

### Parasitism of Lepidopterous Stem Borers in Cultivated and Natural Habitats

Authors: Mailafiya, Duna Madu, Le Ru, Bruno Pierre, Kairu, Eunice Waitherero, Dupas, Stéphane, and Calatayud, Paul-André

Source: Journal of Insect Science, 11(15): 1-19

Published By: Entomological Society of America

URL: https://doi.org/10.1673/031.011.0115

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



# Parasitism of lepidopterous stem borers in cultivated and natural habitats

Duna Madu Mailafiya<sup>1, 2a\*</sup>, Bruno Pierre Le Ru<sup>1b</sup>, Eunice Waitherero Kairu<sup>2c</sup>, Stéphane Dupas<sup>3d</sup>, and Paul-André Calatayud<sup>1e</sup>

<sup>1</sup>Unité de Recherche IRD 072, International Centre of Insect Physiology and Ecology (ICIPE), PO Box 30772, Nairobi, Kenya or Université Paris-Sud II, 91405 Orsay cedex, France

<sup>2</sup> Department of Zoological Sciences, School of Pure and Applied Sciences, Kenyatta University, PO Box 43844, Nairobi, Kenya

<sup>3</sup> Unité de Recherche IRD 072, CNRS, Laboratoire Evolution, Génomes et Spéciation, Bât 13, BP 1, Avenue de la Terrasse, 91198 Gif-sur-Yvette cedex, France et Université Paris-Sud 11, 91405 Orsay cedex, France

### Abstract

Plant infestation, stem borer density, parasitism, and parasitoid abundance were assessed during two years in two host plants, Zea mays (L.) (Cyperales: Poaceae) and Sorghum bicolor (L.) (Cyperales: Poaceae), in cultivated habitats. The four major host plants (Cyperus spp., Panicum spp., *Pennisetum* spp., and *Sorghum* spp.) found in natural habitats were also assessed, and both the cultivated and natural habitat species occurred in four agroecological zones in Kenya. Across habitats, plant infestation (23.2%), stem borer density (2.2 per plant), and larval parasitism (15.0%) were highest in maize in cultivated habitats. Pupal parasitism was not higher than 4.7% in both habitats, and did not vary with locality during each season or with host plant between each season. Cotesia sesamiae (Cameron) and C. flavipes Cameron (Hymenoptera: Braconidae) were the key parasitoids in cultivated habitats (both species accounted for 76.4% of parasitized stem borers in cereal crops), but not in natural habitats (the two *Cotesia* species accounted for 14.5% of parasitized stem borers in wild host plants). No single parasitoid species exerted high parasitism rates on stem borer populations in wild host plants. Low stem borer densities across seasons in natural habitats indicate that cereal stem borer pests do not necessarily survive the non-cropping season feeding actively in wild host plants. Although natural habitats provided refuges for some parasitoid species, stem borer parasitism was generally low in wild host plants. Overall, because parasitoids contribute little in reducing cereal stem borer pest populations in cultivated habitats, there is need to further enhance their effectiveness in the field to regulate these pests.

Keywords: agroecological zones, cereals, habitat types, seasons, wild host plants Correspondence: a\* dmailaflya@gmail.com, b bleru@icipe.org, c eunicekairu@yahoo.com, d dupas@legs.cnrs-gif.r, e pcalatayud@icipe.org, \*Corresponding author Received: 2 November 2009, Accepted: 19 May 2010 Copyright : This is an open access paper. We use the Creative Commons Attribution 3.0 license that permits unrestricted use, provided that the paper is properly attributed. ISSN: 1536-2442 | Vol. 11, Number 15 Cite this paper as:

Mailafiya DM, Le Ru BP, Kairu EW, Dupas S, Calatayud PA. 2011. Parasitism of lepidopterous stem borers in cultivated and natural habitats. *Journal of Insect Science* 11:15 available online: insectscience.org/11.15

Journal of Insect Science | www.insectscience.org

#### Introduction

In sub-Saharan Africa stem borers are major biotic constraints to cereal production. These pests are responsible for losses ranging between 5-73% of potential yield under different agroecological conditions (Seshu Reddy and Walker 1990; De Groote 2002; De Groote et al. 2003). Upon hatching, with the exception of Sesamia calamistis that bore directly into the stem (Bosque-Pérez and Schulthess, 1998), the first instar larvae of most stem borer species initially feed on young leaf tissues, while older larvae tunnel into the stem tissues and feed internally (Nye 1960; Bosque-Pérez and Schulthess 1998). Depending on the species, the larval stage may last 25-58 days and may have 6-8 instars. Pupation normally takes 5-14 days after which adult moths emerge (Harris 1990; Holloway 1998; Maes 1998). In maize, stem borers pupate close to the tunnel exit or even partly outside the stem (Smith et al. 1993), which increases their accessibility to parasitoids (Ndemah et al. 2001). On the contrary, in 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 (Mailafiya 2009).

These stem borers are attacked by a diverse group of both indigenous and exotic parasitoids (Bonhof et al. 1997; Overholt 1998; Zhou et al. 2003; Mailafiya et al. 2009). It is assumed that parasitism is higher on stem borer populations residing in wild grass communities than on those in cultivated crops due to: (1) nonperiodic re-colonization of natural habitats by parasitoids (Conlong 1994), and (2) slow stem borer larval growth rates which increases their temporal window of susceptibility to stagespecific parasitoids (Bowden 1976; Overholt 1998). Parasitization of cereal stem borer pests during the non-cropping (off) season may therefore occur mainly in natural habitats (Schulthess et al. 1997).

Cereal crops are usually grown in small fields surrounded by land occupied by wild host plants of lepidopterous stem borers. Natural habitats have high stem borer diversity (Le Ru et al. 2006a, b), and thus, serve as refugia for sustaining parasitoid diversity within the ecosystem (Ndemah et al. 2002; Mailafiya et al. 2009, 2010). Also, across different ecological regions and seasons, stem borer parasitism is generally positively correlated with parasitoid richness and abundance (Mailafiya et al. 2010). Herbivore parasitism, however, can vary with habitat type depending on the prevailing conditions in a given ecosystem (Landis et al. 2000; Altieri and Nicholls 2004). Hence, it is imperative to understand the ecological role (i.e., herbivore pest population regulation) of natural habitats as a component of the cereal cropping system.

In Kenya, more than 95 parasitoid (Bonhof et al. 1997; Zhou et al. 2003; Mailafiya et al. 2009), 88 stem borer (Khan et al. 1997a; Le Ru et al. 2006a, b; Mailafiya et al. 2009), and 66 host plant (Le Ru et al. 2006a, b; Mailafiya et al. 2009) species have been recorded. However, only laboratory studies have assessed stem borer parasitism in both cereals and wild host plants (Sétamou et al., 2005), and these have particularly focused on one parasitoid, *Cotesia flavipes*; one stem borer, *Chilo partellus*; two cultivated cereals, *Zea mays* and *Sorghum bicolor*; and two wild host plants, *Pennisetum trachyphyllum* and *Sorghum arundinaceum*.

This study assessed the field parasitism of lepidopterous stem borers in various host plant genera found in cultivated habitats (*Z. mays* L. and *S. bicolour* L. (Poales: Poaceae)) and natural habitats (*Cyperus* spp., *Panicum* spp.,

*Pennisetum* spp. and *Sorghum* spp.) during different seasons in four agroecological zones in Kenya. Results obtained can provide crucial information on stem borer parasitism during the off season, or hint at the importance of parasitoids in regulating stem borer populations in different habitats. Ultimately, these should advance basic understanding of the ecological role of natural habitats as reservoir(s) for parasitoids during the off season.

#### **Materials and Methods**

#### Survey sites description

Field surveys were conducted over two years (from December 2005 to December 2007) in four localities representing different agroecological zones in Kenya: Suam (Trans-Nzoia District) in the highland tropics, Kakamega (Kakamega District) in the moist transitional agroecological zones, Mtito Andei (Makueni District) in the dry mid-altitudes, and Muhaka (Kwale District) in the lowland tropics.

Suam (1° 11' N, 34° 47' E, 1995 MASL) has a single cropping season that lasts from March to November. Average annual rainfall and temperature are 1190 mm and 19°C, respectively (Africa AWhere-ACT Database 2002). Local vegetation is characterized by a mosaic of both rain forest and secondary grassland. Suam is a major production region, where 50% of the area is under cereal cultivation at commercial scale mainly with an average field size of 3.4 ha. The area under natural habitats was 50%, of which the total relative cover of all potential wild host plants of stem borers were 11.2% and 10.9% during the rainy and dry seasons, respectively (Otieno et al. 2008).

Kakamega (0° 13' N, 34° 56' E, 1655 MASL) and has a bimodal rainfall distribution with two main cropping seasons occurring from March to August and October to December. Average annual rainfall and temperature are 1570 mm and 21° C, respectively (Africa AWhere-ACT Database 2002). The vegetation mosaic is of the Guineo-Congolian rain forest type. Kakamega is a moderate production region, with 43.3% 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-compact homesteads and along forest edges and the river bank. The area of natural habitats was 51.9%, of which the total relative cover of all potential wild host plants of stem borers were 0.5% and 0.3% during the rainy and dry seasons, respectively (Otieno et al. 2006).

Mtito Andei (2° 39' S, 38° 16' E, 760 MASL) has a single cropping season lasting from November to January. Average annual rainfall and temperature are 665 mm and 23° C, respectively (Africa AWhere-ACT Database 2002). The vegetation consists of Somalia-Masai Acacia-Commiphora deciduous bushland and thicket. Mtito Andei is a minor production region with cereals grown at subsistence level. Area under cereal cultivation was 27.3%, with an average field size of 0.37 ha mainly found surrounding sparsely populated and distant homesteads. The area of natural habitats was 72.7%, of which the total relative cover of all potential wild host plants of stem borers were 13.0% and 8.0% during the rainy and dry seasons, respectively (Otieno et al. 2008).

Muhaka (4° 18' S, 39° 31' E, 40 MASL) has a bimodal rainfall distribution with two main cropping seasons typically occurring from April to August and from October to December. Average annual rainfall and temperature are 1210 mm and 26° C, respectively (Africa AWhere-ACT Database 2002). Local vegetation is the East African coastal grassy and woody mosaic bordering the undifferentiated Zanzibar-

Inhambane forest type. Muhaka is a moderate growing region with about 10.7% 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. The area of natural habitats was 72.3%, of which the total relative cover of all potential wild host plants of stem borers were 2.2% and 1.0% during the rainy and dry seasons, respectively (Otieno et al. 2006).

In Kakamega and Muhaka, cereal crops were planted during the dry season in marshy areas usually bordering streams or rivers. Also, in localities with a single cropping season irrigated crops were found in Mtito Andei, but not in Suam.

#### **Data collection**

Previous studies revealed that stem borer densities were much lower in wild host plants than in adjacent cultivated cereals (Gounou and Schulthess 2004; Ndemah et al. 2007; Matama-Kauma et al. 2008). Therefore, to increase the chances of collecting stem borer parasitoids from different habitats a random sampling scheme was used in cultivated habitats, and both random and non-random sampling schemes were used in natural habitats.

Random sampling in cultivated habitats. Based on the sampling plan developed by Overholt et al. (1994) and the proportion of land under cultivation (Guihéneuf 2004; Goux 2005) 21, 16, 16, and 10 cereal fields were randomly sampled in Kakamega, Mtito Andei, Muhaka, and Suam, respectively. In order to capture parts of early- to mid-whorl (vegetative [4 - 6]weeks]) and late-whorl to tasseling (reproductive [8 - 10 weeks]) stages of plant growth, every field was visited at least twice during each rainy and dry season. To estimate plant infestation, stem borer densities, and parasitism rates (depending on the field size and crop availability during different seasons) 50 to 100 plants were randomly sampled per field (Overholt et al. 1994). The plants collected were dissected in the field, and stem borer larvae or pupae obtained were reared in the laboratory on artificial diet for subsequent recovery of parasitoids.

Random and non-random sampling in natural habitats. To evaluate plant infestation or stem borer densities and parasitism rates in natural habitats, random and non-random sampling schemes were applied, respectively.

#### Random sampling scheme

Grass patches immediately surrounding each sampled cereal field were visited at regular intervals during both dry and rainy seasons as stated above for cultivated habitats. Based on the sampling plan developed by Gounou and Schulthess (2004) to estimate plant infestation and stem borer densities, 50 to 100 plants or tillers (depending on the availability of host plant species during different seasons or due to disturbances [i.e. livestock grazing]) were randomly sampled per plant species at each sampling point, up to 50 m distance from the edge of each cereal field. Each plant or tiller collected was dissected in the field. Stem borer larvae or pupae obtained were reared in the laboratory on artificial diet for subsequent recovery of parasitoids.

#### Non-random sampling scheme

Stem borers living in wild host plants were collected using the non-random sampling procedure applied by Le Ru et al. (2006a, b). During each sampling occasion as described above wild host plants exhibiting infestation symptoms were sampled, where possible up to 100 m of each cereal field was sampled. Depending on both field and crop size, 50 to 100 plants were randomly checked after each

10-15 steps taken in a zigzag manner. At each sampling site, all known host plants belonging to the Poaceae, Cyperaceae, Typhaceae, and Juncaceae families (Le Ru et al. 2006a, b) were inspected for infestation symptoms such as scarified leaves, dead hearts, entrance/exit holes, and frass. Percent parasitism was determined by dividing the number of parasitized larvae/pupae by the total number of larvae/pupae collected (Zhou et al. 2003).

#### Stem borer parasitoid recovery

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 ( $26 \pm 3^{\circ}$  C;  $65 \pm 5$  RH) in the laboratory until puparia or cocoon formation. Parasitoid puparia or cocoons 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. Adult stem borer or parasitoid specimens were preserved in 70 % alcohol.

#### Data analyses

mean Least squares following logistic regression was used to analyze percentage plant infestation (the proportion of plants with stem borers), stem borer density (the number of stem borers per plant), and percentage parasitism (the proportion of parasitized stem borer larvae, pupae, and their total) amongst localities and host plant genera or between seasons per habitat type. All data were analyzed using the Generalized Linear Model (PROC GENMOD; SAS 2001), to cater for binomial error distribution (Collett 1991). Significance was set at  $P \le 0.05$ .

#### Results

**Species occurrence and dominance** 

In this study 10,195 stem borers were collected, of which 7,439 (from six species) and 2,756 (from 13 species) individuals were from cultivated and natural habitats, respectively. Also, 18 and 19 parasitoid species were recovered from stem borer hosts living in cultivated cereals and wild host plants, respectively. The details of parasitoid species found and their multitrophic interactions have been provided in Mailafiya et al. (2009). Stem borers and parasitoids were recovered from two (Z. mays and S. bicolor) and 16 (Cymbopogon spp., Cynodon spp., Cyperus spp., Digitaria Echinochloa spp., spp., Eleusine spp., Eriochloa spp., Euclaena spp., Panicum spp., Pennisetum Rottbellia spp., spp., Schoenoplectus spp., Scleria spp., Setaria spp., Sorghum spp., and Typha spp.) host plant genera in cultivated and natural habitats, respectively. However, due to insufficient collections (data replications) for most host plant genera, analysis in this study was limited to the following: the sedge, Cyperus spp. (Poales: Cyperaceae), and the grasses: Panicum spp., Pennisetum spp., and Sorghum spp. (Poales: Poaceae), as they not only occurred in most or all localities (like the cultivated cereals), but also had adequate replications.

Depending on the locality and host plant, Busseola fusca, Chilo partellus, Sesamia calamistis were the dominant stem borer species in cultivated cereals, while Busseola phaia, Busseola nov 1. Chilo sp. orichalcociliellus, Ematheudes sp., Sesamia nonagrioides were the dominant stem borer species in natural host plants (Table 1). Altogether, percentage stem borer species dominance were computed for 3 and 13 host plant species in cultivated and natural habitats, respectively. Unfortunately, due to very scanty (< 5 individuals) recovery (of single stem borer species each), percentage stem borer species

dominance were not computed for *Eleusine* corocana, Sorghum arundinaceum, Schoenoplectus maritimus in Kakamega; Echinochloa colonum, Eleusine corocana, Eleusine jaegeri, Eriochloa meyerana in Mtito Andei; *Digitaria* sp., *Pennisetum* spp. in Muhaka; and *Cymbopogon nardus*, *Cynodon* sp., *Schoenoplectus confusus*, *Setaria incrassata* in Suam.

Locality / habitat		
type	Host plant	Stem borer species
Kakamega		
Cultivated	Sorghum bicolor	Busseola fusca (90.5%), Busseola phaia (6.3%), Sesamia calamistis (3.2%)
	Zea mays	Busseola fusca (34%), Busseola phaia (33%), Sesamia calamistis (26.6%), Eldana saccharina
		(4%), Sciomesa piscator (2.4%)
	Saccharum officinarum	Busseola phaia (80%), Eldana saccharina (20%)
	Cymbopogon nardus	Busseola phaia (25%), Sciomesa piscator (50%), Tortricidae (25%)
Natural	Cyperus spp .	Sesamia nov sp. 9 (92.9%), Carelis nov sp. 3 (2.8%), Tortricidae (2.8%), Sciomesa piscator (1.5%)
	Euclaena mexicana	Sciomesa piscator (85.7%), Busseola phaia (14.3%)
	Panicum spp.	Busseola phaia (86.7%), Sciomesa
	Pennisetum spp.	Busseola phaia (63.2%), Sciomesa piscator (26.4%), Sciomesa nyei (2.6%), Carelis nov sp. 3 (1.3%),
		Eldana saccharina (1.3%), Poecopa mediopuncta (1.3%), Sesamia calamistis (1.3%),
		Sesamia penniseti (1.3%), Sesamia sp. (1.3%)
	Scleria racemosa	Carelis nov sp. 3 (95.8%), Carelis sp. (4.2%)
	Setaria megaphylla	Busseola nov sp. l (100%)
Mtito Andei		
Cultivated	Sorghum bicolor	Chilo partellus (91.4%), Sesamia calamistis (8.6%)
	Zea mays	Chilo partellus (61.3%), Sesamia calamistis (38.7%)
Natural	Cyperus spp.	Sciomesa nov sp. 3 (68%), Sesamia nonagrioides (12%), Tortricidae (6.7%), Sesamia
		calamistis (5.3%), Schoenobius sp. (4%), Sciomesa piscator (2.7%), Eldana saccharina (1.3%)
	Panicum spp.	Sesamia poephaga (90.2%), Sesamia calamistis (4.9%), Chilo partellus (4.9%)
	Pennisetum spp.	Sesamia calamistis (80%), Chilo partellus (20%)
	Rottbellia cochinchinensis	Ematheudes sp. (100%)
	Setaria verticillata	Sesamia nonagrioides (75%), Sesamia calamistis (23.1%), Sesamia sp. (1.9%)
	Sorghum arundinaceum	Chilo partellus (70.5%), Sesamia calamistis (28.2%), Pyralidae (1.3%)
	Typha domingensis	Sesamia nonagrioides (97.5%), Schoenobius sp. (2.5%)
Muhaka		
Cultivated	Sorghum bicolor	Chilo partellus (83.5%), Sesamia calamistis (15.5%), Chilo orichalcociliellus (1%)
	Zea mays	Chilo partellus (60.6%), Sesamia calamistis (26.5%), Chilo orichalcociliellus (12.9%)
Natural	Cyperus spp.	Tortricidae (50%), Schoenobius sp. (33.3%), Ematheudes sp. (16.7%)
	Echinochloa haploclada	Sesamia nov sp. 4 (33.4%), Sesamia nov sp. (33.3%), Chilo orichalcociliellus (18.5%),
		Sesamia calamistis (7.4%), Acrapex sp. (3.7%), Ematheudes sp.(3.7%)
	Panicum spp.	Chilo orichalcociliellus (85.6%), Sesamia poephaga (5.9%), Manga nubifera (4.5%),
		Chilo partellus (2.3%), Pyralidae (0.9%), Ematheudes sp. (0.5%), Sesamia calamistis (0.5%)
	Rottbellia cochinchinensis	Ematheudes sp. (78.6%), Chilo partellus (10.7%), Chilo orichalcociliellus (8.9%), Pyralidae (1.8%)
	Sorghum arundinaceum	Chilo partellus (88.4%), Chilo orichalcociliellus (6.3%), Sesamia calamistis (4.2%), Ematheudes sp. (1.1
Suam		
Cultivated	Sorghum bicolor	Busseola fusca (100%)
	Zea mays	Busseola fusca (98.7%), Sesamia calamistis (1.3%)
Natural	Cyperus spp.	Sciomesa piscator (53.4%), Tortricidae (20%), Sciomesa venata (13.3%), Sesamia calamistis (13.3%)
	Eleusine corocana	Sesamia calamistis (66.7%), Crambidae (33.3%)
	Panicum spp.	Manga melanodonta (92.7%), Sesamia poephaga (7.3%)
	Pennisetum spp.	Sciomesa nyei (48.4%), Sciomesa piscator (22.5%), Sesamia calamistis (19.4%), Busseola fusca (6.5%)
		Sciomesa venata (3.2%)
	Sorghum arundinaceum	Busseola fusca (85.7%), Sesamia calamistis (14.3%)

<sup>2</sup> (number of traps)

**Table 2.** Least square means (±SE) of plant infestation, stem borer density and parasitism following binomial regression analysis across four localities (AEZs) in cultivated and natural habitats in Kenya

			Local	ity									
		Kakamega	Mtito	Muhaka	Suam					Con	trasts		
Host plant	Parameter	(a)	Andei (b)	(c)	(d)	df	Р	a vs b	a vs c	a vs d	b vs c	b vs d	c vs d
Cultivated ce	ereals												
Zea mays	Plant infestation	-3.2±0.04	-1.5±0.07	-1.7±0.02	-2.7±0.05	3,330	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	Stemborer density	0.7±0.12	0.9±0.03	1.3±0.16	0.9±0.02	3,62	0.01	ns	<0.01	ns	ns	ns	ns
	Larval parasitism	-1.6±0.09	-1.2±0.11	-3.3±0.10	-2.6±0.11	3,233	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
	Pupal parasitism	-8.3±1.61	-4.9±0.70	-5.1±0.35	-4.8±0.44	3,229	ns						
	Total parasitism	-1.3±0.09	-1.3±0.10	-3.0±0.08	-2.6±0.10	3,255	<0.01	0.02	<0.01	<0.01	<0.01	<0.01	<0.01
Sorghum bicolor	Plant infestation	-2.8±0.36	0.8±0.02	2.5±0.39	-5.2±1.00	3,7	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	<0.01
	Stemborer density	2.1±0.73	5.1±1.22	-	-2.3±0.91	2,9	0.01	<0.01	3	0.02	<u></u>	<0.01	
	Larval parasitism	-2.5±0.36	-2.6±0.18	-3.9±0.50	-2.2±0.33	3,21	0.02	ns	0.03	ns	0.02	ns	<0.01
	Pupal parasitism	nc	nc	nc	nc								
	Total parasitism	-2.6±0.36	-2.5±0.18	-3.9±0.50	-2.3±0.33	3,21	0.01	ns	0.03	ns	0.01	ns	ns
Natural host	plants											I	
Cyperus spp.	Plant infestation	-4.4±0.27	-3.1±0.17	-4.8±0.26	-3.9±0.16	3,72	< 0.01	<0.01	ns	ns	<0.01	<0.01	<0.01
	Stemborer density	-3.3±0.09	-3.4±0.18	-4.7±0.23	-4.2±0.16	3,76	<0.01	0.05	<0.01	<0.01	<0.01	<0.01	ns
	Larval parasitism	-2.5±0.23	-2.8±1.04	-1.7±0.76	-3.5±1.01	3,36	ns						
	Pupal parasitism	nc	nc	nc	nc								
	Total parasitism	-2.3±0.22	-2.2±0.60	-2.1±0.74	-3.6±1.00	3,44	ns						
Panicum spp.	Plant infestation	-4.0±0.16	-3.2±0.11	-3.0±0.06	-3.5±0.32	3,122	<0.01	<0.01	<0.01	ns	ns	ns	ns
	Stemborer density	-3.5±0.11	-3.4±0.11	-2.1±0.03	-4.3±0.45	3,143	<0.01	ns	<0.01	ns	<0.01	0.04	<0.01
	Larval parasitism	-2.4±0.42	-2.2±0.51	-3.7±0.22	-2.2±0.22	3,102	<0.01	ns	<0.01	<0.01	ns	<0.01	ns
	Pupal parasitism	-9.7±0.17	-8.2±0.43	-4.6±0.71	-9.5±0.71	3,86	ns						
	Total parasitism	-2.6±0.42	-2.9±0.51	-3.7±0.20	-7.2±0.20	3,119	<0.01	ns	0.02	<0.01	ns	<0.01	ns
Pennisetum spp.	Plant infestation	-3.2±0.10	-2.9±0.29	-	-3.7±0.17	2,80	<0.01	ns		<0.01	-	0.01	-
	Stemborer density	-3.6±0.08	-4.7±0.31	-3.4±0.58	-2.8±0.08	3,84	<0.01	ns	ns	<0.01	ns	<0.01	ns
	Larval parasitism	-3.3±0.45	-2.5±0.34	-0.6±0.02	-3.5±0.50	3,50	ns						
	Pupal parasitism	-8.0±0.19	-7.8±0.50	-	-5.4±0.21	2,41	ns						
	Total parasitism	-3.3±0.45	-5.3±0.28	-0.6±0.12	-3.4±0.45	3,53	ns						
							( · · · · ·						
Sorghum spp.	Plant infestation	-6.5±0.11	-2.0±0.08	-1.9±0.08	-4.1±0.58	3,33	<0.01	ns	ns	ns	ns	<0.01	<0.01
	Stemborer density	-5.9±0.08	-2.1±0.05	-1.5±0.28	-3.0±0.90	3,40	<0.01	ns	ns	ns	<0.01	<0.01	<0.01
	Larval parasitism	-	-3.6±0.50	-3.2±0.29	-1.9±0.66	3,25	0.02	-	-	-	ns	<0.01	<0.01
	Pupal parasitism	nc	nc	nc	nc								
	Total parasitism	-	-3.5±0.50	-3.0±0.26	-1.2±0.65	2,28	0.03	-	-	-	ns	<0.01	<0.01

## Plant infestation, stem borer density and parasitism:

#### a) Based on locality

In maize, plant infestation, stem borer density, larval parasitism and total parasitism were significantly different amongst localities (Table 2). By contrast, pupal parasitism was not significantly different amongst localities. In sorghum, plant infestation, stem borer density, larval parasitism and total parasitism were significantly different amongst localities (Table 2). Pupal parasitism, however, was not computed due to insufficient data.

In *Cyperus* spp., whereas plant infestation and stem borer density were significantly different amongst localities (Table 2), larval and total parasitism were not. Pupal parasitism was not computed due to insufficient data. In *Panicum* spp., plant infestation, stem borer density, larval and total parasitism (Table 2) were significantly different amongst localities. By contrast, pupal parasitism was not significantly different amongst localities. In *Pennisetum*  
 Table 3. Least square means (±SE) following binomial regression analysis of plant infestation (%) during dry and rainy seasons in cultivated and natural habitats in four AEZs in Kenya

	12						Р	lant in	festation							
Host plant		Kakamega	L			Mtito And	ei			Muhak	a			Suam		
genera	DS'	RS	df	Р	DS	RS	df	Р	DS	RS	df	Р	DS	RS	df	Р
Cultivated ha	abitat															
Sgsp <sup>2</sup>	2.3±0.08	1.1±0.05	1,32	ns	-	0.8±0.21	-	-	-	2.5±0.39		-	1.3±0.04	5.9±0.17	1,11	ns
	(0.0%) <sup>3</sup>	(0.0%)				(45.3%)				(0.0%)		6	(0.3%)	(0.4%)		
Zsp	4.0±0.22	3.2±0.08	1,149	<0.01	1.5±0.21	1.4±0.11	1,13	<0.01	0.8±0.08	1.1±0.04	1,56	<0.01	2.3±0.02	2.3±0.09	1,21	ns
	(7.7%)	(0.4%)			(14.8%)	(19.1%)			(23.2%)	(21.2%)			(0.0%)	(9.9%)		
d.f.	1,29	1,59				1,12				1,47			1,18	1,43		
Р	<0.01	<0.01				<0.01				<0.01			<0.01	ns		
Natural habit	tat	8														
Суѕр	2.9±0.05	5.3±0.07	1,12	<0.01	4.2±0.01	2.7±009	1,12	<0.01	4.3±0.13	5.3±0.08	1,20	0.05	5.2±0.05	3.2±0.08	1,20	<0.01
	(0.5%)	(0.7%)			(1.5%)	(0.9%)			(0.9%)	(0.6%)			(0.0%)	(0.9%)		
Pcsp	4.2±0.05	3.9±0.07	1,27	ns	3.8±0.02	3.1±0.02	1,24	0.03	3.3±0.01	2.8±0.05	1,67	<0.01	5.3±0.02	7.3±0.03	1,5	0.03
-	(1.5%)	(1.7%)			(2.6%)	(7.2%)			(3.5%)	(6.4%)			(0.0%)	(5.1%)		
Pnsp	2.3±0.08	3.5±0.03	1,51	<0.01	5.5±0.02	2.6±0.09	1,6	ns	:52		-	-	4.7±0.04	3.7±0.02	1,24	0.05
	(9.8%)	(2.5%)			(0.0%)	(6.6%)							(1.0%)	(2.1%)		
Sgsp	*	6.5±0.04			2.7±0.03	1.6±0.03	1,12	<0.01	2.1±0.12	1.9±0.03	1,13	ns	7.2±0.04	1.7±0.03	1,3	ns
		(0.0%)			(4.4%)	(13.4%)			(20.4%)	(11.3%)		-	(0.0%)	(0.6%)		
Othr	2.0±0.10	4.2±0.06	1,46	<0.01	2.3±0.02	2.7±0.02	1,27	<0.01	4.1±0.18	2.8±0.06	1,75	<0.01	6.3±0.02	4.9±0.05	1,20	ns
	(9.9%)	(1.7%)			(7.8%)	(6.2%)			(15.0%)	(6.5%)			(0.9%)	(4.2%)		
d.f.	3,20	4,123			4,28	4,50			3,58	3,117			4,25	4,47		
Р	<0.01	<0.01			<0.01	<0.01			<0.01	<0.01			<0.01	<0.01		
Pcsp vs Pnsp	<0.01	0.04			ns	ns			ns	ns			ns	ns		
Pcsp vs Cysp	0.05	0.03			ns	ns			<0.01	<0.01			ns	ns	1	
Pcsp vs Sgsp	ns	<0.01			<0.01	<0.01			<0.01	<0.01			<0.01	ns		
Pcsp vs Othr	<0.01	ns			<0.01	0.05			<0.01	ns			ns	ns		
Pnsp vs Cysp	ns	<0.01			ns	ns			ns	ns			ns	ns		
Pnsp vs Sgsp	ns	ns			ns	<0.01			ns	ns			ns	<0.01		
Pnsp vs Othr	ns	<0.01			ns	ns			ns	ns			ns	<0.01		
Cysp vs Sgsp	ns	<0.01			<0.01	<0.01			<0.01	<0.01			<0.01	<0.01		
Cysp vs Othr	0.05	ns			<0.01	ns			ns	<0.01			ns	<0.01		
Sgsp vs Othr	ns	< 0.01			ns	<0.01	10		< 0.01	<0.01			< 0.01	< 0.01		

Season: DS = Dry season and RS = Rainy season

<sup>2</sup>Host plant genera: Cysp = Cyperus spp., Pcsp = Panicum spp., Pnsp = Pennisetum spp., Sgsp = Sorghum spp., Zsp = Zea mays, and Othr = Others

<sup>3</sup>Average values

spp., although plant infestation and stem borer density were significantly different amongst localities (Table 2), larval and total parasitism were not. In *S. arundinaceum*, plant infestation, stem borer density, larval and total parasitism were significantly different amongst localities (Table 2). Pupal parasitism amongst localities, however, was not computed due to insufficient data.

#### b) Based on season per locality

For cultivated habitats, with the exception of Suam, plant infestation was significantly different between maize and sorghum during the rainy season. Likewise, except for Suam, plant infestation was significantly different between seasons in maize (Table 3). Although stem borer density varied significantly between seasons in sorghum in Mtito Andei and Suam, it was not significantly different between seasons in maize in all localities (Table 4). Additionally, across localities, stem borer density was not significantly different between maize and sorghum during all seasons. For natural habitats, across localities, both plant infestation and stem borer density were significantly different amongst host plant genera during all seasons, and between seasons in at least two host plant genera (Tables 3 and 4). Across localities, seasons, and habitat types, 
 Table 4. Least square means (±SE) following binomial regression analysis of stem borer density during dry and rainy seasons in cultivated and natural habitats in four AEZs in Kenya

						S	tem bo	rer de	nsity							
Host plant		Kakam	ega			Mtito An	dei			Muhaka	1			Suam		
genera	DS'	RS	df	Р	DS	RS	df	Р	DS	RS	df	Р	DS	RS	df	P
Cultivated	nabitat															
Sgsp²	-	-	-	-	0.4±0.01	0.6±0.14	1,7	<0.01	-	-	-	-	4.5±0.14	1.2±0.04	1,5	<0.0
SRSh					(0.557) <sup>3</sup>	(1.716)							(0.097)	(0.153)		
Zsp	0.6±0.09	0.5±0.03	1,149	ns	3.9±0.09	1.7±0.01	1,25	ns	0.1±0.02	2.1±1.98	1,122	ns	3.1±0.15	0.8±0.15	-	-
239	(0.695)	(0.591)			(0.643)	(2.216)			(1.873)	(2.148)			(0.556)	(1.131)		
d.f.					1,22	1,21							1,10	4,43		
Р					ns	ns							ns	ns		
Natural hal	oitat															
Суѕр	1.9±0.09	2.8±0.02	1,12	<0.01	4.2±0.08	2.9±0.05	1,10	<0.01	4.3±0.05	4.9±0.03	1,20	ns	4.7±0.07	2.9±0.03	1,21	<0.
Сузр	(0.135)	(0.063)			(0.014)	(0.048)			(0.007)	(0.011)			(0.0006)	(0.008)		
Pcsp	2.8±0.04	3.6±0.03	1,27	<0.01	3.3±0.02	3.4±0.03	1,24	ns	2.1±0.05	2.1±0.04	1,89	ns	3.0±0.08	6.9±0.22	١,6	ns
resp	(0.051)	(0.037)			(0.041)	(0.032)			(0.131)	(0.107)			(0.0001)	(0.226)		
Pnsp	3.2±0.08	3.7±0.10	1,51	<0.01	5.9±0.09	3.6±0.02	1,6	ns	-	3.4±0.38	-	-	4.5±0.05	3.0±0.10	1,27	<0.
пър	(0.033)	(0.027)			(0.001)	(0.025)				(0.0001)			(0.047)	(0.056)		
Sgsp	-	5.9±0.03	-	-	2.3±0.02	2.2±0.02	1,14	ns	2.1±0.04	1.3±0.06	1,18	<0.01	6.9±0.05	2.3±0.05	1,5	ns
SRSh		(0.0001)			(0.077)	(0.117)			(0.137)	(0.204)			(0.0001)	(0.0001)		
Othr	2.3±0.10	3.3±0.07	1,46	<0.01	2.4±0.08	2.2±0.07	1,31	0.04	4.2±0.17	2.8±0.05	1,88	<0.01	6.5±0.05	3.5±0.03	1,24	<0.
Oun	(0.154)	(0.026)			(0.098)	(0.126)			(0.012)	(0.057)			(0.011)	(0.036)		
d.f.	3,20	4,141			4,35	4,50			3,66	4,149			4,26	4,54		
Р	<0.01	<0.01			<0.01	<0.01			<0.01	<0.01			<0.01	<0.01		
Pcsp vs Pnsp	ns	ns			ns	ns			ns	0.02			<0.01	ns		
Pcsp vs Cysp	0.02	<0.01			0.03	ns			<0.01	<0.01			<0.01	ns		
Pcsp vs Sgsp	ns	<0.01			<0.01	<0.01			<0.01	<0.01			<0.01	ns		
Pcsp vs Othr	ns	0.02			<0.01	<0.01			<0.01	<0.01			<0.01	ns		
Pnsp vs Cysp	<0.01	<0.01			ns	ns			ns	0.03			ns	ns		
Pnsp vs Sgsp	ns	ns			ns	<0.01			ns	<0.01			ns	0.02		
Pnsp vs Othr	<0.01	<0.01			ns	<0.01			ns	ns			ns	<0.01		
Cysp vs Sgsp	ns	<0.01			<0.01	<0.01			ns	<0.01			<0.01	0.04		
Cysp vs Othr	ns	<0.01			<0.01	<0.01			ns	<0.01			ns	<0.01		
Sgsp vs Othr	ns	<0.01			ns	ns			<0.01	<0.01			<0.01	<0.01		

<sup>2</sup>Host plant genera: Cysp = Cyperus spp., Pcsp = Panicum spp., Pnsp = Pennisetum spp., Sgsp = Sorghum spp., Zsp = Zea mays, and Othr = Others

<sup>3</sup>Average values

plant infestation and stem borer density were generally highest in maize (Tables 3 and 4).

In both habitats, with the exception of maize in Muhaka, larval parasitism was not significantly different between seasons on all host plants (Tables 5). Whereas in cultivated habitats larval parasitism was significantly different between maize and sorghum during the rainy season in only two localities (Mtito Andei and Muhaka), larval parasitism was significantly different mainly during the rainy season amongst various host plant genera in three different localities (Kakamega, Suam, and Muhaka). Across localities, seasons, and habitat types larval parasitism rates were generally highest in maize. In both cultivated and natural habitats, larval parasitism rates were highest during the rainy season. Across localities and habitat types, in addition to being generally low, pupal parasitism rates were neither significantly different among host plant genera nor across seasons in each host plant (Table 6). In cultivated habitats, with the exception of maize total parasitism Muhaka. was not in significantly different between seasons in maize and sorghum across localities (Table 7). In natural habitats, per host plant genera, total

 Table 5. Least square means (±SE) following binomial regression analysis of larval parasitism (%) during dry and rainy seasons in cultivated and natural habitats in four AEZs in Kenya

							Larva	l par	asitism							
Host plant		Kakameg	a		1	<b>1</b> tito Ande	i			Muhak	a			Suam		
genera	DS	RS	df	Р	DS	RS	df	Р	DS	RS	df	Р	DS	RS	df	F
Cultivated	habitat															
Sgsp²	1.3±0.09	-	-	-	2.7±0.11	2.1±0.06	١,7	ns	-	3.9±0.09	-	-	1.8±0.06	1.9±0.05	1,5	n
	(0.0%) <sup>3</sup>				(4.2%)	(14.1%)				(0.0%)			(7.1%)	(12.0%)		
Zsp	2.9±0.18	2.6±0.07	1,102	ns	2.5±0.19	0.0±0.01	1,36	ns	4.6±0.10	1.3±0.10	1,122	0.02	2.5±0.10	2.9±0.09	1,47	ns
	(5.8%)	(6.8%)			(11.7%)	(15.0%)			(14.0%)	(3.5%)			(12.0%)	(4.8%)		
d.f.	1,20				1,21	1,12				1,49			1,12	1,28		
Р	ns				ns	<0.01				<0.01			ns	ns		
Natural hat	oitat															
Cysp	2.1±0.04	2.0±0.05	1,14	ns	2.6±0.09	0.9±0.03	1,8	ns	1.9±0.06	2.7±0.01	1,18	ns	0.5±0.07	5.1±0.21	1,21	ns
	(0.0%)	(3.7%)			(6.6%)	(0.0%)			(2.8%)	(3.3%)			(0.0%)	(0.0%)		
Pcsp	1.0±0.05	2.5±0.10	1,23	ns	1.1±0.07	1.5±0.07	1,22	ns	4.6±0.11	0.8±0.02	1,87	ns	1.2±0.05	3.3±0.15	١,5	n
	(11.1%)	(6.6%)			(6.7%)	(1.5%)			(1.7%)	(1.9%)			(0.0%)	(0.0%)		
Pnsp	3.3±0.03	3.3±0.12	1,56	ns	2.4±0.05	4.8±0.12	1,8	ns	-	0.6±0.02	-	-	0.3±0.01	2.5±0.04	1,25	n
	(15.0%)	(1.8%)			(0.0%)	(0.0%)				(0.0%)			(2.0%)	(0.0%)		
Sgsp	-	2.8±0.07	-	-	4.0±0.03	3.3±0.06	1,10	ns	2.5±0.05	3.0±0.01	1,16	ns	-	2.7±0.03	-	-
		(0.0%)			(5.5%)	(1.5%)			(0.0%)	(11.5%)				(0.0%)		
Othr	2.8±0.06	3.6±0.03	1,57	ns	2.7±0.05	0.5±0.09	1,30	ns	2.3±0.09	0.6±0.06	1,87	ns	2.0±0.05	3.9±0.07	1,22	ns
	(3.3%)	(3.4%)			(0.0%)	(0.3%)			(0.0%)	(3.1%)			(0.0%)	(0.7%)		
d.f.	3,14	3,147			4,39	4,50			3,68	4,149			3,16	3,35		
Р	ns	<0.01			ns	ns			<0.01	<0.01			ns	<0.01		
Pcsp vs Pnsp		ns							ns	0.03				ns		
Pcsp vs Cysp		ns							0.03	ns				ns		
Pnsp vs Cysp		0.02							ns	ns				0.02		
Pnsp vs Othr		ns							ns	0.03				ns		
Cysp vs Sgsp		ns							<0.01	ns				ns		
Cysp vs Othr		<0.01							ns	ns				ns		$\square$

Season: DS = Dry season and RS = Rainy seaso

<sup>2</sup>Host plant genera: Cysp = Cyperus spp., Pcsp = Panicum spp., Pnsp = Pennisetum spp., Sgsp = Sorghum spp., Zsp = Zea mays, and Othr = Others

<sup>3</sup>Average values

parasitism was not significantly different between seasons in all localities. Also, across habitats, total parasitism rate was highest in maize in cultivated habitats, particularly during the rainy season.

#### Discussion

Although highest total (larval and pupal) parasitism rate (<15.2%) was recorded in maize, stem borer parasitism was generally low in both cultivated cereals and wild host plants across localities and seasons. The results of larval and pupal parasitism in maize and cultivated sorghum align with parasitism rates previously reported by Skövgrad and Päts

(1996) and Zhou et al. (2003). Likewise, larval parasitism recorded in wild host plants in this study fell within the range documented by Khan et al. (1997a) and Overholt et al. (1997). For the first time, this study provided stem borer pupal parasitism rates in wild host plants. However, because wild stem borers generally pupate outside plant stems (Mailafiya et al. 2009) it is very likely that current pupal parasitism rates were underestimated. Given that larval and pupal parasitism rates were highest across seasons in cultivated cereals, present results do not support the assumption by Bowden (1976), Conlong (1994), and Overholt (1998) that stem borer parasitism is higher in wild host plants than in cultivated 

 Table 6.
 Least square means (±SE) following binomial regression analysis of pupal parasitism (%) during dry and rainy seasons in cultivated and natural habitats in four AEZs in Kenya

							Pup	oal pa	rasitism							
Host plant		Kakameg	a			Mtito An	dei			Muhak	a			Suam		
, genera	DS'	RS	df	Р	DS	RS	df	Р	DS	RS	df	Р	DS	RS	df	P
Cultivated h	abitat															
Sgsp²	3.4±0.09	-	-	-	4.9±0.10	4.4±0.21	1,6	ns	-	3.9±0.10	-	-	3.0±0.03	3.1±0.05	1,4	n
	(0.0%) <sup>3</sup>				(5.0%)	(0.0%)				(0.0%)			(0.0%)	(0.0%)		
Zsp	2.0±0.04	4.7±0.11	1,76	ns	5.9±0.06	5.4±0.13	1,32	ns	4.3±0.71	5.8±0.17	1,114	ns	2.3±0.07	5.2±0.06	1,39	n
	(0.0%)	(0.0%)			(0.0%)	(6.0%)			(4.7%)	(1.0%)			(1.8%)	(0.3%)		
d.f.	1,25				1,16	1,17				1,49			1,11	١,35		
Р	ns				ns	ns				ns			ns	ns		
Natural hab	itat															
Суѕр	2.8±0.08	2.0±0.05	1,12	ns	0.5±0.01	2.4±0.03	1,6	ns	3.7 0.11	0.5±0.02	1,20	ns	3.3±0.14	3.2±0.11	1,19	n
	(0.0%)	(5.0%)			(0.0%)	(0.0%)			(0.0%)	(0.0%)			(0.0%)	(0.0%)		
Pcsp	1.0±0.05	2.5±0.06	1,18	ns	0.6±0.07	2.2±0.09	1,19	ns	4.6±0.08	0.2±0.03	1,86	ns	3.7±0.09	2.5±0.09	1,4	n
	(0.0%)	(0.0%)			(0.0%)	(0.0%)			(2.9%)	(0.0%)			(0.0%)	(0.0%)		
Pnsp	3.3±0.12	3.3±0.05	1,41	ns	2.8±0.05	4.8±0.05	1,5	ns	-	0.0±0.00	-	-	3.6±0.03	4.4±0.09	1,21	ns
	(0.0%)	(0.0%)			(0.0%)	(0.0%)				(0.0%)			(0.0%)	(0.0%)		
Sgsp	-	4.6±0.07	-	-	2.1±0.03	5.4±0.07	1,14	ns	2.5±0.05	3.3±0.15	1,17	ns	2.2±0.12	3.8±0.07	1,20	ns
		(0.0%)			(0.0%)	(0.0%)			(0.0%)	(0.0%)				(0.0%)		
Others	2.8±0.06	3.6±0.03	1,49	ns	2.7±0.05	5.0±0.05	1,29	ns	1.1±0.03	2.3±0.09	1,77	ns	3.6±0.07	3.9±0.01	1,20	n
	(0.0%)	(0.0%)			(0.0%)	(10.0%)			(0.0%)	(0.7%)			(0.0%)	(0.0%)		
d.f.	3, 11	4, 1 39			4, 23	4,31			3, 36	4, 77			4, 15	4, 32		
Р	ns	ns			ns	ns			ns	ns			ns	ns		

<sup>3</sup>Average values

cereals. Greater stem borer damage and amounts of larval frass usually produced in maize and sorghum compared to wild host plants (Ngi-Song et al. 1996; Ngi-Song and Overholt 1997), suggests higher herbivore host apparentcy in cultivated cereals than in wild host plants (Van Nouhuys and Via 1999; Barbosa and Calda 2007). Moreover, higher herbivore host densities in cultivated crops generally results in greater attraction/congregation and residence time of parasitoids (Sheehan and Shelton 1989; Connor and Cargain 1994; Umbanhowar et al. 2003) leading to higher host attacks.

Low parasitoid searching efficiency in more complex habitats (i.e. natural habitats with greater host plant species composition and/or plant structures) (Andow and Prokrym 1990; Udayagiri and Welter 2000) might have contributed to low stem borer parasitism rates in wild host plants. For instance, Babendreier et al. (2003) found decreased searching efficiency to be responsible for lower parasitism of egg hosts by Trichogramma brassicae Bezdenko in non-crop plants than in maize. Low parasitism in 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 (Stamp 2001; Nishida 2002). Singer and Stireman (2003) and Singer et al. (2004), for example, found that the woolly bear caterpillars, Grammia geneura (Lepidoptera: Arctiidae), feeding in two host plants that pyrrolizidine contain alkaloids, Senecio longilobus and Ambrosia confertiflora, was **Table 7.** Least square means (±SE) following binomial regression analysis of total (larval and pupal) parasitism (%) during dry and rainy seasons in cultivated and natural habitats in four AEZs in Kenya

							To	tal p	arasitism	า						
Host plant		Kakame	ga		M	ltito And	dei			Muhak	a			Suam		
genera	DS'	RS	d.f.	Р	DS	RS	d.f.	Р	DS	RS	d.f.	Р	DS	RS	d.f.	Р
Cultivated h	abitat															
Sgsp <sup>2</sup>	3.7±0.07	1.0±0.02	1,32	ns	2.4±0.02	2.6±0.09	1,7	ns	-	-	-	-	1.4±0.02	1.9±0.06	1,5	ns
	(0.0%) <sup>3</sup>	(0.0%)			(4.4%)	(10.1%)							(7.0%)	(11.1%)		
Zsp	7.7±0.06	2.4±0.11	1,151	ns	2.8±0.05	1.5±0.07	1,36	ns	2.7±0.19	0.3±0.53	1,122	<0.01	2.4±0.04	2.9±0.05	1,58	ns
	(5.8%)	(6.7%)			(11.7%)	(15.1%)			(6.3%)	(3.7%)			(14.4%)	(5.1%)		
d.f.	1,32	1,59			1,22	1,21							1,18	1,43		
Р	ns	ns			ns	<0.01							ns	<0.01		
Natural hab	itat															
Суѕр	7.1±0.13	1.9±0.23	1,14	ns	1.7±0.08	2.9±0.03	1,8	ns	1.9±0.06	2.3±0.04	1,18	ns	6.3±0.07	2.4±0.04	1,21	ns
	(0.0%)	(4.0%)			(6.6%)	(4.0%)			(2.8%)	(3.3%)			(0.0%)	(0.0%)		
Pcsp	2.7±1.03	2.5±0.46	1,27	ns	2.9±0.02	2.9±0.09	1,22	ns	4.1±0.05	3.5±0.04	1,87	ns	5.1±0.10	8.3±0.13	1,5	ns
	(10.1%)	(6.6%)			(6.6%)	(1.5%)			(2.9%)	(1.9%)			(0.0%)	(0.0%)		
Pnsp	3.4±1.01	3.3±0.50	1,56	ns	-	5.3±0.05	-	-	-	0.6±0.07	-	-	8.2±0.11	3.0±0.04	1,25	ns
	(1.5%)	(1.8%)				(0.0%)				(0.0%)			(0.2%)	(1.2%)		
Sgsp	-	-	-	-	4.2±0.05	3.1±0.09	1,10	ns	3.2±0.08	3.3±0.09	1,16	ns	8.7±0.15	-	-	-
					(5.5%)	(2.8%)			(3.3%)	(11.1%)			(0.0%)			
Others	2.8±0.45	3.5±0.32	1,57	ns	3.3±0.05	4.2±0.08	1,30	ns	7.1±0.05	3.5±0.05	1,87	ns	7.3±0.18	4.1±0.05	1,22	ns
	(3.3%)	(5.6%)			(0.0%)	(0.4%)			(0.0%)	(3.2%)			(0.0%)	(0.8%)		
d.f.	2, 15	3, 95			3, 19	3, 38			2,41	2, 77			3, 22	3, 36		
Р	ns	<0.01			ns	0.04			ns	<0.01			ns	ns		
Pcsp vs Pnsp	ns	ns			ns	ns			ns	0.02			ns	ns		
Pnsp vs Cysp	ns	<0.01			ns	ns			ns	ns			ns	ns		

<sup>2</sup>Host plant genera: Cysp = Cyperus spp., Pcsp = Panicum spp., Pnsp = Pennisetum spp., Sgsp = Sorghum spp., Zsp = Zea mays, and Othr = Others

<sup>3</sup>Average values

detrimental to the development of *Cotesia* sp. and two tachinid flies, *Exorista mella* and *Chetogena tachinomoides*. Meanwhile, information on both direct and indirect effects of plant toxicity in stem borer parasitoids is currently unavailable. Future investigations are needed, particularly because wild stem borers have been recovered from a wide range of host plant species (at least 66) (Le Ru et al. 2006a, b).

Low herbivore host densities across seasons in wild host plants in this study suggests low host encounter rates (Van Alphen 1993; Hemerik et al. 1993; Van Baalen and Hemerik 2008), and perhaps, frequent incidences of super or multiple parasitism (Van Alphen and Visser 1990; Godfray 1994) leading to the mortality of stem borers and associated parasitoids and/or low abundance and fitness of parasitoids. Studies by Agboka et al. (2002), confirmed that parasitism of Sesamia calamistis super Hampson eggs by *Telenomus* spp. within 24 hours after oviposition caused 40% mortality of the host. Additionally, Sétamou et al. (2005), showed the survivorship of parasitized stem borer larvae and parasitoid fitness to be much lower in wild host plants than in cultivated cereals. It will be interesting to have future studies elucidate the incidence and effects of super and multiple parasitism on stem borer parasitoid abundance and fitness in wild host plants.

Most host-parasitoid communities contain one or a few strong interactions, with the majority of parasitoids being opportunists that take advantage of available resources as they exert very weak parasitism rates (Polis and Strong 1996; Rodríguez and Hawkins 2000). In the case of stem borer parasitoid communities in Kenya, present results showed C. flavipes and C. sesamiae to be the key parasitoids species yielding strong interactions in regulating stem borer host populations in cultivated cereals (Mathez 1972; Skövgrad and Päts 1996; Ogol et al. 1998; Zhou et al. 2003). However, in wild host plants neither the two Cotesia species nor other parasitoid species exerted strong parasitism rates in stem borer hosts. This was attributed to the generally low stem borer host densities in wild host plants.

Consistent with the results in this study, Sétamou et al. (2005) also observed lower stem borer (an endogenous host) larval parasitism by C. *flavipes* in wild host plants than in cultivated crops. Benrey et al. (1998), likewise, using hosts recorded lower exogenous larval parasitism of *Pieris rapae* (L.) by *C. glomerata* (L.) in wild *Brassica* sp. and *Phaseolus* sp. than in their cultivated relatives. However, contrary to the above examples, Van Nouhuys and Via (1999) found higher larval parasitism of P. rapae by C. glomerata in wild than in cultivated cabbage. Additionally, on the sunflower moth, Homoeosoma electellum Hulst, with both exogenous (early instars feeding on pollen/floret) and endogenous (late instars as seed feeders) stages Chen and Welter (2007) demonstrated higher parasitism by Dolichogenidea homoeosomae Muesebeck in wild sunflowers than in their agricultural counterparts. Altogether, herbivore parasitism seemed to be high in wild host plants only in cases where: (1) parasitoid foraging efficiency was high owing to greater visual apparency of feeding hosts in less complex (structured) plants (Van Nouhuys and Via 1999), and (2) lack of structural refuge (i.e. hard seed coat) (Chen and Welter 2007) that offers little or no protection to herbivores against attacks.

Altogether, in spite of low stem borer parasitism in natural habitats in this study, natural habitats remain crucial for the sustenance of essential parasitoid diversity in cereal cropping ecosystems, as parasitoid diversity is higher in more diverse host plant communities (Mailafiya et al. 2010). Moreover, several abiotic and biotic factors affect the parasitization of stem borers. Irrespective of habitat type, stem borer parasitism is positively correlated with both parasitoid richness and abundance. Furthermore, being negatively correlated with temperature in natural habitats, parasitoids seem sensitive to harsh/extreme temperatures in this habitat, thereby either lowering their performance or decimating some of their populations (Mailafiya et al. 2010). Also, heavy rainfall, especially at higher altitudes, is detrimental to both stem borers (parastized or not) and parasitoids as well as their activities (Schulthess et al. 2001; Ndemah et al. 2003; Mailafiya et al. 2010)

In conclusion, evidence provided by field data in this study showed that stem borer parasitism was generally low during all seasons in wild host plants, and that cereal stem borers do not necessarily survive the off-season by remaining active in wild host plants. Low larval and pupal (or total) parasitism rates in cultivated cereals further reveal the need for enhancement of parasitoid effectiveness through biological control and/or habitat management practices to regulate cereals stem borer pests.

#### Acknowledgements

The authors are grateful to the entire members of the Noctuid Stem Borer Biodiversity Project

(NSBB) of the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya for assistance with field collections or laboratory work. We also thank G. Delvare of CIRAD (Montpellier, France), D. Barraclough of the University of KwaZulu-Natal (Durban, South Africa), P. Moyal of IRD (France), and S. Muthenge of the East Africa Herbarium (Nairobi, Kenya) for the identification of Hymenopteran parasitoids, Dipteran parasitoids, adult stem borers, and wild host plants, respectively. This research was funded by the German Academic Exchange Service (DAAD) through the African Regional Postgraduate Programme in Insect Science (ARPPIS) at ICIPE and the Institut de Recherche pour le Développement (IRD) in Kenya.

#### References

Africa AWhere-ACT database. 2002. *Mud Springs Geographers*, Inc. Temple, Texas.

Agboka K, Schulthess F, Labo I, Smith H. 2002. Intra and inter specific superparasitism of *Telenomus busseolae* Gahan and *Telenomus isis* Polaszek (Hymenoptera: Scelionidae) two egg parasitoids of the African cereal stem borer *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae). *Journal of Insect Behaviour* 15: 1-12.

Altieri MA, Nicholls CI. 2004. *Biodiversity and pest management in agroecosystems*, 2<sup>nd</sup> editors. The Haworth Press Inc.

Andow DA, Prokrym DR. 1990. Plant structural complexity and host finding by parasitoids. *Oecologia* 82: 162-165.

Babendreier D, Schoch D, Kuhke, S, Dorn, S, Bigler F. 2003. Non-target exploitation by *Trichogramma brassicae* (Hym.: Trichogrammatidae): what are the risks for endemic butterflies? *Agricultural and Forest Entomology* 5: 199-208.

Barbosa P, Caldas A. 2007. Do larvae of species in macrolepidopteran assemblages share traits that influence susceptibility to parasitism? *Environmental Entomology* 36: 329-336.

Benrey B, Callejas A, Rios L, Oyama K, Denno RF. 1998. The effects of domestication of *Brassica* and *Phaseolus* on the interaction between phytophagous insects and parasitoids. *Biological Control* 11: 130–140.

Bonhof MJ, Overholt WA, Van Huis A, Polaszek, A. 1997. Natural enemies of cereal stem borers in east Africa: a review. *Insect Science and its Application* 17: 18-35.

Bosque-Pérez NA, Schulthess F. 1998. Maize: West and Central Africa. In: Polaszek A, editor. *African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control.* CTA/CABI International, Wallingford.

Bowden J. 1976. Stem borer ecology and strategy for control. *Annals of Applied Biology* 84: 107-111.

Chen YH, Welter SC. 2007. Crop domestication creates a refuge from parasitism for a native moth. *Journal of Animal Ecology* 44: 238-245.

Collett D. 1991. *Modelling binary data*. Chapman and Hall.

Conlong DE. 1994. A review and perspectives for the biological control of the African sugarcane stalk borer *Eldana saccharina* 

Walker (Lepidoptera: Pyralidae). *Agriculture, Ecosystems and Environment* 48: 9-17.

Connor EF, Cargain MJ. 1994. Density-related foraging behavior in *Closterocerus tricinctus*, a parasitoid of the leaf-mining moth, *Cameraria hamadryadella*. *Ecological Entomology* 19: 327–334.

De Groote H. 2002. Maize yield loss from stem borers in Kenya. *Insect Science and its Application* 22: 89-96.

De Groote H, Overholt WA, Ouma JO, Mugo S. 2003. *Assessing the impact of Bt maize in Kenya using GIS model.* A paper presented at International Agricultural Economics Conference, August 2003.

Godfray HCJ. 1994. *Parasitoids: behavioural and evolutionary ecology*. Princeton University Press.

Gounou S, Schulthess F. 2004. Spatial distribution of lepidopterous stem borers on indigenous host plants in West Africa and its implications for sampling schemes. *African Entomology* 12: 1-8.

Goux E. 2005. Caracterisation des habitats sauvages et cultives des insects ravageurs des cultures de mais des localites de Mtito Andei et Suam (Kitale) au Kenya. Universite de Paris XII.

Guihéneuf Y. 2004. *Characterisation of wild and cultivated habitats in two ecological areas in Kenya*. Mémoire de D.E.S.S., Université de Paris XII.

Harris KM. 1990. Bioecology of *Chilo* species. *Insect Science and its Application* 11: 467-477.

Hemerik L, Driessen G, Haccou P. 1993. Effects of intra-patch experiences on patch time, search time and searching efficiency of the parasitoid *Leptopilina clavipes*. *Journal of Animal Ecology* 62: 33-44.

Holloway JD. 1998. Noctuidae. In: Polaszek A, editor. *African cereal stem borers: economic importance, taxonomy, natural enemies and control*, pp. 79-86. CTA/CABI International.

Khan ZR, Chiliswa P, Ampong-Nyarko K, Smart, LE, Polaszek A, Wandera J, Mulaa MA. 1997a. Utilization of wild gramineous plants for management of cereal stem borers in Africa. *Insect Science and its Application* 17: 143-150.

Khan ZR, Ampong-Nyarko K, Chiliswa P, Hassanali A, Kimani-Njogu S, Lwande W, Overholt WA, Pickett JA, Smart LE, Wadhams LJ, Woodcock CM. 1997b. Intercropping increases parasitism of pests. *Nature* 388: 631-632.

Landis DA, Wratten SD, Gurr GA. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45: 175-201.

Le Ru BP, Ong'amo GO, Moyal P, Muchugu E, Ngala L, Musyoka B, Abdullah Z, Matama-Kauma T, Lada VY, Pallangyo B, Omwega CO, Schulthess F, Calatayud P-A, Silvain, J-F 2006a. Geographic distribution and host plant ranges of East African noctuid stem borers. *Annales de la Société Entomologique de France* 42: 353-361.

Le Ru BP, Ong'amo GO, Moyal P, Ngala L, Musyoka B, Abdullah Z, Cugala D, Defabachew B, Haile TA, Kauma Matama T, Lada VY, Negassi B, Pallangyo K. Ravolonandrianina J, Sidumo A, Omwega CO, Schulthess F, Calatayud P-A, Silvain J-F,

2006b. Diversity of lepidopteran stem borers on monocotyledonous plants in eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bulletin of Entomological Research* 96: 1–9.

Maes KVN. 1998. Pyraloidea: Crambidae, Pyralidae. In: Polaszek A, editor. *African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control*, pp. 87-98. CTA/CABI International.

Mailafiya DM. 2009. *Diversity and ecological preference of parasitoids associated with lepidopteran stem borers in Kenya*. PhD. Thesis, Kenyatta University.

Mailafiya DM, Le Ru BP, Kairu EW, Calatayud P-A, Dupas S. 2009. Species diversity of lepidopteran stem borer parasitoids in cultivated and natural habitats in Kenya. *Journal of Applied Entomology* 133: 416-429.

Mailafiya DM, Le Ru BP, Kairu EW, Calatayud P-A, Dupas S. 2010. Factors affecting stem borer parasitoid species diversity and parasitism in cultivated and natural habitats. *Environmental Entomology* 39: 57-67.

Matama-Kauma T, Schulthess F, Mueke J, Omwega CO, Ogwang JA. 2006. Effect of wild grasses planted as border rows on stem borer infestations in maize in Uganda. *Annales de la Société Entomologique de France* 42: 455-460.

Matama-Kauma T, Schulthess F, Le Ru BP, Mueke J, Ogwang JA, Omwega CO. 2008. Abundance and diversity of lepidopteran stem borers and their parasitoids on selected wild grasses in Uganda. *Crop Protection* 27: 505– 513.

Mathez FC. 1972. *Chilo partellus* (Swinhoe), *C. oricalcociliellus* (Lepidoptera: Crambidae) and *Sesamia calamistis* Hmps. (Lep.: Noctuidae) on maize in the coast province, Kenya. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 45: 267-289.

McCullagh P, Nelder JA. 1989. *Generalized linear models*. Chapman and Hall.

Ndemah R, Schulthess F, Poehling M, Borgemeister C, Goergen G. 2001. Natural enemies of lepidopterous borers on maize and elephant grass. *Bulletin of Entomological Research* 91: 205-212.

Ndemah R, Gounou S, Schulthess F. 2002. The role of wild grasses in the management of lepidopterous cereal stem borers on maize in western Africa. *Bulletin of Entomological Research* 92: 507–519.

Ndemah R, Schulthess F, Korie S, Borgemeister C, Poehling M, Cardwell KF. 2003. Factors affecting infestations of the stalk borer *Busseola fusca* (Fuller) on maize in the forest zone of Cameroon with special reference to Scelionid egg parasitoids. *Environmental Entomology* 32: 1-70.

Ndemah R, Schulthess F, Le Ru BP, Bame I. 2007. Lepidopteran cereal stem borers and associated natural enemies on maize and wild grass hosts in Cameroon. *Journal of Applied Entomology* 131: 658-668.

Ngi-Song AJ, Overholt WA, Njagi PGN, Dicke M, Ayertey JN, Lwande W. 1996. Volatile infochemicals used in host and host habitat location by *Cotesia flavipes* and *C. sesamiae* (Hymeoptera: Braconidae), larval parasitoids of stem borers on graminae. *Journal of Chemical Ecology* 22: 307-323.

Ngi-Song AJ, Overholt WA. 1997. Host location and acceptance by *Cotesia flavipes* 

Cameron and *C. sesamiae* (Cameron) (Hymeoptera: Braconidae), parasitoids of African gramineous stem borers: Role of frass and other host cues. *Biological Control* 9: 136-142.

Nishida R. 2002. Sequestration of defensive substances from plants by Lepidoptera. *Annual Review of Entomology* 47: 57–92.

Nye IWB. 1960. The insect pest of graminaceous crops in east Africa. *Colonial Research Studies* 31: 1-48.

Ode PJ. 2006. Plant chemistry and natural enemy fitness: effects on herbivore and natural enemy interactions. *Annual Review of Entomology* 51: 163–185.

Ogol CKPO, Spence JR, Keddie A. 1998. Natural enemy abundance and activity in maize-leucaena agroforestry system in Kenya. *Environmental Entomology* 27: 1444-1451.

Onyango FO, Ochieng-Odero JPR. 1994. Continuous rearing of *Busseola fusca* (Lepidopteran: Noctuidae) on an artificial diet. *Entomologia Experimentalis et Applicata* 73: 139-144.

Otieno NA, Le Ru BP, Ong'amo GO, Dupas S, Calatayud P-A, Makobe M, Ochora J, Silvain J-F 2006. Diversity and abundance of wild host plants of lepidopteran stem borers in two different agroecological zones of Kenya. *Annales de la Société Entomologique de France* 42: 371-380.

Otieno NA, Le Ru BP, Ong'amo GO, Moyal P, Dupas S, Calatayud P-A, Silvain J-F 2008. Diversity and abundance of wild host plants of lepidopteran stem borers in two agro-ecological zones of Kenya. *International Journal of Biodiversity Science and Management* 4: 1–12. Overholt WA, Ogedah K, Lammers P. 1994. Distribution and sampling of *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) in maize and sorghum at Kenya Coast. *Bulletin of Entomological Research* 84: 367-378.

Overholt WA, Ngi-Song AJ, Omwega CO, Kimani-Njogu SW, Mbapila J, Sallam MN, Ofomata V. 1997. A review of the introduction and establishment of *Cotesia flavipes* Cameron in east Africa for biological control of cereal stem borers. *Insect Science and its Application* 17: 79-88.

Overholt WA. 1998. Biological control. In: Polaszek A, editor. *African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control*, pp. 349-404. CTA/CABI International.

Polaszek A. 1998. *African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control.* CTA/CABI International.

Polis GA, Strong DR. 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813-846.

Rodríguez MA, Hawkins BA. 2000. Diversity, function and stability in parasitoid communities. *Ecology Letters* 3: 35-40.

SAS Institute. 2001. *PROC User's Manual*, version 6th edition. SAS Institute.

Schulthess F, Bosque-Perez NA, Chabi-Olaye A, Gounou S, Ndemah R, Goergen G. 1997. Exchange of natural enemies of lepidopteran cereal stem borers between African regions. *Insect Science and its Application* 17: 97-108.

Schulthess F, Chabi-Olaye A, Goergen G. 2001. Seasonal fluctuations of noctuid stem borers egg parasitism in southern Benin with special reference to *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Telenomus* species (Hymenoptera: Scelionidae) on maize. *Biocontrol Science and Technology* 11: 745-757.

Sétamou M, Jiang N, Schulthess F. 2005. Effect of the host plant on the survivorship of parasitized *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) larvae and performance of its larval parasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae). *Biological Control* 32: 183-190.

Seshu Reddy KV, Walker PT. 1990. A review of the yield loss in graminaceous crops caused by *Chilo* spp. *Insect Science and its Application* 11: 563-569.

Sheehan W, Shelton AM. 1989. Parasitoid response to concentration of herbivore food plants: finding and leaving plants. *Ecology* 70: 993–998.

Singer MS, Stireman JO. 2003. Does antiparasitoid defense explain host-plant selection by a polyphagous caterpillar? *Oikos* 100: 554– 562.

Singer MS, Carrière Y, Theuring C, Hartmann T. 2004. Disentangling food quality from resistance against parasitoids: diet choice by a generalist caterpillar. *American Naturalist* 64: 423–429.

Skövgrad H, Päts P. 1996. Effects of intercropping on maize stem borers and their natural enemies. *Bulletin of Entomological Research* 86: 599-607.

Smith JWJr, Wiedenmann RN, Overholt WA. 1993. Parasites of lepidopteran stem borers of tropical gramineous plants. ICIPE Science Press.

Stamp N. 2001. Enemy-free space via host plant chemistry and dispersion: assessing the influence of tri-trophic interactions. *Oecologia* 128: 153–163.

Udayagiri S, Welter SC. 2000. Escape of *Lygus hesperus* (Heteroptera: Miridae) eggs from parasitism by *Anaphesiole* (Hymenoptera: Mymaridae) in strawberries: plant structure effects. *Biological Control* 17: 234–242.

Umbanhowar J, Maron J, Harrison S. 2003. Density-dependent foraging behaviors in a parasitoid lead to density-dependent parasitism of its host. *Oecologia* 137: 123–130.

Van Alphen JJM, Visser ME. 1990. Superparasitism as an adaptive strategy for insect parasitoids. *Annual Review of Entomology* 35: 59-79.

Van Alphen JJM. 1993. Patch residence time and encounters with parasitoid hosts: a reaction. *Netherlands Journal of Zoology* 43: 340-349.

Van Baalen M, Hemerik L. 2008. Parasitoid fitness: from a simple idea to an intricate concept. In: Wajnberg E, Bernstein C, van Alphen JJM, editors. *Behavioural ecology of insect parasitoids: from theoretical approaches to field applications*, pp. 31-50. Blackwell Publishing.

Van Nouhuys S, Via S. 1999. Natural selection and genetic differentiation of behaviour between parasitoids from wild and cultivated habitats. *Heredity* 83: 127–137.

Zhou G, Overholt WA, Kimani-Njogu SW. 2003. Species richness and parasitism in assemblage of parasitoids attacking maize stem borer in coastal Kenya. *Ecological Entomology* 28: 109-118.