changes in the *C. sesamiae* population resident in the lowveld as it adjusted to utilizing the invader as a host. Secondly, unlike in the highveld and much of the middleveld where it is not possible to grow maize during the coldest months of the year (May-August), there is nearly year-round cultivation of maize at some lowveld locations, and on these, high infestation levels by *C. partellus* have been observed in mid-winter (July). Thirdly, although the occurrence of *C. sesamiae* on winter-grown maize has not yet been studied in Zimbabwe, *C. sesamiae* reportedly remains active throughout the year as long as actively feeding stemborer larvae are present (Kfir, 1988). Thus, at the beginning of every summer season, there could be a net outward migration from some lowveld locations ("ecological islands") to niches temporarily made vacant by the demise of populations of the parasitoid as a result of a long dry season (May-October) and the consequent diapause-induced host unavailability. The ability of the two *C. sesamiae* populations to utilize the principal stemborers *B. fusca* and *C. partellus* as hosts and gregarious behaviour then enable the parasitoid to multiply rapidly and fill up all the niches in which the two species occur.

On its own, however, the survival of *C. sesamiae* in lowveld "ecological islands" is not a satisfactory seasonal carryover mechanism as it would imply that parasitism in the distant highveld would lag behind that in the lowveld—the time lag being the emigration period from the lowveld. Chinwada and Overholt (2001) recorded *C. sesamiae* parasitism on *B. fusca* at Harare Research Station (highveld) at the beginning of the season (November) clearly showing that such parasitism could not have been due to individuals that had migrated from the lowveld. From Harare, the nearest lowveld "ecological islands" are about 230 km away in the north (Zambezi Valley) and 300 km away in the southeast (Save Valley). Moreover, if lowveld "ecological islands" alone were the sources of *C. sesamiae* populations that parasitize stemborers in the highveld, then the two populations of the parasitoid should not have shown significant behavioural and physiological differences during the present study. However, some pockets of the middleveld which are much nearer to the highveld and where off-season maize is also grown, though on a smaller scale compared to the lowveld, could equally serve as "ecological islands" for *C. sesamiae* and thus be major sources of the parasitoid in the highveld and the middleveld. Thus, intensive surveys covering the period from April to maybe January are needed so as to assess the validity of the "ecological islands" theory as a seasonal carryover mechanism of *C. sesamiae*.

Cocoon quiescence is another possible *C. sesamiae* seasonal carryover mechanism that needs to be investigated. In India, Subba Rao *et al.* (1969) reported that some *C. flavipes* cocoons collected from the field in January only gave rise to adults in the third week of March, indicating that part of the parasitoid population could overwinter in the pupal stage. Ullyett (1935) suggested that *C. sesamiae* could also overwinter as cocoons but did not provide supporting data. However, of all the likely carryover mechanisms, cocoon quiescence would be the most difficult to study under laboratory conditions as numerous permutations of

environmental stimuli levels that are likely to lead to quiescence (photoperiod, temperature, humidity) would need to be tried out. The likelihood that such stimuli may need to be perceived indirectly at the endoparasitic stage through a change in host physiology (Godfray, 1994) would further complicate the study. In the field, parasitism of *C. sesamiae* cocoons by *Aphanogmus fijiensis* (Ferrière) (Hymenoptera: Ceraphronidae) has been observed (refer to Chapter 3). Although low, this parasitism may significantly reduce the number of *C. sesamiae* cocoons that may survive up to the next cropping season and thus make it unlikely for cocoon quiescence to be of major importance as a seasonal carryover mechanism.

There is also a possibility that small populations of stemborers that could sustain *C. sesamiae* do survive on wild grasses in some middleveld and highveld valleys. This is supported by the fact that irrigation of winter-grown wheat and barley usually enables grasses growing on field verges to survive throughout the dry season. Although these winter cereals themselves could also be viewed as possible alternative hosts of stemborers and thus assist in the sustenance of *C. sesamiae* during the dry season, the only stem-boring insects that have been recorded as pests on wheat and barley in Zimbabwe are larvae of agromyzid flies.

In conclusion, the results of the present studies showed that highveld and lowveld *C. sesamiae* populations can develop on all three stemborer species. Thus, any one of the three, but preferably *S. calamistis*, could be used as a host during laboratory culturing of either population. The mating compatibility between the two *C. sesamiae* populations and the overlap of hosts immediately poses questions as to whether it would be possible to enable the early "take-off" of the parasitoid in the highveld through inoculative releases of adults reared from *C. partellus* infesting winter-grown irrigated maize in the lowveld. However, such an exercise may not result in an improvement in *B. fusca* seasonal parasitism in the highveld as the results of the present study already suggest that there is a significant degree of physiological incompatibility between

the lowveld *C. sesamiae* population and *B. fusca*. At most, introducing lowveld *C. sesamiae* into the highveld region might even upset the existing parasitoid-host equilibrium due to outbreeding depression when lowveld *C. sesamiae* males mate with highveld females. On the other hand, it is difficult to predict the outcome of a deliberate introduction of highveld *C. sesamiae* into the lowveld. The poor acceptance of *C. partellus* by highveld *C. sesamiae* does not necessarily imply that parasitization of the stemborer by the parasitoid population will not occur as the results of the present study also show that the lowveld population, while not accepting *C. partellus* in the laboratory tests, actually thrives on the stemborer in the field. Probably, only in the middleveld might a deliberate introduction of lowveld *C. sesamiae* result in improved *C. partellus* parasitism. Finally, it is important to note that the stemborers used in the studies were obtained from Kenya and thus could have had genetic characteristics that are different from the original hosts of the parasitoid in Zimbabwe. Thus, host genetic differences, rather than differences between the two parasitoid populations, could have influenced acceptability/suitability of the borers.

CHAPTER 5

Life History Studies Of *Sturmiopsis parasitica*

5.1 INTRODUCTION

The tachinid fly, *Sturmiopsis parasitica* (Curran) is an important larval parasitoid of cereal stemborers in Africa (Harris, 1998). Described from Zimbabwe (Crosskey, 1980), *S. parasitica* is found in abundance within the Harare area where it parasitizes *Busseola fusca* Fuller (Smithers, 1960a; Rose, 1962; Chinwada and Overholt, 2001). The species has also been recorded in West and East Africa on various stemborers including *B. fusca*, *Chilo orichalcociliellus* (Strand), *Chilo partellus* (Swinhoe), *Coniesta ignefusalis* (Hampson), *Eldana saccharina* (Walker), *Sesamia calamistis* Hampson and *Sesamia nonagrioides botanephaga* Tams & Bowden (Mohyuddin and Greathead, 1970; Nagarkatti and Rao, 1975; Harris, 1998).

Using a colony initiated with individuals recovered from stemborers sampled in Ghana, Nagarkatti and Rao (1975) described the life history of *S. parasitica*. Harare, Zimbabwe, is the type locality of *S. parasitica* but apart from field data on parasitism (Smithers, 1960a; Rose, 1962, Chinwada and Overholt, 2001), there has been no attempt to study its biology in the country. Both the West African and Zimbabwean populations of *S. parasitica* occur in regions that are climatically dissimilar, thus making population-specific biological data essential. Clearly, for a species that along with *Cotesia sesamiae* (Cameron) has been suggested as a candidate for re-distribution within Africa (Mohyuddin and Greathead, 1970), the provision of biological data on as many geographic populations of *S. parasitica* as possible is thus of critical importance. This chapter outlines biological studies conducted on

the Zimbabwean population of *S. parasitica* and discusses its potential as a biological control agent.

5.2 MATERIALS AND METHODS

5.2.1 Insects

Third and fourth instar larvae of *B. fusca*, *C. partellus* and *S. calamistis* were used for the experiments. These were reared on artificial diet (Ochieng *et al.*, 1985; Onyango and Ochieng'-Odero, 1994). A laboratory colony of *S. parasitica* was initiated from pupariating maggots that emerged from *B. fusca* larvae and pupae sampled in maize fields in the Harare area. The rearing procedures used were adapted from Nagarkatti and Rao (1975). In brief, parasitoid puparia were held singly in vials until adult emergence. Each freshly emerged female, distinguished by the presence of whitish frons (smoky grey in males) (Nagarkatti and Rao, 1975), was confined singly with 1-3 males (2-3 day old) in a vial. The vial was then shaken under bright light to stimulate mating. Once mating commenced, the mating pair was removed from the other males and placed away from light. However, when the number of newly-emerged females at any one time was at least 10, mating was allowed to take place inside Perspex® cages (11 x 11 x 8 cm). In this case, a few males were introduced into cages in which the females were held and mating pairs removed periodically. New males were introduced to replace the ones that had mated or those that showed no inclination to mate. At the end of each day, males were removed and returned to their own cages. Males that had mated were held separately from unmated ones. Mated males were sometimes used for one additional mating attempt when necessary.

Once mated, females were held in separate cages (12 x 12 x 12 cm). All females mated on the same day were held in one cage. Shredded paper strips were placed inside the cages to provide a resting platform for the adults. Honey (100%) and distilled water were provided in saturated pieces of cotton wool as food for the adults. The honey was changed every five days and water replenished as often as necessary.

5.2.2 Development on different stemborer hosts

The development of *S. parasitica* on different stemborer species was studied using *B. fusca* (non-diapause), *C. partellus* and *S. calamistis*. Eighteen days after mating (Nagarkatti and Rao, 1975), gravid females were dissected and their uteri ruptured in distilled water so as to release the maggots. Using a fine camel hair-brush, active maggots were transferred to the ventral surface of a larva that had previously been wiped clean using cotton wool soaked in distilled water. Host larvae were inoculated using 2 and 4 maggots or an undetermined number transferred in 2 brush-strokes. For each of the three inoculation methods, at least 100 larvae of each species were used. Irrespective of the number of maggots dissected out of each female, maggots from individual females were used to inoculate not more than 20 larvae of each species. Inoculated larvae were then reared individually on artificial diet inside glass vials (2.5 x 7.5 cm) at 25 ± 0.5°C, 65-80% relative humidity and 12:12 (L:D) hour photoperiod.

Larvae were checked daily until pupation, death or parasitoid emergence. Parasitoid puparia were weighed and then held individually inside 12 ml vials for adult emergence. In order to maintain a high humidity environment inside the vials, each puparium rested on a bed of moistened frass. However, as the high humidity environment inside the vials favoured the growth of saprophytic fungi, the surface of each puparium was periodically wiped clean using a

5.2.4 Fecundity and gestation period

The fecundity and gestation period of *S. parasitica* were determined by dissecting uteri of mated female flies. Starting at four days after mating and thereafter at two-day intervals up to day 20, females were dissected to check for active maggots. Four females were dissected at each interval. At each dissection, the number of eggs and active maggots were counted. The number of active maggots as a percentage of the total egg load (eggs + maggots) produced by each female was then determined and plotted against time (days after mating). The number of days after mating when the mean percentage of maggots was at its highest was noted and used as an indication of the gestation period at which dissection should be conducted in order to obtain the optimum number of maggots.

5.2.5 Adult longevity

Adult longevity was determined by holding freshly-emerged unmated females inside 350 ml plastic jars at 25 ± 0.5°C and 65-80% relative humidity until they died. Flies that emerged on the same day were held in one jar. However, only a maximum of five flies were put in one jar. The mouth of each jar was closed using netting material held in place by a rubber band. Shredded paper strips, honey solution and distilled water were provided to the adult flies as previously described.

5.2.6 Relative sizes of adult flies

The relative sizes of *S. parasitica* adults emerging from different host species were compared by measuring wing and hind tibia lengths of female flies. The wings and hind tibia were

mounted on a microscope glass slide and their lengths determined under a binocular microscope equipped with an ocular micrometer. To reduce variability among flies from the same host, only adults resulting from puparia that emerged singly or in groups of two per host were used. Both left and right hind tibia and wings were measured and a mean measurement determined.

5.2.7 Data analysis

Data were subjected to t-test (PROC TTEST) or Analysis of Variance (PROC GLM) (SAS Institute, 1990b) followed by the SNK multiple range test when ANOVAs were significant ($P < 0.05$). Proportions were arcsine-transformed (Sokal and Rohlf, 1981; Fowler *et al.*, 2000) before being subjected to analysis.

5.3 RESULTS

Of the three species inoculated, *S. parasitica* developed only on *B. fusca* and *C. partellus* (Table 5.1). No parasitoids emerged from *S. calamistis*. Dissections of *S. calamistis* larvae made at seven days after inoculation showed that although maggots were still alive, they were ensheathed within thick fatty-like tissue. By the 10^{th} day, however, the ensheathed maggots were dead and had been melanized. For the two hosts in which *S. parasitica* could develop, the levels of parasitism and parasitoid puparia recoveries were dependent on species and inoculation method. Inoculation of *B. fusca* larvae using 2 maggots, 4 maggots and the '2 brush-strokes' method resulted in 40.7, 53.4 and 83.3% parasitism, respectively. In contrast, the percentage of *C. partellus* larvae successfully parasitized from similar inoculations was 5.2, 8.6 and 15.0%, respectively.

Table 5.1. Comparative parasitism of different stemborer species by *Sturmiopsis parasitica.*

Stemborer host	No. of maggots used for inoculation	n	% parasitism at 4 weeks post-inoculation‡	Number of additional larvae ascertained to be parasitized by dissection at 8 weeks post-inoculation	Adjusted total % parasitism
B. fusca	2	91	40.7 (37)	0	40.7
	4	86	51.2 (43)	2	53.4
	'2 brush-strokes'	96	76.0 (73)	7	83.3
C. partellus	2	96	5.2 (5)	0	5.2
	4	93	8.6 (8)	0	8.6
	'2 brush-strokes'	120	15.0 (18)	0	15.0
S. calamistis§	2	48	0 (0)	0	0
	4	45	0 (0)	0	0
	'2 brush-strokes'	44	0 (0)	0	0

‡ Figure in parentheses represents total number of stemborers (larvae and pupae) parasitized

§ Maggots ensheathed in thick fatty-like tissue

Table 5.2. Frequency distribution per host of *Sturmiopsis parasitica* puparia recovered from *Busseola fusca* larvae and pupae.

Host stage	Number of maggots used for inoculation	Number of hosts each yielding given number of puparia						Total no. of puparia recovered
		1	2	3	4		6	
Larva	2	23	4	-	-	-	-	31
	4	18	12	5	4	-	-	73
	'2-brush strokes'	22	30	13	3	1	1	144
Pupa	2	9	1	-	-	-	-	11
	4	4	1	-	-	-	-	6
	'2 brush-strokes'	3	-	-	-	-	-	3
Totals		79	48	18	7	1	1	268

Table 5.3. Frequency distribution per host of *Sturmiopsis parasitica* puparia recovered from *Chilo partellus* larvae and pupae.

Host stage	Number of maggots used for inoculation	Number of hosts each yielding given number of puparia		Total no. of puparia recovered
		1	2	
Larva	2	1	-	1
	4	1	-	1
	'2 brush-strokes'	10	2	14
Pupa	2	4	-	4
	4	7	-	7
	'2-brush-strokes'	6	-	6
Totals		29	2	33

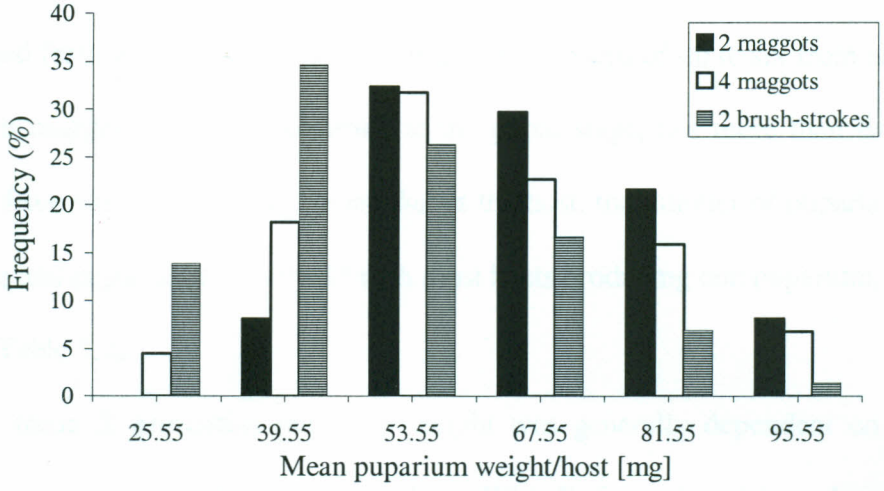


Fig. 5.1. Frequency distribution of weights of *Sturmiopsis parasitica* puparia recovered from *Busseola fusca*.

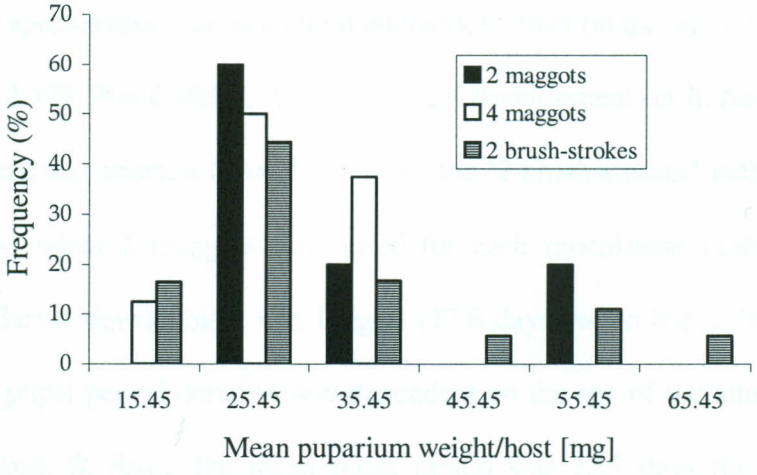


Fig. 5.2. Frequency distribution of weights of *Sturmiopsis parasitica* puparia recovered from *Chilo partellus*.

Parasitoids emerged from both the larval and pupal stages of the host. On *B. fusca*, a total of 144 puparia were recovered when the '2 brush-strokes' inoculation method was used. These puparia were formed from maggots that emerged singly or in groups of up to six from each larva (Table 5.2). When maggot eggression occurred at the pupal stage, not more than two puparia were recovered from each host. With *C. partellus* as the host, the number of puparia recovered from both larvae and pupae totalled only 33 with most hosts producing one puparium, and never more than two (Table 5.3).

The mean *S. parasitica* puparium weight was generally dependent on the number of pupariating maggots emerging from each host. With *B. fusca*, larval inoculations using 2 or 4 maggots resulted in fewer but large-sized puparia being formed. On the other hand, the '2 brush-strokes' method resulted in many but small-sized puparia forming per host (Fig. 5.1). On *C. partellus*, although pupariating maggots emerged mostly singly, the resultant puparia were much smaller compared to those from *B. fusca* (Fig. 5.2).

The species-inoculation method interaction effect on the larval period was significant (F = 9.70; df = 2,178; P = 0.0001). Although larval development on *B. fusca* took 14.2 days overall, development was shortest (13.6 days) when the '2 brush-strokes' method was used and longest (15.3 days) when 2 maggots were used for each inoculation (Table 5.4). However, on *C. partellus*, larval development was longest (17.8 days) when the '2 brush-strokes' method was used. The pupal period duration was dependent on the sex of the adult fly. For parasitoids that emerged from *B. fusca*, the mean pupal period was 13.7 days for males and 15.8 days for females (Table 5.5).

Adults emerged from 77.4 to 88.6% of the puparia recovered from *B. fusca* (Table 5.6). The sex ratio of these adults was almost 1:1. With *C. partellus* as the host, percentage adult emergence ranged from 87.5 to 100%. The male:female sex ratios of adults emerged from

Table 5.4. Larval periods (days) (mean ± SE) of *Sturmiopsis parasitica* developing on *Busseola fusca* and *Chilo partellus* at 25 ± 0.5°C.

Number of maggots used for inoculation	n	*B. fusca*	n	*C. partellus*
2 maggots	37	15.3 ± 0.7 a	5	15.0 ± 1.8 ab
4 maggots	43	14.4 ± 0.6 ab	8	12.1 ± 0.3 b
'2 brush-strokes'	73	13.6 ± 0.3 b	18	17.8 ± 1.1 a
Mean	153	14.2 ± 0.3	31	15.9 ± 0.8
Range		10-34		11-24

Within column means followed by the same letter are not significantly different (SNK).

Table 5.5. Duration of pupal periods (days) of *Sturmiopsis parasitica* emerging from *Busseola fusca* and *Chilo partellus* at 25 ± 0.5°C.

Statistical parameters	*B. fusca*		*C. partellus*	
	Male	Female	Male	Female
n	103	116	15	14
Mean	13.7	15.8	13.5	14.6
Range	12-17	10-20	10-15	13-17
Standard error	0.14	0.13	0.34	0.27
t	10.8183		2.5523	
df	217		27	
P	<0.0001		0.0167	

Table 5.6. Percentage emergence and sexes of *Sturmiopsis parasitica* progeny adults.

Host sp.	Number of maggots used for inoculation	Total number of puparia	Total number of emerged adults	% adult emergence	Sex ratio (M:F)
B. fusca	2	42	36	85.7	1:0.8
	4	79	70	88.6	1:1.2
	'2 brush-strokes'	146	113	77.4	1:1.2
C. partellus	2	5	5	100	1:4
	4	8	7	87.5	1:0.4
	'2 brush-strokes'	19	17	89.5	1:0.9

Table 5.7. Longevity (mean ± SE) of adult *Sturmiopsis parasitica* female flies at 25 ± 0.5°C.

Host sp.	Statistical parameters	n	Longevity [days]
B. fusca		26	28.5 ± 1.50
C. partellus		6	29.0 ± 1.95
	t		0.1638
	df		30
	P		0.8710

Table 5.8. Comparative sizes (mean ± SE) of *Sturmiopsis parasitica* females emerged from *Busseola fusca* and *Chilo partellus.*

Host sp.	Statistical parameters	N	Wing length [mm]	Hind tibia length [mm]
B. fusca		25	6.6 ± 0.13	2.1 ± 0.05
C. partellus		5	5.9 ± 0.34	1.9 ± 0.09
	t		2.1465	2.1047
	df		28	28
	P		0.0406	0.0444

C. partellus were 1:4, 1:0.4 and 1:0.9 for the 2- and 4-maggot and '2 brush-strokes' inoculation methods, respectively (Table 5.6). Unmated adult females lived for about 4 weeks and there were no significant differences ($t = 0.1638$, $P = 0.8710$) in longevity between those that had developed on the two hosts (Table 5.7). However, significant differences ($t = 2.1465$, $P = 0.0406$) in size between the two sets of females were noted (Table 5.8). While females that had developed on *B. fusca* had an average wing length of 6.6 mm, wings of those that had developed on *C. partellus* were shorter (5.9 mm). Hind tibia of flies that had developed on *B. fusca* were also longer than those from *C. partellus*.

When diapausing *B. fusca* larvae were inoculated, the parasitoid larval period was significantly lengthened. Out of 160 larvae that were inoculated on 11 April 2001, no parasitoid emergence occurred within the first six weeks of rearing. One hundred died within the first six weeks without their parasitization status having been ascertained (Table 5.9). When 20 out of the remaining 60 larvae were subsequently transferred to artificial diet and maintained at 25 ± 0.5°C, parasitoids emerged from three larvae at 56 days (6 June), 104 days (24 July) and 136 days (25 August) after inoculation (Table 5.9). Two larvae that had not exhibited signs of parasitization were dissected 150 days after inoculation and found to have live maggots. Of the larvae that were maintained on dry stems at room temperature, parasitoids eventually emerged from seven, starting at 182 days (10 October) and ending 226 days after inoculation (23 November).

The egg maturation period was extended over several days but active maggots were first observed 6 days after mating (DAM) when 7 (0.4% of the total number of eggs) were counted (Table 5.10). The maximum number of active maggots (848) (50.1% of the total number of eggs) was recorded at 12 DAM. Even though there were no significant differences ($P = 0.05$) in the number of eggs that had developed to the active maggot stage from 8 to 20

Table 5.9. Fate of diapausing *Busseola fusca* larvae inoculated with *Sturmiopsis parasitica* maggots and subsequent larval development periods of emerged parasitoid progeny.

Fate	18-26°C (green stems -first 6 weeks)	25.5±0.5°C (artificial diet)	18-26°C (green stems)
No. inoculated	160	(20)	(40)
No. dying during rearing	100	15	19
No. developing to moth stage	0	0	8
No. escaped or unaccounted for	0	0	6
No. confirmed to be parasitized by normal parasitoid emergence	0	3 - 56 days (1p)[a] - 104 days (1p) - 136 days (4p)	7 - 182 days (2p) - 188 days (1p) - 208 days (1p) - 211 days (1p) - 211 days (2p) - 226 days (1p) - 226 days (1p)
No. confirmed to be parasitized by dissection 5 months post-inoculation	-	2 - (2 live maggots) - (3 live maggots)	-

[a] Number of parasitoid puparia/borer in parentheses

Table 5.10. Relative fecundity of *Sturmiopsis parasitica* females dissected at different time intervals†.

Host sp.	Days after mating	Number of eggs/female	Number of active maggots/female‡	% active maggots/female‡
B. fusca	4	1510.0	0	0.0 b
	6	1508.0	7.0 (0-21)	0.4 (0-1.3) b
	8	1434.3	389.8 (305-488)	27.6 (19.2-32.3) ab
	10	1527.5	758.0 (645-893)	49.7 (45.4-57.0) a
	12	1694.3	848.0 (549-1335)	50.1 (34.1-62.4) aA
	14	1615.5	705.8 (467-1031)	44.5 (33.7-66.4) a
	16	1276.3	537.0 (271-849)	45.2 (27.9-69.5) a
	18	1496.3	549.3 (401-688)	38.1 (25.9-56.1)) a
	20	975.8	376.8 (201-679)	37.2 (26.6-44.9) a
C. partellus	12	1289.3	593.8 (327-1053)	49.7 (25.5-83.9) A

† Results are means derived from 4 flies
‡ Range in brackets
Means within a column followed by the same lowercase letter are not significantly different (SNK, P = 0.05)
Means within a column followed by the same uppercase letter are not significantly different (t-test, P = 0.05)

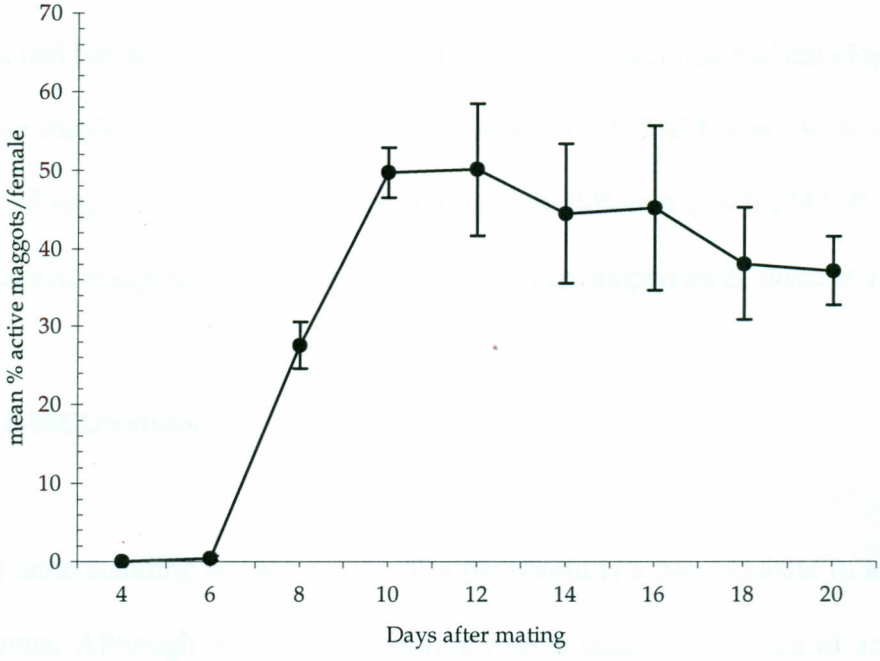


Fig. 5.3. Variation in the percentage (mean ± SE) of active maggots per female *Sturmiopsis parasitica* adult with time.

DAM, the highest proportion was recorded from 10 to 16 DAM. Thereafter, the proportion of maggots that were still alive and active became progressively lower implying that most eggs had matured and hatched before the 18th day (Fig. 5.3). For flies that had developed on *C. partellus*, the mean number of active maggots per female at 12 DAM was 593.8 (49.7% of the total number of eggs). This result was not significantly different (t = 0.1243, P = 0.9052) from the percentage of maggots obtained with flies that had developed on *B. fusca* at 12 DAM.

5.4 DISCUSSION

A good understanding of the biology of a parasitoid is a pre-requisite in a biological control programme. Although *S. parasitica* occurs over a much wider area of sub-Saharan Africa, attacking several species of noctuid and pyralid stemborers (Harris, 1998), reports on its performance on the different host species are very few. Using a population collected in Ghana, Nagarkatti and Rao (1975) gave an account of the biology of *S. parasitica*. At 26°C, they reported a larval period of 12-14 days and a pupal period of 12-19 days. In the present study, the larval and pupal periods recorded at 25 ± 0.5°C are in close agreement with those reported by Nagarkatti and Rao (1975).

Only *B. fusca* and *C. partellus* were suitable hosts for the development of *S. parasitica*. Parasitoid recoveries were, however, much higher on *B. fusca* than on *C. partellus*. *Chilo partellus*, though successfully parasitized in the present study, may only be a partially suitable host due to its smaller size. The large-sized *B. fusca* was more suitable, providing enough food to support the development of more parasitoid immatures, and, hence up to six puparia were recovered from a single host. Chinwada and Overholt (2001) also reported puparia recoveries of one up to six from a single *B. fusca* larva collected at Henderson in

Zimbabwe during the 1995-96 and 1996-97 summer seasons. In the 1999-2000, 2000-01 and 2001-02 recent surveys (refer to Chapter 3), up to eight puparia were recovered from a single larval host.

Sesamia calamistis was an unsuitable host as all maggots got encapsulated. In contrast, Nagarkatti and Rao (1975) reported rearing *S. parasitica* from *E. saccharina* and *Sesamia* spp. in Ghana. However, considering the very low occurrence of *S. calamistis* throughout much of Zimbabwe (Chinwada and Overholt, 2001), it is highly unlikely that maggot encapsulation by *S. calamistis* could explain why recoveries of *S. parasitica* in the country have so far been made only from *B. fusca* (Smithers, 1960a; Rose, 1962; Chinwada and Overholt, 2001). Nonetheless, the observed non-development of *S. parasitica* on *S. calamistis* raises questions as to whether or not, at least in Zimbabwe, the parasitoid has a host-recognition mechanism by which it avoids depositing its maggots on non-*B. fusca* stem tunnel entrance holes. It is highly unlikely that the parasitoid employs such a deliberate discriminatory mechanism as once again the low occurrence of *S. calamistis* within the Harare area ensures that maggot wastage, if any, is negligible.

Parasitoid puparia recoveries were dependent on the stemborer species, inoculation method and host stage (larva or pupa) at which egression of pupariating maggots occurred. More puparia recoveries were made on *B. fusca* than on *C. partellus*. Generally, the larger the number of maggots used for inoculation the better the chances of successful parasitization. Also, for *B. fusca*, more puparia were recovered per host when maggot eggression occurred at the larval as opposed to the pupal stage. However, irrespective of the inoculation method, the resultant weights of puparia recovered from *B. fusca* were dependent on the number of maggots emerging per host. The larger the number of puparia recovered per host the smaller their size and vice versa when only one or two puparia were formed.

From the results, it can be seen that the emergence of a maximum of only two pupariating maggots when parasitoid emergence occurred at the host pupal stage as opposed to six at the larval stage has an important bearing on the rearing of *S. parasitica* in the laboratory. The implication is that wherever practicable, inoculations should be restricted to 3rd and early 4th instars to ensure that *S. parasitica* completes its development before the host pupates. In this manner, more puparia can be recovered from a single host.

Adult female parasitoids that developed on C. *partellus* and *B. fusca* did not differ in their life span. Both sets of flies lived for about four weeks. Significant differences were only noted in their respective sizes, with those that developed on *C. partellus* having shorter wings and hind tibia. Nonetheless, when mated and dissected after a 12-day gestation, adult females that had developed on *C. partellus* were found to be as equally fecund as those that developed on *B. fusca*. However, it can be argued that the longevity data obtained in this study do not have much meaning as only unmated flies were studied. From a point of view of the population dynamics of insect parasitoids, a study of the longevity of mated females gives an indication of how long each can live and thus lay eggs. For males, the same study would have the assumption that the longer a male lives the more females he can inseminate (Jervis and Copland, 1996). In the current study, mated females were not used as it was found that attempts to mate the adults stressed them. Many ended up with broken wings and limbs due to the sometimes vigorous shaking that was required to mate the flies. Ultimately, such physical damage would have resulted in reduced longevity. In retrospect, however, if longevity data had been based on mated flies regardless of the effects of stress and physical damage, their longevity might have better represented natural field situations where longevity is generally expected to be lower, being influenced by various physical and abiotic factors.

One of the problems faced during the course of this study was the inability to know exactly when to dissect mated females in order to obtain the optimum number of maggots for larval inoculation. Although Nagarkatti and Rao (1975) reported a gestation period of 18-19 days, in preliminary studies it was observed that most mated females tended to die before the 18th day. Thus, an experiment was designed with the aim of determining the proportion of eggs that would have developed to the active maggot stage at different time periods during the life span of a mated female. Ultimately, this would give an indication of the dissection date (days after mating) that would result in the optimum number of maggots being realised. In the current study, active maggots were observed starting from the 6th day after mating. There was a rapid rise thereafter followed by a leveling out at 10, 12, 14 and 16 DAM. A sustained decrease at 18 and 20 DAM showed that egg maturation had already been completed and the earliest-formed maggots were starting to die. Thus, rather than allude to a gestation period, it can be concluded that the results of current study showed that 10-16 DAM is the optimum period for dissection in order to recover the highest number of active maggots. This certainly differs with the 18-19 days gestation reported by Nagarkatti and Rao (1975). However, the 537-848 maggots dissected out of each female at 10-16 DAM compare very well with the 500-900 maggots reported by Nagarkatti and Rao (1975) after a gestation of 18-19 days.

Chinwada and Overholt (2001) reported that *S. parasitica* is carried-over from one cropping season to the next in Zimbabwe by synchronizing its larval development with that of diapausing *B. fusca* larvae. However, they were not able to determine the exact duration of this synchronized diapause as their observations were based on field-collected larvae whose parasitization status only became evident at diapause termination. In the present study, the inoculation of already-diapausing larvae was an attempt to show that the physiological state of *B. fusca* larvae at the time of parasitoid ingression or shortly thereafter determined the

duration of development of parasitoid larvae. Still, the study could only give an estimate of the length of the parasitoid larval period inside diapausing hosts as it was based on the inoculation of hosts that were already in diapause. In natural field situations, parasitization by *S. parasitica* would be expected to occur on larvae that will still be actively feeding and thus producing the necessary host-habitat location cues. Although there is no evidence, it would seem unlikely that *S. parasitica* females can locate diapausing larvae in the field, as they would not be actively feeding and thus stimulating the production of volatile signals found to be important for other stemborer larval parasitoids (Mbapila and Overholt, 1997; Ngi-Song and Overholt, 1997).

This study also examined termination of parasitoid diapause. When parasitized diapausing stemborer larvae where transferred to artificial diet and incubated at 25 ± 0.5°C and 65-80% relative humidity, the arrested development appeared to have been interrupted as pupariating maggots emerged starting at 56, then 104 and 136 days after initial inoculation. In contrast, Chinwada and Overholt (2001) reported noting emergence of pupariating maggots some seven months after collecting diapausing larvae and leaving them to terminate diapause without any deliberate manipulation of the environment. The emergence of *S. parasitica* from field-collected diapause-generation *B. fusca* larvae was also reported during the current study (Chapter 3).

Several workers have attributed the arrested development of endoparasitic larval stages to endocrine changes occurring inside host larvae. Lawrence (1986) discussed the host-parasitoid hormonal interactions which result in an obligatory synchronization of the first larval moult of the parasitoid with changes in host ecdysteroid levels. These interactions were explored by Ramadhane *et al.* (1988) who showed that exogenous ecdysteroids that led to diapause termination in the European corn borer, *Ostrinia nubilalis* Hübner, parasitized by the tachinid *Pseudoperichaeta nigrolineata* Walker also led to a resumption of parasitoid

development. Baronio and Sehnal (1980) also reported the close synchronization between the development of first-instar larvae of the tachinid parasitoid *Gonia cinerascens* Rond with its hosts' ecdysteriods levels. In the current study, the provision of an artificial diet to host larvae and warmer temperatures probably triggered a rise in host ecdysteroid levels that were then perceived by the parasitoid as host diapause termination. However, the rate at which ecdysteroid levels rose could have been different among the larvae, hence the emergence of pupariating maggots at different time periods. In contrast, larvae maintained on dry stems at room temperature behaved as if they were in a natural field situation where a rise in host ecdysteroid levels leading to diapause termination only occurs at the onset of the rainy season (October-November) possibly due to a lengthened photoperiod, rising temperature and/or increased humidity. The population of *S. parasitica* found in Ghana could well behave in a manner similar to that of the Zimbabwean population when host larvae diapause. However, the periods of arrested development may not be as noticeable, possibly due to the fact that the hosts with which the parasitoid is associated with in Ghana — *Sesamia* spp. and *E. saccharina* — in contrast to *B. fusca* in Zimbabwe, do not have an obligatory diapause.

In general, this study revealed several important aspects of the biology of *S. parasitica* that could be critical in stemborer biological control programmes. Firstly, the two populations of the species for which some biological data is available seem to show different host preferences. Nagarkatti and Rao (1975) reported collecting the Ghanaian population from *Sesamia* spp. and *E. saccharina*. In addition, they conducted host suitability tests on several Indian stemborers which showed that the tachinid could develop on *Sesamia inferens*, *Chilo partellus*, *C. auricilius*, *C. indicus* and *C. infuscatellus*. Interestingly, there is no information on whether *B. fusca* is a suitable host to the Ghanaian population, even though *B. fusca* does occur there. The current study, though limited in the number of stemborer species

tested, showed that the Zimbabwean population does not develop on *S. calamistis*. *Eldana saccharina* is, however, a suitable host as the South African Sugar Association has, since 2000, been importing *S. parasitica* from Zimbabwe and successfully maintaining a colony on the borer (D.E. Conlong, personal communication). The non-development of the Zimbabwean population on *S. calamistis* as well as its low recovery from *C. partellus* imply that potential release areas must have *B. fusca* as the predominant species. In addition, such areas must have a climate that closely matches that of Harare. Unfortunately, there could be a particular micro-climatic element that is critical as there are several areas in Zimbabwe with a climate and stemborer species composition almost similar to that of Harare, but in which *S. parasitica* has not been found (Chinwada and Overholt, 2001). Also, niches are dynamic in terms of stemborer species composition. In both South Africa and Kenya there is clear evidence showing a competitive displacement of *B. fusca* by *C. partellus* (Kfir *et al.*, 2002).

Secondly, results obtained from the current study showed that egg maturation in *S. parasitica* is extended over several days. This has an important advantage in field situations where low stemborer infestation levels may require the parasitoid to forage for several days. Combined with a long life span and high mobility, a gravid female can live long enough to deposit its full complement of planidia at several stemborer tunnel entrances over a wide area. Ultimately, this enhances the parasitoid's survival chances.

In conclusion, the current study provides new information on the biology of *S. parasitica* in Zimbabwe. However, we still have little insight into why the impact of *S. parasitica* is limited to the Harare area. This parasitoid occurs over a large part of sub-Saharan Africa (Harris, 1998), but its abundance is highly variable. For example, *S. parasitica* has been reported to be abundant in central and southern Tanzania, but not in neighbouring Kenya (Oloo, 1989; Skovgård and Päts, 1996; Songa, 1999) or Uganda

(Matama-Kauma *et al.*, 2001). Redistribution of the Harare population to other areas where *B. fusca* is the dominant stemborer may have potential, but only if it is shown that this population has certain attributes which other populations are lacking. It would seem more likely that there are unknown abiotic or biotic factors which favour this parasitoid in the Harare area. Thus, further studies to elucidate these factors are required. Additionally, it would be interesting to examine the larvipositional behaviour of female flies in the field. Being highly fecund and with an egg maturation period extending over several days, it is clear that a single female distributes its maggots over several borer tunnel entrances. However, it is not known whether or not maggots are distributed in such a way as to minimize inbreeding among offspring adults. Moreover, it would be interesting to see whether *S. parasitica* avoids larviposition on plants infested by the unsuitable host, *S. calamistis*, and/or the partially suitable host, *C. partellus*. If the parasitoid has the ability to discriminate between suitable and unsuitable hosts, then its value as a biocontrol agent will be higher.

CHAPTER 6

Host Suitability Studies of *Cotesia flavipes* in Zimbabwe

6.1 INTRODUCTION

Of the various insect parasitoids associated with gramineous stemborers, the order Hymenoptera by far contains the majority of species that have been introduced in many parts of the world in classical biological control attempts. One species, *Cotesia flavipes* Cameron, has been successfully introduced into more than 40 countries in the tropics and subtropics for classical biological control or as a new association biological control agent against stemborers in the genera *Chilo* and *Diatraea* (Polaszek and Walker, 1991). Until recently, attempts to establish *C. flavipes* in mainland Africa had been unsuccessful (Overholt, 1998). During the period 1968-1972, the Commonwealth Institute of Biological Control (CIBC) (now International Institute of Biological Control) released *C. flavipes* in Kenya, Uganda and Tanzania but there was no evidence of establishment (Omwega *et al.* 1995). The first report of successful establishment of the parasitoid on the mainland, however, came from Kenya after ICIPE conducted releases in the southern coastal region in 1993 (Omwega *et al.*, 1995; Overholt *et al.*, 1997).

Host unsuitability has been cited as one possible explanation for the failure to establish *C. flavipes* in mainland Africa (Overholt, 1998). *Chilo partellus* (Swinhoe) is an introduced species in Africa, having invaded the continent from Asia (Kfir *et al.*, 2002). Throughout its distribution in Asia, *C. partellus* is attacked by *C. flavipes*. Thus, releases of *C. flavipes* in Africa are no more than an attempt to reunite the parasitoid with its old association host. In Zimbabwe, *C. partellus* is the predominant species outside the highveld region (Chinwada *et al.*, 2001). Although *Cotesia sesamiae* (Cameron) is the main larval parasitoid recovered from *B. fusca* and

C. partellus in the country (Chinwada and Overholt, 2001; Chinwada *et al.*, 2001), its impact on the Asian borer is generally low thus justifying the introduction of *C. flavipes*. However, prior to these releases it imperative to obtain information on the suitability of local stemborer species for *C. flavipes* development. The objective of this study was therefore to determine the suitability of the main stemborer species in Zimbabwe — *Busseola fusca* Fuller and *C. partellus* — for development of *C. flavipes*.

6.2 MATERIALS AND METHODS

6.2.1 Stemborer rearing

Two stemborer species, *B. fusca* and *C. partellus* were reared. Initial colonies were set up from larvae and pupae collected at Harare Research Station (*B. fusca*) and Chisumbanje Experiment Station (*C. partellus*). *Sesamia calamistis* Hampson could not be reared due to its low occurrence in the field. *Busseola fusca* larvae were reared individually in plastic vials (4 x 10 cm) and *C. partellus* in groups of 10-20 inside 350 ml plastic jars. Pieces of maize stems and developing cobs were supplied as food for the larvae. The plant material was dissected every two days to inspect larvae for mortality, parasitism or pupation. Pupae present at each checking interval were removed and placed in small wooden cages (30 x 30 x 30 cm) until adult emergence. Emerging moths were transferred to cages (40 x 30 x 60 cm) where 7-9 week old maize stems with intact leaf sheaths and leaves were provided for oviposition. To prevent rapid desiccation, the base of each piece of stem rested on moist cotton wool inside a plastic beaker. Sucrose solution (10%) and distilled water were provided in saturated pieces of cotton wool as food for the moths. Leaves or sheaths were examined each morning for eggs. Egg batches were removed and placed in Petri dishes for hatching. The edges of each

Petri dish were sealed with masking tape in order to prevent newly hatched larvae from escaping.

Upon hatching, larvae were placed inside whorls of 5-6 week old maize plants grown in pots inside a glasshouse. Each pot held 2-3 plants. A camel-hair brush was used to transfer about 10-15 larvae onto a single plant. Ant predation on the young larvae was minimized by applying a light dusting of carbaryl 85 WP around each pot and along the walls of the glasshouse. Larvae were left to feed for 2½-3 weeks after which plants were dissected and larvae taken out for rearing in the laboratory on maize stems. After a further week of rearing in the laboratory, larvae were then used in the experiments.

6.2.2 Host acceptability and suitability studies

The acceptability of *B. fusca* and *C. partellus* was assessed by recording the time to oviposition taken by a one day old mated *C. flavipes* female adult to descend from the top (bottom) of a vial (2.5 x 7.5 cm) inverted over a larva on a flat surface (Ngi-Song *et al.*, 1995). An observation was terminated when the parasitoid stung the larva or after five minutes. The time to oviposition for those females that stung larvae within the five-minute period was recorded. Individual parasitoids and larvae were used only once. Twenty larvae of each host species, replicated four times, were exposed to *C. flavipes*. For each host, the percentage of larvae stung within five minutes was calculated and reported as acceptance.

The suitability of each stemborer species for development of *C. flavipes* was studied by assessing the subsequent development of the parasitoid on each exposed host. Larvae stung during the host acceptance tests above, plus additional ones hand-stung to have a total of at least 100 for each species, were placed individually in plastic vials (4 x 10 cm) at 24-27°C and

55-80% relative humidity and supplied with pieces of maize stems. Three days after exposure, five larvae of each species were randomly selected and dissected to check for encapsulated eggs.

The number of exposed larvae pupating, from which parasitoids emerged, or were still alive 30 days after exposure were recorded. Percentage parasitism, parasitoid larval development period, pupal period, brood size and sex ratio were determined. However, parasitism which was noted within 10 days after exposure was adjudged to be due to *C. sesamiae* as the resultant parasitoid larval period was considered to be too short to have been due to *C. flavipes* parasitization. Previous work showed that some foraging *C. sesamiae* adults would always manage to gain access into the glasshouse and successfully parasitize some of the stemborer larvae being reared on potted maize plants. Considering the biology of *C. sesamiae* (Ullyett, 1935; Mohyuddin, 1971) and the fact that it is very difficult to separate *C. sesamiae* and *C. flavipes* using morphological characters (Kimani-Njogu *et al.*, 1997), the one-week rearing of larvae in the laboratory prior to their exposure, plus the additional 10 days after exposure, was regarded to be a long enough period to eliminate unwanted *C. sesamiae* parasitism and thus ensure that parasitism recorded thereafter would be due to *C. flavipes* only. Thus, effective *C. flavipes* parasitism was the net parasitism calculated after excluding the number of exposed larvae that died and those perceived to have been parasitized by *C. sesamiae*.

Data were subjected to t-test (Proc TTEST, SAS Institute, 1990b). Insect counts and proportions were log-transformed and arcsine square root-transformed, respectively, before being subjected to analysis (Sokal and Rohlf, 1981; Fowler *et al.*, 2000).

6.3 RESULTS

Significantly more *C. partellus* larvae (42.5%) than *B. fusca* (31.3%) were accepted for oviposition by *C. flavipes* ($t = 4.07$, $P < 0.05$) (Table 6.1). Time to parasitoid oviposition was, however, not significantly different ($t = 1.20$, $P = 0.2365$) between the two species. Of the initial number of *B. fusca* and *C. partellus* larvae exposed to *C. flavipes*, about half of them died (Table 6.2). Parasitoid emergence was observed from 6.6% of the *B. fusca* larvae within 10 days after exposure and this was attributed to *C. sesamiae*. In contrast, no parasitoid emergence occurred from *C. partellus* larvae within this period. At greater than 10 days after exposure, parasitoid emergence was noted only on *C. partellus*, where effective *C. flavipes* parasitism was 44.6%. Larval dissections conducted at 3 days after exposure showed that parasitoid eggs had been encapsulated by *B. fusca*. Of the exposed *C. partellus* larvae, 2.2% subsequently pupated while 53.2% were still alive at 30 days after exposure. In the case of *B. fusca*, all the exposed larvae were still alive at 30 days after exposure and no parasitoid emergence was ever recorded on them during the long period of diapause and after diapause termination.

The egg-larval developmental duration of *C. flavipes* on *C. partellus* was 13.8 days and the pupal period 8.1 days (Table 6.3). Overall egg-adult development took 21.9 days. An average of 27.4 adults (70.4% emergence) emerged per host, with 41.3% of them being females.

Table 6.1. Acceptability‡ of *Busseola fusca* and *Chilo partellus* for oviposition by *Cotesia flavipes*.

Species	Statistical parameters	n	Mean % of larvae stung	n	Acceptance time (mins)
B. fusca		80	31.3 ± 2.5 b	25	1.53 ± 0.24 a
C. partellus		80	42.5 ± 1.6 a	34	1.96 ± 0.25 a
	t		4.07		1.20
	df		6		57
	P		0.0066		0.2365

‡ Results are means ± SE.

Means within a column followed by the same letter are not significantly different (t-test, $P < 0.05$).

Table 6.2. Mortality, pupation and parasitism of exposed *Busseola fusca* and *Chilo partellus* larvae.

Species	n	% exposed larvae dying	% parasitism at ≤ 10 days post-exposure	Effective % parasitism‡	Effective % larvae pupating	Effective % larvae still alive 30 days post-exposure
B. fusca	136	49.3	6.6	0.0 (0)*	0.0 (0)*	100 (69)*
C. partellus	158	41.8	0.0	44.6 (41)	2.2 (2)	53.2 (49)

‡ The number of exposed hosts that died and parasitism recorded at ≤ 10 days post-exposure were excluded.

* Number of larvae in parentheses.

Table 6.3. Developmental time, brood size, percentage emergence and sex ratios of adult *Cotesia flavipes* emerging from *Chilo partellus*.

Parameter	n	mean ± SE	Range
Egg-larval period (days)	41	13.8 ± 0.2	12-19
Pupal period (days)	41	8.1 ± 0.1	7-10
Egg-adult period (days)	41	21.9 ± 0.3	20-29
Number of emerged cocoons/female	41	36.9 ± 3.6	5-83
Brood size	41	27.4 ± 3.2	1-69
% adult emergence	41	70.4 ± 3.9	5.9-96.7
% female progeny/female	41	41.3 ± 4.2	0-85.7
Number of parasitoids dying inside cocoons	40	9.7 ± 1.5	1-47

6.4 DISCUSSION

Host incompatibility has been given as one major reason for failure of establishment of the exotic parasitoid *C. flavipes* in mainland Africa (Overholt, 1998). In the current study, both *B. fusca* and *C. partellus* were accepted. However, acceptance for *C. partellus* (42.5%) — an old association host of *C. flavipes* — was unusually low considering the more than 70% acceptance reported by Ngi-Song *et al.* (1995) and Ngi-Song *et al.* (1999).

Cotesia flavipes failed to develop in *B. fusca* due to egg encapsulation. Working in Kenya, Ngi-Song *et al.* (1995) also reported a similar result. In contrast, *C. partellus* was a suitable host and its developmental duration (egg-adult) on *C. partellus* was in agreement with findings by Ngi-Song *et al.* (1995) in Kenya. Despite it being a suitable host, effective *C. partellus* parasitism was very low (44.6%). Rather than indicating that *C. partellus* from Chisumbanje could be a partially suitable host, probably this result and the high larval mortalities that occurred post-exposure (41.8%) were obtained simply because most of the larvae used in the experiment could have been of the 3rd instar. In testing for host age suitability, Ngi-Song *et al.* (1995) reported an effective parasitism of 43.5% and post-exposure mortality of 42.8% when 3rd instar *C. partellus* larvae were used. In contrast, the use of older larvae (4th-6th instar) resulted in high parasitism (78-82%) and low post-exposure mortalities (5-18%). However, it is difficult to explain why there was a high percentage of stung larvae that were still alive and had not produced cocoons at 30 days post-exposure (53.2%). Thus, more studies in which stung larvae are dissected at different time intervals after exposure could clarify whether or not *C. partellus* from Chisumbanje is a partially suitable host for *C. flavipes*.

In general, the non-development of *C. flavipes* in *B. fusca* should not be taken to be a pointer of the expected results from the field after the parasitoid has been released. In Mozambique, Ethiopia and Uganda, *C. flavipes* was recovered from *B. fusca* in the field (Cugala and Omwega, 2001; Getu *et al.*, 2001; Matama-Kauma *et al.,* 2001)). In South Africa, despite reporting failure of establishment, Skoroszewski and van Hamburg (1987) also recovered *C. flavipes* from *B. fusca* during the season of release. While the reported recoveries of *C. flavipes* from *B. fusca* in Mozambique, Ethiopia, Uganda and South Africa differ from observations made in Kenya (Overholt, 1998), Kfir (2001) pointed out that such differences might serve as an indication that different regions of the continent may have different biotypes of *B. fusca*. Thus, these observations from other parts of Africa and the results of the current study underscore the importance of including as many local populations of *B. fusca* and *C. partellus* as possible in host suitability studies and then validating laboratory results with fieldwork.

In conclusion, results of the current study show that *C. partellus* is a suitable host for *C. flavipes* and can be released in the southeastern lowveld and other *C. partellus* "hotpots" in Zimbabwe. Although surveys are yet to be conducted to determine the fate of a preliminary *C. flavipes* release conducted in 1999 (Chinwada *et al.* 2001), the apparent absence or very low impact of the indigenous *C. sesamiae* at some of the *C. partellus* "hotspots" (refer to Chapter 3) highlight the need to release the exotic parasitoid in the country. At the moment, *C. flavipes* is now established in neighbouring Mozambique (Cugala and Omwega, 2001) and whether or not more releases of *C. flavipes* are conducted in the country, there is a strong possibility that the parasitoid could eventually spread from Mozambique into Zimbabwe. In Ethiopia, *C. flavipes* which now accounts for about two-thirds of total stemborer parasitism (Getu *et al.* 2001), was never released in the country. It is speculated that the parasitoid invaded

Ethiopia from Somalia where it was released in 1997 (Overholt, 1998). In Tanzania, it also believed that recoveries of *C. flavipes* which have been made in areas bordering Kenya could have occurred due to the parasitoid spreading from the former where actual releases had been conducted and establishment confirmed much earlier (Omwega *et al.*, 1997; Nsami *et al.*, 2001).

CHAPTER 7

General Discussion, Conclusions and Recommendations

7.1 GENERAL DISCUSSION

Maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* [L.] Moench) are staple food crops in Zimbabwe and attack by Lepidopteran stemborers is among some of the most important biotic constraints limiting potentially harvestable yields in these crops. *Busseola fusca* Fuller, *Chilo partellus* (Swinhoe) and *Sesamia calamistis* Hampson were the three stemborer species recorded attacking maize and sorghum in the country. Their distribution, abundance, percentage composition and interactions with natural enemies within the different ecological zones are discussed in Chapter 3. The seasonal occurrence of the larval parasitoids *Cotesia sesamiae* (Cameron) and *Sturmiopsis parasitica* (Curran) on the highveld (Harare area) is also described in Chapter 3. Studies to investigate the relative suitability of *B. fusca*, *C. partellus* and *S. calamistis* for development of two local populations of *C. sesamiae* (highveld versus lowveld), their mating compatibility and implications for stemborer control are outlined in Chapter 4. Chapter 5 describes laboratory studies which were conducted on *S. parasitica* in order to give a better understanding of its biology. Lastly, Chapter 6 describes host suitability studies conducted on the exotic parasitoid *Cotesia flavipes* Cameron using local populations of *B. fusca* and *C. partellus*, discusses implications of the results and assesses the need to introduce the parasitoid.

Based on the frequencies of occurrence at each of the various study sites, *C. partellus* was the most abundant and widely distributed stemborer species. It was predominant in both the lowveld (< 600 m) and the middleveld (600-1200 m). *Busseola fusca* was the second most abundant species but predominated only in the highveld (> 1200 m). Although *S. calamistis*

appeared to show a preference for the highveld, its overall frequency of occurrence was very low overall and thus, compared to the other two species, seems to be of minor economic importance.

Several natural enemies including larval and pupal parasitoids, an entomogenous nematode and two hyperparasitoid species were recorded in association with stemborers in Zimbabwe. *Cotesia sesamiae* was the most widely occurring stemborer larval parasitoid followed by *S. parasitica*. The latter was, however, only confined within the Harare area (highveld) where it parasitized *B. fusca*. A study of the seasonal fluctuations in *B. fusca* parasitism by the two parasitoids showed that parasitism by *S. parasitica* predominated for about the first half of the season (December-February), with peak parasitism being attained between end of January and mid-February. Thereafter *S. parasitica* parasitism declined steeply such that by the end of March the parasitoid could no longer be recovered from the field. In contrast, *C. sesamiae* was generally active throughout much of the season, with parasitism fluctuating below that of *S. parasitica* for the first half of the season before attaining a peak soon after the latter's parasitism had declined.

Of all the parasitoids recorded, only *S. parasitica* had a clear and easily verifiable seasonal carryover mechanism. The tachinid overwintered in diapausing *B. fusca* larvae from which it emerged in October-December when larvae terminated diapause and resumed development. The seasonal carryover mechanism of *C. sesamiae* could not be identified. However, cocoon quiescence and/or survival as slowly developing endoparasitic larval stages inside diapausing hosts are some of its probable seasonal carryover mechanisms.

Although *C. sesamiae* had a much wider distribution compared to other parasitoids, it apparently was not recorded at the lowveld site of Muzarabani. This result was surprising given the ease with which it was recovered from Birchenough — another lowveld site —

where a much smaller number of *C. partellus* larvae were sampled compared to Muzarabani. This result and the almost complete absence of the parasitoid at the middleveld site of Bushu point to the need to consider introducing *C. flavipes* in order to improve *C. partellus* natural control.

Laboratory studies showed that the lowveld population of *C. sesamiae* accepted far fewer *B. fusca* and *S. calamistis* larvae for oviposition than its highveld counterpart. Although both populations could develop on *C. partellus*, neither accepted the species for oviposition. Probably this low acceptance of *C. partellus* is further evidence to show that the association between *C. sesamiae* and the stemborer is new. The three stemborer species also showed differential suitability for the development of highveld and lowveld *C. sesamiae*. While all three were highly suitable for development of highveld *C. sesamiae*, *B. fusca* was partially suitable for the development of the lowveld population. However, egg encapsulation was not evident suggesting that the observed partial suitability could be due to other host immune responses. Crosses between highveld and lowveld *C. sesamiae* adults were compatible, producing progeny of mixed sexes. However, the lowveld ♂ x highveld ♀ cross resulted in depressed brood sizes compared to the reciprocal cross.

Based on the results of the host suitability and mating compatibility studies, it is possible to conclude that one of the seasonal carryover mechanisms of *C. sesamiae* in Zimbabwe could be just a simple sustenance of the parasitoid on non-diapause *C. partellus* larvae in some lowveld locations ("ecological islands") during the coldest months (May-August) when it is not possible to grow maize in the cooler highveld and middleveld. Thus, every year once the winter season is over, there could be an outward migration of *C. sesamiae* from these "ecological islands" to other niches where populations of the parasitoid would have died out at the end of each cropping season due to unavailability of host stemborers through diapause.

However, on its own the yearly sustenance of *C. sesamiae* in "ecological islands" and outward migration to fill up "empty" niches is not a satisfactory seasonal carryover mechanism. This is because *C. sesamiae* has been recovered in the highveld at the beginning of the season (November) showing that its presence so early in the season could only mean that it somehow overwintered there. Furthermore, the significant degree of physiological incompatibility between lowveld *C. sesamiae* and *B. fusca* already shown during the host suitability studies suggests that this carryover mechanism may very likely not apply to the highveld region.

Laboratory studies showed that the most suitable host for development of *S. parasitica* was *B. fusca*. *Chilo partellus* was partially suitable probably due to its much smaller size. *Sesamia calamistis*, on the other hand, was an unsuitable host due to encapsulation of maggots. The development of *S. parasitica* in non-diapause *B. fusca* larvae largely corroborated results reported from earlier life history studies of the tachinid conducted in India using flies collected in Ghana. The prolonged larval development period of the parasitoid after deliberate inoculation of diapausing hosts demonstrated that the seasonal carryover of *S. parasitica* observed in Zimbabwe occurs as a result of parasitization of diapause-state larvae. Thus, it is the state of host larvae, diapause or non-diapause, which determines the ultimate duration of the larval period of *S. parasitica*. In addition to differences in the suitability of African stemborers (both indigenous and introduced) to development of *S. parasitica*, the life history studies conducted showed that there could be some fundamental biological differences between the different populations of the tachinid in Africa. Among others, studies on larvipositional behaviour of females in the field are needed in order to determine the biological control potential of the *S. parasitica* population occurring in Zimbabwe.

Finally, studies conducted in Zimbabwe to determine the suitability of local populations of *B. fusca* and *C. partellus* for development of *C. flavipes* showed that only the latter was a

suitable host. Although the results appeared to show that there was some degree of physiological incompatibility between the parasitoid and *C. partellus*, the apparent absence or very low impact of the indigenous *C. sesamiae* in some of the *C. partellus* "hotspots", highlighted the need to release *C. flavipes* in the country.

7.2 GENERAL CONCLUSIONS

Several conclusions can be drawn from the results of the current study. Firstly, *B. fusca* and *C. partellus* are the only stemborer species of economic importance in Zimbabwe. While *B. fusca* is clearly predominant in the highveld, *C. partellus* is the most damaging stemborer in the middleveld and lowveld. Secondly, the most important *B. fusca* natural mortality factors in the Harare area (highveld) appear to be the larval parasitoids *C. sesamiae* and *S. parasitica*, the pupal parasitoid *P. nigromaculatus* and an entomogenous nematode *Hexamermis* sp. Outside the highveld, *C. partellus* parasitism was mainly due to *C. sesamiae*, the egg-larval parasitoid *C. curvimaculatus* and the pupal parasitoid *D. busseolae.* An analysis of the fluctuations in *B fusca* seasonal parasitism patterns by *C. sesamiae* and *S. parasitica* in the Harare area showed that *S. parasitica*'s importance as a parasitoid is mainly restricted to first-generation larvae. Second-generation larvae are mainly utilized for seasonal carryover. The seasonal carryover mechanism of *C. sesamiae*, on the other hand, could not be identified but likely mechanisms that warrant further study are cocoon quiescence and survival in "ecological islands". Thirdly, the impact of *C. sesamiae* at various non-highveld locations differed significantly. The apparent absence of the parasitoid at Muzarabani (lowveld) and an almost complete absence at Bushu (middleveld) probably indicate that there are niches in Zimbabwe where the invasive borer *C. partellus* is poorly parasitized. Life

history studies of *S. parasitica* showed that *B. fusca* is the most suitable host while *C. partellus* is partially suitable. *Sesamia calamistis* is totally unsuitable because of maggot encapsulation. Thus, if the *S. parasitica* population/biotype from Zimbabwe is ever to be considered as a stemborer classical biological control agent, release locations should ideally be those in which *B. fusca* is the predominant species. Host suitability studies involving a *C. sesamiae* population from the highveld (Harare) and another from the lowveld (Chisumbanje) and the stemborers *B. fusca*, *C partellus* and *S. calamistis* revealed that there is some degree of physiological incompatibility between the highveld population and *C. partellus* and the lowveld population and *B. fusca*. Evidence of significant genetic differences between the two populations was shown by depressed brood sizes when lowveld *C. sesamiae* males were mated with highveld females. These results, although showing that there could actually be some degree of outbreeding between the two populations, may imply that an improvement in *C. partellus* parasitism in the middleveld might occur following a deliberate introduction of *C. sesamiae* from the lowveld. Lastly, *C. partellus* is suitable for development of *C. flavipes* and its introduction into Zimbabwe should be considered.

7.3 RECOMMENDATIONS

1. Stemborer and natural enemy surveys, covering cultivated and potential wild hosts of stemborers during the summer and the dry seasons, need to be extended to cover the whole country.
2. The occurrence of stemborers and their natural enemies in the dry season should be studied, particularly with the view of determining which natural enemies are active throughout the year and whose activity could be enhanced.

3. The biology and seasonal occurrence of the pupal parasitoid *P. nigromaculatus* should be studied.
4. The larvipositional behaviour of *S. parasitica* needs to be studied so as to determine the potential number of host larvae each female can parasitize in the field and also to determine if the parasitoid has a mechanism by which it can discriminate between suitable and unsuitable hosts. If it has such a discriminatory mechanism then its value as a biological control agent would be much greater.
5. Limited field trials need to be conducted to determine the possibility of redistributing *S. parasitica* within the highveld where *B. fusca* is the dominant stemborer species. This might present an opportunity to determine why the parasitoid seems to be confined to the Harare area while its host, *B. fusca*, has a much wider distribution within the highveld.
6. The possible seasonal carryover of *C. sesamiae* as quiescent cocoons during the winter season or slowly-developing endoparasitic larval stages inside diapausing hosts need to be studied.
7. More host acceptance and suitability studies of *C. flavipes* using as many local populations of stemborers as possible should be conducted.
8. Releases of *C. flavipes* need to be conducted throughout the lowveld and parts of the middleveld where *C. partellus* is the predominant stemborer species.

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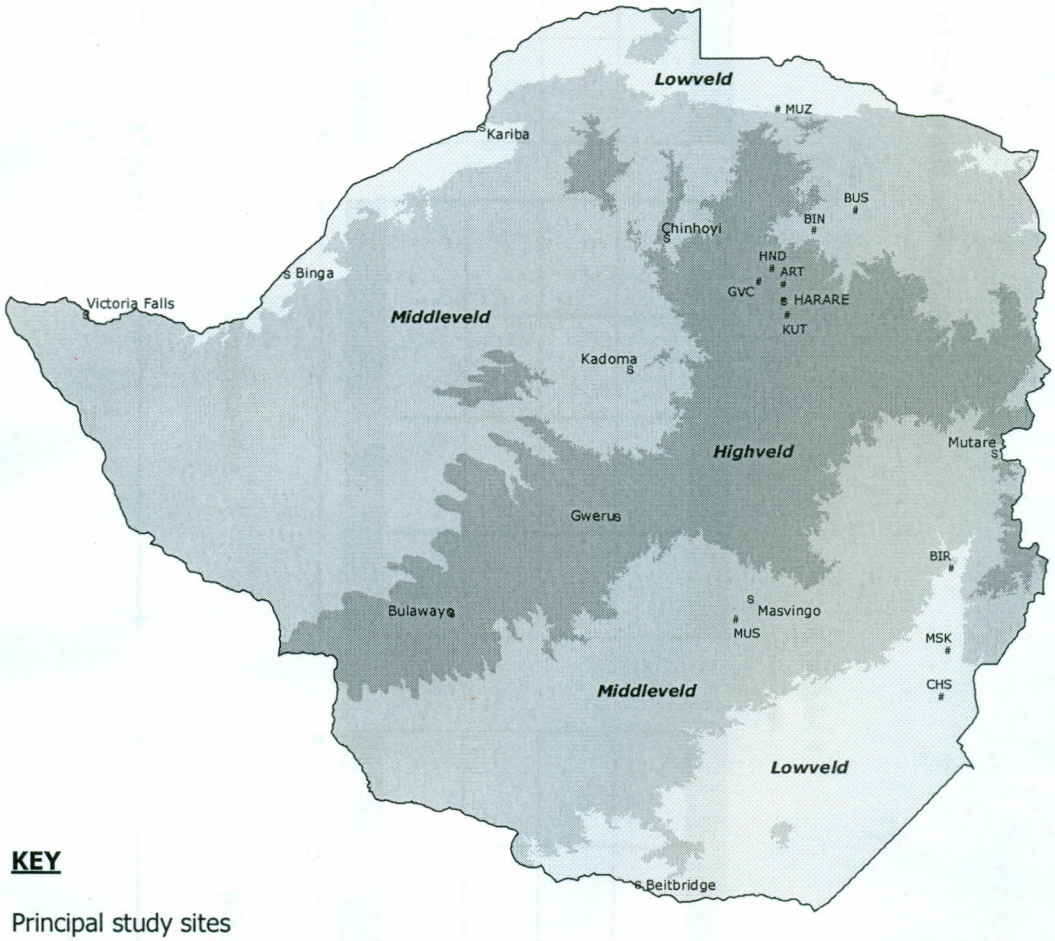
APPENDICES

Appendix 1. Map of Zimbabwe showing the relative locations of the various study sites within the different ecological zones.



KEY

Principal study sites

HND, Henderson Research Station
CHS, Chisumbanje Experiment Station

General survey sites

Harare area (highveld)

ART, Agricultural Research Trust Farm; **GVC**, Gwebi Variety Testing Centre; **HRE**, Harare Research Station; **KUT**, Kutsaga Research Station

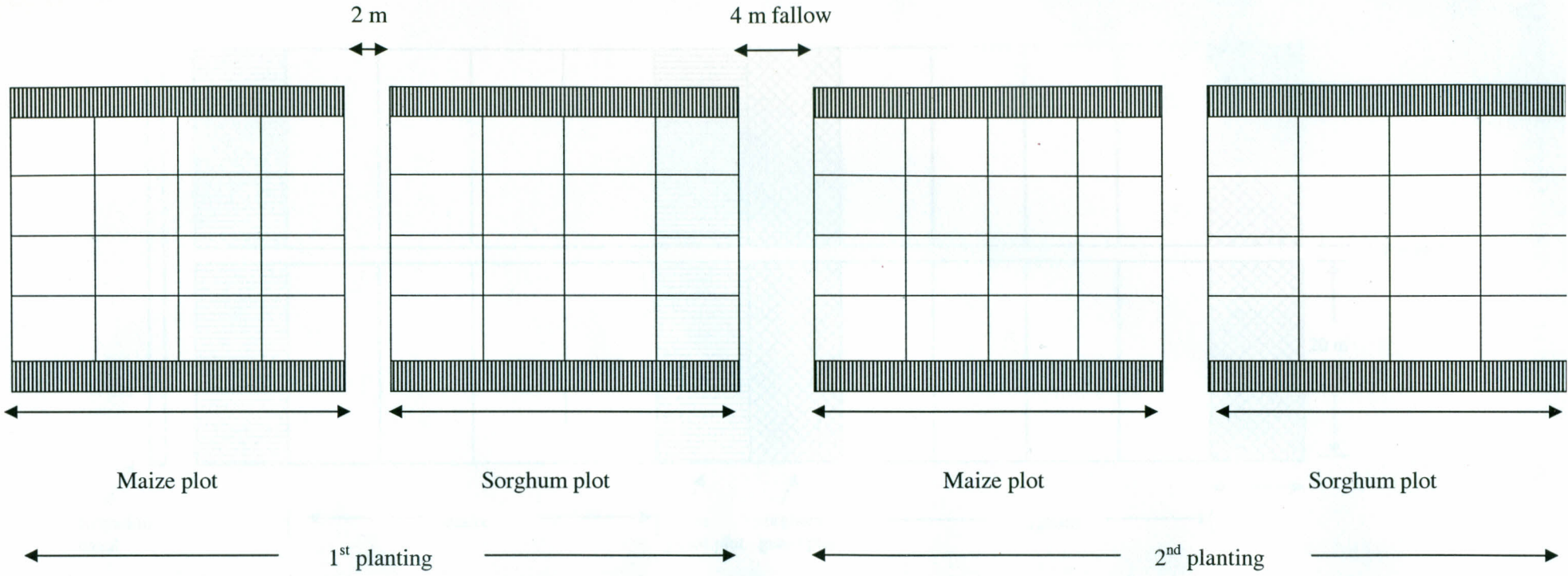
Non-highveld

BIN, Bindura; **BIR**, Birchenough; **BUS**, Bushu
MUS, Mushandike; **MSK**, Musikavanhu; **MUZ**, Muzarabani

Ecological zones

Highveld: above 1200 m; **Middleveld**: 600-1200 m; **Lowveld**: below 600 m

Appendix 2. Layout of trial plots at Henderson



Appendix 2. Layout of trial plots at Chisumbanje