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DIVERSITY AND ECOLOGICAL PREFERENCE OF PARASITOIDS ASSOCIATED WITH LEPIDOPTERAN STEM BORERS IN KENYA

By

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DECLARATION

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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DEDICATION

To my beloved mother, Adama Hena. God bless you for all that you have been through.

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ABSTRACT

Field surveys were carried out from 2005 to 2007 to assess parasitoid species diversity and stemborer parasitism in cultivated and natural habitats in four agroecological zones in Kenya. To increase the chances of collecting stemborer parasitoids, random sampling was employed in cultivated habitats, while both random and non-random samplings were applied in natural habitats. During this study, 7443 and 3676 stemborers were collected from cultivated and natural habitats, respectively. A total of 33 parasitoid species were recorded, of which 18 species were recovered from 6 stemborer species feeding on cereal crops, while 27 species were recovered from 21 stemborer species feeding on 19 wild host plant species. The most common parasitoid species in cultivated habitats were *Cotesia flavipes* (Hymenoptera: Braconidae), *C. sesamiae* (Hymenoptera: Braconidae), *Pediobius furvus* (Hymenoptera: Bethylidae) and *Siphona* sp. (Diptera: Tachinidae). In natural habitats, *Siphona* sp. was the most common. Parasitoid species diversity was significantly higher in natural than in cultivated habitats. Most of the parasitoid species recovered from cultivated habitats were also found in natural habitats. Natural habitats surrounding cereal crops appeared to serve as refugia for sustaining the diversity of stemborer parasitoids in adjacent cereal fields. Given that parasitoid diversity was higher in natural habitats with more diverse plant communities, but parasitoid abundance was higher in cultivated habitats, this study provided partial support for the 'natural enemy' hypothesis. Across agroecological zones, stemborer parasitism was positively dependent on parasitoid species richness and abundance during different seasons in both cultivated and natural habitats. Rainfall had a significant negative effect on parasitoid abundance as well as stemborer parasitism in both cultivated and natural habitats. The negative relationship between parasitism and temperature in natural habitats only, suggested greater sensitivity of parasitoids to extreme temperatures in natural habitats. Across seasons, stemborer densities were generally higher on maize and sorghum in cultivated habitats than on wild host plants in natural habitats. Stemborer parasitism rates were generally low (<15.00%) in both cultivated and natural habitats. Neither larval nor pupal parasitism differed significantly between seasons in natural habitats. *Cotesia sesamiae* was found in Kakamega and Suam in the Western and Rift Valley regions, respectively, where *Busseola fusca* (Lepidoptera: Noctuidae) predominates. By contrast, *C. flavipes* was found in Mtito Andei and Muhaka in the Eastern and Coastal regions, respectively, where *Chilo partellus* (Lepidoptera: Pyralidae) predominates. There was no indication of host plant and stemborer species specificity by *C. sesamiae*, as its host ranges varied with both habitat type and locality. Conversely, *C. flavipes* exhibited a high level of specificity to its target host *C. partellus* on maize and sorghum in cultivated habitats and on *S. arundinaceum* in natural habitats. Of the two *Cotesia* species, natural habitats served as a reservoir for *C. flavipes* only, because these habitats sustained some of the individuals on *C. partellus* during both rainy and dry seasons. This was however not applicable to *C. sesamiae*, as its cereal stemborer hosts *B. fusca* and *Sesamia calamistis* (Lepidoptera: Noctuidae) were scarce in wild host plants.

CHAPTER ONE

GENERAL INTRODUCTION

1.1 Background

Diverse natural systems generally support more complex food webs, with a network of mutualistic and antagonistic interactions among community members, allowing for many alternative paths of energy and material flow through it than in modified agricultural systems (Altieri and Nicholls, 2004; Landis *et al.*, 2005; Tylianakis *et al.*, 2007). These natural systems are often more stable and less subject to fluctuations in populations of destructive herbivores as they exhibit higher resistance (i.e., the ability to avoid or withstand disturbances) and resilience (i.e., the ability to recover following a disturbances) resulting from natural control (Altieri and Nicholls, 2004; Nicholls and Altieri, 2004). On the contrary, the simplification of agricultural landscapes mainly through the practice of monoculture, usually lead to a decrease in natural enemy diversity and activities (Dempster and Coaker, 1974; Landis and Haas, 1992; Barbosa, 1998). Consequently, agricultural landscapes generally lack stability and insect pest outbreaks are more prevalent (Nicholls and Altieri, 2004).

Multitrophic interactions among host plants, herbivores and natural enemies are complex and unpredictable in nature (Andow, 1991; Altieri, 2002; Altieri and Nicholls, 2004). Although negative or indifferent responses may result, diversified landscapes hold more potential for the conservation of agroecosystem biodiversity and the sustenance of pest control functions (Russel, 1989; Altieri, 2002; Altieri and Nicholls, 2004; Duffy *et al.*, 2007). Risch *et al.* (1983), reviewed 150 agroecosystem diversification studies, covering 198 herbivore species. They found that 53% of the herbivore species were less abundant in more diversified systems, 18% were more abundant in diversified systems, 20% showed a variable (inconsistent results) response and 9% showed no difference. Bianchi *et al.* (2006) reported that, out of 24 landscape composition studies, 74% of them showed that landscape complexity enhanced natural enemy populations. Likewise, out of ten biodiversity studies on natural pest control, 45% of the cases reported decreased pest pressures in complex landscapes.

The importance of natural habitats in providing prerequisites to parasitoids has long been recognized (Landis *et al.*, 2000, 2005; Bianchi *et al.*, 2006). Adult food such as pollen and nectar provided by non-crop vegetation have been reported to increase the longevity/fecundity (Costamagna and Landis, 2004; Lee *et al.*, 2004), abundance (Landis and Haas, 1992), searching efficiency (Gurr *et al.*, 1998), parasitism rates (Baggen and Gurr, 1998; Tylianakis *et al.*, 2004), dispersal (Freeman Long *et al.*, 1998; Nicholls *et al.*, 2001), distribution (Doutt and Nakata, 1973; Girma *et al.*, 2000; Landis *et al.*, 2005) and diversity of parasitoids (Powell, 1986; Dennis and Fry, 1992; Landis *et al.*, 2005). Extra-field vegetation also habour alternative hosts for parasitoids (Landis and Menalled, 1998), thus contributing to their perpetuation within the ecosystem (Maier, 1981; Bianchi and van der Werf, 2004). Additionally, extra-field habitats provide more moderate microclimate for parasitoids to survive harsh temperatures than inside fields, thereby positively influencing the abundance and diversity of parasitoids (Forman and Baudry, 1984; Landis *et al.*, 2000, 2005; Gurr *et al.*, 2003). The diversity of natural habitats within agroecosystems therefore contributes to stable pest systems by supporting greater parasitoid diversity and activities in adjacent crop fields (Risch *et al.*, 1983; Powell, 1986; Dennis and Fry, 1992; Landis *et al.*, 2005; Bianchi *et al.*, 2006). In view of this, it is essential that pest management strategies aimed at enhancing parasitoid efficiency be ecologically based. As such, there is need to understand the beneficial effects of agroecosystem biodiversity, and the various multitrophic interactions among organisms of different tropnhic levels on parasitoid diversity and efficiency (Altieri and Nicholls, 2000, 2004; Barbosa, 1998; Landis *et al.*, 2000, 2005).

1.2 Problem statement

In sub-Saharan Africa, the bulk of cereal crops such as maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) are mainly grown at subsistence level by resource-poor farmers, usually on small farms surrounded by patches of natural habitats that habour wild host plants of stem borers (Polaszek and Khan, 1998). Parasitoids as important antagonists attack different developmental stages of stem borer pests, thereby contributing to their overall population regulation (Bonhof *et al.*, 1997; Overholt, 1998). Khan *et al.* (1997), Schulthess *et al.* (1997) and Bonhof *et al.* (2001) all argued that natural habitats adjacent to cultivated cereals provide refuge for parasitoids to perpetuate their populations across seasons. Unfortunately, little or no data exist to prove the role of natural habitats on stem borer parasitoid diversity and parasitism rates in the cereal agroecosystem.

Although stem borer parasitoid diversity has been extensively studied on cultivated cereals in Kenya (Mohyuddin and Greathead, 1970; Bonhof *et al.*, 1997; Zhou *et al.*, 2003), very scanty details exist for wild host plants (Khan *et al.*, 1997a; Songa *et al.*, 2002). For both cultivated and natural habitats, information on factors that affect parasitoid species diversity, abundance and stem borer parasitism are lacking. There is also speculation that the impact of parasitism is much greater on stem borer populations residing in wild grass communities than on populations residing in cultivated habitats (Conlong, 1994; Overholt, 1998). However, no empirical evidence exists to prove this fact. Since parasitoids not only develop and function in a multitrophic context, but also in different habitats, it is essential to understand their diversity and impact on stem borer pest regulation in both cultivated and natural habitats.

The two main larval parasitoids of cereal stem borer pests in Kenya are *Cotesia sesamiae* (Cameron) and *C. flavipes* Cameron (Overholt, 1998; Zhou *et al.*, 2003). Whereas, *C. sesamiae* is indigenous to Africa, *C. flavipes*, a native of Asia, was released in Kenya in 1993 for classical control of the invasive *Chilo partellus* (Swinhoe), a major pest of cereal crops in the Coastal region (Overholt *et al.*, 1994b). For both *Cotesia* species, information on their geographic range, host plant and/or stem borer ranges/specificity and parasitism exists to an extent (i.e., mainly available for the Coastal region, but very scanty details for other ecological regions in Kenya) for cultivated habitats, but is almost unavailable for natural habitats. Furthermore, information is lacking on the role of natural habitats as a reservoir for these *Cotesia* species, especially during the non-cropping season.

1.3 Justification

Intensive agriculture often results in diminished or modified biodiversity through the loss of natural habitats of associated species of plants and animals (Bianchi *et al*., 2006). It is no longer acceptable to modify landscapes solely for the purpose of increasing cultivated areas (Tscharntke *et al*., 2005). Therefore, ecological perspective must be incorporated into crop production planning to ensure sustainable management of natural resources in agricultural systems (Altieri, 2002; Duffy *et al*., 2007; Lindenmayer *et al*., 2007). Understanding how evolutionary, ecological and socio-economic processes drive biodiversity changes and how knowledge of these changes must be incorporated into crop production planning remain a main goal for the future (Altieri, 2002; Gurr *et al*., 2003). However, achieving this in the cereal agroecosystem requires thorough understanding of lepidopteran stem borers and their natural enemies (predators and parasitoids) or in the context of both cultivated and natural habitats. Hence, there is need to establish the diversity of stem borer parasitoids in both cultivated and natural habitats, as well as among various stem borers and host plants in Kenya. In addition, it is essential to provide information on biotic and abiotic factors that affect stem borer parasitoid species diversity, abundance and effectiveness in cultivated and natural habitats. Moreover, information on parasitoid species diversity and their multitrophic interactions in both cultivated and natural habitats may serve as a baseline for future assessment of the effects of biodiversity changes on stem borer parasitoids. Detailed knowledge of host plant and stem borer ranges of parasitoids could help identify important host plant and alternative stem borer species that habour high parasitoid diversity or abundance in natural habitats for utilization in habitat management. Furthermore, the enhancement of parasitoid function (parasitism) requires thorough understanding of their population dynamics and inter-relationships with host plants and stem borers, as well as factors that affect these inter-relationships. Ultimately, the results of such a study should increase our understanding of the role of natural habitats as refugia or reservoir for stem borer parasitoids during either or both rainy and dry seasons.

1.4 Research questions

a) Does stem borer parasitoid species diversity or parasitoid host ranges (stem borers and host plants) differ with habitat type?

b) What are the biotic and abiotic factors that influence parasitoid diversity/abundance and stem borer parasitism in cultivated and natural habitats?

c) Does the impact of stem borer parasitism differ with habitat type?

d) Do natural habitats serve as refugia for *C. sesamiae* and *C. flavipes* during different seasons?

1.5 Hypotheses

a) Species diversity or host ranges of stem borer parasitoids are not significantly different in cultivated and natural habitats.

b) Biotic and abiotic factors do not affect the species richness, abundance and parasitism of stem borer parasitoids.

c) Stem borer parasitism in cultivated and natural habitats are not significantly different.

d) Natural habitats do not serve as a reservoir for *C. sesamiae* and *C. flavipes* during different seasons.

1.6 Objectives

1.6.1 General objective

To investigate the species diversity and impact (parasitism) of stem borer parasitoids in cultivated and natural habitats in Kenya.

1.6.2 Specific objectives

a) To determine the species diversity and host ranges (stem borers and host plants) of stem borer parasitoids in cultivated and natural habitats.

b) To evaluate biotic and abiotic factors that influence the species richness, abundance and parasitism of stem borer parasitoids in cultivated and natural habitats.

c) To assess stem borer parasitism rates in cultivated and natural habitats.

d) To investigate whether natural habitats act as a reservoir for *C. sesamiae* and *C. flavipes* during the dry season.

CHAPTER TWO

LITERATURE REVIEW

2.1 Cereal stem borers

The full potential yield of cereal crops is difficult to realize due to various constraining factors which include climate, plant diseases, weeds and damage by insect pests. Lepidopteran stem borers are generally considered to be the most damaging insect pest of cereal crops in Africa (Nye, 1960; Polaszek, 1998). Twenty-one economically important stem borer species belonging to three families: the Noctuidae, Crambidae and Pyralidae have been reported to attack cereal crops in various parts of the continent (Maes, 1997; Polaszek, 1998). In Kenya, the most economically important species of stem borers include the exotic *C. partellus* and the indigenous maize stalk borer *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). Other minor species include the pink stem borer, *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), the coastal stem borer, *C. orichalcociliellus* (Strand) (Lepidoptera: Crambidae) and the sugarcane stem borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae) (Seshu Reddy and Walker, 1990; Seshu Reddy, 1998; De Groote, 2002; De Groote *et al.*, 2003; Muhammad and Underwood, 2004).

2.2 Generalized life cycle of cereal stem borer insect pests

Two to three days after emergence, adult females mate with males and lay eggs which hatch four to eight days after oviposition. Generally, the first instar larvae migrate from the emergence site to the leaf whorl where they feed on young leaf tissue. An exception is *S. calamistis* whose young larvae bore directly into the stem or initially feed on basal leaf sheaths for two or three days. Generally, older larvae tunnel into the stem tissue and feed internally. Depending on the species, larval stage may last 25 to 58 days and may have six to eight instars. Pupation normally takes five to fourteen days after which adult moths emerge (Harris, 1990; Holloway, 1998; Maes, 1998; Polaszek, 1998).

2.3 Stem borer distribution

Stem borers occur in diverse ecological conditions and their complex differs throughout the African continent. The distribution of stem borer species is influenced by altitude and environmental conditions, particularly temperature, rainfall and humidity (Megenasa, 1982; Sithole, 1987). In Eastern Africa, *B. fusca* is found in cool high altitude areas, over 1140 meters above sea level (m a.s.l.) (Nye, 1960; Kfir *et al.*, 2002; Ong'amo *et al.*, 2006). *Chilo partellus* and *C. orichalcociliellus* are mainly found in warm low altitude areas, 21 to 1670 m a.s.l. (Mathez, 1972; Megenasa, 1982; Ong'amo *et al.*, 2006). Although *S. calamistis* is a cosmopolitan species, it is most prevalent in medium and low elevation areas, 700 to 900 m a.s.l., (Ingram, 1958; Kfir *et al.*, 2002; Ong'amo *et al.*, 2006). *Eldana saccharina* is found throughout sub-Saharan Africa, but mainly in sugarcane growing areas (Nye, 1960; Kfir *et al.*, 2002).

2.4 Damage and loss caused by cereal stem borers

Brenière (1971), Leuschner (1989) and Bosque-Pérez and Mareck (1991) have described the details of crop damage caused by lepidopteran stem borers. Crop damage generally varies greatly among ecological zones or regions and seasons. The severity and nature of damage further depend on the stem borer species, crop growth stage, number of larvae feeding on the plant, plants reaction to borer feeding, prevailing environmental conditions and agronomic practices. For *B. fusca* and *Chilo* species, their first and second instar larvae cause foliar damage during plant whorl stage (Bosque-Pérez and Schulthess, 1998). At this stage, larvae feed by scrapping off the epidermal and parenchyma cells on one side of the leaf, often leaving it intact but transparent. The resultant lesions become windows when the leaves unfold. Young larvae may also feed through the leaves of the intact whorl, which give an array of shot-holes when unfolded. Stem tunneling is usually caused by older larvae (3rd to 8th instars) that bore into the stem through the mid-rib. For *S. calamistis* and *E. saccharina*, their larvae do not feed on plant leaves, but penetrate plant stems shortly after egg hatch (Bosque-Pérez and Schulthess, 1998). In addition, on mature crops, the larvae attack and damage maize cobs.

Leaf feeding by stem borers results in the reduction of plant photosynthetic tissue area. The destruction of meristematic tissues causes deadheart, which is responsible for total plant loss in maize. Other crops like sorghum are able to compensate for death of the main stem by producing additional lateral shoots or tillers. Stem tunneling destroys the central pith and conductive tissues causing a reduction in nutrient uptake, with consequent interruption of grain filling. Secondary effects of stem tunneling include peduncle breakage, poor pollen production, interruption of fertilization, stem breakage or ear drop. Injured plant parts also create avenues for entry by pathogens. Damage caused by the various larval stages ultimately results in stunted plant growth and reduced yields. Estimated yield losses in Kenya vary greatly but are typically in the range of 14% - 40% of the potential yield (Seshu Reddy, 1998; De Groote, 2002; De Groote *et al.*, 2003).

2.5 Stem borer management strategies

Biological, chemical, cultural and host plant resistance are the four main strategies used by farmers to manage stem borer pests in cereal crops (Mugo *et al.*, 2001; Kfir *et al.*, 2002).

2.5.1 Chemical control methods

This practice entails the application of pesticides for the regulation of cereal stem borer pests. Insecticides such as Bulldock (beta-cyfluthrin), Dipterex (tricholorfon) and Ambush (permethrin) are fast acting and effective when supplied at the right time. Timing of sprays is crucial, as the effectiveness of insecticides is hampered by the biology of stem borers. Insecticide application is effective only against young larvae. Older larvae penetrate the stalks and cannot be reached by conventional insecticides. In addition, overlapping stem borer generations, especially of *C. partellus* result in infestation through out the season often rendering insecticide application undesirable (Kfir *et al.*, 1989). Insecticides are also very expensive and may not be economical to use at subsistence level. Furthermore, biological control is often incompatible with the use of insecticides. This is because insecticides usually have toxic effects on natural enemies and can thereby severely reduce their populations or interfere with their activities (Barlett, 1964; Johnson and Tabashnik, 1999). To further complicate the issues, such disruption of natural biological control may cause outbreaks of secondary pests previously suppressed by beneficial natural enemies.

2.5.2 Cultural control methods

Cultural practices involve tactical use of regular farm management practices to either delay or reduce insect pest attack (Seshu Reddy, 1985). It is an important component of integrated pest management programmes. It is considered to be the first line of defense. It involves no additional expenditure at subsistence level, it is safe to use and is compatible with other pest control strategies. Practices such as crop rotation, intercropping, destruction or heat treatment of crop residues, stalk shredding and deep ploughing increase the mortality of diapaused larvae; thereby reducing stem borer populations in the following cropping season (Oloo and Ogedah, 1990; Skovgard and Päts, 1996). Well calculated manipulation of sowing dates can decrease damage by evading the most susceptible plant growth stage corresponding with peak periods of egg and larval abundance of stem borers. Yield losses from dropped ears and lodged plants can also be reduced through early harvest. However, these cultural practices have their limitations. For instance, heat treatment of crop residue and manipulation of sowing dates are strongly influenced by rainfall. Furthermore, the destruction of crop residue is very unpopular. This is because dry stems are used locally for domestic purposes such as fuel and for improvement of soil fertility, and also as fodder or building materials (Päts, 1996). Also developed is the habitat management tactic that uses two kinds of crops that are planted together with maize, such that one plant repels stem borer pests (as the push, i.e. molasses grass *Melinis minutifolia* or the leguminous silverleaf *Desmodium* sp.) while the other plant attracts (as the pull, i.e., Sudan grass *S. vulgare sudanese*) natural enemies such as *C. sesamiae* against these pests (Khan *et al.*, 1997b). In large scale-productions, cultural control is constrained by high labour demand and lack of management capabilities of farmers especially in areas where farming communities lack the support of an adequate extension service. Moreover, the application of a single tactic is less likely to result in high sustainable yields (Nwanze and Mueller, 1989). Therefore, integrated pest management strategy which entails the useful combination of various control tactics (i.e., integration of plant resistance, biological control and cultural practices) might be most appropriate for managing cereal stem borer pest (Nwanze and Mueller, 1989; Overholt *et al.*, 1994b; Sehu Reddy, 1998b).

2.5.3 Host plant resistance

This tactic involves the use of resistant cultivars against cereal stem borer pests. Resistant crop cultivars have no environmental hazards, and are generally compatible with other stem borer control strategies such as the use of natural enemies. However, plant breeders have not yet been able to select agronomically acceptable cultivars with adequate levels of stem borer resistance (Leuschner *et al.*, 1985). It is a great challenge to produce cultivars that combine high quality, drought tolerance and insect or disease resistance to suit the wide variations in agroecological conditions found in most cereal growing areas (Mihm, 1994). Even if that succeeds, experience has shown that insect populations may evolve biotypes capable of attacking formerly resistant cultivars (Roush and McKenzie, 1987). Moreover, the adoption of resistant maize cultivars in the past by subsistence farmers was not impressive, primarily because these cultivars tend to perform poorly under low-input conditions (CIMMYT, 1992). Genetically modified (GM) plants with insecticidal properties are widely grown in other parts of the world and may eventually be adopted in Africa (Bagnara, 2000). However, the use of GM crops remain controversial due to uncertainties about its harmful effects on human health and agroecosystem biodiversity at large (IUCN, 2004).

2.5.4 Biological control methods

This approach involves the use of natural enemies such as predators, parasitoids and pathogens for the regulation of herbivore pest populations. The objective of efficient biological control program is to enhance the abundance and activities (i.e. parasitism/predation) of natural enemy populations (Altieri *et al.,* 1978; Altieri and Nicholls, 2004). This can be achieved either through the importation and release or augmentation of potential biological control agents against target hosts or prey. The aim is for natural enemy populations to self-perpetuate in time and space when established, and thereby regulate the population of its target pests (Huffaker and Messenger, 1976). The use of natural enemies is one of the most desirable methods of managing stem borer pest populations because it is safe and cost effective (Overholt *et al.*, 1997). It also requires little or no farmers contribution and has no adverse effects on the environment.

Several indigenous natural enemies have been reported in Kenya, of which predators cause high stem borer mortality in some regions. However, their abundance is highly dependent on the location and season (Bonhof *et al.*, 1997). The major predators of stem borers include ants (*Camponotus* spp., *Crematogaster* spp., *Tetramorium guineense* F., *Pheidole megacephala* F., *Cardio condyla badonei* Arnold and *C. emeryi* Forel.), earwig (*Diaperasticus erythrocephala* Olivier), spiders (Thomisidae), coccinellids (*Cheilomenes propinqua propinqua* (Mulsant) and *Cheilomenes sulphurea* Olivier), cockroaches (*Blatella* spp.), praying mantids and staphylinids (*Paederus sabaeus* Erichson) (Bonhof *et al.,* 1997; Overholt, 1998). The most commonly reported indigenous parasitoids of stem borers in Kenya are the egg parasitoids *Telenomus* species (Scelionidae) and *Trichogramma* species (Trichogrammatidae), the larval parasitoids *C. sesamiae*, *C. flavipes* and *Goniozus indicus* Ashmead, and pupal parasitoids *Pediobius furvus* (Gahan) (Hymenoptera: Eulophidae) and *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae) (Mohyuddin and Greathead, 1970; Mathez, 1972; Oloo and Ogedah, 1990; Bonhof *et al.,* 1997; Zhou *et al.*, 2003). Furthermore, entomopathogens like *Bacillus thuringiensis* Berlinger and botanical pesticides such as neem (*Azadirachta indica* A. Juss) have been reported to have great potential for controlling stem borer pests (Bonhof *et al.,* 1997). However, the commercial products of entomopathogens are usually not available or affordable to low income subsistence farmers in Africa (Mihm, 1994). Moreover, the impact of naturally occurring fungi, bacteria, protozoa, viruses and nematodes is often mitigated by long dry seasons and by lack of physical contact with stem borer larvae embedded within plant stems.

2.5.4.1 Biology of *Cotesia* species and their stem borer pest regulation potential

Cotesia sesamiae and *C. flavipes* share similar biology and ecology (Overholt, 1998; Niyibigira *et al.*, 2003). Adults preferably emerge in bright light. Males emerge first and wait near the cocoon for the females to emerge, after which sib-mating takes place (Ullyet, 1935). Adult females oviposit in medium and large sized stem borer larvae (Smith *et al.*, 1993; Ngi-Song *et al.*, 1996). A single female clutch size can range between 40 and 60 eggs (Potting *et al.*, 1999; Mochiah *et al.*, 2001). Fully developed larvae emerge from stem borer larvae and spin white cocoons, which are loosely held together by strands of fine silk. The average egg to adult developmental time is 18 days at 25°C (Ngi-Song *et al.*, 1995; Mochiah *et al.*, 2001). Longevity of adult wasps ranges from two to ten days depending on the availability and type of food resource (Sathe *et al.*, 2001).

The two *Cotesia* species parasitize stem borers belonging to the Crambidae and Noctuidae families (Mohyuddin and Greathead, 1970; Kfir and Bell, 1993). *Cotesia flavipes* have been reported to have high host searching ability that allows it to seek out its hosts even at low densities (Wiedenmann and Smith, 1993). Both *Cotesia* species employ an efficient attack strategy, the ingress and sting method, whereby they enter tunnels inside plant stems and parasitize stem borer larvae directly (Smith *et al.*, 1993). The short generation time (18 days) of the two *Cotesia* species (Ngi-Song *et al.*, 1995; Mochiah *et al.*, 2001) compared to that of stem borer hosts (30 - 58 days) (Polaszek, 1998) and their high reproductive rates with a female biased sex ratio (Omwega and Overholt, 1997) demonstrates a high potential for stem borer pest regulation.

Cotesia species as biological control agents are not without limitations. Mbapila and Overholt (1997) reported that these *Cotesia* species lack the ability to locate and parasitize diapaused larvae in dried maize stems. Furthermore, laboratory studies have indicated that the two species can mate in a no choice situation, but cannot produce viable progeny (Overholt, 1998). Meaning that, if the two *Cotesia* species were to breed in nature, their reproductive success will be limited.

2.6 Stem borer parasitism

Lepidopteran stem borers are parasitized, at different developmental stages, by egg larval or pupal parasitoids. Parasitoids of cereal stem borers in Eastern Africa have been reviewed by Bonhof *et al.* (1997). In Kenya, at least 85 species (in two Orders, sixteen Families and fifty-five Genera) of parasitoids have been reported on seven species of stem borers feeding on maize and sorghum. In natural habitats, ten species (belonging to two Orders, five Families and eight Genera) of parasitoids were recovered from six species of stem borers found on ten species of wild host plants (Khan *et al.*, 1997a; Overholt *et al.*, 1997; Polaszek and Khan, 1998; Conlong, 2000; Songa *et al.*, 2002) (see Table 2.1). Parasitoids play an important role in curtailing stem borer pest populations, because without their activities, the annual yield losses would be much higher. Parasitism is generally influenced by several factors such as stem borer species, stem borer growth stage or size, location, host plant species and season (Bonhof *et al.*, 1997; Jiang *et al.*, 2004; Sétamou *et al.*, 2005; Muturi *et al.*, 2005). Additionally, successful parasitism can be influenced by the accessibility of parasitoids to stem borer larvae or pupae living inside plant stems, as well as the attraction of parasitoids by kairomones from plants and stem borers and synomones from infested plants (Overholt, 1998; Chabi-Olaye *et al.*, 2001).

2.6.1 Parasitism in cultivated habitats

In Western Africa, larval and pupal parasitoids of stem borers are generally rare (Shanower *et al.*, 1991; Gonou *et al.*, 1994), while egg parasitism rates are reported to be high, reaching up to 76.4% (Sétamou and Schulthess, 1995). In contrast, egg

Table 2.1: Species of stem borer parasitoids reported in cultivated and natural habitats in Kenya

Parasitoid species	Stem borer		Host plant species	Reference
	species	growth stage		
Cultivated habitats				
Hymenoptera				
Bethylidae				
Goniozus sp.	C. sp	L	Zm	Mohyuddin and Greathead, 1970
Goniozus indicus Ashmead	Bf, Co, Cp, Sc	L	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Odontepyris transvaalensis (De Buyson)	Bf, ?	L	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Braconidae				
Amyosom nyanzaense (Quicke & Wharton)	Bf, Co, Cp, Sc	L	Sb, Zm	Quicke and Wharton, 1989; Zhou *et al.*, 2003
Apanteles sp. (ater group)	Cp	L	Sb, Zm	Milner, 1967; Mohyuddin and Greathead, 1970
Apanteles sp. nr *laevigatus* (Ratzeburg)	Co, Cp	L	Sb, Zm	Mohyuddin and Greathead, 1970; Mathez, 1972
Bassus sp.	Co	L	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Bassus sublevis (Granger)	Cp, Es	L	Zm	van Achterberg and Polaszek, 1996
Bracon (Glabrobracon) sp.	Co, Cp	L	Sb, Zm	Mathez, 1972; Oloo, 1989
Bracon chinensis Szepligeti	Cp	L	Sb	Seshu Reddy, 1989
Bracon sesamiae Cameron	Bf, Co, Cp, C. sp	L	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Chelonus sp.	?	P	Zm	Mathez, 1972
Chelonus curvimaculatus Cameron	Bf, Co, Cp, Sc	E/L	Sb, Zm	Milner, 1967; Mohyuddin and Greathead, 1970; Zhou *et al.*, 2003
Cotesia flavipes Cameron	Bf, Co, Cp, Sc	L	Zm	Overholt *et al.*, 1997; Zhou *et al.*, 2003
Cotesia ruficrus (Haliday)	Cp, Sc	L	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003

Parasitoid species	**Stem borer**		**Host**	**Reference**
	species	**growth stage**	**plant species**	
Cotesia sesamiae Cameron	Bf, Co, Cp, Es, Sc, S. sp.	L	Sb, Zm	Mohyuddin and Greathead, 1970; Mathez, 1972; Oloo, 1989; Zhou *et al.*, 2003
Dolichogenidea fuscivora Walker	Bf, Cp, Sc	L	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Dolichogenidea polaszeki Walker	Sc, Bf	L	Zm	Zhou *et al.*, 2003
Euvipio rufa Szepligeti	Cp	L	Sb, Zm	Oloo, 1989; Greathead, 1990
Glyptapanteles africanus (Cameron)	Cp, Sc	L	Zm	Zhou *et al.*, 2003
Glyptapanteles maculitarsis (Cameron)	Cp, Sc	L	Zm	Zhou *et al.*, 2003
Glyptomorpha spp.	Co, Cp	L	Zm	La Croix, 1967
Macrocentrus sesamivorus van Achterberg	Cp, Sc	L	Zm	van Achterberg and Polaszek, 1996
Macrocentrus sp.	Co, Cp, Sc	L	Zm	Zhou *et al.*, 2003
Meteorus sp.	Bf, Cp	L	Zm	Milner, 1967; van Achterberg and Polaszek, 1996; Zhou *et al.*, 2003
Myosoma nyanzaensis Quicke & Wharton	Cp, ?	L	Sb, Zm	Quick and Wharton, 1989; Mohyuddin, 1990
Phanerotoma leucobasis Kriechbaumer	Bf	E/L	Zm	van Achterberg and Polaszek, 1996
Rhaconotus sp.	Cp	L	Sb, Zm	Mohyuddin and Greathead, 1970
Rhaconotus scirpophagae Wilkinson	Cp, C. sp.	L	Zm	Mathez, 1972; van Achterberg and Polaszek, 1996; Zhou *et al.*, 2003
Stenobracon rufus (Szepligeti)	Co, Cp, S. sp	L	Zm	Mathez, 1972; Zhou *et al.*, 2003
Tropobracon anntenatus (Granger)	Co	L	Zm	Zhou *et al.*, 2003
Tropobracon sp.	?		Zm	Bonhof *et al.*, 1997
Ceraphronidae				
Aphanobmus fijiensis (Ferrière)	Sc	H	Zm	Zhou *et al.*, 2003

Parasitoid species	**Stem borer**		**Host plant species**	**Reference**
	species	**growth stage**		
Chalcididae				
Antrhocephalus mitys Walker	Cp	P	Zm	Skovgard and Päts, 1996; Zhou *et al.*, 2003
Brachymeria spp.	Bf, Co, Cp, C. sp., Es	P	Sb, Zm	Mohyuddin and Greathead, 1970; Chacko and Ogedah, 1990; Skovgard and Päts, 1996
Brachymeria dunbrodyensis Cram.	C. sp.	?	Zm	La Croix, 1967
Brachymeria kassalensis Kirby	Cp	?	Zm	La Croix, 1967
Brachymeria olethria Waterston	Co, Cp	P, ?	Zm	La Croix, 1967; Zhou *et al.*, 2003
Psilochalchis soudanensis (Steffan)	Bf, Co, Cp, Es	P	Sb, Zm	Oloo,1989; Skovgard and Päts, 1996; Zhou *et al.*, 2003
Encrytidae				
Exoristobia dipterae (Risbec)	Co	H	Zm	Zhou *et al.*, 2003
Eulophidae				
Pediobius sp.	?	?	Zm	Bonhof *et al.*, 1997
Pediobius furvus (Gahan)	Bf, Co, Cp, C. sp. S. sp.	P, ?	Sb, Zm	Mohyuddin and Greathead, 1970; Mathez, 1972; Oloo,1989; Zhou *et al.*, 2003
Tetrastichus sp.	Co, Cp, Sc, ?	P	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Eurytomidae				
Eurytoma braconidis (Ferrière)	Co, Cp, Bf	H	Zm	Zhou *et al.*, 2003
Eurytoma oryzivora Delvare	Cp, Sc	P	Zm	Zhou *et al.*, 2003
Ichneumonidae				
Charops spp.	C. sp.	?	Zm	La Croix, 1967; Greathead, 1990
Dentichasmias busseolae Heinrich	B. sp., Co, Cp, Sc	P	Sb, Zm	Oloo, 1989; Seshu Reddy, 1989; Skovgard and Pits, 1996; Zhou *et al.*, 2003

Parasitoid species	**Stem borer**		**Host plant species**	**Reference**
	species	**growth stage**		
Isotima sp.	Bf, Cp	L/P	Zm	Mohyuddin and Greathead, 1970
Pimpla sp.	Cp	P	Zm	Zhou *et al.*, 2003
Pristomerus sp.	C. sp., Sc	L, ?	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Procerochasmias nigromaculatus (Cameron)	Bf, Cp, Es, Sc	P	Zm	Bonhof *et al.*, 1997
Syzeuctus sp.	Co, Cp, Sc	L	Zm	Mathez, 1972; Zhou *et al.*, 2003
Syzeuctus ruberrimus Benoit	Co, Cp	L	Zm	Benoit, 1959
Temelucha sp.	Cp, C. sp.	L, ?	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Temelucha sp.	Cp, C. sp.	L, ?	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Vadonina nimbipennis (Seyrig)	Bf, Co, Cp, ?	P, ?	Zm	Bonhof *et al.*, 1997; Zhou *et al.*, 2003
Xanthopimpla sp.	Co, Cp	P	Zm	Zhou *et al.*, 2003
Xanthopimpla luteola Toiq	C. sp.	?	Zm	La Croix, 1967
Xanthopimpla stemmator Thunberg	?	?	Zm	Bonhof *et al.*, 1997
Pteromalidae				
Norbanus sp.	Cp	L	Zm	Bonhof *et al.*, 1997
Scelionidae				
Telenomus busseolae (Gahan)	Bf	E	Sb, Zm	Oloo, 1989
Telenomus spp.	Cp, ?	E	Sb, Zm	Oloo, 1983; Greathead, 1990; Midega *et al.*, 2004
Telenomus applanatus Bin & Johnson	Es	E	Zm	Polaszek and Kimani-Njogu, 1990
Telenomus nemesis Polaszek and Kimani	Co, C. sp.	E	Zm	Polaszek, 1995
Telenomus thestor Nixon	?	E	Zm	Polaszek, 1995

Parasitoid species	**Stem borer**		**Host**	**Reference**
	species	**growth stage**	**plant species**	
Trichogrammatidae				
Trichogramma spp.	Co, Cp, Sc, ?	E	Sb, Zm	Mathez, 1972; Seshu Reddy, 1989; Greathead, 1990; Midega *et al.*, 2004
Trichogramma bournieri Pintureau and Babault	Cp, Sc	E	Zm	Haile *et al.*, 2002; Zhou *et al.*, 2003
Trichogramma sp. nr. *mwanzai* Schulten and Feijen	Cp, Sc	E	Sb, Zm	Haile *et al.*, 2002; Zhou *et al.*, 2003
Trichogrammatoidea sp.	?	E	Zm	Bonhof *et al.*, 1997
Diptera				
Chloropidae				
Scollophthalmus trapezoides (Beck)	?	L	Zm	Mathez, 1972
Polyodaspis sp.? *robusta* Lamp	Co, Cp	L	Zm	Mathez, 1972
Anatrichus erinaceus Loew	?	?	Zm	Mathez, 1972
Muscidae				
Atherigona sp.	C. sp.	L	Zm	La Croix, 1967; Mathez, 1972
Atherigona sp. (orientalis group)	Bf, Co, Cp	L	Zm	Bonhof *et al.*, 1997
Phaonia sp.	?	L	Zm	Mathez, 1972
Phoridae				
Plethysmochacta sp.	Bf	?	Zm	Bonhof *et al.*, 1997
Sarcophagidae				
Sarcophaga spp.	Bf, Cp, S. sp.	L	Sb, Zm	Mohyuddin and Greathead, 1970; Mohyuddin, 1990
Sarcophaga villa Curran	Bf, Cp, S. sp.	L	Zm	Milner, 1967

Parasitoid species	**Stem borer**		**Host**	**Reference**
	species	**growth stage**	**plant species**	
Tachinidae				
Unidentified species	Bf	L	Zm	Mohyuddin and Greathead, 1970
Actia sp.	?	L	Zm	Mohyuddin and Greathead, 1970
Atherigona sp	Cp	L	Sb, Zm	Mohyuddin and Greathead, 1970
Nemoraea discoidalis Villeneuve	Bf	P	Zm	Milner, 1967
Peribaea orbata (Wiedemann)	Cp	L	Zm	Milner, 1967; Mohyuddin and Greathead, 1970
Schembria eldana Barraclough	Co, Cp, Sc	L/P	Zm	Zhou *et al.*, 2003
Siphona (Crocuta) *murina* Mesnil	Bf, Cp, Es, Sc	L	Zm	Nye, 1960; Mohyuddin and Greathead, 1970
Sturmiopsis parasitica (Curran)	Co, Cp, C. sp., Sc	L, P	Sb, Zm	La Croix, 1967; Mohyuddin and Greathead, 1970; Zhou *et al.*, 2003
Natural habitats				
Braconidae				
Brconid sp.	Es	L	Cf	Conlong, 2000
Cotesia flavipes Cameron	Bs, Cp	L	Ci, Cd, Sv	Khan *et al.*, 1997a; Songa *et al.*, 2002
Cotesia sesamiae Cameron	Pb, P. sp., Cp	L	Ep, Ph sp., Pm, Pp, Sv	Khan *et al.*, 1997a; Songa *et al.*, 2002
Chelonus curvimaculatus Cameron	Cp	L	Sv	Songa *et al.*, 2002
Stenobracon rufus Szépligeti	Pb	L	?	Khan *et al.*, 1997a
Bethylidae				
Goniozus indicus Ashmead	C sp.	L	Sa	Conlong, 2000

Parasitoid species	**Stem borer**		**Host**	**Reference**
	species	**growth stage**	**plant species**	
Ichneumonidae				
Ichneumonid sp.	Es	L	Cp	Conlong, 2000
Pristomerus sp.	Cp	L	Sv	Songa *et al.*, 2002
Pteromalidae				
Norbanus sp.	Cp	L	Sv	Songa *et al.*, 2002
Diptera				
Schembria eldana Barraclough	Es	L	Cp	Conlong, 2000

Bf = *Busseola fusca,* Bs = *Bactra stagnicolana,* B. sp. = *Busseola* sp., Co = *Chilo orichcalcilliellus,* Cp = *Chilo partellus,* C. sp = *Chilo* sp., Es = *Eldana saccharina,* Pb = *Phragmatecia boisduvalii,* Pe sp. = *Poeonoma* sp., Sc = *Sesamia calamistis,* S. sp. = *Sesamia* sp., ? = Unknown; E = Egg, H = Hyperparasitoid, L = Larva, P = Pupa
Cyd = *Cyperus distans,* Cyf = *C. fastigiatus,* Cyi = *C. immensis,* Cyp = *C. papyrus,* Ep = *Echinochloa pyramidalis,* Ph sp.. = *Phragmites* sp., Pm = *Pennisetum macrourum,* Pp = *P. purpureum,* Sa = *Sorghum arundinaceum,* Sb = *Sorghum bicolor,* Sv = *S. versicolar,* Zm = *Zea mays*

parasitoids are extremely rare in southern Africa, whereas larval and pupal parasitoids of stem borers are quite abundant (Kfir, 1995, 2000). Kfir and Bell (1993) and Kfir (2000) reported that, the parasitism of stem borer larvae and pupae in southern Africa range from 20.0% to 70.0% and 0% to 100%, respectively. In Eastern Africa, whereas egg parasitism was reported to be very low (Mohyuddin and Greathead, 1970), larval parasitism was between 3.0% and 37.0% (Bonhof *et al.*, 1997; Matama-Kauma, 2000; Rwomushana *et al.*, 2005), while pupal parasitism was generally less than 5.0% (Bonhof *et al.*, 1997).

In Kenya, egg parasitism at the coast was estimated to range between 19% and 76% (Mathez, 1972; Skövgrad and Päts, 1996). By contrast, egg predation and disappearance were major mortality factors (97.6%) in the western parts of Kenya, where egg parasitism was less common and ranged between 5.0% and 50.0% (Mohyuddin and Greathead, 1970; Oloo, 1989; Oloo and Ogedah, 1990). Young stem borer larvae often suffer heavy mortalities from cannibalism, predation and abiotic factors such as wind and rain (Bonhof *et al.,* 1997). On the contrary, the impact of parasitoids on stem borer larvae was generally low, with parasitism not more than 10.0% (Mathez, 1972; Oloo and Ogedah, 1990; Ogol *et al.,* 1998; Midega *et al.*, 2004). Although sessile stem borer pupae are often protected inside plant stems, they have been reported to suffer high mortalities of up to 88%, with disappearance (representing predation and other unknown factors) as the major mortality factor (Oloo, 1989). Pupal parasitism was generally low, and parasitization rates varied from 0.0% to 58.0% in Western Kenya (Mathez, 1972; Oloo and Ogedah, 1990) and between 0% and 26.0% at the coast of Kenya (Mathez, 1972; Skovogard and Päts, 1996).

In spite of the large number of indigenous species reported in cultivated habitats in Kenya, research findings indicated that these parasitoids are not able to prevent economic damage or reduce pest populations to below economic threshold levels (Bonhof *et al.*, 1997; Overholt, 1998). Therefore, *C. flavipes* was introduced in Coastal Kenya from Asia to compliment the mortality of *C. partellus* by indigenous parasitoids. *Cotesia flavipes* has since become successfully established (Omwega *et al.*, 1995; Omwega *et al.*, 2006), and is contributing to the regulation of its target host, *C. partellus,* with field parasitism rates of up to 25.80% (Songa *et al.*, 2001).

2.6.2 Parasitism in natural habitats

There are no records of stem borer egg and pupal parasitism in natural habitats in Kenya. Larval parasitism of stem borers feeding on wild host plants range between 0.6% and 16.6% (Khan *et al.*, 1997a; Overholt *et al.*, 1997; Conlong, 2000; Songa *et al.*, 2002). In spite of the low parasitism rates reported on wild host plants, the impact of parasitism by indigenous parasitoids on stem borer populations residing in natural habitats might be high based on the following assumptions:

1. Parasitoids do not have to migrate periodically to recolonize stem borers residing in natural habitats. Therefore, stem borers and parasitoids tend to be more stable in natural habitats (Conlong, 1994).
2. Larval growth of stem borers is much slower on wild host plants than on cereal crops, thereby creating a wider temporal window of susceptibility for parasitoid attacks (Bowden, 1976).
3. Stem borer survival is quite low on wild host plants (Ofomota *et al.*, 2000). Thus, it is expected that parasitoids and other natural enemies will effectively maintain

stem borer populations below an epidemic pest level (Wiedenmann and Smith, 1993).

4. Parasitoids that utilize the "Drill-and-Sting" or "Planidial-Ingress" foraging strategies might be highly effective on small-diameter stems of wild host plants compared to the relatively thick-stemmed cereal crops (Overholt, 1998).

2.7 The role of wild host plants in stem borer pest management

In tropical and sub-tropical Africa, stem borers originally attacked wild gramineous and other plant species (Mally, 1920) without special consequences. However, with extensive cultivation of cereal crops, some stem borer species followed the cultivated forms of their wild host plants, and became more widely distributed and economically important. Possibly this was because, cereal crops supplied readily available and highly nutritious food sources with relatively little inherent resistance to stem borer attack (Polaszek and Khan, 1998). An example of a species that became economically important is *E. saccharina* that was formerly restricted to wild host plants in Uganda. However, *E. saccharina* drastically changed its pest status in the 1970's, when it expanded its host range to include maize, cultivated sorghum and sugarcane (*Saccharum officinarum* L.) (Girling, 1978).

In the past, most stem borer species were generally thought to be polyphagous, having several graminaceous host plant families (Polaszek and Khan, 1998). Therefore, various authors recommended the removal and destruction of wild host plants surrounding cultivated cereal crops, as a measure for reducing stem borer pest populations (Nye, 1960; Seshu Reddy, 1985). However, recent findings by Le Ru *et al.* (2006a,b) indicated that the majority of stem borer species in natural habitats were monophagous rather than polyphagous. Moreover, several scientists emphasized that wild host plants adjacent to cultivated crops can be beneficial in providing refugia to parasitoids and other natural enemies, as well as adult food sources such as nectar or pollen, and alternate hosts or prey during the non-cropping season (Altieri *et al.*, 1977; Altieri and Whitcomb, 1979; Herzog and Funderburg, 1986; Khan *et al.*, 1997a). It has therefore been postulated that natural habitats may play a role in sustaining populations of stem borer parasitoids during the off-season (Bonhof *et al.*, 2001). This in turn, is expected to contribute to the reduction of stem borer pest infestations in cultivated cereal crops, by facilitating carry-over of parasitoids or natural enemies of stem borers from one season to the next. For instance, Khan *et al.* (1997a) reported three parasitoids of economically important cereal stem borer pests on three non-economically important stem borer species on wild host plants in Kenya. *Cotesia sesamiae* and *Stenobracon rufus* Szépligeti were recovered from the stem borer *Phragmataecia boisduvalli* (Herrich-Shaeffer) (Cossidae) on *Echinochloa pyramidalis* (Lam.) Hitchc. & Chase and *Phragmites* sp. *Cotesia sesamiae* was also recovered from the stem borer *Poeonoma serrata* (Hampson) (Noctuidae) on *Pennisetum purpureum* Schumach and *P. macrourum* Trin. In another example, Songa *et al.* (2002) recorded *C. flavipes, C. sesamiae, Chelonus curvimaculatus* Cameron, *Norbanus* sp. and *Pristomerus* sp. on *Sorghum versicolar* Anderss.

CHAPTER THREE

GENERAL MATERIALS AND METHODS

3.1 Study localities and field survey

Surveys were conducted in four localities in Kenya: Suam (Rift valley), Kakamega (Western Kenya), Mtito Andei (Eastern Kenya) and Muhaka (Coast) (Figure 3.1). These localities not only varied with agroecological zones but also in altitude and climatic conditions (Corbett, 1998), vegetation mosaics (White, 1983) and stem borer species composition (Ong'amo *et al*., 2006). Descriptions of all study sites are presented in table 3.1.

It should be noted that for Kakamega and Muhaka, in addition to the two main cropping seasons, cereal crops were usually available in the fields in-between the main cropping seasons. This was due to brief rain spells that were experienced during dry seasons and sometimes, cereal crops were planted in marshy areas usually bordering streams or rivers. In localities with a single cropping season, irrigation was practiced in Mtito Andei but not in Suam.

Field surveys were carried out for two years consecutively, from December 2005 to December 2007. In all localities, sampling was regularly done at two months interval during each rainy and dry season to include both the vegetative and harvest stages of cereal

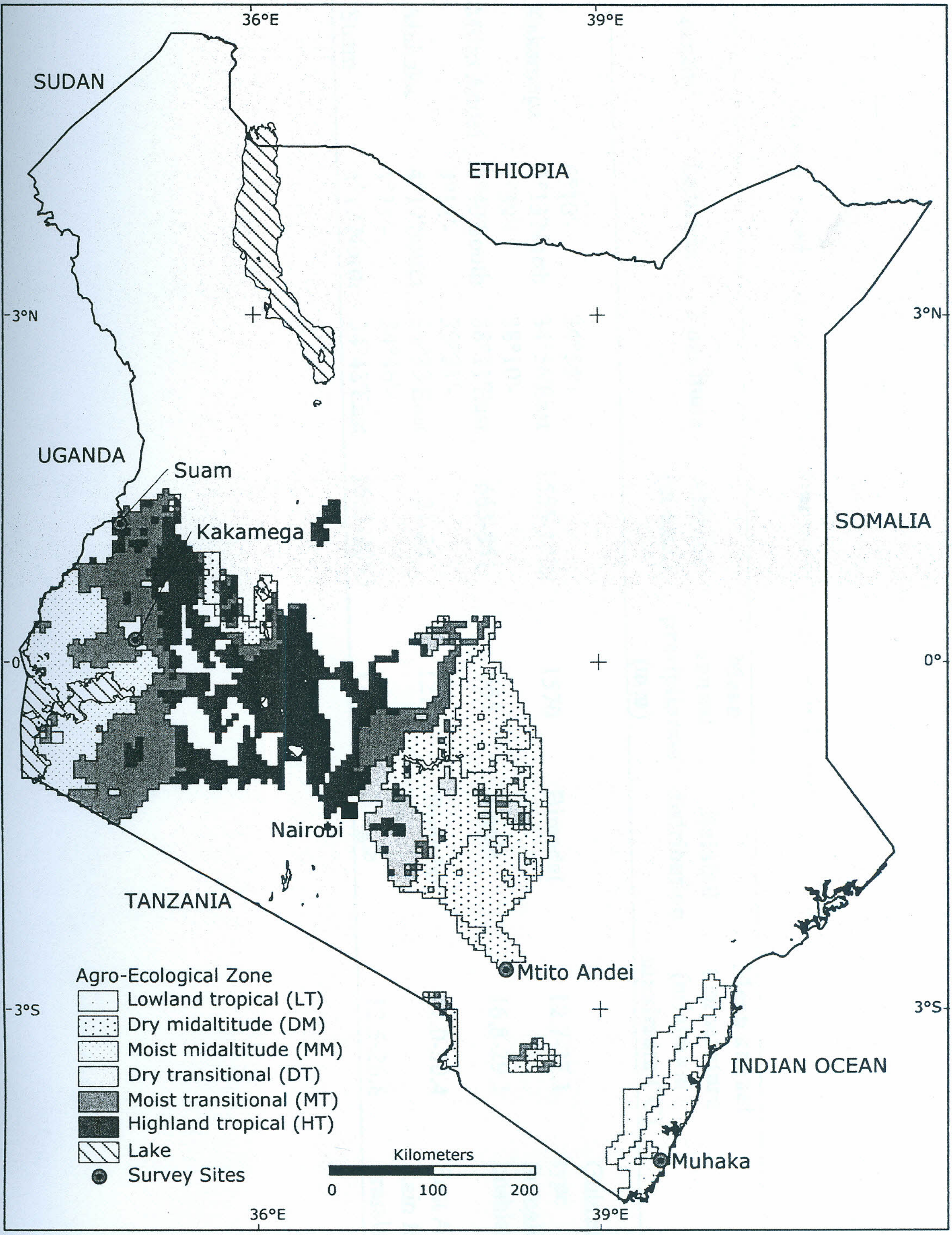

Figure 3.1: Map of Kenya showing localities and agroecological zones where the study was conducted

Table 3.1: Summarized description of the four study localities in Kenya

Locality	Latitude	Longitude	Altitude (m a.s.l.)	Mean annual precipitation (mm)	Rainfall distribution	Mean annual temperature (minimum - maximum (°C)	Vegetation mosaic
Kakamega	0°10'-0°13'North	34°54'-34°56'East	1555-1702	1570	Bimodal	12.7-27.1	Guineo-Congolian rain forest type
Mtito Andei	2°39'-2°40'South	38°10'-38°21'East	663-851	665	Single	16.8-29.1	Somalia and Masai Acacia bushland/thicket mosaic
Muhaka	4°18'-4°19'South	39°31'-39°33'East	21-54	1210	Bimodal	22.0-30.4	East African coastal mosaic
Suam	1°11'-1°12'North	34°46'-34°48'East	1665-2035	1190	Single	12.5-26.8	Rain forest and secondary grassland mosaic

crops, and to enable sampling of different life stages of stem borers. Sampling was done in such a way that it caused minimal disturbance to the stem borer populations within the study sites.

3.2 Data collection

Guihéneuf (2004) and Goux (2005) used high resolution satellite images to provide maps of the survey sites (25 km^2 per locality), characterizing the landscape of each site into cultivated and non-cultivated areas. The Arc View 3.2 (1992) software was used to generate random sampling points in each survey site. There after, a GARMIN 12X portable Global Positioning System (GPS) receiver was used to locate and identify each sampling point in the field.

Evidence from previous studies had showed that stem borer densities were much lower on wild host plants than on adjacent cultivated cereal crops (Nye, 1960; Gounou and Schulthess, 2004; Le Ru *et al.*, 2006a,b; Ndemah *et al.*, 2007; Matama-Kauma *et al.*, 2008). Therefore, to increase the chances of collecting stem borers and their parasitoids in both cultivated and natural habitats, the sampling methods employed differed with habitat type. Whereas, only random sampling method was carried out in cultivated habitats, both random and non-random sampling methods were applied in natural habitats.

3.2.1 Sampling in cultivated habitats

The number of farmers cereal fields visited per study site was determined based on the area under cereal cultivation in relation to the total area of that site. This proceeded in three steps. Firstly, the total number of cereal plants collected per study site (n_1) was calculated using the formula described by Cochran (1977):

$$n_1 = Z^2_{\alpha/2} / \delta^2 (q / p) \tag{1}$$

where n_1 is the total number of cereal plants required in each site, $Z_{\alpha/2}$ is the standard normal deviate at 95 % confidence level (1.96), δ is the reliability level of statistical significance (0.05), p is the proportion of land area under cereal cultivation, q is proportion of land area without cereal (1 - p).

Secondly, within each study site, the number of cereal plants sampled per farmers cereal field (n_2) was calculated using the formula described by Zar (1999):

$$n_2 = Z^2_{\alpha(2)} / 4Dd^2 \tag{2}$$

where n_2 is the number of cereal plants sampled per field, $Z_{\alpha(2)}$ is the standard normal deviate at 95 % confidence level (1.96), d is permitted error (0.1), D is the design effect (1).

Thirdly, the number of farmers cereal field visited per site (n_3) was determined by combining equations 1 and 2 above:

$$n_3 = [(Z^2_{\alpha/2} / \delta^2 (q / p)) / (Z^2_{\alpha(2)} / 4Dd^2)] = 4Dqd^2 / p\delta^2 \tag{3}$$

After applying the formulae, 21, 16, 16 and 10 farmers cereal fields were randomly selected for sampling in Kakamega, Mtito Andei, Muhaka and Suam, respectively. Each field was visited at least twice during each long rains, short rains and dry season throughout the study period (Plates 3.1a,b,c, 3.2a,b,c, 3.3a,b,c and 3.4a,b,c). To estimate stem borer parasitoid diversity and density, depending on the field size and crop availability during different seasons, 50 to 100 plants were randomly sampled per field (Overholt *et al.* 1994a). The plants collected were dissected in the field, and stem borer larvae or pupae obtained were transported to the laboratory for rearing and subsequent recovery of parasitoids.

3.2.2 Sampling in natural habitats

To evaluate stem borer density and parasitoid diversity in natural habitats, random and non-random sampling methods were employed, respectively.

3.2.2.1 Random sampling method

Based on the sampling plan developed by Gounou and Schulthess (2004), grass patches immediately surrounding sampled cereal field were inspected. The same grass patch was visited at regular time intervals during rainy and dry seasons as stated above for cultivated habitats (Plates 3.1d,e,f, 3.2d,e,f, 3.3d,e,f and 3.4d,e,f). To estimate stem borer densities on wild host plants, during each sampling occasion, depending on the availability of host plant species during different seasons or due to disturbances (i.e., livestock overgrazing), 50 to 100 plants/tillers were randomly sampled per plant species in each patch, up to a distance of 50 m from the edge of each cereal field. Each plant/tiller selected was dissected in the field. Stem borer larvae or pupae collected were labeled and transported to the laboratory for rearing and subsequent recovery of parasitoids.

Plate 3.1: Pictures of Kakamega study site. (a) maize plants during the rainy season, (b and c) standing and heaped stalks during the dry season, (d) wild host plants during the rainy and (e and f) dry seasons

Plate 3.2: Pictures of Mtito Andei study site. (a) maize plants during the rainy season, (b and c) dry and grazed stalks during the dry season, (d) wild host plants during the rainy and (e and f) dry seasons

Plate 3.3: Pictures of Muhaka study site. (a) maize plants during the rainy season, (b and c) standing stalks during the dry season, (d) wild host plants during the rainy and (e and f) dry seasons

Plate 3.4: Pictures of Suam study site. (a) maize plants during the rainy season, (b and c) standing or heaped stalks during the dry seasons, (d) wild host plants during the rainy and (e and f) dry seasons

3.2.2.2 Non-random sampling method

To estimate parasitoid species diversity on wild host plants, stem borers were collected using a slight modification of the non-random sampling procedure applied by Le Ru *et al.* (2006a,b). During each sampling occasion as described above, wild host plants were sampled where possible up to 100 m distance of each sampled cereal field including grass patches found along road sides, in open forest grass patches, on the banks of streams, dams or rivers and in swamps. At each sampling site, all known or potential host plants belonging to the Poaceae, Cyperaceae and Typhaceae families (Khan *et al.*, 1997a; Le Ru *et al.*, 2006a,b) were checked for infestation symptoms such as scarified leaves (window panes and pin holes) (Plate 3.5a,b,c), frass (Plate 3.5d), dry leaves and shoots (dead hearts) (Plate 3.5e), bored (entrance or exit) hole (Plate 3.5f). All plants/tillers collected were dissected in the field. Stem borer larvae or pupae obtained were labeled and transported to the laboratory for rearing and subsequent recovery of parasitoids (Plate 3.6a,b,c,d,e).

3.3 Stem borer/parasitoid recovery and identification

The stem borer larvae recovered were reared on artificial diet developed by Onyango and Ochieng-Odero (1994) in glass vials (2.5 cm diameter x 7.5 cm depth) plugged with cotton wool, which were kept under ambient conditions in the laboratory (26 ± 1 °C; 65 ± 5 RH) until pupation or cocoon formation. Parasitoid cocoons or puparia recovered from stem borer larvae or pupae were kept separately in plastic vials (2.5 cm diameter x 7.5 cm depth) until adult emergence (Plate 3.7a,b,c). Adult stem borer or parasitoid

Plate 3.5: Pictures of stem borer infestation symptoms. (a, b and c) different forms of leave scarification and (d) bored hole clogged with frass on maize, (e) dead heart and (f) entrance or exit hole on *Cynodon aethiopicus*

Plate 3.6: Pictures of stem borer recovery and rearing. (a) stem borer larva and (b) pupa on dissected plant stems, (c and d) field collection of stem borers on artificial diet in labeled vials, and (e) rearing and observation for adult stem borer or parasitoid puparia/cocoon emergenence in the laboratory

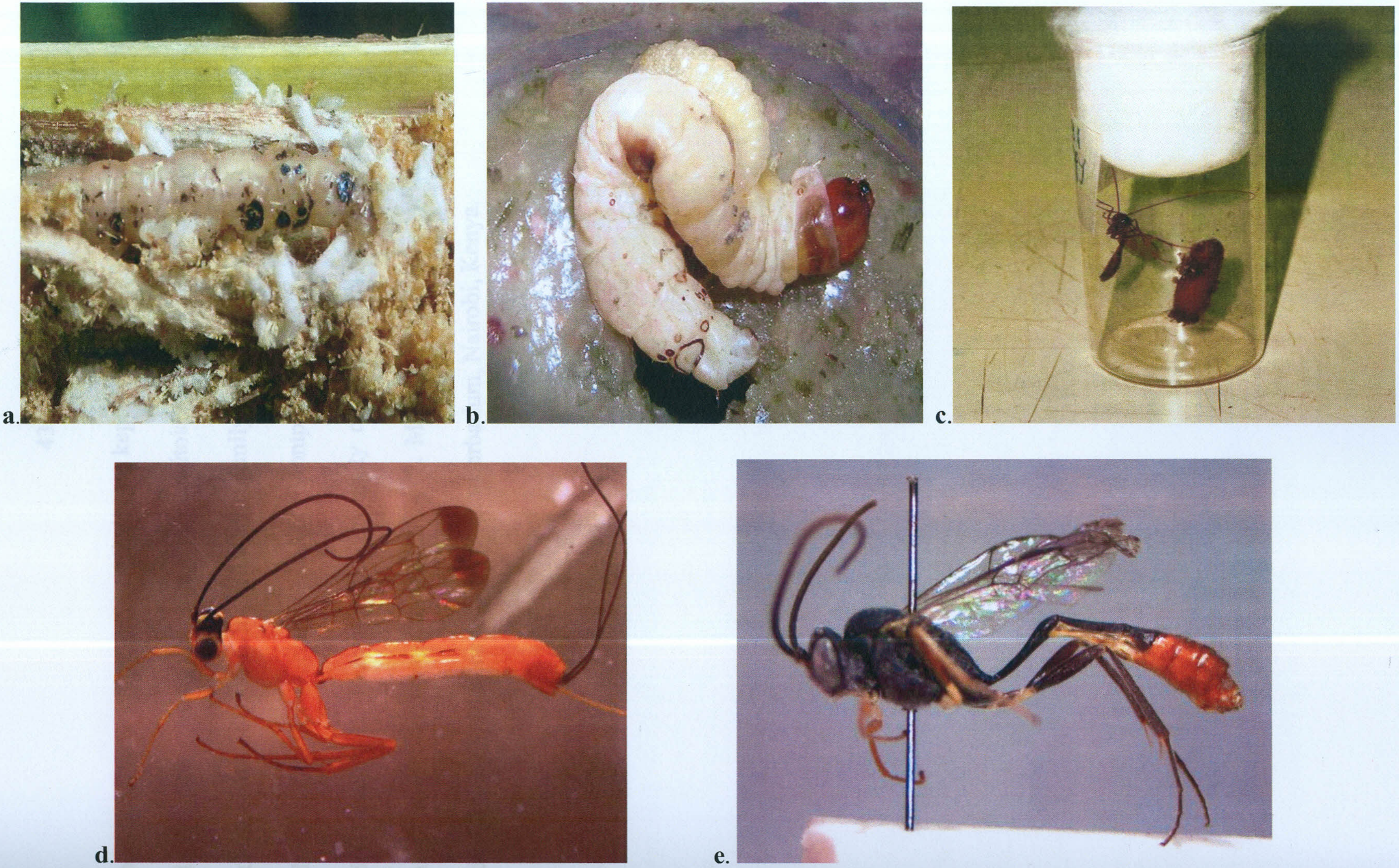

Plate 3.7: Pictures of parasitoids. (a and b) parasitoid larvae emerged from stem borer larvae, (c) an adult parasitoid emerged from a pupal case and (d and e) wet and dry adult parasitoid specimens

specimens were either preserved dry or kept in 70 and 100% alcohol (Plate 3.7d,e). Identifications of stem borers and parasitoids were conducted to species level where possible, or otherwise to genera or family levels. Hymenopteran parasitoids were identified by G. Delvare, CIRAD, Montpellier, France. Dipteran parasitoids were identified by D. Barraclough, University of KwaZulu-Natal, Durban, South Africa. Adult stem borers were identified by P. Moyal, IRD, France. Wild host plants were identified by S. Muthenge, East Africa Herbarium, Nairobi, Kenya.

CHAPTER FOUR

DIVERSITY, HOST RANGES AND MULTITROPHIC INTERACTIONS OF STEM BORER PARASITOIDS

4.1 Introduction

In sub-Saharan Africa, cereal crops are mainly grown at subsistence level by resource-poor farmers. The bulk of cereal fields are usually small and surrounded by patches of natural habitats that habour wild host plants (i.e., grasses and sedges) of cereal stem borer pests. Lepidopteran stem borers, amongst others, are the major biotic constraints to increased cereal production (Polaszek, 1998) and have been reported to cause losses ranging between 5% and 73% of potential crop yield (Seshu Reddy and Walker, 1990; De Groote, 2002; De Groote *et al.*, 2003). In Kenya, the species diversity of stem borer parasitoids has been intensively studied in cultivated habitats. Where at least 85 species of parasitoids have been reported attacking seven species of stem borer pests on maize and cultivated sorghum (Mohyuddin and Greathead, 1970; Bonhof *et al.*, 1997; Zhou *et al.*, 2003). On the contrary, inspite of the high diversity of stem borer species on wild host plants (Le Ru *et al.*, 2006a,b), only ten species of parasitoids have been reported attacking six other species of stem borers on ten species of wild host plants (Khan *et al.*, 1997a; Overholt *et al.*, 1997; Polaszek and Khan, 1998; Conlong, 2000; Songa *et al.*, 2002). In view of the high diversity of stem borers living in natural habitats, parasitoid diversity has likely been underestimated.

Though lepidopteran stem borers have been an important subject of study for the past 50 years (Polaszek, 1998), the role of natural habitats on stem borer parasitoid diversity remain unclear. Currently, some scientists suggest that stem borer parasitoids can persist and increase their populations across season in natural habitats (Khan *et al.*, 1997a; Schulthess *et al.*, 1997; Bonhof *et al.*, 2001; Muturi *et al.*, 2005), arguing that wild host plants adjacent to cultivated crops provide important refuge and food resources such as pollen and nectar for parasitoids to sustain their populations during non-cropping seasons. Having been reported that parasitoids develop and function in a multitrophic context (Landis *et al.*, 2000, 2005; Wilkinson and Landis, 2005; Bianchi *et al.*, 2006), it is crucial to understand the diversity and ecology of stem borer parasitoids in the context of both cultivated and natural habitats. Moreover, future design of successful sustainable stem borer pest management strategies would require sufficient knowledge of not only parasitoid species diversity, but also their host ranges and multitrophic interactions in cultivated and natural habitats. The focus of this study was (1) to provide a catalogue of stem borer parasitoid species, along with their stem borer and host plant ranges in cultivated and natural habitats, (2) to assess the diversity of stem borer parasitoids on different stem borer and host plant genera or families and (3) to assess the diversity of stem borer parasitoids in cultivated and natural habitats in different agroecological zones, and also during different seasons.

4.2 Materials and methods

4.2.1 Field survey

Field surveys were carried out in 4 localities in Kenya: Kakamega, Mtito Andei, Muhaka and Suam, all found in different AEZs as described in Chapter 3 sub-section 3.1. Surveys were conducted during both dry and rainy seasons from December 2005 to

December 2007. Random sampling method was applied in cultivated habitats, while both random and non-random sampling methods were applied in natural habitats, respectively. Details are provided in Chapter 3 sub-section 3.2.

4.2.2 Stem borer parasitoid recovery and their identification

Infested cereal and wild host plants were destructively sampled in the field. Stem borer larvae collected were transported to the laboratory and reared on artificial diet. All stem borer pupae and parasitoid cocoons or puparia recovered were kept in separate vials until the emergence of adults. The details are provided in Chapter 3 sub-section 3.3. Additionally, parasitoids, stem borers and host plants collected were identified to species level where possible, or else to genera or family levels as described in Chapter 3 sub-section 3.3.

4.2.3 Data analyses

Due to scarcity of data for some species, parasitoid data obtained from various stem borer and host plant species were pooled according to their respective genera for appropriate analysis or presentation. The Shannon diversity index (*H'*) which takes into account the number of species (species richness) and their relative abundance (equitability) was used to compute parasitoid species diversity in cultivated and natural habitats (Magurran, 1988):

$$H' = -\Sigma\, Pi ln Pi$$

where *i* is the parasitoid species, *Pi* is the proportional abundance of the *i*th species and *ln* is the natural logarithm.

Because the Shannon diversity index is inappropriate for estimating species diversity when species richness is extremely low, the index was used only in cases where parasitoid species richness was $\geq$ five. *t*-tests were used to examine differences in parasitoid species diversity in cultivated and natural habitats on different stem borer or host plants genera and families (pooled data), in each locality (pooled data) and during different seasons (pooled data) (Magurran, 1988). Significance was set at $P \leq 0.05$. However, this test was not performed for host plant genera or families that did not occur in both habitats. Additionally, differences in stem borer parasitoid species composition in cultivated and natural habitats was compared by calculating the Morista-Horn index (C_{mH}) (Magurran, 1988):

$$C_{mH} = [2\Sigma(n_{ia}\, n_{ib})]/[(d_a + d_b)\, N_a N_b]$$

where N_a and N_b are the total number of individuals in cultivated and natural habitats, respectively; n_{ia} and n_{ib} are number of individuals of a particular species i in cultivated and natural habitats, respectively; $d_a = \Sigma\, n_{ia}^2/N_a^2$ and $d_b = \Sigma\, n_{ib}^2 / N_b^2$. High values of C_{mH} indicate increasing similarity between the two habitats, with a maximum of 1.

4.3 Results

4.3.1 Parasitoid species composition

During the two years field surveys, 7443 and 3676 stem borers were collected from cultivated and natural habitats, respectively. A total of 33 parasitoid species were recovered (Table 4.1). In cultivated habitats, 18 species of parasitoids (eleven larval and seven pupal parasitoids) were recovered from six species of stem borers feeding on

Table 4.1: Parasitoids recovered from lepidopteran stem borers feeding on cereal and wild host plants

Parasitoid species	H	L	Season	Stem borer species	Host plant species	BS	IB	FS	PA	AS
Hymenoptera										
Bethylidae										
Goniozus indicus Ashmead	C	Su	Ds	Bf (1)	Zm	L	i	Ec	G	IS
	C	Ma	Sr	Cp (1)	Zm					
	N	Mu	Sr	Em (1)	Re					
Braconidae										
Bracon sp.	N	Ma	Sr	Sn (1)	Cs	L	i	Ec	G	DS
Bracon sesamiae Cameron	C	Ka	Sr	Bp (1)	Zm	L	i	Ec	G	DS
	N	Ka	Lr	Bnsp1 (1)	Sm					
	N	Su	Lr	Sc (1)	Si					
Chelonus curvimaculatus Cameron	C	Ma	Sr	Cp (4)	Sb, Zm	L	k	En	S	DA
	N	Ka	Sr	Bnsp1 (1)	Sm					
	N	Mu	Sr	Cp (2)	Pp					
Cotesia flavipes Cameron	C	Ma	Ds,Sr	Cp (121), Sc (7)	Sb, Zm	L	k	En	G	IS
	C	Mu	Lr,Sr	Cp (117), Sc (18)	Sb, Zm					
	N	Ma	Sr	Cp (1)	Sa					
	N	Mu	Lr,Sr	Cp (16)	Sa					
Cotesia sesamiae (Cameron)	C	Ka	Ds,Lr,Sr	Bf (76), Bp (12), Sc (7)	Sb, Zm	L	k	En	G	IS
	C	Su	Lr	Bf (90), Sc (2)	Sb, Zm					
	N	Ka	Sr	Bp (1)	Pm					
	N	Su	Lr	Bf (1)	Sa					
Cotesia sp.	N	Ka	Lr	Snsp9 (3)	Cp	L	k	En	G	IS
Dolichogenidea polaszeki Walker	C	Su	Lr	Bf (5)	Zm	L	k	En	S	IS
	N	Ka	Lr	Snsp9 (1)	Cp					
	N	Ma	Sr	Cp (1)	Sa					
Iphiaulax pilisoma van Achterberg	N	Mu	Sr	Em (1)	Re	L	i	Ec	S	WS

Parasitoid species	H	L	Season	Stem borer species	Host plant species	BS	IB	FS	PA	AS
Macrocentrus sp.	N	Mu	Ds	Tr (1)	Cr	L	k	En	S/G	PS
Apanteles fuscivorus (Walker)	N	Ka	Sr	N (1)	Pp	L	k	En	G	IS
Ceraphronidae										
Aphanogmus fijiensis (Ferrière)	C	Su	Lr	Bf (3)	Sb	L	i	Ec	S	IS
	C	Mu	Sr	Cp (1)	Zm					
Eurytomidae										
Pediobius furvus Gahan	C	Su	Lr	Bf (1)	Zm	P	i	En	G	IS
	C	Mu	Sr	Cp (2), Sc (1)	Zm					
	N	Ka	Lr	Snsp9 (2)	Cp					
	N	Ma	Sr	Sn (1)	Td					
Tetrastichus sp.	C	Su	Ds	Bf (1)	Zm	P	i	En	G	IS
Ichneumonidae										
Amouramorpha sp.	N	Ka	Lr	Tr (1)	Cd	L	i	Ec	S	PS
Dentichasmias busseolae Heinrich	C	Ma	Sr	Cp(1)	Zm	P	i	En	S	IS
Enicospilus ruscus Gauld & Mitchell	N	Ka	Sr,Lr	Snsp9 (17)	Cp, Sm	L	k	En	S	?
Enicospilus antefurcalis Szépligeti	N	Ka	Ds	Bnsp1 (1)	Sm	L	k	En	S	?
Gambroides nimbipennis Seyrig	C	Mu	Lr	Cp (1)	Zm	P	i	En	S	PS?
Ichneumoninae 1	N	Ka	Lr	Bnsp1 (1)	Sm	L	?	En	S	?
Ichneumoninae 2	N	Ka	Lr	? (1)	Sm	P	?	En	S	?
Ichneumoninae 3	N	Su	Sr	C (1)	Ec	L	?	En	S	?
Ichneumoninae 4	C	Su	Lr	Bf (1)	Zm	P	?	En	S	?
Procerochasmias nigromaculatus Cameron	C	Su	Ds,Lr	Bf (3)	Zm	P	i	En	S	IS
Pristomerus nr. bullis Fitton	N	Mu	Lr	Em (5)	Re	L	k	En	S	PS
Syzeuctus ruberrimus Benoist	N	Mu	Ds,Lr,Sr	Co (18)	Pm	L	k	En	S	PS
Unidentified Genera nr. Bathyplectes	N	Su	Lr	Scn (1)	Pt	L	?	En	S	?

Parasitoid species	**H**	**L**	**Season**	**Stem borer species**	**Host plant species**	**BS**	**IB**	**FS**	**PA**	**AS**
Venturia sp.	N	Su	Lr	C (1), Scn (1)	Ec, Pt	L	k	En	S	PS
Xanthopimpla stemmator (Thunberg)	C	Ma	Ds	Cp (2)	Sb	P	i	En	S	DS
	C	Mu	Lr,Sr	Cp (4)	Zm					
	N	Mu	Lr,Sr	Co (1), Em (1), Mn (1)	Pm, Re					
Diptera										
Tachinidae										
Linnaemyia sp.	C	Ka	Sr	Bf (3)	Zm	L	k	En	S	PI
	C	Su	Lr	Bf (1)	Zm					
	N	Ka	Ds,Lr,Sr	Bnsp1 (4), Bp (4)	Sm, Pm					
	N	Su	Lr	Bf (1), Scp (1)	Sa, Pc					
Metoposisyrops sesamiae Mesnil	C	Ma	Sr	Cp (2)	Zm	L	k	En	S	PI
	N	Ma	Sr	Co (1), Cp (2), Em (1), Sn (4), Sp (2)	Ci, Cs, Pm, Re, Sa, Td					
Siphona sp.	C	Ka	Ds,Lr,Rs	Bf (16), Bp (6), Sc (29)	Sb, Zm	L	k	En	S/G	PI
	C	Su	Lr	Bf (34)	Sb, Zm					
	C	Mu	Sr	Cp (3), Sc (1)	Zm					
	N	Ka	Ds,Lr,Sr	Bnsp1 (1), Bp (2), Msp (1), Scn (1), Scp (2)	Em, Pc, Pm, Pp, Sm					
	N	Su	Lr	Bf (1), Scn (2)	Pt, Sa					
	N	Mu	Lr	Scnsp3 (1)	Eh					
Sturmiopsis parasitica (Curran)	C	Mu	Lr	Cp (6)	Zm	L	k	En	S/G	PI
	N	Mu	Sr	Co (4), Csp (1)	Cr, Pm					

H = Habitat; C = Cultivated, N = Natural.
L = Locality; Ka = Kakamega, Ma = Mtito Andei, Mu = Muhaka, Su = Suam.
Ds = Dry season, Lr = Long rains, Sr = Short rains.

Bf = *Busseola fusca*, Bnsp.1 = *Busseola s.l. nov* sp.1, Bp = *Busseola phaia*, C = Crambidae, Co = *Chilo orichalcociliellus*, Cp = *Chilo partellus*, Csp = *Chilo* sp., Em = *Ematheudes* sp., Ichneumoninae 1/2/3/4, Mn = *Manga nubifera*, Msp. = Manga sp., N = Noctuidae, Sc = *Sesamia calamistis*, Scn = *Sciomesa nyei*, Scnsp.3 = *Sciomesa nov* sp.3, Scp = *Sciomesa piscator*, Sn = *Sesamia nonagrioides*, Snsp.9 = *Sesamia nov* sp.9, Sp = *Sesamia poephaga*, Tr = Tortricidae.

In parenthesis are numbers of specimen recovered.

Ca = *Cynodon aethiopicus*, Cd = *Cyperus dichroostachyus*, Ci = *C. involucratus*, Cs = *C. distans*, Cv = *C. dives*, Cp = *C. papyrus*, Cr = *C. rotundus*, Ec = *Eleusine corocana*, Eh = *Echinochloa haploclada*, Em = *Euclaena mexicana*, Pc = *Pennisetum macrourum*, Pm = *Panicum maximum*, Pp = *P. purpureum*, Pt = *P. trachyphyllum*, Re = *Rottboellia exaltata*, Sa = *Sorghum arundinaceum*, Sb = *S. bicolor*, Si = *Setaria incrassata*, Sm = *S. megaphylla*, Td = *Typha domingensis*, Zm = *Zea mays*.

BS = Borer growth stage; L = Larva, P = Pupa.
IB = Interaction with borer; i = idiobiont, k = koinobiont.
FS = Feeding site; Ec = Ectoparasite, En = Endoparasite.
PA = Progeny allocation; G = Gregarious, S = Solitary.
AS = Attack strategy; DA = Direct attack, DS = Drill-and-sting, IS = Ingress-and-sting, PI = Planidial ingress, PS = Probe-and-sting, WS = Wait-and-sting.

maize and cultivated sorghum, while in natural habitats, 27 species (twenty-four larval and three pupal parasitoids) were recovered from 21 species of stem borers feeding on 19 species of wild host plants. Not a single parasitoid was recovered from an additional 11 species of stem borers obtained from 19 other wild host plant species. Only four species of dipteran parasitoids were recovered from stem borers in both cultivated and natural habitats. Koinobiont parasitoid richness was highest on stem borer larvae in both cultivated (73%) and natural (73%) habitats. By contrast, idiobiont parasitoid richness was highest on sessile pupae in both cultivated (100%) and natural (100%) habitats. The number of endoparasitic species was three and four times higher than ectoparasitic species in cultivated and natural habitats, respectively. In cultivated habitats, the ingress-and-sting (59%) attack was the most common strategy utilized by parasitoids, followed by the planidial ingress (23%), drill-and-sting (12%) and direct attack (6%) methods. However, more attack methods were utilized by parasitoids in natural habitats, with the ingress-and-sting (43%) method being the most common strategy, followed by the planidial ingress (24%), drill-and-sting (14%), direct attack (9%), probe-and-sting (5%) and wait-and-sting (5%) methods. About 52% and 39% of the parasitoid species found in cultivated and natural habitats, respectively, were strictly solitary species, while 22% and 28% other species were both solitary and gregarious in cultivated and natural habitats, respectively. Majority of the parasitoid species were recovered during the rainy season. Only 5% and 7% of parasitoid species were recovered during the dry season in cultivated and natural habitats, respectively. Most parasitoid species were found in one or two AEZ(s). Only *P. furvus* was recovered from all four AEZs.

4.3.2 Parasitoid species diversity on stem borers and host plants in different localities and seasons

Parasitoid and stem borer diversity, richness and abundance varied with habitat type on different stem borer families (Tables 4.2a,b,c) and genera (Tables 4.3a,b,c). Noctuidae and Crambidae were the only families that were heavily parasitized (Tables 4.2a,b,c). For these two families, parasitoid diversity was significantly higher in natural than in cultivated habitats (Tables 4.2a,b,c). *Chilo*, *Busseola* and *Sesamia* species were the major stem borer genera found in both cultivated and natural habitats (Tables 4.3a,b,c). For these genera, parasitoid diversity was significantly higher in natural than in cultivated habitats (Tables 4.3a,b,c).

The results of parasitoid and stem borer diversity, richness, abundance and average densities in cultivated and natural habitats on different host plant families and genera are provided in Tables 4.4a,b,c,d and Tables 4.5 a,b,c,d, respectively. Only host plants belonging to the family Poaceae occurred in both cultivated and natural habitats, and parasitoid diversity was significantly higher in natural than in cultivated habitats (Tables 4.4a,b,c,d). In addition, on the same plant family, parasitoid species and individuals utilizing the ingress-and-sting attack method were more than those utilizing other attack strategies. Among host plant genera, only *Sorghum* spp. occurred in both cultivated and natural habitats. However, parasitoid diversity on *Sorghum* spp. was not significantly different in both habitats (Table 4.5a,b,c,d).

Table 4.2a: Diversity of parasitoids recovered from four stem borer families in cultivated and natural habitats (pooled data, 2005-2007)

Parasitoid diversity / abundance	**Stem borer family**							
	Noctuidae		**Crambidae**		**Pyralidae**		**Tortricidae**	
	Cultivated	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Species richness (*S*)	11	19	11	9	2	6	0	2
Number of individuals (*N*)	322	67	271	54	2	11	0	2
Shannon diversity index (*H'*)	1.19	2.37	0.62	1.61	-	1.42	-	-
t-test (*H'* between habitats)	8.72		6.58		-		-	
P-value	<0.001		<0.001		-		-	
Morista-Horn Index (C_{mH})	0.24		0.53		-		-	

Table 4.2b: Species richness and abundance of parasitoids recovered from four stem borer families in cultivated and natural habitats (pooled data, 2005-2007)

	Parasitoid		Stem borer family							
Order	**Family**		**Noctuidae**		**Crambidae**		**Pyralidae**		**Tortricidae**	
			Cultivated	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Hymenoptera	Braconidae	Richness	4	7	2	3	1	1	0	1
		Abundance	221	12	243	22	2	1	0	1
	Ichneumonidae	Richness	1	8	3	4	0	3	0	1
		Abundance	3	25	10	24	0	8	0	1
	Others	Richness	4	1	3	0	0	1	0	0
		Abundance	8	3	7	0	0	1	0	0
	Total	Richness	9	16	8	7	1	5	0	2
		Abundance	232	40	260	46	2	10	0	2
Diptera	Tachinidae	Richness	2	3	3	2	1	1	0	0
		Abundance	90	27	11	8	1	1	0	0
			Parasitoid interaction with host							
	Idiobionts	Richness	6	7	6	1	0	3	0	1
		Abundance	12	10	17	1	0	3	0	1
	Koinobionts	Richness	5	11	5	7	2	3	0	1
		Abundance	310	56	254	52	3	8	0	1

Table 4.2c: Species richness and abundance of stem borers recovered from four families in cultivated and natural habitats (pooled data, 2005-2007)

Stem borer richness / abundance	Stem borer family							
	Noctuidae		Crambidae		Pyralidae		Tortricidae	
	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural
Richness	4	22	2	5	1	3	0	1
Abundance	3601	1809	3897	1911	23	240	0	19

Table 4.3a: **Diversity of parasitoids recovered from three stem borer genera in cultivated and natural habitats (pooled data, 2005-2007)**

Parasitoid diversity / abundance	**Stem borer genera**							
	Busseola		***Sesamia***		***Chilo***		**Others**	
	Cultivated	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Species richness (*S*)	10	10	5	8	11	7	2	13
Number of individuals (*N*)	256	25	66	30	270	52	2	26
Shannon diversity index (*H'*)	0.91	1.93	1.13	1.59	0.62	1.47	-	2.21
t-test (*H'* between habitats)	4.54		2.56		6.13		-	
P-value	< 0.001		0.02		< 0.001		-	
Morista-Horn Index (C_{mH})	0.26		0.01		0.54		-	

Table 4.3b: Species richness and abundance of parasitoids recovered from three stem borer genera in cultivated and natural habitats (pooled data, 2005-2007)

Parasitoid			Stem borer genera							
Order	**Family**		***Busseola***		***Sesamia***		***Chilo***		**Others**	
			Cultivated	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Hymenoptera	Braconidae	Richness	3	4	2	5	2	3	1	2
		Abundance	187	5	34	7	242	22	2	2
	Ichneumonidae	Richness	1	4	0	1	4	2	0	7
		Abundance	3	7	0	14	14	22	0	14
	Others	Richness	4	0	2	1	2	0	0	1
		Abundance	6	0	2	3	3	0	0	1
	Total	Richness	8	8	4	7	8	5	1	10
		Abundance	196	12	36	24	259	44	2	17
Diptera	Tachinidae	Richness	2	2	1	1	3	2	1	3
		Abundance	60	13	30	6	11	8	1	9
			Parasitoid interaction with host							
	Idiobionts	Richness	6	2	2	3	6	1	0	5
		Abundance	10	2	2	5	17	1	0	6
	Koinobionts	Richness	4	7	3	5	5	6	0	7
		Abundance	246	22	64	25	253	51	0	19

Table 4.3c: Species richness and abundance of stem borers recovered from three stem borer genera in cultivated and natural habitats (pooled data, 2005-2007)

Stem borer richness / abundance	Stem borer genera							
	Busseola		*Sesamia*		*Chilo*		Others	
	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural
Richness	2	4	1	8	2	3	1	15
Abundance	2626	465	959	636	3897	1900	16	812

Table 4.4a: Diversity of stem borer parasitoids recovered from three host plant families in cultivated or natural habitats (pooled data, 2005-2007)

Parasitoid diversity / abundance	**Host plant family**			
	Poaceae		**Cyperaceae**	**Typhaceae**
	Cultivated	**Natural**	**Cultivated**	**Natural**
Species richness (*S*)	17	23	10	2
Number of individuals (*N*)	595	104	27	3
Density per plant/tiller	0.18	0.03	0.08	0.02
Shannon diversity index (*H'*)	1.43	2.59	1.70	-
t-test (*H'* between habitats)	11.24		-	-
P-value	< 0.001		-	-
Morista-Horn Index (C_{mH})	0.45		-	-

Table 4.4b: Species richness and abundance of stem borer parasitoids recovered from three host plant families in cultivated or natural habitats (pooled data, 2005-2007)

Parasitoid			Host plant family			
Order	**Family**		**Poaceae**		**Cyperaceae**	**Typhaceae**
			Cultivated	**Natural**	**Natural**	**Natural**
Hymenoptera	Braconidae	Richness	5	7	5	0
		Abundance	465	29	7	0
	Ichneumonidae	Richness	4	11	2	0
		Abundance	13	43	15	0
	Others	Richness	4	1	1	1
		Abundance	15	1	2	1
	Total	Richness	13	19	8	1
		Abundance	493	73	24	1
Diptera	Tachinidae	Richness	4	4	2	1
		Abundance	102	31	3	2
		Parasitoid interaction with host				
	Idiobionts	Richness	9	9	3	1
		Abundance	29	12	4	1
	Koinobionts	Richness	8	14	7	1
		Abundance	566	92	23	2

Table 4.4c: Attack strategies utilized by parasitoids on stem borers found in three host plant families in cultivated or natural habitats (pooled data, 2005-2007)

Parasitoid attack strategy		Host plant families			
		Poaceae		Cyperaceae	Typhaceae
		Cultivated	Natural	Natural	Natural
Direct attack	Richness	1	2	0	0
	Abundance	4	7	0	0
Drill and sting	Richness	2	2	1	0
	Abundance	7	5	1	0
Ingress and sting	Richness	10	7	5	1
	Abundance	482	60	21	1
Planidial ingress	Richness	4	4	2	1
	Abundance	102	31	3	2
Probe and sting	Richness	0	0	1	0
	Abundance	0	0	1	0
Wait and sting	Richness	0	1	0	0
	Abundance	0	1	0	0

Table 4.4d: Species richness and abundance of stem borers recovered from three host plant families in cultivated or natural habitats (pooled data, 2005-2007)

Stem borer richness / abundance	Host plant families			
	Poaceae		Cyperaceae	Typhaceae
	Cultivated	Natural	Cultivated	Natural
Richness	7	29	11	2
Abundance	7446	3178	343	131
Density per plant/tiller	2.54	0.98	0.75	0.56

Table 4.5a: Diversity of stem borer parasitoids recovered from six host plant genera in cultivated or natural habitats (pooled data, 2005-2007)

Parasitoid diversity / abundance	Host plant genera							
	Sorghum		*Zea*	*Cyperus*	*Panicum*	*Pennisetum*	*Setaria*	Others
	Cultivated	Natural	Cultivated	Natural	Natural	Natural	Natural	Natural
Species richness (*S*)	6	6	18	10	7	6	8	10
Number of individuals (*N*)	70	23	525	27	35	15	15	18
Density per plant/tiller	0.09	0.07	0.17	0.08	0.02	0.02	0.04	0.02
Shannon diversity index (*H'*)	1.27	0.98	1.44	1.70	1.35	1.58	1.88	2.03
t-test (*H'* between habitats)	1.13		-	-	-	-	-	-
P-value	0.20		-	-	-	-	-	-
Morista-Horn Index (C_{mH})	0.71		-	-	-	-	-	-

Table 4.5b: Species richness and abundance of stem borer parasitoids recovered from six host plant genera in cultivated or natural habitats (pooled data, 2005-2007)

	Parasitoid		**Host plant genera**							
Order	**Family**		***Sorghum***		***Zea***	***Cyperus***	***Panicum***	***Pennisetum***	***Setaria***	**Others**
			Cultivated	**Natural**	**Cultivated**	**Natural**	**Natural**	**Natural**	**Natural**	**Natural**
Hymenoptera	Braconidae	Richness	3	3	5	5	1	2	2	1
		Abundance	57	19	408	7	1	5	3	1
	Ichneumonidae	Richness	1	0	5	2	2	2	4	5
		Abundance	2	0	12	15	23	2	7	10
	Others	Richness	1	0	4	1	0	0	0	2
		Abundance	3	0	12	2	0	0	0	2
	Total	Richness	5	3	14	8	3	4	6	8
		Abundance	62	19	432	24	24	7	10	13
Diptera	Tachinidae	Richness	1	3	4	2	4	2	2	2
		Abundance	8	4	93	3	11	8	5	5
			Parasitoid interaction with host							
	Idiobionts	Richness	2	0	10	3	1	1	2	4
		Abundance	5	0	25	4	2	1	3	4
	Koinobionts	Richness	4	6	8	7	6	5	5	5
		Abundance	65	23	500	23	33	14	11	13

Table 4.5c: Attack strategies utilized by parasitoids on stem borers found in six host plant genera in cultivated or natural habitats (pooled data, 2005-2007)

Parasitoid attack strategy		**Host plant genera**							
		Sorghum		***Zea***	***Cyperus***	***Panicum***	***Pennisetum***	***Setaria***	**Others**
		Cultivated	**Natural**	**Cultivated**	**Natural**	**Natural**	**Natural**	**Natural**	**Natural**
Direct attack	Richness	1	0	1	0	0	2	1	1
	Abundance	1	0	3	0	0	5	1	1
Drill and sting	Richness	1	0	2	1	1	0	1	1
	Abundance	2	0	5	1	2	0	2	1
Ingress and sting	Richness	3	3	10	5	1	1	2	2
	Abundance	59	19	431	21	1	1	5	2
Planidial ingress	Richness	1	3	4	2	3	2	2	2
	Abundance	8	4	93	3	11	8	5	5
Probe and sting	Richness	0	0	0	1	0	0	0	0
	Abundance	0	0	0	1	0	0	0	0
Wait and sting	Richness	0	0	0	0	0	0	0	1
	Abundance	0	0	0	0	0	0	0	1

Table 4.5d: Species richness and abundance of stem borers recovered from six host plant genera in cultivated or natural habitats (pooled data, 2005-2007)

Stem borer richness / abundance	**Host plant genera**							
	Sorghum		***Zea***	***Cyperus***	***Panicum***	***Pennisetum***	***Setaria***	**Others**
	Cultivated	**Natural**	**Cultivated**	**Natural**	**Natural**	**Natural**	**Natural**	**Natural**
Richness	5	6	6	10	10	12	4	19
Abundance	776	495	6665	231	1382	267	398	879
Density per plant/tiller	1.86	1.13	2.48	0.87	1.08	0.87	2.11	0.70

Parasitoid and stem borer diversity, richness and abundance varied with habitat type in different localities (both individual localities and all localities pooled together) (Tables 4.6a,b,c) or during different seasons (both separate seasons within each locality and pooled data for all localities) (Tables 4.7a,b). Within each and across all localities, parasitoid diversity was significantly higher in natural than in cultivated habitats (Table 4.6a,b,c). Although parasitoid and stem borer diversity/richness and abundance varied with habitat type during different seasons (Table 4.7a,b,c,d,e,f), for pooled data, parasitoid diversity was significantly higher in natural than in cultivated habitats during both dry and rainy seasons (Table 4.7a). In a similar trend, with the exception of Kakamega, parasitoid diversity was significantly higher in natural than in cultivated habitats during the rainy season in all localities (Table 4.7d).

Table 4.6a: Diversity of stem borer parasitoids recovered from cultivated and natural habitats in four AEZs (pooled data, 2005-2007)

Parasitoid diversity and abundance	**Locality**									
	Suam		**Kakamega**		**Mtito Andei**		**Muhaka**		**Total**	
	Cultivated	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Species richness (*S*)	10	7	5	14	6	5	8	10	18	27
Number of individuals (*N*)	144	11	154	48	140	14	158	60	596	133
Shannon diversity index (*H'*)	1.07	1.85	0.81	2.03	0.43	0.99	0.65	1.76	1.44	2.75
t-test (*H'* between habitats)	6.35		7.69		2.60		7.34		14.15	
P-value	< 0.001		< 0.001		0.05		< 0.001		< 0.001	
Morista-Horn Index (C_{mH})	0.38		0.19		0.11		0.48		0.36	

Table 4.6b: Species richness and abundance of stem borer parasitoids recovered from cultivated and natural habitats in four AEZs (pooled data, 2005-2007)

Parasitoid			Locality									
Order	**Family**		**Suam**		**Kakamega**		**Mtito Andei**		**Muhaka**		**Total**	
			Cultivated	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Hymenoptera	Braconidae	Richness	2	2	2	6	2	3	1	4	5	10
		Abundance	99	2	98	9	132	3	136	22	465	36
	Ichneumonidae	Richness	2	3	0	5	2	0	3	3	5	11
		Abundance	4	4	0	22	4	0	6	31	14	57
	Others	Richness	4	0	1	1	1	1	2	1	4	2
		Abundance	6	0	1	2	2	1	6	1	15	4
	Total	Richness	8	5	3	12	5	4	6	8	14	23
		Abundance	109	6	99	33	138	4	148	54	494	97
Diptera	Tachinidae	Richness	2	2	2	2	1	1	2	2	4	4
		Abundance	35	5	55	15	2	10	10	6	102	36

Table 4.6c: Species richness and abundance of stem borers recovered in cultivated and natural habitats in four AEZs (pooled data, 2005-2007)

Stem borer richness / abundance	**Locality**									
	Suam		**Kakamega**		**Mtito Andei**		**Muhaka**		**Total**	
	Cultivated	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Richness	3	9	5	13	2	13	3	11	7	32
Abundance	1763	380	1001	839	983	621	3696	1836	7443	3676

Table 4.7a: Diversity of stem borer parasitoids recovered during rainy and dry seasons in cultivated and natural habitats (pooled data according to season for all localities, 2005-2007)

Parasitoid diversity / abundance	**Season**			
	Rainy		**Dry**	
	Cultivated	**Natural**	**Cultivated**	**Natural**
Species richness (*S*)	17	24	9	11
Number of individuals (*N*)	455	103	141	30
Shannon diversity index (H')	1.47	2.69	1.20	2.15
t-test (H' between habitats)	12.09		6.73	
P-value	< 0.001		< 0.001	
Morista-Horn Index (C_{mH})	0.37		0.24	

Table 4.7b: **Species richness and abundance of stem borer parasitoids recovered during rainy and dry seasons in cultivated and natural habitats (pooled data according to season for all localities, 2005-2007)**

Parasitoid			Season			
			Rainy		Dry	
Order	**Family**	**No. species abundance**	**Cultivated**	**Natural**	**Cultivated**	**Natural**
Hymenoptera	Braconidae	Richness	5	8	2	4
		Abundance	347	30	118	6
	Ichneumonidae	Richness	5	10	2	4
		Abundance	10	46	4	11
	Others	Richness	3	2	4	0
		Abundance	9	4	6	0
	Total	Richness	13	20	8	8
		Abundance	366	80	128	15
Diptera	Tachinidae	Richness	4	4	1	3
		Abundance	89	23	13	13

Table 4.7c: Species richness and abundance of stem borers recovered during rainy and dry seasons in cultivated and natural habitats (pooled data according to season for all localities, 2005-2007)

Stem borer richness / abundance	**Season**			
	Rainy		**Dry**	
	Cultivated	**Natural**	**Cultivated**	**Natural**
Richness	5	7	22	28
Abundance	5642	2594	1801	1082

Table 4.7d: Diversity of stem borer parasitoids recovered during rainy and dry seasons in cultivated and natural habitats (pooled data, 2005-2007)

Parasitoid diversity / abundance	Locality															
	Kakamega				Suam				Mtito Andei				Muhaka			
	Rainy		Dry		Rainy		Dry		Rainy		Dry		Rainy		Dry	
	C	N	C	N	C	N	C	N	C	N	C	N	C	N	C	N
Species richness (*S*)	4	13	3	3	8	5	6	4	5	5	3	1	7	8	4	5
Number of individuals (*N*)	126	41	28	7	116	5	28	8	112	11	28	3	101	46	57	14
Shannon diversity index (*H'*)	-	1.97	-	-	1.08	1.48	0.71	-	0.38	1.16	-	-	0.79	1.69	-	1.33
t-test (*H'* between habitats)	-		-		2.25		-		2.74		-		5.61		-	
P-value	-		-		0.05		-		0.02		-		0.001		-	
Morista-Horn Index (C_{mH})	-		-		0.01		-		0.14		-		0.81		-	

C = Cultivated habitats, N = Natural habitats

Table 4.7e: Species richness and abundance of stem borer parasitoids recovered during rainy and dry seasons in cultivated and natural habitats (pooled data, 2005-2007)

Parasitoid			Locality															
Order	Family		Suam				Kakamega				Mtito Andei				Muhaka			
			Rainy		Dry		Rainy		Dry		Rainy		Dry		Rainy		Dry	
			C	N	C	N	C	N	C	N	C	N	C	N	C	N	C	N
Hymenoptera	Braconidae	Richness	2	1	1	1	2	7	1	0	2	3	1	0	1	2	1	3
		Abundance	76	1	23	1	82	10	16	0	107	3	25	0	82	17	54	5
	Ichneumonidae	Richness	3	3	1	1	0	3	0	1	2	0	1	0	3	3	1	2
		Abundance	3	3	1	1	0	20	0	1	2	0	2	0	5	22	1	9
	Others	Richness	1	0	2	0	0	0	1	0	1	1	1	0	1	1	2	0
		Abundance	1	0	2	0	0	0	1	0	1	1	1	0	4	1	2	0
	Total	Richness	6	4	4	2	2	11	2	1	4	4	3	0	5	6	4	5
		Abundance	83	4	26	2	82	32	17	1	110	4	28	0	91	40	57	14
Diptera	Tachinidae	Richness	2	1	2	2	2	2	1	2	1	1	0	1	2	2	0	0
		Abundance	33	1	2	4	44	9	11	6	2	7	0	3	10	6	0	0

C = Cultivated habitats, N = Natural habitats

Table 4.7f: Species richness and abundance of stem borers recovered during rainy and dry seasons in cultivated and natural habitats (pooled data, 2005-2007)

Stem borer richness / abundance	**Locality**															
	Kakamega				**Suam**				**Mtito Andei**				**Muhaka**			
	Rainy		**Dry**		**Rainy**		**Dry**		**Rainy**		**Dry**		**Rainy**		**Dry**	
	C	**N**	**C**	**N**	**C**	**N**	**C**	**N**	**C**	**N**	**C**	**N**	**C**	**N**	**C**	**N**
Richness	5	13	3	5	3	10	2	3	2	8	2	14	3	12	3	8
Abundance	338	205	128	44	598	124	107	13	241	237	261	187	1144	255	298	152

C = Cultivated habitats, N = Natural habitats

4.4 Discussion

Prior to this work only ten species of stem borer parasitoids had been reported from natural habitats in Kenya (Khan *et al.*, 1997a; Overholt *et al.*, 1997; Polaszek and Khan, 1998; Conlong, 2000; Songa *et al.*, 2002), in contrast to 27 species in the present study, of which the tachinid *Siphona* sp. was the most common species. In cultivated habitats, corroborating results by Ogol *et al.* (1998) and Zhou *et al.* (2003) from Western and Coastal Kenya, respectively, *C. flavipes, C. sesamiae* and *P. furvus* were the dominant species in addition to *Siphona* sp. These results further confirmed the establishment of the exotic species *C. flavipes* in Kenya, not only in cultivated habitats as reported by Overholt *et al.* (1997) and Omwega *et al.* (2006), but also in natural habitats.

The richness of pupal parasitoids was quite high on cultivated cereals. Perhaps this is because, on cereal crops, stem borers frequently pupate inside plant stems, whereas on wild host plants, stem borers seldom pupate within plant stems, but rather on the outside, often at the bottom of plants close to the roots in the soil (B.P Le Ru, personal communication). As such, it is most probable that both the richness and abundance of pupal parasitoids is generally underestimated in natural habitats. Another possible explanation is that many more stem borers survive to pupal stage in cultivated grasses either due to high nutritive value (Ofomata *et al.*, 2000) or due to low predation rates of both parasitized and unparasitized larvae or pupae (Bonhof *et al.*, 1997). These findings revealed that *Xanthopimpla stemmator* (Thunberg) a pupal parasitoid which was not released in Kenya, was recovered for the first time parasitizing stem borers in both cultivated and natural habitats. Considering that *X. stemmator* was released in Ethiopia, Eritrea, Tanzania, Uganda and Zanzibar (C. Omwega, personal communication), it was assumed that the parasitoid might have crossed borders into Kenya from neighbouring countries.

Ndemah *et al.* (2007) in Cameroon and Matama-Kauma *et al.* (2008) in Uganda, likewise reported a high diversity of stem borer parasitoids on wild host plants. By contrast, on cultivated cereals, Zhou *et al.* (2003) reported a much higher parasitoid diversity from only the Coastal region of Kenya. Differences of parasitoid diversity at the Kenyan coast in this study and that by Zhou *et al.* (2003) might have been due to two reasons. Firstly, parasitoid diversity is not static in a given locality, and could therefore change considerably over time as their herbivoure host densities change (Menalled *et al.*, 2003). Secondly, it is very likely that the higher parasitoid species diversity recorded by Zhou *et al.* (2003) compared to what was recorded in this study was due to a longer survey duration (i.e., 8 vs 2 years, respectively) and higher stem borer host collection (i.e., 174663 vs 11119 stem borers, respectively).

The results of Bonhof *et al.* (1997) and Zhou *et al.* (2003), in conjunction with those presented here showed that the majority of species recovered are common to both cultivated and natural habitats, whereas only an unknown *Cotesia* sp. was exclusive to natural habitats. As defined by Smith *et al.* (1993), in this study, stenophagous parasitoids refered to those parasitoids that were recovered from a narrow range of host species, while monophagous parasitoids were those that were recovered from only one host species. Most of the parasitoid species recovered were stenophagous, and only four species *Cotesia* sp., *Enicospilus ruscus, Pristomerus* sp. and *Syzeuctus ruberrimus* were monophagous. The reasons for this were not clear. However, it is possible that, in addition to reduced host and habitat specificity, the availability of several alternative stem borer hosts enables parasitoids to switch between different habitats when necessary, as a survival strategy (Askew, 1994; Hoffmeister and Vidal, 1994). Further, for both habitats, more than half of the parasitoid species collected were found restricted to specific AEZ(s), indicating variability in parasitoid species composition among different AEZs. This is possibly due to differences in the stem borer host species composition (Shaw, 1994; Sheehan, 1994; Tscharntke and Brandl, 2004) or local ecological conditions (Askew and Shaw, 1986; Hawkins and Sheenan, 1994; Tscharntke and Brandl, 2004). It is also very likey that most of the parasitoid species found were near the edge of their distribution.

The lower species diversity of parasitoids in cultivated compared to natural habitats in this study was most likely due to low stem borer and host plant species diversity in cultivated habitats. In addition, regular disturbances experienced in modified habitats through agricultural practices such as land tillage, pesticides or fertilizer applications and crop harvest often alter or reduce species interactions across different trophic levels, causing parasitoids to re-colonize crop fields each growing season (Levins and Wilson, 1980; Tylianakis *et al.*, 2007). In contrast, high parasitoid diversity in natural habitats may have been supported by the presence of high stem borer species diversity in perennial habitats (Kruess, 2003; Le Ru *et al.*, 2006a,b; Ndemah *et al.*, 2007; Matama-Kauma *et al.*, 2008). Likewise, high parasitoid diversity during the cropping season in both habitats was probably due to high host plant richness and abundance, which enhance the diversity and abundance of stem borer hosts. The findings also revealed a higher diversity of parasitoids on maize than on sorghum in cultivated habitats, and thus was very likely due to the higher number of stem borers collected on maize. However, the low abundance of parasitoids in natural habitats, coupled with the fact that most parasitoid species were stenophagous, suggests that higher diversity of parasitoids on wild host plants than on cultivated cereals was supported by the availability of alternative stem borer hosts. Parasitoid diversity was high on different dominant wild host plant species with high stem borer infestation levels in various AEZs in this study in Kenya, as well as in Cameroon (Ndemah *et al*., 2007) and Uganda (Matama-Kauma *et al*., 2008). This showed that parasitoid diversity was not only varied with the local host plant species composition, but is also very likely higher on dominant host plant species harbouring higher stem borer diversity and abundance than other host plant species. Nevertheless, the abundance of parasitoids from wild host plants was lower than on cultivated cereals. This was probably due to three reasons. Firstly, since parasitoid fitness and clutch size is positively correlated to host size (Mackauer and Sequeira, 1993; Godfray, 1994; Ode, 2006; Jervis *et al.*, 2008), it is very likely that gregarious species revert to a solitary status by lowering their clutch size (Waage, 1986; Godfray, 1994) in response to the small size of stem borers encountered in wild host plants (Haile and Hofsvang, 2002; Sétamou *et al.*, 2005). This is supported by the fact that the majority of parasitoids recovered from wild host plants were solitary compared to the higher number of gregarious species recorded on cultivated cereals. Secondly, it could have been due to low fitness of parasitoids on wild host plants as a result of poor quality host (both herbivores and host plants) (Sétamou *et al.*, 2005; Ode, 2006; Jervis *et al.*, 2008). Thirdly, it might have also been due to low host availability resulting from low stem borer densities (Ndemah *et al.*, 2007; Matama-Kauma *et al.*, 2008), high stem borer larval mortality (Sétamou *et al.*, 1993) and host-finding difficulties in natural habitats (Vinson, 1976; Takabayashi *et al.*, 1991; Gauld and Gaston, 1994).

Given that the ingress-and-sting attack method was the most common attack strategy utilized by parasitoids on both cereals and wild host plants, present results contradict earlier suggestion (Hawkins *et al.*, 1987; Muturi *et al.*, 2005) that the drill-and-sting attack method would be more common on wild host plants due to ease of accessing stem borers within thin-stemmed wild plants. The differences observed in these studies might be attributed to the number of parasitoid and host plant species studied. Both Hawkins *et al.* (1987) and Muturi *et al.* (2005) conducted investigations on a single parasitoid species on at most two wild host plant species. By contrast, the current study assessed 33 parasitoid and 38 wild host plant species in natural habitats.

The observation that the stem borer parasitoid diversity was much higher in natural than in cultivated habitats, and that most parasitoids species were stenophagous, attacking several stem borer species in both habitats, implied that natural habitats surrounding cereal crops might serve as refugia for sustaining the diversity of stem borer parasitoids in adjacent cereal fields.

CHAPTER FIVE

EFFECTS OF BIOTIC AND ABIOTIC FACTORS ON PARASITOID SPECIES DIVERSITY AND STEM BORER PARASITISM

5.1 Introduction

The relationships between beneficial ecosystem services and biodiversity have been a major research goal of agroecology over the past decade (Kremen, 2005; Tscharntke *et al.*, 2005; Lindenmayer *et al.*, 2007). Natural pest regulation is reported to be influenced by the biodiversity of organisms, and that diversified landscapes hold most potential for the conservation of natural enemies and the sustenance of pest control functions (Gurr *et al.*, 2003; Altieri and Nicholls, 2004; Duffy *et al.*, 2007; Bianchi *et al.*, 2006). The reason for differences in natural pest control in simple and diverse plant communities within agroecosystems has been explained by two main hypotheses: (i) the 'Natural enemy and (ii) 'Resource concentration' hypotheses. Firstly, the 'Natural enemy hypothesis' predicts higher diversity and abundance of parasitoids and predators in more diverse or heterogeneous plant communities due to availability of alternate hosts/prey and food, leading to a reduction in herbivore populations (Root, 1973; Vandermeer, 1990). Secondly, the 'Resource concentration hypothesis' postulates that in simple monocultures or homogeneous plant communities, where host plants are concentrated in time and space, herbivores will build up their populations, while in more diverse plant communities, a reduction in pest incidence may result from impediment of herbivore movement and colonization (Tahvanainen and Root, 1972; Root, 1973). Nonetheless, it was established that increase of plant diversity in agroecosystems does not necessarily translate into increased control of herbivoure pests (Risch *et al.*, 1983; Andow, 1991;

Bianchi *et al.*, 2006). The composition and processes of ecological systems are a function of their location, physical/chemical environment, spatial context and surroundings, history and current level or type of human use (Lindenmayer *et al.*, 2007). As such, the relationship between farmland biodiversity and natural pest control cannot be generalized for different agroecosystems, but rather each system should be evaluated on a context-dependent basis for large-scale conservation of natural enemies and pest management decisions.

Parasitoid diversity and parasitism rates were shown to be higher in structurally complex landscapes composed of arable fields intermingled with non-crop habitat than in simple landscapes composed of mainly arable fields (Kruess and Tscharntke, 1994; Thies and Tscharntke, 1999; Steffan-Dewenter, 2003; Kruess, 2003; Weibull and Östman, 2003). Relatively undisturbed or perennial non-crop habitats such as field margins, fallows, hedgerows and woody vegetation in agricultural landscapes, supply parasitoids with alternative hosts, sources of food (pollen and nectar) for adults and moderate microclimate which increases parasitoid longevity, fecundity, populations and spread to surrounding crops. Also it may enhance early season abundance and parasitism rates, thus, contributing to timely herbivore pest suppression (Forman and Baudry, 1984; Dyer and Landis, 1996, 1997; Landis and Menalled, 1998; Nicholls *et al.*, 2001; Lee *et al.*, 2004).

In Kenya, lepidopteran stem borers are the most damaging group of cereal crop pests (Warui and Kuria, 1983; Seshu Reddy, 1989, 1998). Although these pests are attacked by several species of parasitoids in major cereal cropping regions (Mohyuddin and

Greathead, 1970; Mathez, 1972; Oloo, 1989; Oloo and Ogeda, 1990; Bonhof *et al.*, 1997; Zhou *et al.*, 2001, 2003), no information exists on factors that influence parasitoid species diversity/richness and function. Meanwhile, the simplification of agricultural landscapes through deforestation, agricultural land or field size enlargement, destruction of non-crop habitat, as well as excessive and frequent insecticide or fertilizer applications and inappropriate land management practices continue unabated with consequent decline of farmland biodiversity (Cohen, 2002; Muhammad and Underwood, 2004; Bai and Dent, 2006). This study assessed the effects of biotic (across trophic levels) and abiotic factors on parasitoid richness and/or abundance, and also on stem borer parasitism rates during different seasons in landscapes consisting of cultivated and natural habitats in four agroecological zones (AEZs) in Kenya.

5.2 Materials and methods

5.2.1 Landscape characteristics and data collections

From December 2005 to December 2007, field surveys were conducted in landscapes consisting of a matrix of cultivated and natural habitats in four localities Kakamega, Mtito Andei, Muhaka and Suam which fall in different AEZs (see Chapter 3 sub-section 3.1). Kakamega is a moderate cereal production region, with 43.58% of the area under cereal cultivation. Cereals were grown at subsistence level, with an average field size of 0.28 ha located in open forest patches, or scattered around non-compacted homesteads, and along forest edges and the river bank. In addition to growing *P. purpureum* for fodder, wild grass patches were numerous, mainly around crop fields or homesteads, along road sides and the river bank, with a moderate level of connection between patches. Mtito Andei is a minor cereal production region with cereals grown at subsistence level. Area under cereal cultivation was 29.33%, with an average field size of 0.37 ha mainly found surrounding sparsely populated and distant homesteads. In addition to high grazing activities, wild grass patches were very few and small, mainly existing in water trenches bordering crop fields, or in swamps and along irrigation canals, with a low level of connection between patches. Muhaka is a moderate cereal growing region, with about 11.7% of the area under cereal cultivation, and an average field size of 0.15 ha. Cereals were grown at subsistence level, in fields scattered around a more compact homestead settlement. Numerous wild grass patches were available surrounding crop fields, along major roads and around ponds, with a fairly high level of connection between grass patches. Suam is a major cereal production region, of which 62.91% of the area was under cereal cultivation mainly at commercial scale, with an average field size was of 3.40 ha. Human settlement was clearly separated from cultivated areas, with very few wild grass patches found mainly along field edges and road sides, and a very low level of connection between grass patches.

Random sampling method was applied in cultivated habitats, while both random and non-random sampling methods were applied in natural habitats as described in Chapter 3 sub-section 3.2. Temperature and rainfall records were sourced from Africa AWhere-ACT Database (2002) and the Spatial Characterization Tool - Africa (Corbett and O'Brien, 1997).

5.2.2 Parasitoid recovery and identification

Infested cereal and wild host plants were destructively sampled in the field. Stem borer larvae collected were transported to the laboratory and reared on artificial diet. All stem borer pupae and parasitoid cocoons or puparia recovered were kept in separate vials until the emergence of adults as explained in Chapter 3 sub-section 3.3. Parasitoids, stem borers and host plants collected were identified to species level where possible, or else to genera or family levels as described in Chapter 3 sub-section 3.3.

5.2.3 Statistical analyses

Parasitoid species diversity was assessed using the Shannon diversity index. The diversity indices for cultivated and natural habitats were compared using *t*-tests (Magurran, 1988). Significance was set at $P \leq 0.05$. The generalized linear model (PROC GENMODE Regression, SAS 2001), was used to analyze: (i) count data and environmental variables (parasitoid/stem borer/host plant richness and abundance, altitude, rainfall and temperature) using a Poisson error distribution with a logarithmic link function (McCullagh and Nelder, 1989), (ii) proportion data (stem borer density and parasitism rates) using a binomial error distribution with a logistic link function (Collett, 1991). The goodness of fit was evaluated using the deviance statistic (McCullagh and Nelder, 1989). Additionally, deviance statistic was used to test the effects of interaction between factors that contribute in explaining the dependent variable selected. Pearson's correlation analysis was performed to assess relationships between different components of the system. Prior to correlation analysis, insect counts were log $(x + 1)$ transformed and proportion data arcsine-transformed (Zar, 1999).

5.3 Results

5.3.1 Species diversity/richness or abundance for parasitoids, stem borers and host plants in different habitats

Species richness and abundance of parasitoids, stem borers and host plants in cultivated and natural habitats were summarized for all landscapes in Table 5.1. Host plant and stem borer richness were generally higher in natural than in cultivated habitats in all localities. The results of *t*-tests showed that parasitoid diversity was significantly higher in natural than in cultivated habitats in all localities: Kakamega ($t = 7.69$, $P < 0.001$), Mtito Andei ($t = 2.56$, $P = 0.05$), Muhaka ($t = 7.34$, $P < 0.001$) and Suam ($t = 6.35$, $P < 0.001$). In contrast, stem borer and parasitoid abundance were relatively higher in cultivated than in natural habitats.

5.3.2 Parasitoid richness

The biotic and abiotic factors affecting parasitoid richness are presented in Table 5.2 and Table 5.3, respectively. All biotic factors investigated namely stem borer richness, abundance or density and host plant richness were positively (+) correlated (Pearson's correlation) to parasitoid species richness. Across all landscapes and seasons, for cultivated habitats, with the exception of Kakamega, parasitoid richness was not significantly related to stem borer richness or abundance. By contrast, in natural habitats, parasitoid richness was mainly explained by stem borer abundance during the rainy season. Although stem borer density and its interaction with stem borer richness significantly influenced parasitoid richness, for each habitat type, this effect varied with either AEZs or between seasons within a given AEZ. Parasitoid richness was not

Table 5.1: Summary of species richness and/or abundance of parasitoids, stem borers and host plants collected during different seasons in cultivated and natural habitats.

Locality	Habitat	Parasitoids		Stem borers		Host plants	
		Rainy	Dry	Rainy	Dry	Rainy	Dry
		Richness/ Abundance	Richness/ Abundance	Richness/ Abundance	Richness/ Abundance	Richness	Richness
Kakamega	Cultivated	7/128	2/27	5/733	3/268	2	1
	Natural	14/40	3/7	13/687	5/152	31	19
Mtito Andei	Cultivated	10/128	2/27	2/489	2/494	2	2
	Natural	8/15	1/3	8/365	14/256	25	20
Muhaka	Cultivated	8/104	4/57	3/2916	3/780	2	1
	Natural	11/46	5/12	12/1246	8/590	26	18
Suam	Cultivated	7/113	5/28	3/1504	2/259	2	2
	Natural	4/4	4/6	10/296	3/84	37	34

Table 5.2: Generalized linear model results (parameter estimates and Type 3 likelihood tests) of biotic factors affecting parasitoid species richness in cultivated and natural habitats in four localities

Biotic factors	Cultivated habitats						Natural habitats					
	Rainy			Dry			Rainy			Dry		
	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*
						Kakamega						
Constant	83.54	68		25.95	27		64.08	52		16.75	14	
Stemborer richness	47.48	1	<.01	23.73	1	ns	56.18	1	0.01	16.25	1	ns
Stemborer abundance	58.17	1	<.01	16.64	1	0.02	38.53	1	<.01	6.89	1	0.01
Host plant richness	62.34	1	ns	25.65	1	ns	63.49	1	ns	12.01	1	ns
Stemborer richness * abundance	30.40	1	<.01	15.88	1	ns	35.92	1	ns	4.67	1	ns
Stemborer richness * host plant richness	46.71	1	ns	23.32	1	ns	52.5	1	ns	12.45	1	ns
Constant	24.80	43		15.96	22		59.98	40		13.04	14	
Stemborer density	23.59	1	ns	14.79	1	0.01	58.91	1	<.01	12.95	1	0.05
Stemborer richness * density	14.02	1	0.02	9.52	1	0.02	44.06	1	ns	9.62	1	ns
						Mtito Andei						
Constant	9.99	22		5.87	9		13.18	18		7.22	10	
Stemborer richness	7.31	1	ns	3.83	1	ns	13.08	1	ns	5.56	1	ns
Stemborer abundance	7.24	1	ns	4.31	1	ns	9.57	1	0.05	6.01	1	ns
Host plant richness	9.95	1	ns	4.99	1	ns	9.61	1	0.05	5.87	1	ns
Stemborer richness * abundance	5.64	1	ns	2.13	1	ns	4.36	1	ns	6.11	1	ns
Stemborer richness * host plant richness	5.41	1	ns	3.54	1	ns	3.62	1	ns	5.83	1	ns
Constant	5.31	13		3.61	9		9.53	9		6.01	9	
Stemborer density	4.98	1	ns	3.51	1	ns	9.37	1	<.01	5.87	1	ns
Stemborer richness * density	3.16	1	0.01	1.02	1	0.03	2.95	1	ns	4.16	1	ns

Table 5.2 (continued).

Biotic factors	Cultivated habitats						Natural habitats					
	Rainy			Dry			Rainy			Dry		
	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*
						Muhaka						
Constant	58.61	58		14.09	23		45.43	52		25.45	26	
Stemborer richness	57.09	1	ns	11.12	1	ns	43.35	1	ns	24.39	1	ns
Stemborer abundance	57.37	1	ns	12.36	1	ns	39.75	1	0.01	25.31	1	ns
Host plant richness	58.41	1	ns	14.09	1	ns	45.04	1	ns	25.43	1	ns
Stemborer richness * abundance	56.74	1	ns	11.04	1	ns	39.29	1	ns	24.26	1	ns
Stemborer richness * host plant richness	57.02	1	ns	11.12	1	ns	42.96	1	ns	23.83	1	ns
Constant	17.95	55		13.75	19		43.40	50		22.52	25	
Stemborer density	16.96	1	0.02	13.01	1	0.01	42.34	1	0.01	21.62	1	<.01
Stemborer richness * density	7.09	1	ns	11.07	1	ns	33.28	1	ns	13.53	1	ns
						Suam						
Constant	4.96	21		9.13	10		4.46	18		9.95	10	
Stemborer richness	4.87	1	ns	6.39	1	ns	2.56	1	ns	8.52	1	ns
Stemborer abundance	4.82	1	ns	7.17	1	ns	1.15	1	ns	8.11	1	ns
Host plant richness	4.96	1	ns	9.05	1	ns	4.12	1	ns	9.90	1	ns
Stemborer richness * abundance	4.36	1	ns	4.85	1	ns	0.89	1	ns	6.13	1	ns
Stemborer richness * host plant richness	4.54	1	ns	6.22	0	ns	0.76	1	ns	7.53	1	ns
Constant	4.68	10		7.91	10		3.36	7		6.53	7	
Stemborer density	3.61	1	ns	7.37	1	ns	3.25	1	ns	5.94	1	0.01
Stemborer richness * density	1.02	1	ns	4.37	1	ns	1.15	1	ns	3.82	1	ns

Table 5.3: Generalized linear model results (parameter estimates and Type 3 likelihood tests) of environmental variables affecting parasitoid species richness in cultivated and natural habitats across all localities.

Abiotic factors	Cultivated habitats								Natural habitats							
	Rainy				Dry				Rainy				Dry			
	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*
Constant		193.45	149			60.29	65			135.48	119			60.96	56	
Altitude	-	191.18	1	ns	-	59.86	1	ns	+	135.38	1	ns	+	59.09	1	ns
Rainfall	-	185.71	1	0.05	-	60.29	1	ns	-	135.19	1	ns	-	60.91	1	ns
Temperature	+	191.37	1	ns	+	59.25	1	ns	-	135.45	1	ns	-	57.49	1	ns
Altitude * Rainfall		177.68	1	ns		59.39	1	ns		134.76	1	ns		57.52	1	ns
Altitude * Temperature		188.53	1	ns		57.57	1	ns		135.05	1	ns		55.84	1	ns
Rainfall * Temperature		177.6	1	ns		59.15	1	ns		134.66	1	ns		55.59	1	ns

SC = SC = signs of correlation coefficient related to host plant richness in both cultivated and natural habitats, for all seasons and all AEZs, with the exception of Mtito Andei where there was slight significance. Amongst abiotic factors, only rainfall had a significantly negative effect on parasitoid richness during the rainy season in cultivated habitats, but not during the dry season.

5.3.3 Parasitoid abundance

Results of the effects of biotic and abiotic factors on parasitoid abundance are presented in Table 5.4 and Table 5.5, respectively. All biotic factors were positively (+) correlated (Pearson's correlation of transformed data) with parasitoid abundance. Across all AEZs and between seasons, parasitoid abundance was mostly affected by stem borer abundance, and to a very low extent by stem borer richness. Likewise, stem borer density and its interaction with stem borer richness showed a significantly positive effect on parasitoid abundance. However, for each habitat type, this effect varied with either AEZ or between seasons within a given AEZ. For both cultivated and natural habitats, across all AEZs and between seasons, host plant richness had a negligible effect on parasitoid abundance. Altitude, rainfall and temperature mainly influenced parasitoid abundance during the dry season in cultivated habitats, with both altitude and rainfall exerting a significantly negative effect.

Table 5.4: Generalized linear model results (parameter estimates and Type 3 likelihood tests) of biotic factors affecting parasitoid abundance in cultivated and natural habitats in four localities.

Biotic factors	Cultivated habitats						Natural habitats					
	Rainy			Dry			Rainy			Dry		
	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*
Kakamega												
Constant	338.99	68		60.32	27		162.69	52		20.79	14	
Stemborer richness	201.38	1	<.01	55.19	1	0.02	151.47	1	0.01	20.21	1	ns
Stemborer abundance	178.91	1	<.01	26.90	1	<.01	85.11	1	<.01	6.82	1	0.02
Host plant richness	238.59	1	ns	53.31	1	ns	161.0942	1	ns	15.22	1	ns
Stemborer richness * abundance	112.78	1	<.01	26.74	1	ns	81.27	1	ns	4.67	1	ns
Stemborer richness * host plant richness	183.62	1	ns	55.18	1	ns	145.529	1	ns	15.61	1	ns
Constant	24.80	43		46.93	22		59.98	40		12.56	14	
Stemborer density	24.59	1	<.01	45.01	1	0.04	56.09	1	0.04	12.17	1	0.03
Stemborer richness * density	17.78	1	0.05	36.11	1	0.01	29.17	1	0.01	9.58	1	ns
Mtito Andei												
Constant	186.67	22		40.41	9		19.85	18		9.36	10	
Stemborer richness	130.38	1	<.01	28.49	1	0.06	16.93	1	ns	7.27	1	ns
Stemborer abundance	48.31	1	<.01	21.31	1	<.01	9.31	1	0.01	8.45	1	0.01
Host plant richness	184.43	1	ns	36.32	1	0.04	9.28	1	0.01	9.32	1	ns
Stemborer richness * abundance	32.55	1	0.01	35.01	1	0.02	4.28	1	ns	6.57	1	0.05
Stemborer richness * host plant richness	102.54	1	<.01	27.26	0	ns	3.21	1	0.05	6.31	1	0.021
Constant	122.24	13		32.76	9		19.07	9		8.62	9	
Stemborer density	122.02	1	ns	31.92	1	0.02	18.52	1	ns	8.13	1	ns
Stemborer richness * density	87.43	1	0.02	18.15	1	0.01	11.93	1	0.01	4.90	1	ns

Table 5.4 (continued).

Biotic factors	Cultivated habitats						Natural habitats					
	Rainy			Dry			Rainy			Dry		
	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*
Muhaka												
Constant	222.56	58		84.29	23		78.21	52		42.83	26	
Stemborer richness	197.22	1	<.01	34.04	1	<.01	73.74	1	0.03	39.45	1	ns
Stemborer abundance	179.01	1	<.01	49.51	1	<.01	72.22	1	0.01	42.17	1	ns
Host plant richness	172.11	1	ns	84.29	1	ns	77.39	1	ns	42.72	1	ns
Stemborer richness * abundance	175.65	1	ns	30.36	1	ns	68.22	1	0.05	39.31	1	ns
Stemborer richness * host plant richness	159.23	1	ns	34.04	1	ns	72.89	1	ns	39.18	1	ns
Constant	17.95	55		32.62	19		43.40	50		38.00	25	
Stemborer density	17.31	1	0.04	32.07	1	ns	42.17	1	ns	37.99	1	<.00
Stemborer richness * density	10.04	1	ns	25.36	1	ns	23.09	1	ns	28.00	1	ns
Suam												
Constant	59.49	21		24.55	10		6.72	18		11.21	10	
Stemborer richness	56.17	1	ns	18.65	1	0.01	3.07	1	0.05	9.81	1	ns
Stemborer abundance	32.05	1	<.01	13.96	1	0.01	2.66	1	0.04	7.21	1	0.04
Host plant richness	58.58	1	ns	24.04	1	ns	6.41	1	ns	10.56	1	ns
Stemborer richness * abundance	11.40	1	0.03	9.71	1	0.04	1.71	1	ns	5.47	1	ns
Stemborer richness * host plant richness	32.29	1	<.01	18.38	1	ns	1.07	1	ns	7.51	1	ns
Constant	13.24	10		21.95	10		6.51	7		8.68	7	
Stemborer density	13.13	1	ns	20.52	1	0.04	5.11	1	ns	7.32	1	ns
Stemborer richness * density	9.54	1	<.01	11.66	1	0. 01	1.36	1	ns	6.55	1	ns

Table 5.5: Generalized linear model results (parameter estimates and Type 3 likelihood tests) of environmental variables affecting parasitoid abundance in cultivated and natural habitats across all localities

Abiotic factors	Cultivated habitats								Natural habitats							
	Rainy				Dry				Rainy				Dry			
	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*
Constant		1093.48	149			239.83	65			271.60	119			86.31	56	
Altitude	-	1068.47	1	<.01	-	229.46	1	0.01	-	271.61	1	ns	-	85.40	1	ns
Rainfall	-	976.04	1	<.01	-	220.94	1	<.01	-	271.60	1	ns	-	86.12	1	ns
Temperature	+	1082.30	1	0.03	+	237.99	1	ns	-	271.36	1	ns	-	84.07	1	ns
Altitude * Rainfall		844.42	1	0.03		211.49	1	ns		261.71	1	0.01		83.50	1	ns
Altitude * Temperature		1040.01	1	ns		217.71	1	ns		269.74	1	ns		82.60	1	ns
Rainfall * Temperature		871.15	1	<.01		218.76	1	ns		262.63	1	0.03		82.32	1	ns

SC = signs of correlation coefficient

5.3.4 Stem borer parasitism

Results of the effects of biotic and abiotic factors on stem borer parasitism are presented in Table 5.6 and Table 5.7, respectively. Stem borer parasitism was significantly positively affected by parasitoid richness and abundance. Although, stem borer richness, abundance or density and host plant richness had some significant effect on stem borer parasitism, for each habitat type, these effects varied with either landscape or between seasons within a given landscape. For both cultivated and natural habitats, altitude, rainfall and temperature had some effect on stem borer parasitism during the rainy season. However, across seasons, whereas altitude and rainfall had a negative effect in both habitats, temperature had a positive effect in cultivated habitats, but a negative effect in natural habitats.

Table 5.6: Generalized linear model results (parameter estimates and Type 3 likelihood tests) of biotic factors affecting stem borer parasitism in cultivated and natural habitats in four localities

Biotic factors	Cultivated habitats						Natural habitats					
	Rainy			Dry			Rainy			Dry		
	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*
						Kakamega						
Constant	1326.86	68		324.38	27		404.11	52		167.20	14	
Parasitoid richness	591.35	1	<.01	177.76	1	<.01	246.50	1	<.01	128.52	1	<.01
Parasitoid abundance	774.36	1	<.01	212.98	1	<.01	306.81	1	<.01	139.24	1	<.01
Stemborer richness	985.91	1	<.01	296.57	1	<.01	365.58	1	<.01	115.95	1	<.01
Stemborer abundance	1108.69	1	<.01	270.59	1	<.01	362.51	1	<.01	165.88	1	ns
Host plant richness	1326.08	1	ns	310.23	1	0.05	384.64	1	<.01	115.32	1	0.02
Parasitoid richness * abundance	290.77	1	<.01	76.44	1	<.01	206.2857	1	<.01	35.33	1	<.01
Parasitoid richness * stemborer richness	468.54	1	<.01	169.32	1	ns	223.03	1	0.05	39.44	1	<.01
Stemborer richness * host plant richness	947.09	1	ns	279.49	1	0.02	333.628	1	ns	113.31	1	0.01
Constant	136.02	43		30.95	22		96.68	40		9.28	14	
Stemborer density	134.32	1	<.01	29.28	1	ns	82.66	1	<.01	8.84	1	ns
Parasitoid richness * stemborer density	110.75	1	0.01	15.36	1	0.05	71.18	1	<.01	2.03	1	<.01

Table 5.6 (continued).

Biotic factors	Cultivated habitats						Natural habitats					
	Rainy			Dry			Rainy			Dry		
	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*	Deviance	d.f.	*P*
Mtito Andei												
Constant	230.99	22		112.56	9		85.87	18		34.39	10	
Parasitoid richness	76.13	1	<.01	51.14	1	<.01	80.65	1	0.02	1.36	1	<.01
Parasitoid abundance	126.98	1	<.01	86.97	1	<.01	73.28	1	0.04	5.56	1	<.01
Stemborer richness	131.85	1	<.01	112.49	1	ns	61.54	1	<.01	26.42	1	0.04
Stemborer abundance	137.49	1	<.01	112.43	1	ns	81.01	1	0.02	23.54	1	<.01
Host plant richness	230.90	1	ns	108.66	1	0.04	79.61	1	0.01	34.28	1	ns
Parasitoid richness * abundance	20.65	1	<.01	51.01	1	0.01	0.22	1	<.01	13.46	1	<.01
Parasitoid richness * stemborer richness	62.21	1	0.04	3.81	1	ns	22.76	1	<.01	5.87	1	<.01
Stemborer richness * host plant richness	58.41	1	ns	14.09	1	ns	44.18	1	ns	25.92	1	ns
Constant	65.74	13		24.79	9		10.24	9		11.40	9	
Stemborer density	64.45	1	0.05	23.54	1	<.01	9.95	1	ns	10.87	1	ns
Parasitoid richness * stemborer density	32.22	1	0.03	10.29	1	0.02	4.79	1	ns	2.01	1	ns

Table 5.6 (continued).

Biotic factors	**Cultivated habitats**						**Natural habitats**					
	Rainy			**Dry**			**Rainy**			**Dry**		
	Deviance	**d.f.**	***P***	**Deviance**	**d.f.**	***P***	**Deviance**	**d.f.**	***P***	**Deviance**	**d.f.**	***P***
	Muhaka											
Constant	518.01	58		184.98	23		566.51	52		220.09	26	
Parasitoid richness	235.74	1	<.01	82.01	1	<.01	336.47	1	<.01	95.89	1	<.01
Parasitoid abundance	394.23	1	<.01	148.48	1	<.01	380.76	1	<.01	127.47	1	<.01
Stemborer richness	517.39	1	ns	167.43	1	<.01	538.34	1	<.01	219.28	1	ns
Stemborer abundance	508.13	1	0.01	184.82	1	ns	537.22	1	<.01	218.14	1	ns
Host plant richness	510.87	1	0.01	184.98	1	ns	566.45	1	ns	0.0075	1	ns
Parasitoid richness * abundance	163.72	1	<.01	25.63	1	<.01	268.59	1	<.01	16.77	1	0.02
Parasitoid richness * stemborer richness	232.17	1	ns	44.78	1	<.01	259.85	1	<.01	30.32	1	<.01
Stemborer richness * host plant richness	510.74	1	ns	167.43	1	ns	529.03	1	ns	208.23	1	0.05
Constant	150.06	55		62.63	19		79.76	50		90.36	25	
Stemborer density	149.64	1	ns	61.75	1	<.01	78.92	1	0.02	89.13	1	0.01
Parasitoid richness * stemborer density	96.54	1	0.01	45.93	1	0.01	67.54	1	<.01	77.51	1	ns

Table 5.6 (continued).

Biotic factors	Cultivated habitats						Natural habitats					
	Rainy			Dry			Rainy			Dry		
	Deviance	**d.f.**	***P***	**Deviance**	**d.f.**	***P***	**Deviance**	**d.f.**	***P***	**Deviance**	**d.f.**	***P***
	Suam											
Constant	24.36	21		68.51	10		68.29	18		82.76	10	
Parasitoid richness	20.59	1	0.05	45.02	1	<.01	5.92	1	<.01	18.56	1	<.01
Parasitoid abundance	4.68	1	<.01	50.36	1	<.01	6.62	1	<.01	16.65	1	<.01
Stemborer richness	22.59	1	ns	45.81	1	<.01	16.21	1	<.01	69.51	1	0. 03
Stemborer abundance	19.77	1	0.03	68.04	1	ns	15.97	1	<.01	70.52	1	0. 05
Host plant richness	24.31	1	ns	66.52	1	ns	50.42	1	<.01	82.64	1	ns
Parasitoid richness * abundance	4.54	1	ns	29.35	1	0.02	2.88	1	ns	23.17	1	<.01
Parasitoid richness * stemborer richness	17.18	1	ns	32.85	1	0.03	2.56	1	ns	7.38	1	ns
Stemborer richness * host plant richness	10.71	1	0.04	42.73	1	0.01	5.65	1	0.01	19.31	1	ns
Constant	19.44	10		60.77	10		4.93	7		77.31	7	
Stemborer density	18.94	1	0.02	58.91	1	0.04	4.48	1	ns	75.44	1	0.01
Parasitoid richness * stemborer density	10.44	1	ns	47.13	1	0.01	3.08	1	ns	35.31	1	ns

Table 5.7: **Generalized linear model results (parameter estimates and Type 3 likelihood tests) of environmental variables affecting stem borer parasitism in cultivated and natural habitats across all localities**

Abiotic factors	Cultivated habitats								Natural habitats							
	Rainy				Dry				Rainy				Dry			
	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*	SC	Deviance	d.f.	*P*
Constant		2264.61	149			715.37	65			1185.96	119			535.89	56	
Altitude	-	2231.09	1	<.01	-	713.52	1	ns	-	1164.46	1	<.01	-	518.04	1	<.01
Rainfall	-	2119.82	1	<.01	-	715.23	1	ns	-	1175.51	1	0.01	-	535.63	1	ns
Temperature	+	2246.77	1	<.01	+	706.61	1	0.03	-	1178.49	1	0.05	-	498.52	1	<.01
Altitude * Rainfall		1965.35	1	<.02		692.05	1	<.01		1149.28	1	0.05		487.20	1	<.01
Altitude * Temperature		2122.35	1	<.01		680.60	1	<.01		1139.61	1	ns		484.43	1	0.05
Rainfall * Temperature		1999.17	1	<.02		664.99	1	<.01		1168.74	1	ns		470.03	1	<.01

SC = signs of correlation coefficient

5.4 Discussion

The results revealed a higher diversity of parasitoids in natural than in cultivated habitats. This can be attributed to the presence of various alternative hosts owing to the high richness of stem borers. This was further supported by the fact that the majority of stem borer parasitoids were stenophagous and exploited two or more host borer species (Bonhof *et al.,* 1997; Zhou *et al.,* 2003). Additionally, the higher diversity of parasitoids in natural habitats was probably due to the availability of adult food resources (i.e., pollen, floral and extrafloral nectar) and/or favorable microclimate for surviving harsh temperatures and adverse agricultural management practices (i.e., tillage and pesticides/fertilizers). Adult food resources have been proven to enhance parasitoid longevity, fecundity and effectiveness (Landis *et al.,* 2000, 2005; Wilkinson and Landis, 2005; Bianchi *et al.,* 2006). This suggested that non-crop habitats, particularly undisturbed, might play an important role in sustaining stem borer parasitoid diversity by providing refugia for parasitoids to escape periodic disturbances that occur in cultivated habitats.

By comparing the two habitat types, these results provide partial support for the 'natural enemy hypothesis' (Root, 1973; Andow, 1991), in that, parasitoid diversity was higher in natural habitats (with higher host plant richness) than in cultivated ones (with lower host plant richness). In light of the 'resource concentration hypothesis' (Root, 1973; Andow, 1991), stem borer abundance was very low in natural habitats. Perhaphs, this was due to the difficulty of host-finding by the parasitoids in more diverse plant communities. Consequently, this might have also increased the emigration of ovipositing females from this habitats, and at the same time reduced stem borer abundance by lowering their immigration into this habitat. Chabi-Olaye *et al.* (2005) reported reduced host-finding ability of ovipositioning female moths in a maize-cassava intercrop compared to a maize monocrop, and attributed this difference to host-finding difficulties. Similar to the findings by Benrey *et al.* (1998), Sétamou *et al.* (2005) and Tylianakis *et al.* (2007), parasitoid abundance was higher on herbivores attacking cultivated crops than on those attacking wild host plants. This most likely might be due to increased fitness of parasitoids on stem borers feeding on cultivated crops. Cultivated crops are often subjected to artificial selection for improved yield, nutrient content, taste or appearance, accompanied by a reduction in toxic compounds (Evans, 1993) and supply high quality resource to herbivores and their associated parasitoids (Ofomata *et al.*, 2000; Haile and Hofsvang, 2002; Sétamou *et al.*, 2005). The latter authors also pointed out that reduced fitness of parasitoids on wild host plants was probably due to poor herbivore quality, in consequence of low quality or amounts of plant resources. Furthermore, because parasitoids do not metabolize plant secondary compounds assimilated from their host's diet (Campbell and Duffey, 1979; Quicke, 1997), plant allelochemistry might affect stem borer-parasitoid interactions negatively by altering parasitoid behaviour or physiology (Vinson, 1976; Takabayashi *et al.*, 1991; Gauld and Gaston, 1994; Ode, 2006). Another likely reason for low abundance of parasitoids in natural habitats might be prolonged developmental rates or low reproduction capabilities (Waage, 1986; Godfray, 1994; Jervis *et al.*, 2008) in response to small-sized stem borers feeding on wild host plants (Ofomata *et al.*, 2000; Haile and Hofsvang, 2002). Sétamou *et al.* (2005) reported a decline in progeny production by *Cotesia flavipes* Cameron on small stem borers attacking wild host plants than on relatively bigger ones feeding on maize and cultivated sorghum.

The stem borer parasitism was positively related to parasitoid richness and abundance during both rainy and dry seasons in all AEZs and habitat types. This conforms to the findings reported by Kruess and Tscharntke (2000) and Kruess (2003). However, differential response of parasitoid richness/abundance to the richness/abundance of stem borers and host plants at lower trophic levels clearly indicated that these effects not only varied with the landscape composition of different AEZs, but also with habitat type in a given AEZ, as well as between seasons within a particular habitat.

The significant negative relationship between parasitoid abundance/stem borer parasitism and rainfall during the rainy season in both cultivated and natural habitats, might have been due to a decrease in host availability, most probably because of the death of stem borers following heavy rainfall. Heavy rainfall is reported to inflict considerable mortality on stem borer populations (Oloo, 1989; Moyal, 1998; Schulthess *et al.,* 2001; Haile and Hofsvang, 2002) or disrupt their mating and oviposition activities (Jerath, 1968; Sampson and Kumar, 1983). As rainfall increases with altitudes (Corbett, 1998), its negative effects are expected to be more severe at high elevations, especially in areas with bimodal rainfall distribution.

Other studies have shown that both altitude and temperature play an important role in determining the distribution and abundance of stem borer hosts (Ingram, 1958; Nye, 1960; Sithole, 1987; Ong'amo *et al.*, 2006). However, in this study, it was assumed that the negative significant relationships between parasitoid abundance and stem borer parasitism to altitude in all seasons and habitat types, was artificially created as a result of the presence of the invasive borer *C. partellus* and its introduced parasitoid *C. flavipes* predominating the warm mid- and lowland altitudes. Logically, excluding the above two species, altitude alone might not have had an effect on parasitoid abundance or stem borer parasitism. This is because, the Noctuidae (i.e., *Busseola* spp., *Sesamia* spp., *Sciomesa* spp., *Poeonoma* spp. and *Acrapex* spp.) are not only relatively abundant in the cool Kenya highlands, but are also more diverse than the Pyralidae.

The lower richness of parasitoids in Suam, but higher abundance of parasitoids in Kakamega, suggested that altitude had little or no effect on parasitoid richness and abundance, since both localities were situated in the Kenya highlands. The two possible explanations for the observed differences are that, the lower richness and abundance of parasitoids in Suam may have resulted from landscape degradation and simplification. This was mainly because, commercial maize production is carried out in very large fields with scanty and disconnected patches of natural habitats within the landscape of this locality. On the other hand, the higher richness and abundance of parasitoids in Kakamega must have been due to a more spatial and temporal availability of suitable host plants that sustains actively feeding stem borers during different seasons, owing to the bimodal rainfall distribution in this locality. The latter explanation is further supported by the fact that, parasitoid richness and abundance were much higher in Muhaka with a bimodal rainfall distribution than in Mtito Andei with a single rainfall distribution.

In summary, the present results highlight the importance of non-crop habitats within the cereal agroecosystem as refugia for stem borer parasitoids. Furthermore, these results established the functional (positive) dependence of stem borer parasitism on parasitoid richness and abundance irrespective of habitat types and seasons in all localities. However, any attempt to enhance stem borer parasitism by increasing parasitoid richness or abundance in a given landscape, would require thorough understanding of the effects of both biotic and abiotic factors operating locally, since these factors could vary with landscape composition, habitat type and season.

CHAPTER SIX

STEM BORER PARASITISM ON CULTIVATED CEREALS AND NATURAL HOST PLANTS

6.1 Introduction

Variations in the abundance of parasitoids and their parasitism of herbivores from cultivated crops and natural host plants have been reported (Benrey *et al.*, 1998; Tylianakis *et al.*, 2007). Habitat attributes such as plant species composition and architecture directly influence parasitoid behaviour, which in turn affect parasitism (Andow and Prokrym, 1990; Landis and Haas, 1992). In cultivated habitats, reduced chemical defense and the high nutrition of domesticated crops were shown to encourage accelerated development and abundance of parasitoids, as they derive these indirectly via their herbivore hosts (Clancy and Price, 1987; Benrey and Denno, 1997; William, 1999). In addition, modified or enlarged crop structures can create structural refuge that limits the accessability of parasitiods to herbivore (Andow and Prokrym, 1990; Brown *et al.*, 1995; Chen and Welter, 2007). However, in natural habitats, the high complexity of diverse plant communities was reported to decrease plant apparency and individual parasitoid searching efficiency (Andow and Prokryn, 1990; Udayagiri and Welter, 2000). Likewise, high levels of plant allelochemical in their host diet exerts negatively on parasitoid fitness and ultimately parasitism (Benrey *et al.*, 1998; Harvey *et al.*, 2003). Several studies have compared parasitism rates in cultivated and natural habitats, and so far the evidence available appears to be mixed. For instance, Benrey *et al.* (1998), Sétamou *et al.* (2005) and Tylianakis *et al.* (2007) observed higher parasitim rates on cultivated crops, while Seaman *et al.* (1990), van Nouhuys and Via (1999) and Haye and

Kenis (2004) instead recorded higher parasitim rates on wild plants. This reflects the unpredictable nature of parasitism for either habitat type. Further, since it is essential to conserve beneficial interactions and functions of herbivore pest management in agroecosystems, it is imperative to understand the ecological role of natural habitats as a component of a particular cropping system.

Lepidopteran stem borers are a major biotic constraint to cereal production and cause between 5% and 73% loss of potential yield in Kenya (Seshu Reddy and Walker, 1990; De Groote, 2002; De Groote *et al.*, 2003). These stem borers are attacked by a diverse group of both indigenous and exotic parasitoids (Mohyuddin and Greathead, 1970; Mathez, 1972; Bonhof *et al.*, 1997; Overholt, 1998; Zhou *et al.*, 2003). Cereal crops are usually grown in small fields surrounded by land occupied by natural host plants of lepidopteran stem borers. These natural habitats have high stem borer diversity (Le Ru *et al.*, 2006a,b), and there in can serve as refugia to parasitoids (Altieri *et al.*, 1977; Altieri and Nicholls, 2004). It is assumed that parasitism is higher on stem borer populations residing in wild grass communities than on those in cultivated crops due to non-periodic habitat re-colonization by parasitoids (Conlong, 1994) and the relatively wide-temporal window of susceptibility of stem borer larvae to parasitoid attacks (Bowden, 1976; Overholt, 1998). As such, cereal stem borer pest regulation during the off-season might occur mainly in natural habitats (Schulthess *et al.*, 1997). This study tried to appraise the impact of stem borer parasitism on various host plant genera found in cultivated and natural habitats during different seasons in four AEZs in Kenya. Information obtained should advance our basic understanding of the ecological role of natural habitats in regulating stem borer pest populations, especially during the non-cropping season.

6.2 Materials and methods

6.2.1 Field survey

Field surveys were carried out in four localities namely Kakamega, Mtito Andei, Muhaka and Suam, all in different AEZs as described in Chapter 3 sub-section 3.1. Surveys were conducted during both dry and rainy seasons from December 2005 to December 2007. Random sampling method was applied in cultivated habitats, while both random and non-random sampling methods were applied in natural habitats, respectively. Details are provided in Chapter 3 sub-section 3.2.

6.2.2 Parasitoid recovery and identification

Infested cereal and wild host plants were destructively sampled in the field. Stem borer larvae collected were transported to the laboratory and reared on artificial diet. All stem borer pupae and parasitoid cocoons or puparia recovered were kept in separate vials until the emergence of adults. The details are provided in Chapter 3 sub-section 3.3. Parasitoids, stem borers and host plants collected were identified to species level where possible, or else to genera or family levels as described in Chapter 3 sub-section 3.3.

Parasitoid abundance represents the number of individual parasitoids. Adult parasitoid emergence per stem borer host was also recorded. Larval and pupal parasitism were estimated as the proportion of susceptible stem borers parasitized (Zhou *et al*., 2003). Stem borer density was expressed as larvae/pupae per plant (Zhou *et al*., 2001).

6.2.3 Data analyses

The generalized linear model (PROC GENMODE, SAS 2001) was used to analyze count data (i.e., parasitoid abundance and adult emergence per host) and proportion data (i.e., percentage plant infestation, stem borer density and percentage parasitism) assuming a Poisson error distribution with a logarithmic link function (McCullagh and Nelder, 1989) and a binomial error distribution with a logistic link function (Collett, 1991), respectively. Significance level was set at $P \leq 0.05$.

6.3 Results

6.3.1 The incidence of plant infestation, stem borer density and parasitism among localities

The incidence of plant infestation by stem borers, stem borer density and parasitism for different localities are shown in Table 6.1. In cultivated habitats (Table 6.1), although the incidence of plant infestation by stem borers in Mtito Andei, Suam and Muhaka were not significantly different during the dry season, the incidence of plant infestation varied significantly with locality. Stem borer densities per plant did not vary with locality during the dry season. In the rainy season, however, Mtito Andei had significantly lower stem borer densities compared to Suam and Kakamega. Pupal parasitism in cultivated habitats were generally low and did not differ significantly among localities. Larval parasitism on the other hand varied with localities during the rainy season but not during the dry season except for Muhaka where there was no parasitism. It is worthy noting that Kakamega and Suam were similar in stem borer densities, larval and pupal parasitism levels.

Table 6.1: Least square means (±SE) following binomial regression analysis (generalized linear model) of plant infestation (%), stem borer density and parasitism (larval/pupal) (%) during different seasons in cultivated and natural habitats.

Locality	Plant infestation (%)				Stem borer density (per plant/tiller) (mean)				Larval parasitism (%)				Pupal parasitism (%)			
	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*
								Cultivated habitats								
Kakamega (a)	3.2±0.11	3.3±0.08	1,81	0.89	0.6±0.12	0.5±0.03	1,76	0.89	2.4±0.07	1.5±0.08	1,85	0.79	0.8±0.06	1.7±0.08	1,16	0.93
	(5.97%)	(3.98%)			(0.60)	(0.58)			(5.84%)	(6.64%)			(0.00%)	(0.00%)		
Suam (b)	1.8±0.09	2.3±0.09	1,35	0.01	4.5±0.08	0.9±0.05	1,11	0.03	1.9 0.03	2.3 0.09	1,35	0.98	2.6±0.03	1.3±0.09	1,14	0.90
	(1.11%)	(9.49%)			(1.13)	(2.01)			(11.25%)	(5.22%)			(1.55%)	(0.37%)		
Mtito Andei (c)	1.5±0.10	1.2±0.10	1,29	0.32	0.4±0.03	1.5±0.06	1,20	<.01	2.5±0.09	0.0±0.01	1,33	<.01	1.5±0.07	2.6±0.08	1,14	0.87
	(3.08%)	(22.70%)			(0.98)	(2.64)			(9.58%)	(14.99%)			(0.15%)	(0.59%)		
Muhaka (d)	1.6±0.07	0.9±0.04	1,59	0.08	1.8±0.07	1.1±0.04	1,63	0.81	0.0±0.00	3.5±0.04	1,62	0.87	1.9±0.05	1.0±0.04	1,32	0.95
	(21.60%)	(22.66%)			(1.54)	(2.14)			(1.49%)	(3.58%)			(4.76%)	(0.99%)		
d.f.	3, 56	3, 143			3, 46	3, 131			3, 58	3, 145			3, 25	3, 139		
P	<.0001	<.0001			0.5714	0.0018			<.0002	<.0001			0.9999	<.0001		
a vs b	<.0001	<.0001			ns	ns			ns	ns			ns	ns		
a vs c	<.0001	<.0001			ns	0.0384			ns	0.0002			ns	ns		
a vs d	<.0001	<.0001			ns	ns			ns	<.0001			ns	ns		
b vs c	ns	<.0001			ns	0.0580			ns	<.0001			ns	ns		
b vs d	ns	<.0001			ns	ns			0.0102	0.0467			ns	ns		
c vs d	ns	0.0075			ns	ns			0.0005	<.0001			ns	ns		

Table 6.1 (continued).

Locality	Plant infestation (%)				Stem borer density (per plant/tiller) (mean)				Larval parasitism (%)				Pupal parasitism (%)			
	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*
								Natural habitats								
Kakamega (a)	2.4±0.10	3.2±0.13	1,66	<.01	2.6±0.08	3.4±0.04	1,156	<.01	2.9±0.05	2.8±0.07	1,166	0.87	2.7±0.10	4.6±0.07	1,68	0.90
	(7.04%)	(1.85%)			(0.058)	(0.021)			(3.12%)	(2.88%)			(0.00%)	(0.04%)		
Suam (b)	5.2±0.31	3.6±0.09	1,71	<.01	4.5±0.08	0.9±0.04	1.80	<.01	2.9±0.03	3.5±0.03	1,77	0.91	2.9±0.09	2.3±0.06	1,56	0.78
	(0.74%)	(2.59%)			(0.022)	(0.033)			(1.67%)	(0.26%)			(0.00%)	(0.00%)		
Mtito Andei (c)	2.8±0.09	0.8±0.04	1,83	0.08	2.6±0.06	2.5±0.09	1,85	0.44	4.2±0.18	3.8±0.08	1,87	0.57	2.5±0.05	3.2±0.05	1,51	0.57
	(3.40%)	(7.77%)			(0.073)	(0.066)			(2.99%)	(0.88%)			(0.00%)	(0.03%)		
Muhaka (d)	3.3±0.07	1.4±0.03	1,189	<.01	2.6±0.04	1.1±0.04	1,215	<.01	4.6±0.10	3.3±0.05	1,198	0.01	0.0±0.00	5.5±0.13	1,113	0.31
	(3.51%)	(4.78%)			(0.089)	(0.082)			(1.05%)	(3.59%)			(1.47%)	(0.33%)		
d.f.	3, 141	3, 385			3, 145	3, 383			3, 144	3, 379			3, 83	3, 341		
P	<.0001	<.0001			<.0001	<.0001			0.0045	0.0416			0.9999	0.9566		
a vs b	<.0001	0.0148			<.0001	0.0040			ns	ns			ns	ns		
a vs c	0.0039	<.0001			ns	<.0001			ns	0.0206			ns	ns		
a vs d	<.0001	<.0001			ns	<.0001			0.0081	ns			ns	ns		
b vs c	<.0001	<.0001			<.0001	<.0001			ns	ns			ns	ns		
b vs d	<.0001	<.0001			<.0001	<.0001			ns	ns			ns	ns		
c vs d	0.0002	0.0270			ns	0.0173			ns	ns			ns	ns		

Larval parasitism on the other hand varied with localities during the rainy season but not during the dry season except for Muhaka where there was no parasitism. It is worthy noting that Kakamega and Suam were similar in stem borer densities, larval and pupal parasitism levels.

In all localities, the incidence of plant infestation by stem borers in natural habitats (Table 6.1) varied significantly with season. Infestation was higher during the dry season except in Kakamega where the reverse was true. Suam had the highest incidence of plant infestation by stem borers in both seasons while Mtito Andei tended to have lowest. Stem borer density was higher in the dry season in all localities and varied significantly between localities especially in the rainy season. Pupal and larval parasitism was neither affected by season nor by locality.

6.3.2 Total stem borer parasistism, parasitoid abundance and adult emergence per host in different localities

Table 6.2 provides summarized results on total stem borer parasistism and parasitoid abundance or adult emergence per host. In cultivated habitats (Table 6.2), total parasitism was higher during the rainy season than during the dry season except for Suam and Muhaka. Likewise, total parasitism was significantly different between seasons in a given locality except in Kakamega. Total parasitism varied among localities during the rainy season but was not significantly different during the dry season except for Kakamega where it was generally higher than in other localities.

Table 6.2: Least square means (±SE) following binomial or Poisson regression analysis (generalized linear model) of total parasitism (%), parasitoid abundance and number of off-springs in different seasons and habitats.

Locality	Total parasitism (%)				Parasitoid abundance (mean)				Adult parasitoid emergence per host (mean)			
	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*
					Cultivated habitats							
Kakamega (a)	2.1±0.05 (5.84%)	2.2±0.09 (6.57%)	1, 86	0.998	0.9±0.05 (28)	1.0±0.09 (123)	1, 86	0.052	2.0±0.07 (11.21)	1.7±0.05 (23.19)	1, 84	0.002
Suam (b)	1.9±0.03 (13.36%)	2.9±0.09 (5.34%)	1, 40	0.001	0.3±0.04 (23)	0.6±0.07 (92)	1, 37	0.701	3.5±0.05 (16.55)	2.6±0.05 (38.62)	1, 40	<.001
Mtito Andei (c)	2.7±0.08 (9.64%)	1.0±0.06 (15.32%)	1, 33	<.001	0.2±0.04 (31)	1.1±0.05 (112)	1, 33	0.168	2.8±0.05 (18.55)	5.9±0.07 (52.90)	1, 33	0.946
Muhaka (d)	2.2±0.09 (6.33%)	3.6±0.05 (3.73%)	1, 63	0.003	1.6±0.16 (57)	3.2±0.08 (101)	1, 63	0.987	1.2±0.11 (41.89)	2.3±0.09 (29.89)	1, 63	0.008
d.f.	3, 56	3, 153			3, 69	3, 154			3, 66	3, 154		
P	0.0028	<.0001			0.0006	<.0001			<.0001	<.0001		
a vs b	ns	0.0266			ns	0.0011			<.0001	<.0001		
a vs c	ns	<.0001			0.0048	0.0009			<.0001	<.0001		
a vs d	ns	<.0001			ns	ns			<.0001	0.0114		
b vs c	0.0136	<.0001			ns	ns			<.0001	<.0001		
b vs d	ns	0.0024			ns	0.0021			<.0001	<.0001		
c vs d	ns	<.0001			0.0035	0.0014			<.0001	<.0001		

Table 6.2 (continued).

Locality	Total parasitism (%)				Parasitoid abundance (mean)				Adult parasitoid emergence per host (mean)			
	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*
					Natural habitats							
Kakamega (a)	3.0±0.08	2.4±0.09	1, 161	0.710	0.9±0.05	1.3±0.11	1, 163	0.291	0.2±0.02	1.3±0.04	1, 66	<.001
	(3.12%)	(3.49%)			(7)	(39)			(3.40)	(9.32)		
Suam (b)	2.0±0.05	3.5±0.05	1, 83	0.938	0.3±0.01	2.6±0.50	1, 87	0.053	0.9±0.11	2.1±0.17	1, 83	<.001
	(1.59%)	(0.62%)			(6)	(4)			(2.46)	(0.12)		
Mtito Andei (c)	4.4±0.08	2.5±0.09	1, 89	0.165	0.2±0.03	1.5±0.04	1, 89	0.106	2.5±0.07	0.1±0.01	1, 89	<.001
	(2.99%)	(1.49%)			(3)	(11)			(1.00)	(5.88)		
Muhaka (d)	3.8±0.23	1.1±0.04	1, 215	0.116	1.6±0.06	1.2±0.05	1, 217	0.152	0.8±0.05	0.5±0.06	1, 217	<.001
	(1.98%)	(3.66%)			(12)	(42)			(4.67)	(1.72)		
d.f.	3, 144	4, 395			3, 151	3, 403			3, 154	3, 403		
P	0.0408	<.0001			0.0125	<.0001			<.0001	<.0001		
a vs b	ns	0.0534			ns	0.0099			<.0001	<.0001		
a vs c	0.0496	0.0423			0.0189	ns			0.0002	<.0001		
a vs d	ns	0.0183			ns	ns			0.0279	<.0001		
b vs c	ns	ns			ns	0.0469			<.0001	<.0001		
b vs d	ns	ns			ns	0.0071			<.0001	<.0001		
c vs d	ns	ns			0.004	ns			0.0058	0.0001		

Parasitoid abundance in a locality did not differ between seasons in cultivated habitats. The trend of parasidoid abundance among localities was not very clear but Muhaka had higher than other localities in both seasons. Adult parasitoid emergence per host varied significantly with season. In Mtito Andei and Muhaka, adult parasitoid emergence per host was higher during the rainy season while in Suam and Kakamega the reverse was true. In both seasons, adult parasitoid emergence per host varied significantly with locality. Adult parasitoid emergence per host were generally higher in Kakamega and Mtito Andei than in Muhaka and Suam.

In natural habitats (Table 6.2), both total parasitism and parasitoid abundance were generally not significantly different between seasons in a locality. Total parasitism and parasitoid abundance were generally higher during the rainy season except in Mtito Andei and Muhaka. Total parasitism and parasitoid abundance varied significantly among most localities during the rainy than during the dry season. Adult parasitoid emergence per host was highest during the rainy season except for Suam and Muhaka. Between seasons, adult parasitoid emergence per host varied significantly in all localities. Likewise, in both rainy and dry seasons, adult parasitoid emergence per host differed significantly among localities.

6.3.3 Comparison of the incidence of plant infestation, stem borer density/parasitism and parasitoid abundance/adult emergence per host between and among host plant genera in different habitats

In cultivated habitats the incidence of plant infestation by stem borers was higher on maize than on sorghum with the exception of Suam where the incidence of plant infestation was higher in sorghum during the wet season. In natural habitats the incidence of plant infestation by stem borers generally differed significantly among host plant genera in both seasons (Table 6.3). The incidence of plant infestation by stem borers was significantly different between season on at least three host plant genera in all localities. The incidence of plant infestation by stem borers in cultivated habitats ranged from 0.35% (on sorghum) in Suam to 23.22% (on maize) in Muhaka, both in the dry season. While in natural habitats, the incidence of plant infestation by stem borers ranged from 0.00% (on *Cyperus* spp.) in Kakamega to 15.48% (on *S. arundinaceum* in Muhaka), both in dry seasons.

In cultivated habitats, stem borer density was significantly different between seasons on only *Sorghum* spp. (in Suam and Mtito Andei), but not between host plant genera during rainy and dry seasons in most localities (Table 6.4). In natural habitats, stem borer density significantly varied among host plant genera in both rainy and dry seasons, and also between seasons on at least two host plant genera in all localities. The mean (±SD) stem borer density was highest on maize in cultivated habitats, and ranged between 0.59 (±0.08SD) and 2.14 (±0.22SD) stem borers per plant in the rainy season in Kakamega and in the dry season in Muhaka, respectively. In general, stem borer density was low in natural habitats, ranging from 0.00 (±0.00SD) to 0.22 (±0.07SD) stem borers per tiller on *S. arundinaceum* in the rainy season in Kakamega and Muhaka, respectively.

In cultivated habitats, larval parasitism was generally not significantly different between host plant genera during both rainy and dry seasons (Tables 6.5). Additionally, per host plant genera, except on maize in Muhaka, larval parasitism was not significantly

Table 6.3: Least square means (±SE) following binomial regression analysis (generalized linear model) of plant infestation (%) during dry and rainy seasons in cultivated and natural habitats

	Plant infestation															
Host plant	**Kakamega**				**Suam**				**Mtito Andei**				**Muhaka**			
genera	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***
Cultivated habitat																
Sorghum	2.3±0.0	1.1±0.0	1,32	0.08	1.3±0.0	5.9±0.1	1,11	0.99	-	0.8±0.2			-	2.5±0.3		
Zea	4.0±0.2	3.2±0.0	1,149	<.01	2.3±0.0	2.3±0.0	1,21	0.89	1.5±0.2	1.4±0.1	1,13	0.05	0.8±0.0	1.1±0.0	1,56	0.01
d.f.	1,29	1,59			1,18	1,43				1,12				1,47		
P	<.0001	<.0002			0.0004	0.9996				<.0001				<.0001		
Natural habitat																
Cyperus (a)	2.9±0.0	5.3±0.0	1,12	0.01	5.2±0.0	3.2±0.0	1,20	0.01	4.2±0.0	2.7±0.0	1,12	0.01	4.3±0.1	5.3±0.0	1,20	0.05
Panicum (b)	4.2±0.0	3.9±0.0	1,27	0.66	5.3±0.0	7.3±0.0	1,5	0.05	3.8±0.0	3.1±0.0	1,24	0.03	3.3±0.0	2.8±0.0	1,67	0.02
Pennisetum (c)	2.3±0.0	3.5±0.0	1,51	<.01	4.7±0.0	3.7±0.0	1,24	0.05	5.5±0.0	2.6±0.0	1,6	0.99	-	-		
Sorghum (d)	-	6.5±0.0			7.2±0.0	1.7±0.0	1,3	0.98	2.7±0.0	1.6±0.0	1,12	<.01	2.1±0.1	1.9±0.0	1,13	0.28
Others (e)	2.0±0.1	4.2±0.0	1,46	<.01	6.3±0.0	4.9±0.0	1,20	0.19	2.3±0.0	2.7±0.0	1,27	0.07	4.1±0.1	2.8±0.0	1,75	<.01
d.f.	3,20	4,123			4,25	4,47			4,28	4,50			3,58	3,117		
P	<.0001	<.0001			<.0001	<.0001			<.0001	<.0001			<.0001	<.0001		
b vs a	0.0584	0.0271			ns	ns			ns	ns			0.0073	<.0001		
b vs d	ns	<.0001			<.0001	ns			0.0075	<.0001			0.0001	<.0001		
b vs e	<.0001	ns			ns	ns			<.0001	0.0461			0.0001	ns		
c vs e	ns	0.0012			ns	0.0036			ns	ns			ns	ns		
a vs d	ns	<.0001			<.0001	<.0001			0.0028	<.0001			<.0001	<.0001		
a vs e	0.0599	ns			ns	<.0001			<.0001	ns			ns	<.0001		
d vs e	ns	<.0001			<.0001	<.0001			ns	<.0001			0.0001	<.0001		

Table 6.4: Least square means (±SE) following binomial regression analysis (generalized linear model) of stem borer density during dry and rainy seasons in cultivated and natural habitats

Host plant	Stem borer density (per plant/tiller)															
	Kakamega				Suam				Mtito Andei				Muhaka			
genera	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*
Cultivated habitat																
Sorghum	-	-	-	-	4.5±0.1	1.2±0.0	1,5	0.01	0.4±0.0	0.6±0.1	1,7	<.01	-	-		
Zea	0.6±0.0	0.5±0.0	1,149	0.89	-	0.8±0.1			3.9±0.0	1.7±0.0	1,25	0.17	0.1±0.0	2.1±1.9	1,122	0.288
d.f.						4,43			1,22	1,21						
P						0.1284			0.8287	09288						
Natural habitat																
Cyperus (a)	1.9±0.0	2.8±0.0	1,12	0.04	4.7±0.0	2.9±0.0	1,21	<.01	4.2±0.0	2.9±0.0	1,10	0.03	4.3±0.0	4.9±0.0	1,20	0.263
Panicum (b)	2.8±0.0	3.6±0.0	1,27	0.02	3.0±0.0	6.9±0.2	1,6	0.19	3.3±0.0	3.4±0.0	1,24	0.62	2.1±0.0	2.1±0.0	1,89	0.324
Pennisetum (c)	3.2±0.0	3.7±0.1	1,51	0.01	4.5±0.0	3.0±0.1	1,27	<.01	5.9±0.0	3.6±0.0	1,6	0.99	-	3.4±0.3		
Sorghum (d)	-	5.9±0.0			6.9±0.0	2.3±0.0	1,5	0.99	2.3±0.0	2.2±0.0	1,14	0.07	2.1±0.0	1.3±0.0	1,18	<.001
Others (e)	2.3±0.1	3.3±0.0	1,46	<.01	6.5±0.0	3.5±0.0	1,24	0.01	2.4±0.0	2.2±0.0	1,31	0.04	4.2±0.1	2.8±0.0	1,88	<.001
d.f.	3,20	4,141			4,26	4,54			4,35	4,50			3,66	4,149		
P	0.0001	<.0001			<.0001	<.0001			<.0001	<.0001			<.0001	<.0001		
b vs c	ns	ns			0.0010	ns			ns	ns			ns	0.0215		
b vs a	0.0189	<.0001			0.0006	ns			0.0333	ns			<.0001	<.0001		
b vs d	ns	<.0001			<.0001	ns			0.0001	<.0001			<.0001	<.0001		
b vs e	ns	0.0197			0.0009	ns			<.0001	<.0001			<.0001	<.0001		
c vs a	0.0002	<.0001			ns	ns			ns	ns			ns	0.0300		
c vs d	ns	ns			ns	0.0169			ns	<.0001			ns	0.0002		
c vs e	<.0001	0.0004			ns	0.0025			ns	<.0001			ns	ns		
a vs d	ns	<.0001			<.0001	0.0409			<.0001	<.0001			ns	<.0001		
a vs e	ns	0.0001			ns	0.0016			<.0001	<.0001			ns	<.0001		
d vs e	ns	<.0001			<.0001	<.0001			ns	ns			<.0001	<.0001		

Table 6.5: Least square means (±SE) following binomial regression analysis (generalized linear model) of larval parasitism (%) during dry and rainy seasons in cultivated and natural habitats

	Larval parasitism															
Host plant	**Kakamega**				**Kitale**				**Mtito Andei**				**Muhaka**			
genera	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***
Cultivated habitat																
Sorghum	1.3±0.0	-			1.8±0.0	1.9±0.0	1,5	0.84	2.7±0.1	2.1±0.1	1,7	0.19	-	3.9±0.1		
Zea	2.9±0.1	2.6±0.0	1,102	0.47	2.5±0.1	2.9±0.0	1,47	0.07	2.5±0.1	0.0±0.0	1,36	0.07	4.6±0.1	1.3±0.1	1,122	0.016
d.f.	1, 20	8			1, 12	1, 28			1, 21	1, 12				1, 49		
P	0.6703				0.8775	0.8140			0.7982	0.0065				0.0021		
Natural habitat																
Cyperus (a)	2.1±0.0	2.0±0.0	1,14	0.95	0.5±0.0	5.1±0.2	1,21	0.72	2.6±0.1	0.9±0.0	1,8	0.84	1.9±0.16	2.7±0.0	1,18	0.826
Panicum (b)	1.0±0.0	2.5±0.1	1,23	0.28	1.2±0.0	3.3±0.1	1,5	0.86	1.1±0.1	1.5±0.1	1,22	0.78	4.6±0.1	0.8±0.0	1,87	0.074
Pennisetum (c)	3.3±0.0	3.3±0.1	1,56	0.97	0.3±0.0	2.5±0.0	1,25	0.79	2.4±0.1	4.8±0.1	1,8	0.86	-	0.6±0.0		
Sorghum (d)	-	2.8±0.0			-	2.7±0.0			4.0±0.0	3.3±0.1	1,10	0.53	2.5±0.1	3.0±0.0	1,16	0.934
Others (e)	2.8±0.0	3.6±0.0	1,57	0.16	2.0±0.0	3.9±0.0	1,22	0.81	2.7±0.1	0.5±0.1	1,30	0.95	2.3±0.1	0.6±0.1	1,87	0.997
d.f.	3,14	3,147			3,16	3,35			4,39	4,50			3,68	4,149		
P	0.3414	<.0001			0.9333	0.0071			0.1418	0.6357			<.0001	<.0001		
b vs c	ns	ns			ns	ns			ns	ns			ns	0.026		
b vs a	ns	ns			ns	ns			ns	ns			0.0282	ns		
c vs a	ns	0.0209			ns	0.0181			ns	ns			ns	ns		
c vs e	ns	ns			ns	ns			ns	ns			ns	0.0251		
a vs d	ns	ns			ns	ns			ns	ns			<.0001	ns		
a vs e	ns	0.0001			ns	ns			ns	ns			ns	ns		

different between seasons (Tables 6.5). In natural habitats, larval parasitism did not vary between seasons on various host plant genera. However, among host plant genera larval parasitism generally varied significantly in the rainy season except in Mtito Andei. Larval parasitism was relatively higher in cultivated than in natural habitats, with the highest level of 15.00% on maize in the rainy season in Mtito Andei and 9.50% on *S. arundinaceum* during the dry season in Muhaka, respectively.

In cultivated habitats (Tables 6.6), pupal parasitism was generally not significantly different between host plant genera in both seasons except in Muhaka. Pupal parasitism was not significantly different between seasons on all plant genera in each locality. In natural habitats, across localities, pupal parasitism was neither significantly different among host plant genera during different seasons nor between seasons on all plant genera. Pupal parasitism was slightly higher in cultivated than in natural habitats. Pupal parasitism was highest on maize (4.72%) in the dry season in Muhaka and on *Panicum* spp. (2.50%) during the dry season in Muhaka, in cultivated and natural habitats, respectively.

Total parasitism followed a similar trend as larval parasitism (Tables 6.7). In cultivated habitats, larval parasitism was generally not significantly different between host plant genera in both seasons and between seasons on each host plant genera except in Mtito Andei and on maize in Muhaka, respectively. In natural habitats, total parasitism did not vary between seasons on various host plant genera. However, among host plant genera, total parasitism was only significantly different in the rainy season except in Suam. Total parasitism was relatively higher in cultivated than in natural habitats, with the

Table 6.6: Least square means (±SE) following binomial regression analysis (generalized linear model) of pupal parasitism (%) during dry and rainy seasons in cultivated and natural habitats

Host plant genera	Pupal parasitism															
	Kakamega				Kitale				Mtito Andei				Muhaka			
	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*
Cultivated habitat																
Sorghum	3.4±0.1	-			3.0±0.0	3.1±0.1	1,4	0.73	4.9±0.1	4.4±0.2	1,6	0.89	-	3.9±0.1		
Zea	2.0±0.0	4.7±0.1	1,76	0.91	2.3±0.1	5.2±0.1	1,39	0.81	5.9±0.1	5.4±0.1	1,32	0.81	4.3±0.1	5.8±0.2	1,114	0.56
d.f.	1, 25				1, 11	1, 35			1, 16	1, 17				1, 49		
P	0.8721				0.8829	0.9822			0.9885	0.8599				0.0021		
Natural habitat																
Cyperus (a)	2.8±0.1	2.0±0.1	1,12	0.92	3.3±0.1	3.2±0.1	1,19	0.91	0.5±0.0	2.4±0.0	1,6	0.75	3.7 0.1	0.5±0.0	1,20	0.97
Panicum (b)	1.0±0.1	2.5±0.1	1,18	0.98	3.7±0.1	2.5±0.1	1,4	0.73	0.6±0.1	2.2±0.1	1,19	0.84	4.6±0.1	0.2±0.0	1,86	0.83
Pennisetum (c)	3.3±0.1	3.3±0.1	1,41	0.97	3.6±0.0	4.4±0.1	1,21	0.52	2.8±0.1	4.8±0.0	1,5	0.53	-	0.0±0.0		
Sorghum (d)	-	4.6±0.1			2.2±0.1	3.8±0.1	1,20	0.78	2.1±0.0	5.4±0.1	1,14	0.73	2.5±0.1	3.3±0.1	1,17	0.31
Others (e)	2.8±0.06	3.6±0.0	1,49	0.97	3.6±0.1	3.9±0.0	1,20	0.85	2.7±0.1	5.0±0.1	1,29	0.55	1.1±0.0	2.3±0.1	1,77	0.77
d.f.	3,11	4,139			4,15	4,32			4,23	4,31			3,36	4,77		
P	0.9127	0.8477			0.9332	0.9992			0.9855	0.8115			0.9911	0.8743		

Table 6.7: Least square means (±SE) following binomial regression analysis (generalized linear model) of total (larval and pupal) parasitism (%) during dry and rainy seasons in cultivated and natural habitats

	Total parasitism															
Host plant	Kakamega				Suam				Mtito Andei				Muhaka			
genera	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*	Dry	Rainy	d.f.	*P*
Cultivated habitat																
Sorghum	3.7±0.1	1.0±0.0	1,32	0.99	1.4±0.0	1.9±0.1	1,5	0.29	2.4±0.0	2.6±0.1	1,7	0.25	-	-		
Zea	7.7±0.1	2.4±0.1	1,151	0.99	2.4±0.0	2.9±0.1	1,58	0.07	2.8±0.1	1.5±0.1	1,36	0.99	2.7±0.2	0.3±0.5	1,122	0.07
d.f.	1,32	1,59			1,18	1,43			1,22	1,21						
P	0.5346	0.8677			0.1717	0.9997			0.398	0.0113						
Natural habitat																
Cyperus (a)	7.1±0.1	1.9±0.2	1,14	0.99	6.3±0.1	2.4±0.0	1,21	0.64	1.7±0.1	2.9±0.0	1,8	0.64	1.9±0.1	2.3±0.0	1,18	0.81
Panicum (b)	2.7±1.0	2.5±0.4	1,27	0.87	-	8.3±0.1			2.9±0.0	2.9±0.1	1,22	0.95	4.1±0.1	3.5±0.0	1,87	0.21
Pennisetum (c)	3.4±1.0	3.3±0.5	1,56	0.95	8.2±0.1	3.0±0.0	1,25	0.99	-	5.3±0.1			-	0.6±0.1		
Sorghum (d)	-	-			8.7±0.2	-			4.2±0.1	3.1±0.1	1,10	0.33	3.2±0.1	3.3±0.1	1,16	0.73
Others (e)	2.8±0.4	3.5±0.3	1,57	0.24	7.3±0.2	4.1±0.1	1,22	0.99	3.3±0.1	4.2±0.1	1,30	0.99	7.1±0.1	3.5±0.1	1,87	0.99
d.f.	3,14	3,141			3,16	3,35			3,34	4,45			3,64	4,144		
P	0.6326	<.0001			0.9500	08773			0.4187	0.0446			0.0617	<.0001		
b vs c	ns	ns			ns	ns			ns	ns			ns	0.024		
c vs a	ns	0.0110			ns	ns			ns	ns			ns	ns		
c vs e	ns	ns			ns	ns			ns	ns			ns	0.0251		
a vs e	ns	<.0001			ns	ns			ns	0.0012			ns	ns		

highest value recorded on maize (15.18%) in Mtito Andei and on *S. arundinaceum* (9.53%) in Muhaka both in the rainy season, respectively.

Parasitoid abundance in cultivated habitats was not significantly different between seasons on all host plant genera (Tables 6.8). While parasitoid abundance was generally not significantly varied between host plant genera in both seasons except in Mtito Andei. In natural habitats, parasitoid abundance was generally not significantly different between seasons on various host plant genera. However, among host plant genera, parasitoid abundance was significantly different during the rainy season in Kakamega and Muhaka only. Parasitoid abundance was generally higher in cultivated than in natural habitats, with the highest values recorded on maize (average (±SD) 5.8±0.21) in Mtito Andie and on *Cyperus* spp. (0.8±0.02) in Kakamega both during the rainy season, respectively.

Adult parasitoid emergence per host in cultivated habitats was not significantly different between seasons on all host plant genera (Tables 6.9). Likewise, adult parasitoid emergence per host was generally not significantly different between host plant genera in both seasons except in Mtito Andei. For natural habitats, adult parasitoid emergence per host was significantly different between seasons on at least one host plant genera in all localities. Among host plant genera, adult parasitoid emergence per host was significantly varied during both seasons in Kakamega and Muhaka only. Adult parasitoid emergence per host was relatively higher in cultivated than in natural habitats, with the highest values observed on maize (24.0±0.13) during the rainy season in Mtito

Table 6.8: Least square means (±SE) following poisson regression analysis (generalized linear model) of parasitioid abundance during dry and rainy seasons in cultivated and natural habitats

	Parasitoid abundance															
Host plant	**Kakamega**				**Suam**				**Mtito Andei**				**Muhaka**			
genera	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***
Cultivated habitat																
Sorghum	0.1±0.0	-			0.2±0.0	1.0±0.0	1,5	0.20	1.2±0.2	1.25±0.3	1,9	0.96	-	-		
Zea	2.8±0.1	1.8±0.1	1,151	0.39	1.2±0.0	0.5±0.2	1,58	0.51	2.6±1.0	0.86±0.4	1,36	0.99	1.9±0.1	2.7±0.5	1,122	0.37
d.f.	1,32				1,18	1,43			1,22	1, 21						
P	0.9998				0.5775	0.9999			<.0001	0.0004						
Natural habitat																
Cyperus (a)	0.2±0.0	0.3±0.0	1,15	0.09	0.0±0.0	0.0±0.0	1,25	0.71	1.6±0.0	0.91±0.7	1,10	0.57	1.6±0.0	2.7±0.0	1,20	0.43
Panicum (b)	1.0±0.0	1.6±0.0	1,29	0.61	8.0±0.2	0.0±0.0	1,21	0.99	0.5±0.0	1.84±0.5	1,24	0.83	1.4±0.2	1.2±0.1	1,89	0.52
Pennisetum (c)	2.0±0.0	2.5±0.0	1,58	0.68	2.0±0.1	2.7±0.0	1,27	0.16	2.8±0.0	5.0±0.1	1,8	0.99	-	0.0±0.0		
Sorghum (d)	-	2.6±0.0			2.1±0.0	0.6±0.1	1,25	0.19	1.2±0.1	0.6±0.1	1,15	0.28	0.6±0.1	0.1±0.0	1,18	0.22
Others (e)	0.1±0.0	1.6±0.0	1,57	0.16	5.0±0.0	2.8±1.0	1,22	0.99	2.8±0.1	1.6±0.5	1,32	0.99	2.9±0.01	1.7±0.1	1,89	0.99
d.f.	3,21	4,146			4,26	4,58			4,39	4,50			3,68	4,149		
P	0.1687	<.0001			0.9999	0.4298			0.3358	0.3585			0.4275	0.0002		
b vs a	ns	<.0001			ns	ns			ns	ns			ns	ns		
b vs d	ns	ns			ns	ns			ns	ns			ns	0.0018		
c vs a	ns	<.0001			ns	ns			ns	ns			ns	0.0555		
c vs d	ns	<.0001			ns	ns			ns	ns			ns	ns		
a vs d	ns	<.0001			ns	ns			ns	ns			ns	0.0093		
a vs e	ns	<.0001			ns	ns			ns	ns			ns	ns		
d vs e	ns	<.0001			ns	ns			ns	ns			ns	<.0001		

Table 6.9: Least square means (±SE) following poisson regression analysis (generalized linear model) of the number of parasitoid off-springs per borer host during dry and rainy seasons in cultivated and natural habitats

	Parasitoid proney															
Host plant	**Kakamega**				**Suam**				**Mtito Andei**				**Muhaka**			
genera	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***	**Dry**	**Rainy**	**d.f.**	***P***
Cultivated habitat																
Sorghum	1.8±0.1	-			4.3±0.1	4.3±0.1	1,5	0.85	3.6±0.2	3.1±0.0	1,9	0.46	-	-		
Zea	1.2±0.0	1.7±0.1	1,151	0.11	2.8±0.1	2.1±0.1	1,34	0.20	1.9±0.1	2.7±0.1	1,36	0.99	0.9±0.1	1.0±0.1	1,122	0.604
d.f.	1, 32				1, 18	1, 43			1, 22	1, 21						
P	0.1267				0.5561	0.9996			<.0001	0.0401						
Natural habitat																
Cyperus (a)	-	3.5±0.0	1,15	0.99	5.2±0.1	0.0±0.0	1,25	0.88	0.5±0.0	0.9±0.0	1,10	0.57	1.6±0.0	2.7±0.0	1,20	0.437
Panicum (b)	0.9±1.4	2.8±0.0	1,29	0.04	5.0±0.3	0.0±0.0	1,21	0.65	0.5±0.0	1.5±0.1	1,24	0.96	1.4±0.1	0.8±0.0	1,89	0.130
Pennisetum (c)	2.0±1.0	1.9±0.3	1,58	0.91	4.7±0.5	4.6±0.1	1,27	0.81	2.8±0.1	4.8±0.1	1,8	0.86	-	0.0±0.0		
Sorghum (d)	-	4.0±0.3			4.0±0.1	6.5±0.1	1,25	0.93	2.1±0.0	0.8±0.1	1,15	0.03	1.1±0.1	2.7±0.0	1,18	<.001
Others (e)	2.7±1.0	0.7±0.2	1,57	<.01	2.0±0.1	5.0±0.7	1,22	0.99	2.1±0.1	0.5±0.1	1,32	0.98	2.0±0.1	0.6±0.1	1,89	0.999
d.f.	2,21	4,146			4,26	4,58			4,39	4,50			3,68	4,149		
P	0.0512	<.0001			0.9999	0.1384			0.3358	<.0001			<.0001	<.0001		
b vs c	ns	<.0000			ns	ns			ns	ns			ns	ns		
b vs a	ns	<.0001			ns	ns			ns	ns			ns	ns		
b vs d	ns	ns			ns	ns			ns	<.0001			<.0001	<.0001		
b vs e	ns	<.0001			ns	ns			ns	0.0001			ns	ns		
c vs a	ns	<.0001			ns	ns			ns	ns			ns	0.0555		
c vs d	ns	<.0001			ns	ns			ns	ns			ns	0.0054		
c vs e	0.0087	<.0001			ns	ns			ns	ns			ns	ns		
a vs d	ns	<.0001			ns	ns			ns	0.0196			0.0071	<.0001		
a vs e	ns	<.0001			ns	ns			ns	0.0495			ns	0.0409		
d vs e	ns	<.0001			ns	ns			ns	ns				<.0001		

Andie and on S. arundinaceum (6.53±0.09) during the rainy season in Muhaka, respectively.

6.4 Discussion

Results from the current study indicated that stem borer larval/total parasitism and parasitoid abundance varied with locality or season in a given habitat type. Presumably, these variations were due to related differences in host plant-stem borer-parasitoid species composition or complex existing in different localities, as well as their abundance in both time and space. Additionally, the fact that the incidence of plant infestation by stem borers, stem borer density/parasitism, parasitoid abundance/adult emergence per host were generally low in natural habitats which have been reported to have a high richness of wild host plants. This suggested that host plant diversity had a strong influence on the abundance of parasitoids, and consequently, the availability of stem borer hosts for parasitization. This can be attributed to disruption of host finding due to a variety of physical characteristics or chemical stimuli in natural habitats that either decreases immigration or increases emigration of herbivores, which consequently decreases herbivoure abundance in more diverse host plant communities (Root, 1973; Vinson, 1976; Kareiva, 1983; Andow, 1991; Tumlinson *et al.*, 1992; Vet and Dicke, 1992). According to Chabi-Olaye *et al.* (2005), olfactory and visual cues produced by non-host plants, was the reason for reduced abundance of the stem borer *B. fusca* in maize intercropped with legume or cassava rather than on maize monocrops. In another study, Päts *et al.* (1997) reported that under maize and cowpea intercrop, *C. partellus* and *C. orichalcociliellus* had a 50% chance of locating non-suitable host, thus hampering their movement on crops by increasing the time spent in finding suitable hosts.

In line with previous findings by Oloo (1989), Oloo and Ogedah (1990), Bonhof *et al.* (1997) and Midega *et al.* (2004), larval parasitism was generally less than 10% in both cultivated and natural habitats. However, compared to cultivated habitats, stem borer larval/total parasitism were relatively lower in natural habitats. Low parasitism in natural habitats could have resulted from low parasitoid searching efficiency (Hassell and Southwood, 1978; Price *et al.*, 1980; Andow and Prokrym, 1990; Udayagiri and Welter, 2000), in more complex (both host plant composition and plant structure) habitats. Evidence by Babendreier *et al.* (2003) proved decreased searching efficiency to be responsible for lower parasitism of egg hosts by *Trichogramma brassicae* Bezdenko on plants in non-crop habitats than on maize. Low parasitism on wild host plants might have also been due to high mortality of parasitoids from toxic phytochemicals or their metabolites in the tissue and hemolymph of their herbivorous host (Ode, 2006). Through sequestration, some herbivores utilize plant secondary chemicals in defense against their parasitoids to create enemy-free space (Jeffries and Lawton, 1984; Gauld *et al.*, 1992; Stamp, 2001; Nishida, 2002). For instance, Singer and Stireman (2003) and Singer *et al.* (2004) found that the woolly bear caterpillars, *Grammia geneura* (Lepidoptera: Arctiidae), when fed on two host plants, *Senecio longilobus* and *Ambrosia confertiflora*, that contain pyrrolizidine alkaloids, was detrimental to the development of *Cotesia* sp. and two tachinid flies, *Exorista mella* and *Chetogena tachinomoides*. Although stem borers have been reported from 66 wild host plant species (Le Ru *et al.*, 2006a), details of direct or indirect plant toxicity on stem borer parasitoids is lacking, thus, requiring future studies.

Low herbivore host densities across seasons on wild host plants in this study suggested low host encounter rates (van Alphen, 1993; Hemerik *et al.*, 1993; Hassell, 2000; Outreman *et al.*, 2001; van Baalen and Hemerik, 2008), and perhaps, high incidences of super or multiple parasitism (Charnov and Skinner, 1985; van Alphen and Visser, 1990; Godfray, 1994), leading to either the mortality of stem borers and their associated parasitoids or low abundance and fitness of parasitoids. Facts exist for only cultivated habitats. Agboka *et al.* (2002), for example, demonstrated that super parasitism of *Sesamia calamistis* Hampson eggs by *Telenomus* spp. within 24 hours after oviposition caused 40% mortality of the host. On wild host plants, although Sétamou *et al.* (2005) did not investigate super parasitism, they found the survivorship of parasitized stem borer larvae and parasitoid fitness to be much lower on wild host plants than on cultivated cereals. Future studies should elucidate the incidence and effects of super and multiple parasitism on stem borer parasitoid abundance and fitness in natural habitats. Specifically, low parasitoid fitness might provide partial explanation for longer developmental periods observed for most parasitoids (Godfray, 1994; Jervis *et al.*, 2008) recovered from stem borers feeding on wild host plants compared to their counterparts on cultivated cereals.

For the first time, this study provides stem borer pupal parasitism rates in natural habitats. However, given that wild stem borers generally pupate outside plants stems (B.P. Le Ru, personal observations), it is very likely that pupal parasitism reported here was underestimated. Altogether, present results do not support the assumption by Bowden (1976), Conlong (1994) and Overholt (1998) that stem borer parasitism is higher in natural than in cultivated habitats. Predation may rather be high in natural habitats owing to high abundance and activities of generalist predators attacking stem borers (Bonhof *et al.*, 1997; Bonhof, 1998) and other herbivorous prey in perennial wild grasses. It will be interesting to compare stem borer predation in maize and wild grasses, especially because, larval migration among plants might be high in wild grasses due to low plant-stem carrying capacity (Haile and Hofsvang, 2002; Mohamed *et al.*, 2004; Sétamou *et al.*, 2005), exposing more stem borer prey to attacks.

Generally, stem borer parasitism and parasitoid abundance/adult emergence per host varied among localities during different seasons, as well as between seasons within a given locality. Though stem borer parasitism was generally low in both cultivated and natural habitats, parasitism rates were much lower in natural habitats. Given that parasitism was generally low during the dry season, there was no indication that non-diapaused larvae of cereal stem borer pests were controlled on wild host plants during the off-season.

CHAPTER SEVEN

GEOGRAPHIC DISTRIBUTION, HOST RANGE AND SEASONAL OCCURRENCE OF *COTESIA SESAMIAE* (CAMERON) AND *COTESIA FLAVIPES* CAMERON (HYMENOPTERA: BRACONIDAE)

7.1 Introduction

The braconid wasp *Cotesia sesamiae* (Cameron) (Plate 7.1a) is the most common indigenous gregarious larval endoparasitoid of cereal stem borers in Kenya (Mohyuddin and Greathead, 1970; Zhou *et al.*, 2003). However, the generational mortality of the invasive stem borer pest *Chilo partellus* (Swinhoe) by *C. sesamiae* on maize at the Kenya coast was typically less than 0.5% (Overholt *et al.*, 1994b). As such, *C. flavipes* Cameron (Plate 7.1b), an exotic parasitoid of *C. partellus* from Asia, was released in Coastal Kenya in 1993 for classical biological control of this pest species (Overholt *et al.*, 1994b). Evidence shows that *C. flavipes* has since become established and is playing a key role in suppressing the populations of *C. partellus* in the Coastal and Eastern regions of Kenya (Zhou *et al.*, 2001; Omwega *et al.*, 2006). The two *Cotesia* species attack medium and large larval instars of stem borers belonging to two economically important families, Noctuidae and Crambidae (Overholt and Smith, 1990; Zhou *et al.*, 2003). Though *C. sesamiae* and *C. flavipes* are taxonomically related and are reported to occupy an ecologically similar niche (Omwega *et al.*, 1995; Kimani-Njogu and Overholt, 1997), laboratory studies suggested differences in their stem borer host range

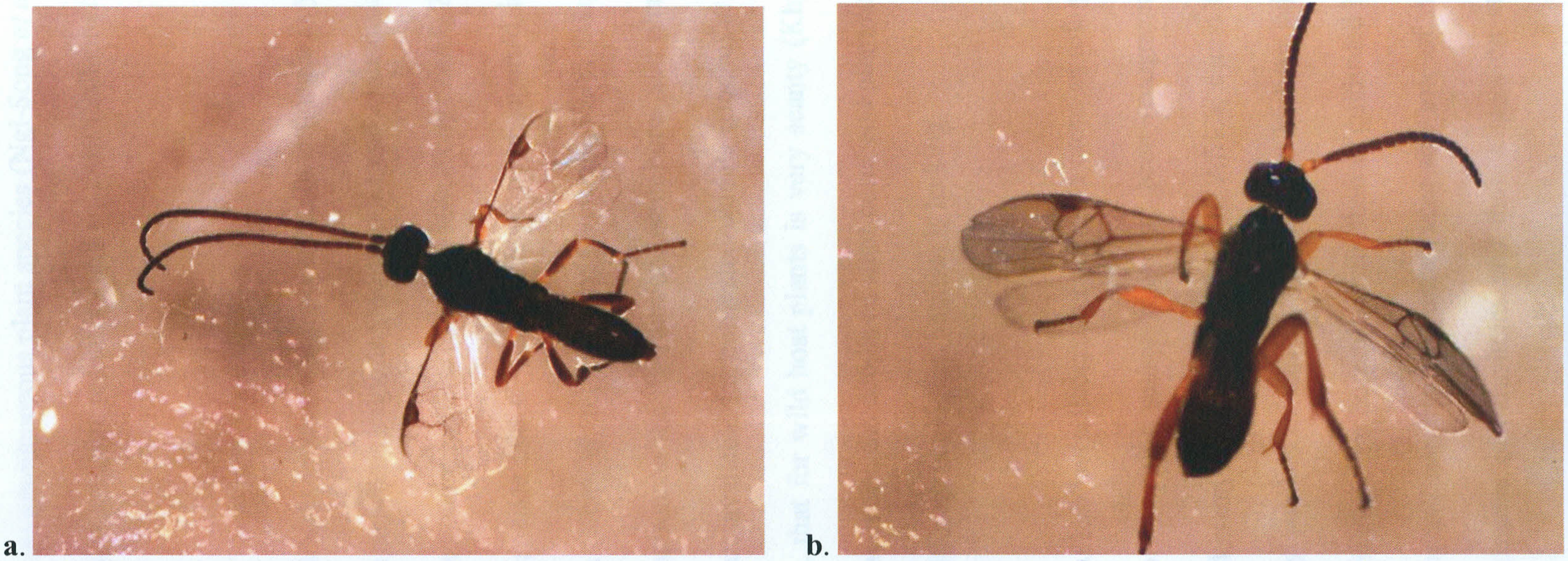

Plate 7.8: Wet specimens of (a) *Cotesia sesamiae* and (b) *C. flavipes*

and their attraction to various graminaceous plant species (Ngi-Song *et al.*, 1995, 1996). Thus, the two *Cotesia* species partition resources and co-exist (Sallam *et al.*, 2001; Jiang *et al.*, 2008).

The distribution of both *Cotesia* species was reported to be influenced by climate, in that *C. sesamiae* was common in wetter regions (Mohyuddin and Greathead, 1970), and *C. flavipes* common to dry and warm regions (Songa, 1999; Songa *et al.*, 2001; Niyibigira, 2003). So far, both *C. sesamiae* and *C. flavipes* have been reported in cultivated and natural habitats in Kenya (Khan *et al.*, 1997a,b; Overholt, 1998; Songa *et al.*, 2002). However, whereas information on the distribution, stem borer and plant host range for the two *Cotesia* species are available for cultivated cereals (Bonhof *et al.*, 1997; Oloo, 1989; Zhou *et al.*, 2003), that for wild host plants is very scanty (Khan *et al.*, 1997a; Songa *et al.*, 2002). Furthermore, the details of stem borer and plant host specificity for both *Cotesia* species in different ecological habitats is lacking.

The importance of natural habitats adjacent to cultivated crops as refugia for parasitoids especially during the non-cropping season has long been recognized (Powell, 1986; Landis *et al.*, 2005; Wilkinson and Landis, 2005). In Africa, cereal fields are usually small and surrounded by patches of natural habitats that harbour wild host plants of cereal stem borers with higher stem borer diversity than in cultivated habitats (Le Ru *et al.*, 2006a,b). It is therefore, important to understand the role of natural habitats in maintaining stable populations of parasitoids and their impact on stem borers across seasons.

In this study, field surveys were carried out over two years in both cultivated and natural habitats in four agroecological zones (AEZs) in Kenya. Data obtained were used to reveal: (i) the geographic range for *C. sesamiae* and *C. flavipes*, (ii) the range of stem borer and plant hosts for both *Cotesia* species and (iii) the variations of parasitism, cocoon mass, brood size and adult emergence by the two *Cotesia* species across seasons. Altogether, the result findings should shed more light on the effects of habitat type and ecological regions on the distribution of these *Cotesia* species. This might also give an insight into the role of natural habitats as refugia for *Cotesia* species during the non-cropping seasons.

7.2 Materials and methods

7.2.1 Field collection

Field surveys were carried out in four localities in Kenya namely Kakamega, Mtito Andei, Muhaka and Suam, all located in different AEZs as described in Chapter 3 sub-section 3.1. Surveys were conducted during both dry and rainy seasons from December 2005 to December 2007. Random and non-random sampling methods were applied in cultivated and natural habitats, respectively (see Chapter 3 sub-section 3.2).

7.2.2 Parasitoid recovery and identification

Infested cereal and wild host plants were destructively sampled in the field. The numbers of small, medium and large stem borer larvae collected were recorded, then transported to the laboratory and reared on artificial diet. All *Cotesia* cocoons recovered were kept in separate vials until the emergence of adults as explained in Chapter 3 sub-section 3.3. *Cotesia* species, stem borers and host plants collected were identified to species level as described in Chapter 3 sub-section 3.3.

The number of cocoon mass and brood size of *Cotesia* species obtained were recorded. Percentage parasitism was calculated as the proportion of susceptible stem borer larvae parasitized by *Cotesia* species (Zhou *et al.*, 2001, 2003). Percentage adult emergence was computed as the proportion of cocoons that yielded adult parasitoids (Omwega and Overholt, 1997; Hailemichael *et al.*, 1997). Sex ratio was calculated as the proportion of females over the total number of adult parasitoids (Schulthess *et al.*, 2001; Ndemah *et al.*, 2003).

7.2.3 Data analyses

Generalized linear model (PROC GENMODE, SAS 2001) was used to analyze count data (cocoon mass and brood size) and proportion data (percentage parasitism or adult emergence and sex ratio) assuming a Poisson error distribution with a logarithmic link function (McCullagh and Nelder, 1989) and a binomial error distribution with a logistic link function (Collett, 1991), respectively. Significance level was set at $P \leq 0.05$.

7.3 Results

7.3.1 Geographic distribution, stem borer and plant host range for *Cotesia* species

The two parasitoid species, *C. sesamiae* and *C. flavipes,* were separated in their spatial distribution (Table 7.1). While *C. sesamiae* was found in Western (Kakamega) and Rift valley (Suam) regions of Kenya highlands, *C. flavipes* was found in Eastern (Mtito

Table 7.1: Stem borer and host plant range for *C. sesamiae* and *C. flavipes* in cultivated and natural habitats

Parasitoid species	Locality	Habitat	Season	Host plant species	Stem borer species
Cotesia sesamiae	Kakamega	Cultivated	Dry, Long rains, Short rains	*S. bicolor, Z. mays*	*B.fusca, B.phaia, S. calamistis*
		Natural	Short rains	*P. maximum*	*B.phaia*
	Suam	Cultivated	Dry, Long rains	*S. bicolor, Z. mays*	*B.fusca, S. calamistis*
		Natural	Dry	*S. arundinaecium*	*B.fusca*
Cotesia flavipes	Muhaka	Cultivated	Dry, Long rains, Short rains	*S. bicolor, Z. mays*	*C. partellus, S. calamistis*
		Natural	Long rains, Short rains	*S. arundinaecium*	*C. partellus*
	Mtito Andei	Cultivated	Dry, Short rains	*S. bicolor, Z. mays*	*C. partellus, S. calamistis*
		Natural	Short rains	*S. arundinaecium*	*C. partellus*

Andei) and Coastal (Muhaka) regions situated in the mid and low-lands of Kenya respectively. In Mtito Andei and Muhaka, *C. flavipes* had the same host plant and stem borer ranges in either habitat type. By contrast, the host plant and stem borer ranges for *C. sesamiae* varied with both habitat type and locality (Kakamega and Suam) (Table 7.1). Whereas the cocoon mass of both *Cotesia* species (Table 7.2a) and stem borer abundance (Table 7.2b) were generally higher in cultivated habitats, host plant richness (Table 7.2c) was generally higher in natural habitats.

7.3.2 Parasitism, cocoon mass, brood size, adult emergence and sex ratio for *Cotesia* species in different seasons and habitats

In each habitat, stem borer hosts of both *Cotesia* species were restricted to a maximum of two host plant species (Table 7.3). Across localities, parasitism by either *Cotesia* species varied with stem borer species found on the various host plant species, and also according to season and year (Table 7.3). Highest parasitism rate by both *Cotesia* species was recorded during the rainy season on stem borers feeding on *Sorghum bicolor* L. and *S. arundinaceum* (Desv.) Stapf in cultivated and natural habitats (Table 7.3).

In cultivated habitats, parasitism by both *Cotesia* species was significantly different between seasons on the predominant stem borer species *B. fusca* and *C. partellus* in Kakamega and Muhaka, respectively (Table 7.4). Both localities had a bimodal rainfall distribution. However, in natural habitats, across all localities, parasitism by the two *Cotesia* species was not significantly different between seasons on all stem borer species.

Table 7.2a: Abundance of parasitoids in cultivated and natural habitats

Parasitiod species	Number of *Cotesia* cocoon mass							
	Kakamega		Suam		Mtito Andei		Muhaka	
	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural
	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy
Cotesia sesamiae	16/80	0/2	23/71	3/0	0/0	0/0	0/0	0/0
Cotesia flavipes	0/0	0/0	0/0	0/0	25/103	0/1	54/81	3/13
Others parasitiods	12/45	7/39	5/44	5/4	3/9	3/10	3/19	11/33

Table 7.2b: Species richness and abundance of stem borers in cultivated and natural habitats

Stem borer Family	Species	Number of stem borer individuals							
		Kakamega		Suam		Mtito Andei		Muhaka	
		Cultivated	Natural	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural
		Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy
Noctuidae	*B. fusca*	155/335	0/0	258/1488	13/1	0/0	0/0	0/0	0/0
	B. pphaia	24/189	42/115	0/0	0/9	0/0	0/0	0/0	0/0
	S. calamistis	56/111	0/1	0/19	0/24	67/86	75/33	268/442	1/8
	Others	0/23	132/674	1/7	69/258	0/0	111/236	0/0	49/116
Crambidae	*C. partellus*	0/0	0/0	0/0	0/0	427/404	49/74	484/2197	174/479
	C. orichalcociliellus	0/0	0/0	0/0	0/0	0/0	0/0	28/281	336/338
	Others	0/1	0/11	0/0	2/9	0/0	15/0	0/0	0/5
Pyralidae	*E. sacharrina*	0/23	0/1	0/0	0/0	0/0	1/0	0/0	0/0
	Others	0/0	20/0	0/0	0/4	0/0	6/22	0/0	30/300
Tortricidae	?	0/0	0/6	0/0	0/4	0/0	3/3	0/0	1/5

Table 7.2c: Species richness of host plants in cultivated and natural habitats

Host plant family	Host plants richness							
	Kakamega		Suam		Mtito Andei		Muhaka	
	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural	Cultivated	Natural
	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy	Dry/Rainy
Poaceae	3/3	14/24	2/2	27/30	2/2	16/19	2/2	15/22
Cyperacae	-	4/6	-	6/6	-	3/5	-	3/4
Typhacae	-	1/1	-	1/1	-	1/1	-	0/0

Table 7.3: Percentage parasitism by *C. sesamiae* and *C. flavipes* on different stem borers and host plants. In parenthesis are the number of parasitized stem borers collected

Locality	**Species**			**Percent parasitism**			
				2006		**2007**	
	Host plants	**Stem borers**	**Parasitoids**	**Dry season**	**Rainy season**	**Dry season**	**Rainy season**
Kakamega	*Z.mays*	*B. fusca*	*C. sesasmiae*	10.42 (5)	6.32 (12)	2.22 (1)	12.00 (9)
	Z.mays	*S. calamistis*	*C. sesasmiae*	2.22 (1)	7.41 (6)	-	0.00
	Z.mays	*B. phaia*	*C. sesasmiae*	18.51 (5)	20.00 (25)	-	29.67 (27)
	S. bicolor	*B. fusca*	*C. sesasmiae*	-	0.00	3.78 (4)	-
	P. maximum	*B. phaia*	*C. sesasmiae*	0.00	9.09 (2)	0.00	0.00
			C. sesasmiae				
Suam	*Z.mays*	*B. fusca*	*C. sesasmiae*	12.39 (14)	2.91 (6)	2.08 (1)	20.43 (48)
	Z.mays	*S. calamistis*	*C. sesasmiae*	-	0.00	-	25.00 (2)
	S. bicolor	*B. fusca*	*C. sesasmiae*	42.11 (8)	-	-	57.89 (11)
	S. arundinaceum	*B. fusca*	*C. sesasmiae*	14.29 (1)	-	-	0.00
Mtito Andei	*Z.mays*	*C. partellus*	*C. flavipes*	17.24 (5)	7.54 (8)	3.23 (1)	45.93(79)
	Z.mays	*S. calamistis*	*C. flavipes*	0.00	0.00	0.00	15.55 (7)
	S. bicolor	*C. partellus*	*C. flavipes*	0.00	19.14 (9)	6.44 (19)	0.00
	S. arundinaceum	*C. partellus*	*C. flavipes*	0.00	2.27 (1)	0.00	0.00
			C. flavipes				
Muhaka	*Z.mays*	*C. partellus*	*C. flavipes*	24.24 (8)	7.12 (57)	16.99 (35)	1.72 (15)
	Z.mays	*S. calamistis*	*C. flavipes*	0.00	4.17 (6)	7.86 (11)	0.00
	S. bicolor	*C. partellus*	*C. flavipes*	-	50.00 (4)	-	-
	S. arundinaceum	*C. partellus*	*C. flavipes*	0.00	60.00 (12)	20.00 (3)	4.11 (1)
	P. maximum	*C. orichalcociliellus*	*C. flavipes*	0.00	0.00	0.00	0.00

Table 7.4: Binomial regression analysis of stem borer parasitism (%) by *C. sesamiae* and *C. flavipes* between seasons on different host species

Species		Percent parasitism							
		Cultivated habitats				Natural habitats			
		Parameter estimate (SE)				Parameter estimate (SE)			
Cotesia	Stem borer	Intercept	Dry vrs Rainy	*P*-value	Odds ratio	Intercept	Dry vrs Rainy	*P*-value	Odds ratio
Kakamega									
C. sesamiae	*B. fusca*	-0.97(0.09)	-1.54 (0.05)	<.0001	0.21	-	-	-	
	S. calamistis	-2.49 (0.04)	-0.57 (0.09)	0.1491	0.57	-4.03 (0.08)	-1.38 (0.05)	0.9999	0.25
	B. phaia	1.87 (0.09)	-0.92 (0.08)	0.0011	0.40	-1.04 (0.05)	0.45 (0.03)	0.5512	1.57
Suam									
C. sesamiae	*B. fusca*	-2.13 (0.10)	0.15 (0.07)	0.5626	1.16	-7.36 (0.04)	0.56 (0.03)	0.3754	1.75
	S. calamistis	1.25 (0.08)	0.44 (0.03)	0.7112	1.55	-7.00 (0.11)	-0.30 (0.06)	0.5737	0.74
Mtito Andei									
C. flavipes	*C. partellus*	-1.00 (0.02)	-0.70 (0.04)	0.8223	0.50	-6.93 (0.05)	-0.36 (0.03)	0.2665	0.70
	S. calamistis	-2.06 (0.04)	-0.75 (0.03)	0.9999	0.47	-7.00 (0.08)	-1.30 (0.06)	0.8875	0.27
Muhaka									
C. flavipes	*C. partellus*	-3.17 (0.02)	-0.94 (0.08)	<.0001	0.39	-3.97 (0.05)	-1.28 (0.03)	0.9999	0.28

For *C. sesamiae*, in cultivated habitats, whereas its cocoon mass was significantly different between seasons on two stem borer species in only one locality (Table 7.5), its brood size and percentage adult emergence were significantly different between seasons on at least one stem borer species in both localities of occurrence (Tables 7.6 and 7.7). By contrast, in natural habitats, the cocoon mass, brood size and percentage adult emergence of *C. sesamiae* were not significantly different between seasons on all stem borer hosts in both localities of occurrence (Tables 7.5, 7.6 and 7.7).

For *C. flavipes*, in cultivated habitats, its cocoon mass and brood size were significantly different between seasons on at least one stem borer host in both localities of occurrence (Tables 7.5 and 7.6), while its percentage adult emergence was significantly different between seasons on all stem borer hosts in only one locality (Table 7.7). By contrast, in natural habitats, the cocoon mass, brood size and percentage adult emergence of *C. partellus* were significantly different between seasons on at least one stem borer host in both localities of occurrence (Tables 7.5, 7.6 and 7.7).

In cultivated habitats, the sex ratio of both *C. sesamiae* and *C. flavipes* was significantly different between seasons on at least one stem borer species in all localities (Table 7.8). On the contrary, in natural habitats, the sex ratio of both *Cotesia* species was not significantly different between seasons on all stem borer species in all localities (Table 7.8).

Table 7.5: Logistic regression analysis of cocoon mass(es) produced by *C. sesamiae* and *C. flavipes* between seasons on different stem borers

Species		Cocoon mass							
Cotesia	Stem borer	Cultivated habitats				Natural habitats			
		Parameter estimate (SE)				Parameter estimate (SE)			
		Intercept	Dry vrs Rainy	*P*-value	Odds ratio	Intercept	Dry vrs Rainy	*P*-value	Odds ratio
Kakamega									
C. sesamiae	*B. fusca*	0.59 (0.03)	-1.06 (0.08)	0.0002	0.35	-	-	-	-
	S. calamistis	-1.29 (0.04)	-0.89 (0.08)	0.4058	0.41	-0.67 (0.02)	-0.22 (0.04)	0.9999	0.80
	B. phaia	1.37 (0.14)	-0.55 (0.08)	0.0013	0.58	-0.88 (0.05)	0.45 (0.03)	0.8917	1.57
Suam									
C. sesamiae	*B. fusca*	0.41 (0.02)	-0.26 (0.04)	0.2820	0.77	-0.74 (0.09)	0.50 (0.06)	0.8821	1.65
	S. calamistis	0.25 (0.07)	0.08 (0.01)	0.5987	1.08	-0.55 (0.03)	-0.13 (0.04)	0.7919	0.88
Mtito Andei									
C. flavipes	*C. partellus*	1.79 (0.03)	-0.51 (0.02)	0.0209	0.60	-1.60 (0.05)	-1.39 (0.02)	<.0001	0.25
	S. calamistis	0.15 (0.03)	-0.56 (0.09)	0.9999	0.57	-3.00 (0.13)	-1.32 (0.07)	0.5331	0.27
Muhaka									
C. flavipes	*C. partellus*	-0.61 (0.11)	0.37 (0.09)	<.0001	1.45	-1.47 (0.07)	-0.85 (0.04)	0.1808	0.43
	S. calamistis	-1.99 (0.07)	0.46 (0.05)	0.0004	1.58	-3.00 (0.03)	-1.03 (0.06)	0.9117	0.36

Table 7.6: Logistic regression analysis of brood size produced by *C. sesamiae* and *C. flavipes* between seasons on different stem borers

Species		Brood size per host							
		Cultivated habitats				Natural habitats			
		Parameter estimate (SE)				Parameter estimate (SE)			
Cotesia	**Stem borer**	**Intercept**	**Dry vrs Rainy**	***P*-value**	**Odds ratio**	**Intercept**	**Dry vrs Rainy**	***P*-value**	**Odds ratio**
Kakamega									
C. sesamiae	*B. fusca*	4.06 (0.01)	-1.28 (0.05)	<.0001	0.28	-	-	-	-
	S. calamistis	0.27 (0.06)	-1.47 (0.03)	<.0001	0.23	-3.00 (0.09)	-0.86 (0.05)	0.7752	0.42
	B. phaia	1.55 (0.10)	-0.97 (0.06)	0.0008	0.38	-0.73 (0.09)	0.41 (0.05)	0.9722	1.51
Suam									
C. sesamiae	*B. fusca*	3.87 (0.02)	-0.26 (0.04)	<.0001	0.77	-3.88 (0.02)	0.40 (0.03)	0.8881	1.49
	S. calamistis	4.87 (0.06)	-1.30 (0.04)	0.8773	0.27	-3.00 (0.03)	-0.99 (0.01)	0.9894	0.37
Mtito Andei									
C. flavipes	*C. partellus*	2.22 (0.01)	-1.07 (0.05)	<.0001	0.34	1.60 (0.07)	-1.39 (0.05)	0.9999	0.25
	S. calamistis	0.76 (0.06)	-0.35 (0.04)	0.9993	0.70	-3.00 (0.02)	-0.73 (0.01)	0.9173	0.48
Muhaka									
C. flavipes	*C. partellus*	2.16 (0.02)	0.68 (0.04)	<.0001	1.97	1.26 (0.07)	-1.01 (0.03)	<.0001	0.36
	S. calamistis	2.00 (0.05)	-0.36 (0.07)	<.0001	0.70	-3.00 (0.09)	-1.51 (0.07)	0.9855	0.22

Table 7.7: Binomial regression analysis of adult emergence (%) by *C. sesamiae* and *C. flavipes* between seasons on different stem borers

Species		Percent adult emergence							
Cotesia	Stem borer	Cultivated habitats				Natural habitats			
		Parameter estimate (SE)				Parameter estimate (SE)			
		Intercept	Dry vrs Rainy	*P*-value	Odds ratio	Intercept	Dry vrs Rainy	*P*-value	Odds ratio
Kakamega									
C. sesamiae	*B. fusca*	1.48 (0.24)	-1.10 (0.20)	<.0001	0.33	-	-	-	-
	S. calamistis	5.35 (0.13)	-0.94 (0.09)	0.9999	0.39	2.55 (0.19)	-1.02 (0.07)	0.5117	0.36
	B. phaia	1.66 (0.12)	-0.83 (0.08)	0.0002	0.44	-0.67 (0.09)	0.28 (0.06)	0.6714	1.32
Suam									
C. sesamiae	*B. fusca*	1.10 (0.05)	0.13 (0.03)	<.0001	1.14	2.96 (0.29)	0.10 (0.02)	0.9783	1.11
	S. calamistis	0.43 (0.02)	0.21 (0.02)	0.3551	1.23	-3.35 (0.18)	-1.27 (0.13)	0.7853	0.28
Mtito Andei									
C. flavipes	*C. partellus*	1.92 (0.05)	0.21 (0.07)	0.2244	1.23	-0.58 (0.05)	0.43 (0.02)	0.8416	1.54
	S. calamistis	2.37 (0.22)	0.36 (0.09)	0.7761	1.43	-1.09 (0.07)	0.33 (0.03)	0.9125	1.39
Muhaka									
C. flavipes	*C. partellus*	1.58 (0.06)	-0.63 (0.09)	<.0001	0.53	3.04 (0.34)	-1.14 (0.19)	<.0001	0.32
	S. calamistis	1.91 (0.16)	-0.79 (0.19)	<.0001	0.45	-7.53 (0.17)	-1.44 (0.21)	0.4731	0.24

Table 7.8: Binomial regression analysis of sex ratio for *C. sesamiae* and *C. flavipes* between seasons on different stem borers

Species		**Sex ratio (proportion of females)**							
		Cultivated habitats				**Natural habitats**			
		Parameter estimate (SE)				**Parameter estimate (SE)**			
Cotesia	**Stem borer**	**Intercept**	**Dry vrs Rainy**	***P*-value**	**Odds ratio**	**Intercept**	**Dry vrs Rainy**	***P*-value**	**Odds ratio**
Kakamega									
C. sesamiae	*B. fusca*	1.16 (0.05)	-0.85 (0.17)	<.0001	0.43	-			
	S. calamistis	1.92 (0.10)	-0.18 (0.05)	0.7733	0.84	1.16 (0.19)	0.65 (0.07)	0.9135	1.92
	B. phaia	1.82 (0.11)	-0.98 (0.09)	0.0023	0.38	-1.11 (0.08)	0.61 (0.04)	0.4377	1.84
Suam									
C. sesamiae	*B. fusca*	0.95 (0.05)	0.23 (0.04)	0.0327	1.26	1.56 (0.34)	-1.28 (0.14)	0.4532	0.28
	S. calamistis	0.63 (0.06)	0.49 (0.03)	0.5945	1.63	1.79 (0.11)	-1.30 (0.09)	0.5767	0.27
Mtito Andei									
C. flavipes	*C. partellus*	1.07 (0.04)	0.43 (0.04)	0.0031	1.54	0.33 (0.08)	0.21 (0.03)	0.8122	1.23
	S. calamistis	1.42 (0.06)	0.56 (0.04)	0.5666	1.75	1.52 (0.05)	-0.59 (0.04)	0.5587	0.55
Muhaka									
C. flavipes	*C. partellus*	1.15 (0.05)	-0.02 (0.10)	0.8266	0.98	0.96 (0.11)	-0.19 (0.05)	0.7076	0.83
	S. calamistis	0.64 (0.02)	0.62 (0.08)	0.0006	1.86	1.32 (0.13)	-1.04 (0.08)	0.5743	0.35

7.4 Discussion

These results showed that the occurrence of the two *Cotesia* species in different ecological regions was clearly influenced by the geographic range of their respective suitable stem borer hosts (Ngi-Song *et al.*, 1995; Hailemichael *et al*, 1997, 2008) and temperature (Mohyuddin and Greathead, 1970; Songa, 2001). *Cotesia sesamiae* was found in the cool Kenyan highlands whether wet (Kakamega) or partially dry (Suam) where *B. fusca* predominates (Nye, 1960; Harris and Nwanze, 1992; Ong'amo *et al.*, 2006). While *C. flavipes* was found in the warm mid- and low-altitudes where *C. partellus* predominates (Nye, 1960; Songa, 1999; Zhou *et al.*, 2003; Ong'amo *et al.*, 2006).

In this study, the two *Cotesia* species were not found living together in a single locality. However, *C. sesamiae* and *C. flavipes* coexist in areas surrounding Mount Kenya (in the central region) at altitudes between 1200 and 1500 m asl, where intermediate climatic conditions support mixed populations of *B. fusca* and *C. partellus* (Le Ru, Unpublished data). This implied that, with the spread of *C. partellus* to high elevation areas (Overholt *et al.*, 2000; Wale *et al.*, 2006), *C. flavipes* will consequently increase its geographic range by invading such regions. This is likely to occur with heightened effects of global warming, as the wet and cool highlands might get drier and hotter (Funk *et al.*, 2005; Case, 2006; Osbahr and Viner, 2006), thereby turning favourable for the development and spread of both *C. partellus* and *C. flavipes* as previously reported by Mbapila and Overholt (2001) and Mbapila *et al.* (2002). Additionally, *C. flavipes* is capable of successfully developing on *B. fusca* in cases of multiple parasitism when the host species is parasitized by *C. sesamiae* prior to attack by *C. flavipes* (Ngi-Song *et al*., 2001). In view of the above stated findings, there is a need to monitor if increased temperatures will aid the spread of *C. partellus* and its biological control agent *C. flavipes* to high altitude areas, so as to elucidate the consequences of global warming on the interactions between *B. fusca* and *C. sesamiae* that currently predominate in the Kenya highlands, as well as the effectiveness of *C. flavipes* on *C. partellus* in such regions.

Cotesia sesamiae was not recovered in Muhaka, and this might have been due to its very low abundance or parasitism in this region. Earlier findings by Overholt *et al*. (1994b) had pointed out the need to introduce *C. flavipes* at the Kenyan Coast, as a result of the low abundance and inefficiency of *C. sesamiae* in controlling *C. partellus*. Not surprising, Le Ru (Unpublished data), from field surveys in cultivated and natural habitats (33 and 11 localities in Eastern and Coastal regions in Kenya, respectively [during 2001 to 2003]) recorded less than 4% of *C. sesamiae* among *Cotesia* species recovered from 25000 stem borer larvae collected. The continuation of this study in natural habitats only (43 and 15 localities in Eastern and Coastal regions of Kenya, respectively [during 2003 to 2008]), likewise showed that *C. sesamiae* was less than 1% among *Cotesia* species recovered from 5000 stem borer larvae collected.

There was no sign of host specificity for *C. sesamiae* in either cultivated or natural habitats, as its host plant and stem borer ranges varied with both habitat type and locality. By contrast, *C. flavipes* was found restricted to a narrow range of host plants and stem borers, with a high level of specificity to its target host *C. partellus* on maize

(90.17%) and sorghum (100%) in cultivated habitats and on *S. arundinaceum* (98.50%) in natural habitats. In another study, extensive surveys carried out by Le Ru (Unpublished data) in seven countries of Eastern and Southern Africa (during 2001 to 2008), confirmed that in natural habitats *C. sesamiae* had a much broader range of hosts (twenty stem borer and nine wild host plant species) than *C. flavipes* that was highly specific to *C. partellus* on *S. arundinaceum*, *P. purpureum* and *Arundo donax* L. The high host specificity of *C. flavipes* to *C. partellus* could have been due to the high physiological suitability of this host for its development as reported by Ngi-Song *et al.* (1995) and Sétamou *et al.* (2005). A major objective of classical biological control is the ability of an exotic natural enemy to maintain high specificity to its target host species with minimal or no impact on other non-target hosts in the ecosystem (Howarth, 1991; Greathead, 1995). For the current result findings, *C. flavipes* appeared to be an appropriate biological control agent against *C. partellus* in Eastern Africa.

The present results also showed that both *C. sesamiae* and *C. flavipes* played an important role in regulating stem borer pest populations in their respective regions of occurrence. For both *Cotesia* species, parasitism varied with season, year and habitat type, as parasitism was generally higher in cultivated habitats during the rainy season. Though parasitism of *C. partellus* by *C. sesamiae* had never been greater than 3% on maize before the introduction of *C. flavipes* (Overholt *et al.*, 1994b), this study showed that the parasitism of this particular pest by *C. flavipes* had greatly increased with a high of 45.93% on maize and 50.00% on sorghum in cultivated habitats, and 60.00% on *S. arundinaceum* in natural habitats.

These results further suggested that the perennation of both *Cotesia* species across seasons occured mainly in cultivated habitats and to a lesser extent in natural habitats for *C. flavipes* only. Non-perennation of *C. sesamiae* in natural habitats was most probably due to the scarcity (in Suam) and absence (in Kakamega) of its suitable cereal stem borer pests on wild host plants.

The availability of *C. sesamiae* and *C. flavipes* across seasons was not only influenced by the presence of actively feeding stem borer larvae on cereal plants, but also by the duration of the dry season in different localities. For instance, in Kakamega, where dry conditions did not exceed two months, *C. sesamiae* maintained its population during the dry season by parasitizing *B. fusca* and *S. calamistis*, feeding on maize and sorghum plants available in few crop fields. Seshu Reddy (1989) and Le Ru (Unpublished data) had pointed out that *B. fusca* is capable of feeding actively throughout the year without any intervening diapause in areas where the dry season rarely exceeds two months. In Suam, where dry conditions remained at least five months, though rare, *C. sesamiae* was recovered from *B. fusca* larvae mainly during the rainy and earlier parts of the dry seasons prior to host diapause inside dry maize root stalks. Thus, suggesting that *C. sesamiae* is well adapted to surviving harsh dry conditions in this locality. Given that *C. sesamiae* lacks the ability to locate diapaused larvae in dried maize stalks (Mbapila and Overholt, 1997), it is possible that this parasitoid species survives severe dry periods in the field by parasitizing non-diapausing larvae prior to aestivation, and then assume a resting stage within diapausing larvae. In Muhaka, though some *C. partellus* larvae diapaused inside dry maize stalks, *C. flavipes* survived the dry season by parasitizing actively feeding *C. partellus* larvae on the few maize stems found in marshy areas. In the semi-arid Mtito Andei, where dry conditions last more than eight months, some *C. flavipes* individuals survived the dry season parasitizing actively feeding *C. partellus* and *S. calamistis* larvae on maize in irrigated fields. In addition, it is believed that some other *C. flavipes* individuals probably entered a resting stage along with their host larvae in dried maize and sorghum stalks.

CHAPTER EIGHT

GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

8.1 General discussion

In total twenty-seven and eighteen parasitoid species were found in natural and cultivated habitats, respectively. Of the parasitods recovered in natural habitats, seventeen species were reported for the first time attacking stem borers on wild host plants in Kenya. For cultivated habitats, in Coastal Kenya, Zhou *et al.* (2003) recorded a much higher parasitoid diversity on maize. The discrepancy of stem borer parasitoid diversity between the two studies was attributed to differences in the study duration and the numbers of stem borers collected. Moreover, parasitoid diversity is not static, and can change over time along with changes in their herbivore host densities (Menalled *et al.*, 2003). These results and those of Bonhof *et al.* (1997) and Zhou *et al.* (2003), clearly showed that the majority of parasitoid species recovered were not only stenophagous, but were common to both cultivated and natural habitats. This suggested that most of the species have a low host and habitat specificity, probably as a survival strategy to enable them switch habitats when necessary (Askew, 1994; Hoffmeister and Vidal, 1994).

Parasitoid species composition varied among different AEZs, as more than half of the species collected were restricted to specific AEZ(s). Perhaphs, this was due to differences in the herbivore host species composition or local ecological conditions (Askew and Shaw, 1986; Shaw, 1994; Sheehan, 1994; Tscharntke and Brandl, 2004). It seemed that uncommon parasitoid species were very likely found near the edge of their distribution, and do not necessarily survive in high numbers in natural habitats to occasionally spill over onto cereal stem borers.

Results obtained indicated that, in all AEZs, stem borer parasitoid diversity was significantly higher in natural than in cultivated habitats. Ndemah *et al.* (2007) in Cameroon and Matama-Kauma *et al.* (2008) in Uganda, likewise found a high diversity of stem borer parasitoids on wild host plants. The low diversity of parasitoids in cultivated habitats was thought to be as a result of the low diversity of stem borers and host plant species in this habitat, and also because parasitoids have to re-colonize crop fields periodically owing to crop harvest and disturbances caused by agricultural practices (i.e., pesticides applications) that generally alter or reduce species interactions across different trophic levels in modified habitats (Levins and Wilson, 1980; Tylianakis *et al.*, 2007). By contrast, the high diversity of parasitoids in natural habitats was very likely supported by the availability of alternative herbivore hosts, adult food resources (i.e., pollen, floral and extrafloral nectar) and shelter from adverse management practices or temperatures in the perennial habitat (Kruess, 2003). Adult food resources have been shown to enhance parasitoid longevity, fecundity and effectiveness (Landis *et al.*, 2000, 2005; Wilkinson and Landis, 2005; Bianchi *et al.*, 2006). Benrey *et al.* (1998), Sétamou *et al.* (2005) and Tylianakis *et al.* (2007) have reported similar findings where parasitoid abundance was generally higher on cultivated crops than on natural host plants. This could be attributed to the much lower larval mortality on cultivated crops than on wild host plants (Sétamou *et al.*, 1993; Haile and Hofsvang, 2002). In addition, the higher nutritional content of selected crops translates into higher fitness for stem borers and subsequently that of parasitoids, which in turn supports high clutch size in parasitoids (Ode, 2006; Jervis *et al.*, 2008).

In line with the findings of Kruess and Tscharntke (2000) and Kruess (2003), this study found that, across all AEZs, stem borer parasitism was positively related to parasitoid richness and abundance during the rainy and dry seasons in both cultivated and natural habitats. These results further showed that the relationship between stem borers and host plants richness/abundance on parasitoid richness/abundance was not always positive, as it varied with AEZs, habitat type and season. A significantly negative relationship between parasitoid richness/abundance or stem borer parasitism and rainfall during the rainy and dry seasons in both cultivated and natural habitats in all AEZs, pointed out the decrease in host availability owing to high stem borer mortality following heavy rainfall. Earlier studies have shown that heavy rainfall either inflicts considerable mortality on stem borer populations directly (Oloo, 1989; Moyal, 1998; Schulthess *et al.,* 2001; Haile and Hofsvang, 2002) or indirectly disrupts their mating and oviposition activities (Jerath, 1968; Sampson and Kumar, 1983). As rainfall increases with altitudes (Corbett, 1998), its negative effects are expected to be more severe at high elevations, especially in areas with bimodal rainfall distribution.

The low incidence of plant infestation by stem borers, stem borer density/parasitism and parasitoid abundance/adult emergence per host in natural habitats suggest that host plant diversity has a strong influence on the abundance, and consequently, the availability of stem borer hosts. This is because more diverse host plant communities are characterized by decreased immigration or increased emigration of herbivores owing to host-finding disruption in habitats with a high variety of physical characteristics or chemical stimuli (Root, 1973; Vinson, 1976; Kareiva, 1983; Andow, 1991; Tumlinson *et al.*, 1992; Vet and Dicke, 1992).

The results also showed that larval/total parasitism varied among agroecological regions. Possibly, this was because of different host plant-herbivore-parasitoid species composition existing in different localities, as well as the seasonal variations of their densities (Shaw, 1994; Sheehan, 1994; Askew and Shaw, 1986; Tscharntke and Brandl, 2004). However, similar to the findings reported by Oloo (1989), Oloo and Ogedah (1990), Bonhof *et al.* (1997) and Midega *et al.* (2004), larval/total parasitism was generally less than 10% in both cultivated and natural habitats. In particular, stem borer parasitism was much lower in natural habitats. This was most probably due to low stem borer densities on wild host plants (Ofomata *et al.*, 2000; Mohamed *et al.*, 2004; Sétamou *et al.*, 2005), and perhaphs, low herbivoure host encounter rates or multiple parasitism of the few encountered herbivore hosts (van Baalen and Hemerik, 2008). Alternatively, the low larval parasitism in natural habitats, may be explained by high mortality of parasitoids when exposed to plant allelochemicals in their host diet (Ode, 2006). Although pupal parasitism was generally low in both habitats, it was slightly higher in cultivated than in natural habitats, may be due to the ease of accessing stem borers living inside thick stemmed cereal plants (Muturi *et al.*, 2005), or due to the underestimation of parasitization rates on wild host plants in the field, since stem borers seldom pupate within plant stems, but rather outside their host plant stems in the soil. The fact that, in natural habitats, parasitism rates were generally low across seasons, suggests that cereal stem borer pests are not necessarily controlled on wild host plants during the off-season.

The distribution of *C. sesamiae* and *C. flavipes* in different agroecological regions was most influenced by the geographic range of their suitable cereal stem borer host (Ngi-Song *et al.*, 1995; Hailemichael *et al*, 1997, 2008). *Cotesia sesamiae* and *C. flavipes* were found in parts of the Kenyan highlands (cool areas) and Eastern/Coastal regions in mid- and lowland altitudes (warm/dry areas), where *B. fusca* and *C. partellus* predominate, respectively (Nye, 1960; Harris and Nwanze, 1992; Songa, 1999; Ong'amo *et al.*, 2006). Since both *Cotesia* species coexist in areas of intermediate climatic conditions (Le Ru, Unpublished data), the geographic range for *C. flavipes* might increase with increased effects of global warming, as it may invade the Kenya highland. Whereas *C. sesamiae* showed no signs of host specificity in either habitats, *C. flavipes* was highly specific to its target host *C. partellus* on maize/sorghum in cultivated habitats and on *S. arundinaceum* in natural habitats. Evidently, *C. flavipes* is a suitable biological control agent against *C. partellus* in Kenya, seemingly without any adverse effects on non-target hosts in the ecosystem (Howarth, 1991; Greathead, 1995).

Furthermore, evidence showed that each *Cotesia* species contributed in regulating stem borer populations in both habitats, but in their respective regions of occurrence. This was expected, because, stem borer parasitism could vary with season, year and habitat type (Overholt, 1998). These results also showed that both *Cotesia* species perennated across seasons in cultivated habitats. Nonetheless, natural habitats served as a reservoir for *C. flavipes*, as some of its individual were sustained across seasons on *C. partellus* feeding in *S. arundinaceum*. On the contrary, natural habitats did not serve as a reservoir for *C. sesamiae*, as its cereal stem borer hosts were scarce on wild host plants.

This study indicated that the availability of either *Cotesia* species across seasons was influenced by the availability of actively feeding cereal stem borer pests and the duration of the dry season in different localities. In AEZs with bimodal rainfall distribution, some individuals of either *Cotesia* species were sustained during the dry season on actively feeding *B. fusca* and *C. partellus* on maize. This was possible because few maize plants were available during the dry season due to either brief rain spells or they grew in marshy areas along the river banks. However, in AEZs with a single rainfall distribution, these *Cotesia* species survived the harsh dry periods either on hosts actively feeding in irrigated plots, or perhaphs assumed a quiescent stage within diapausing larvae so as to resume growth the next cropping season when favourable conditions resume.

8.2 Conclusions

1. Stem borer parasitoid diversity was higher in natural than in cultivated habitats in all agroecological zones.
2. Natural habitats surrounding cereal crops appeared to serve as refugia for sustaining the diversity of stem borer parasitoids from adjacent cereal fields.
3. Parasitoid diversity was much higher in agroecological zones with bimodal rainfall distribution pattern (Kakamega and Muhaka) than those with a single distribution pattern (Kitale and Mtito Andei).

4. In both habitats, stem borer parasitism was positively related to parasitoid species richness and abundance during both rainy and dry seasons.
5. Parasitoid richness and abundance were mainly influenced by stem borer density. These effects, however, varied with locality, habitat type or season.
6. Parasitoid abundance and stem borer parasitism were negatively correlated with rainfall.
7. Stem borer parasitism was positively and negatively correlated with temperature in cultivated and natural habitats, respectively.
8. Stem borer parasitism was generally low in both cultivated and natural habitats.
9. The distribution of *C. sesamiae* and *C. flavipes* in different AEZs was mainly affected by the geographic range of their suitable cereal stem borer host and temperature.
10. *Cotesia flavipes* proved to be an appropriate biological control agent in Kenya by maintaining high specificity to its target host *C. partellus* on both cultivated cereals and natural host plants, with very little effect on non-target hosts.
11. Both *C. sesamiae* and *C. flavipes* played an important role in regulating stem borer pest populations in different agroecological regions.
12. Natural habitats served as a reservoir for *C. flavipes* across seasons, but not for *C. sesamiae*.

8.3 Recommendations

1. To gain further insight into the role of natural habitats as refugia for stem borer parasitoids, there is a need to understand the suitability of wild stem borer species to parasitoids of cereal stem borer pests.
2. To successfully practice habitat management in the cereal agroecosystems, it is important to identify wild host plants that supply essential nutrients to adult parasitoids, and also the most effective means of incorporating non-crop habitats for the provision of refuge, food resources and suitable micro-climate to parasitoids.
3. Future studies should investigate the effects of size, vegetation species composition and fragmentation/connectivity of natural habitats on stem borer parasitoid diversity, survivorship, dispersal and parasitism in the cereal cropping system.
4. Sustenance of *Cotesia* species or the enhancement of their impact will require thorough understanding of their survivorship across seasons. Thus, it will be intresting to establish whether *Cotesia* species assume quiescence in diapausing stem borer host larvae during severe dry conditions.
5. Further investigations are necessary to determine the effects of *S. arundinaceum* and *P. maximum* (that haboured *Cotesia* species) as intercrop or border row plants around cereal crops on the abundance of both *Cotesia* species and their parasitism rates.

6. To fully comprehend the role of natural habitats in sustaining stable stem borer parasitoid populations, it is essential to establish the direct or indirect effects of phytochemicals or their toxic metabolites on stem borer parasitoid development, fitness and impact.
7. To appraise the possible consequences of global warming on the stem borer parasitoid communities in Kenya, it will be intresting to monitor whether increased environmental temperature would facilitate the spread of *C. partellus* to the Kenyan highlands. If *C. partellus* were to spread to other agroecological regions in the country; would *C. flavipes* remain an effective biological control agent against its populations? Further, what might be the consequences of such spread on the interactions between *B. fusca* and *C. sesamiae* that currently predominate in the Kenya highlands.

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