Biological Control 54 (2010) 1–8

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Geographic distribution, host range and perennation of *Cotesia sesamiae* and *Cotesia flavipes* Cameron in cultivated and natural habitats in Kenya

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A R T I C L E I N F O

Article history:
Received 3 February 2009
Accepted 16 November 2009
Available online 20 November 2009

Keywords:
Cotesia sesamiae
Cotesia flavipes
Busseola fusca
Busseola phaia
Chilo partellus
Chilo orichalcociliellus
Sesamia calamistis
Zea mays
Sorghum bicolor
Sorghum arundinaceum
Panicum maximum
Ecoregional distribution, Host range
Cultivated and natural habitats
Seasonal occurrence
Biological control agent

A B S T R A C T

Field surveys were carried out in four agroecological zones to assess the geographic distribution, host range and perennation of *Cotesia sesamiae* and *Cotesia flavipes* in cultivated and natural habitats in Kenya. The distribution of the two *Cotesia* species in different ecological regions was most affected by the suitability of the local stem borer species for parasitoid development, and temperature, as both species were found in localities dominated by their suitable host(s) where temperature favoured their occurrence. Fourteen years after its release, *C. flavipes* has maintained a high level of specificity to its target host *Chilo partellus* on maize and sorghum in cultivated habitats and on *Sorghum arundinaceum* in natural habitats. *Cotesia flavipes* appeared to be an appropriate biological control agent against *C. partellus* in eastern Africa, with minimal or no effects on non-target hosts in different habitats. Conversely, *C. sesamiae* lacked host specificity in different habitats, as its stem borers or host plants varied with both locality and habitat type. Perennation by both *Cotesia* species occurred mainly in cultivated habitats. Furthermore, natural habitats played a role in sustaining some individuals of *C. flavipes* during both rainy and dry seasons. These areas acted as refuges for *C. flavipes*, but not for *C. sesamiae*, because its hosts were scarce on natural host plants. The availability of these *Cotesia* species across seasons was mainly influenced by the presence of actively feeding stem borers on cereal plants during different seasons, as well as the duration of the dry season in different localities.

1. Introduction

The braconid *Cotesia sesamiae* (Cameron) 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) inflicted by *C. sesamiae* on maize at the Kenya Coast was typically less than 0.5% (Overholt et al., 1994b). Therefore, *C. flavipes* Cameron, a native of the Indo-Australian region was introduced to coastal Kenya in 1993 (Overholt et al., 1994b). *Cotesia flavipes* has become established and is playing a key role in suppressing *C. partellus* in coastal Kenya (Zhou et al., 2001, 2003). 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* occupy an ecologically similar niche (Omwega et al., 1995; Kimani-Njogu and Overholt, 1997), laboratory studies suggest differences in their host range and their attraction to various graminaceous plant species (Ngi-Song et al., 1995, 1996). Thus, the two *Cotesia* species can partition resources and coexist (Sallam et al., 2001; Jiang et al., 2008).

The distribution of both *Cotesia* species is influenced by climate, in that *C. sesamiae* is common in wetter regions (Mohyuddin and Greathead, 1970), and *C. flavipes* is common in dry and warm regions (Songa, 1999; Songa et al., 2001; Niyibigira, 2003). Thus far, both *C. sesamiae* and *C. flavipes* have been reported in cultivated and natural habitats in Kenya (Khan et al., 1997; Overholt, 1998; Songa et al., 2002). However, whereas information on the distribution, stem borer and plant host range for the two *Cotesia* species

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1049-9644/$ - see front matter © 2010 Published by Elsevier Inc.
doi:10.1016/j.biocontrol.2009.11.008

are available for cultivated cereals (Bonhof et al., 1997; Oloo, 1989; Zhou et al., 2003), similar information for natural host plants is very scarce (Khan et al., 1997; Songa et al., 2002). Furthermore, the details of stem borer and plant host specificity for both *Cotesia* species in different ecological habitats are lacking.

The importance of natural habitats adjacent to cultivated crops as refuges 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 (i.e., ⩽1 ha) and surrounded by patches of natural habitats that harbour wild host plants of cereal stem borers and have higher stem borer diversity than the cultivated habitats (Le Ru et al., 2006a,b). It is therefore important to understand the role of natural habitats in the population ecology of parasitoids and their effect on levels of parasitism of stem bores in cereal crops.

In this study, field surveys were carried out over 2 years in both cultivated (in maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.)) and natural (in all potential natural host plants) habitats in four agroecological zones in Kenya. Data obtained were used to examine: (i) the geographic range of *C. sesamiae* and *C. flavipes*, (ii) the range of stem borer and plant hosts for both *Cotesia* species, as well as the specificity of these parasitoids to their hosts, and (iii) seasonal variations in the number of cocoon masses for both *Cotesia* species.

2. Materials and methods

2.1. Study site description

From December 2005 to December 2007, field surveys were conducted in four agroecological zones in Kenya (Corbett, 1998), namely in Kakamega (Kakamega District) in the moist transitional agroecological zone in the Western region of Kenya, Mtito Andei (Makueni District) in the dry mid-altitudes in the Eastern region, Muhaka (Kwale District) in the lowland tropics in the Coastal region and Suam (Trans-Nzoia District) in the highland tropics in the Rift Valley region (Fig. 1). Kakamega (0°13′N, 34°56′E) is 1655 metres above sea level (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 (Corbett, 1998). The vegetation mosaic is of the Guineo-Congolian rain forest type (White, 1983). Kakamega is a moderate production region (Muhammad and Underwood, 2004), with 43.3% of the area under cereal cultivation. Cereals were grown at subsistence levels, with an average field size of 0.28 ha located in open forest patches, or scattered around non-compact homesteads, and also 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 was 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 (Corbett, 1998). The vegetation consists of Somalia-Masai Acacia-Commiphora deciduous bushland and thicket (White, 1983). Mtito Andei is a minor production region with cereals grown at subsistence level (Muhammad and Underwood, 2004). Area under cereal cultivation was 27.3%, with an average field size of 0.37 ha. The area of natural habitats was 72.7%, of which the total relative cover of all potential wild host plants of stem borers was 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 (Corbett, 1998). Local vegetation is the East African coastal grassy and woody mosaic bordering the undifferentiated Zanzibar-Inhambane forest type (White, 1983). Muhaka is a moderate growing region (Muhammad and Underwood, 2004), with about 10.7% of the area under cereal cultivation, and an average field size of 0.15 ha. The area of natural habitats was 72.3%, of which the total relative cover of all potential wild host plants of stem borers was 2.2% and 1.0% during the rainy and dry seasons, respectively (Otieno et al., 2006).

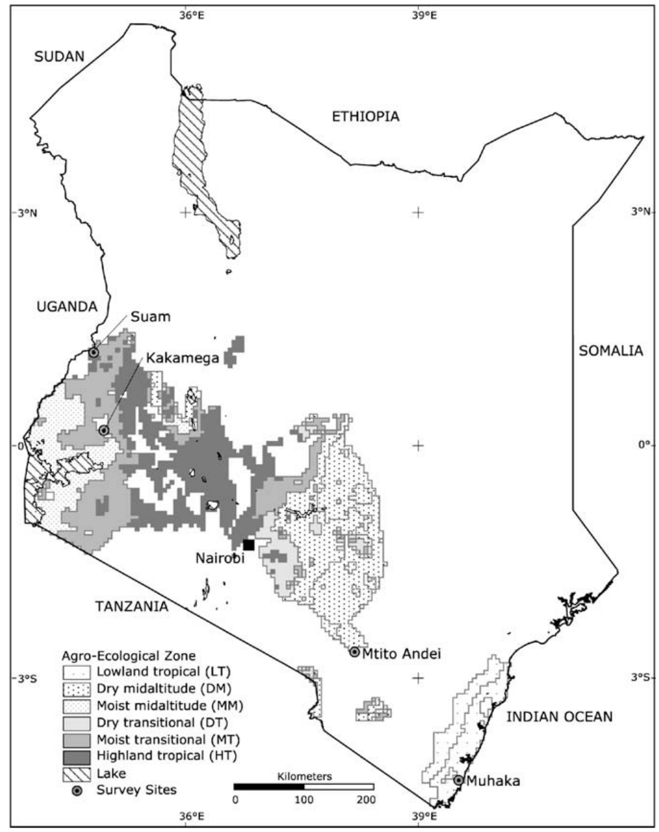

Fig. 1. Map of Kenya showing surveyed sites in four agroecological zones.

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 (Corbett, 1998). Local vegetation is characterized by a mosaic of both rain forest and secondary grassland (White, 1983). Suam is a major production region (Muhammad and Underwood, 2004), 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 was 11.2% and 10.9% during the rainy and dry seasons, respectively (Otieno et al., 2008).

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, because of brief rain spells experienced during dry seasons. Also, cereal crops were sometimes planted in marshy areas usually bordering streams or rivers. Besides the single cropping seasons in Mtito Andei and Suam, during the dry season, irrigation was practiced in the former locality (in a few fields surrounding the local water reservoir) as opposed to the latter locality.

2.2. Field collections

2.2.1. Random sampling in cultivated habitats

Based on the sampling plan developed by Overholt et al. (1994a) and the proportion of land under cultivation (Guihéneuf, 2004; Goux, 2005), we randomly sampled 21, 16, 16 and 10 cereal (maize and sorghum) fields in Kakamega, Mtito Andei, Muhaka and Suam, respectively. In order to include both vegetative and reproductive stages of plant growth, every field was visited at least twice during each rainy and dry season. Depending on the plot size and crop availability during different seasons, 50–100 plants were randomly sampled per field (Overholt et al., 1994a). The plants were dissected in the field, and stem borer larvae or pupae obtained were transported to the laboratory for rearing and subsequent recovery of parasitoids.

2.2.2. Non-random sampling in natural habitats

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 in natural habitats found surrounding each sampled cereal field were sampled where possible up to 100 m from the field edge. At each sampling site, all known host plants belonging to the Poaceae, Cyperaceae, Typhaceae and Juncaceae (Le Ru et al., 2006a,b) were inspected for infestation symptoms such as scarified leaves (window panes and pin holes), dry leaves and shoots (dead hearts), entrance or exit holes, and frass. Infested wild host plants found were destructively sampled. The numbers of small (first and second instars), medium (third and fourth instars) and large (fifth instars and above) (Overholt et al., 1994a; Ngi-Song et al., 1995) larvae collected were recorded. Afterwards, the stem borer larvae were transported to the laboratory for rearing and subsequent recovery of *Cotesia* cocoons.

2.3. 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 × 7.5 cm depth) plugged with cotton wool and kept under ambient conditions in the laboratory (26 ± 1 °C; 65 ± 5% RH) until cocoon formation. Each parasitoid cocoon mass recovered was kept separately in an empty plastic vial (2.5 cm diameter × 7.5 cm depth) until adult emergence. Adult stem borer or parasitoid specimens were preserved in 70% or 100% ethanol. Stem borers and parasitoids were identified to species level. *Cotesia* species were identified at the biosystematics unit of the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya and by G. Delvare, CIRAD, Montpellier, France. Adult stem borers were identified by P. Moyal, IRD, France. Wild host plants were identified by S. Muthenge, East Africa Herbarium, Nairobi, Kenya.

Each *Cotesia* cocoon mass obtained was recorded. Percentage parasitism was calculated as the proportion of medium and large stem borer larvae parasitized by *Cotesia* species (Zhou et al., 2001, 2003).

2.4. Statistical analyses

The number of cocoon mass(es) recovered was analysed using the generalized linear model (PROC GENMOD, SAS, 2001), with a logarithmic link function to cater for Poisson error distribution (McCullagh and Nelder, 1989). Significance level was set at $P \leqslant 0.05$.

3. Results

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

General field collections made are presented in Table 1. Both *C. sesamiae* and *C. flavipes* were generally more abundant in cultivated than in natural habitats (Table 1). *Cotesia sesamiae* and *C. flavipes* were restricted to two different regions, with no coexistence of the two species in any locality (Table 2). Whilst *C. sesamiae* was found in western and rift valley regions of the Kenyan highlands, *C. flavipes* was found in the dry mid-altitudes and lowland tropics of the eastern and coastal regions of Kenya, respectively. According to habitat type, the stem borer and plant host ranges for *C. flavipes* did not differ with locality, whilst the stem borer and plant host ranges for *C. sesamiae* varied with locality (Table 2). In each habitat, the stem borer hosts for both *Cotesia* species were restricted to two host plant species (Table 2).

3.2. Parasitism and the number of cocoon mass for *Cotesia* species in different seasons and habitats

Across all localities, parasitism by both *Cotesia* species varied with season and stem borer species found on the various host plant species (Table 3). The highest parasitism rate by both *Cotesia* species was recorded during the rainy season on stem borers feeding on *S. bicolor* and *Sorghum arundinaceum* (Desv.) Stapf in cultivated and natural habitats, respectively (Table 3).

For *C. sesamiae* in cultivated habitats, the number of cocoon mass was significantly different between seasons on two stem borer species in only one locality (Table 4). By contrast, in natural habitats, the number of cocoon mass was not significantly different between seasons on all stem borer hosts in both localities of occurrence (Table 4).

For *C. flavipes* in cultivated habitats, the number of cocoon masses was significantly different between seasons on at least one stem borer host in both localities of occurrence (Table 4). By contrast, in natural habitats, the number of cocoon mass was significantly different between seasons on at least one stem borer host in both localities of occurrence (Table 4).

4. Discussion

4.1. Geographic distribution

Our results showed that the occurrence of the two *Cotesia* species in different ecological regions was influenced by the geographic range of their respective suitable stem borer hosts (Ngi-Song et al., 1995; Hailemichael et al., 1997, 2008), with *Busseola fusca* (Fuller) predominating in cool areas either wet (Kakamega) or partially dry (Suam) and *C. partellus* predominating in warm areas either wet (Muhaka) or dry (Mtito Andei) (Nye, 1960; Harris and Nwanze, 1992; Songa, 1999; Zhou et al., 2003; Ong'amo et al., 2006). These results suggest that temperature is a key factor in the distribution of these *Cotesia* species and their stem borer hosts (Mohyuddin and Greathead, 1970; Songa et al., 2001).

Although this study did not find both *Cotesia* species living together in a particular locality, *C. sesamiae* and *C. flavipes* coexist in areas surrounding Mount Kenya (in the central region) at altitudes between 1200 and 1500 masl, where intermediate climatic conditions support mixed populations of *B. fusca* and *C. partellus* (Le Ru, Unpublished data). This implies that, with the spread of *C. partellus* to high elevation areas (Overholt et al., 2000; Wale et al., 2006), *C. flavipes* may 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; Verdin et al., 2005; Case, 2006; Osbahr and Viner, 2006), thereby turning favourable for the development of both *C. partellus* and *C. flavipes* (Mbapila and Overholt, 2001; Mbapila et al., 2002). Moreover, *C. flavipes* is capable of successfully developing on *B. fusca* in cases of multiple parasitism when parasitized by *C. sesamiae* prior to that by *C. flavipes*

Table 1

Species richness and abundance of parasitoids (or number of cocoon masses for *Cotesia* species), stem borers and host plants found in cultivated and natural habitats in four AEZs in Kenya.

Order/family	Species	Locality							
		Kakamega		Suam		Mtito Andei		Muhaka	
		Cultivated Dry/rainy season	Natural Dry/rainy season	Cultivated Dry/rainy season	Natural Dry/rainy season	Cultivated Dry/rainy season	Natural Dry/rainy season	Cultivated Dry/rainy season	Natural Dry/rainy season
Parasitoids									
Braconidae	*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
Hymenoptera and Diptera	Other species	(2)[a] 12/(3) 45	(3) 7/(11) 39	(4) 5/(6) 44	(4) 5/(4) 4	(2) 3/(4) 9	(1) 3/(4) 10	(3) 3/(6) 19	(4) 11/(7) 33
	Total	28/125	7/41	28/115	8/4	28/112	3/11	57/100	14/46
Stem borers									
Noctuidae	*Busseola fusca*	155/335	0/0	258/1488	13/1	0/0	0/0	0/0	0/0
	Busseola phaia	24/189	42/115	0/0	0/9	0/0	0/0	0/0	0/0
	Sesamia calamistis	56/111	0/1	0/19	0/24	67/86	75/33	268/442	1/8
	Other species	(0) 0/(1) 23	(5) 132/(10) 674	(1) 1/(1) 7	(3) 69/(7) 258	(0) 0/(0) 0	(6) 111/(5) 236	(0) 0/(0) 0	(4) 49/(6) 116
Crambidae	*Chilo partellus*	0/0	0/0	0/0	0/0	427/404	49/74	484/2197	174/479
	Chilo orichalcociliellus	0/0	0/0	0/0	0/0	0/0	0/0	28/281	336/338
	Other species	(0) 0/(1) 1	(0) 0/(1) 11	(0) 0/(0) 0	(1) 2/(1) 9	(0) 0/(0) 0	(2) 15/(0) 0	(0) 0/(0) 0	(0) 0/(1) 5
Pyralidae	*Eldana sacharrina*	0/23	0/1	0/0	0/0	0/0	1/0	0/0	0/0
	Other species	(0) 0/(0) 0	(1) 20/(0) 0	(0) 0/(0) 0	(0) 0/(1) 4	(0) 0/(0) 0	(2) 6/(1) 22	(0) 0/(0) 0	(2) 30/(2) 300
Tortricidae	Unidentified species	(0) 0/(0) 0	(0) 0/(1) 6	(0) 0/(0) 0	(0) 0/(1) 4	(0) 0/(0) 0	(1) 3/(1) 3	(0) 0/(0) 0	(1) 1/(1) 5
	Total	235/682	194/808	259/1514	84/309	494/490	260/368	780/2920	591/1251
Host plants									
Cyperacae	*Cyperus dives*		(+)/(+)[b]		(+)/(+)				
	Cyperus rotundus								(+)/(+)
	Cyperus papyrus		(−)/(+)						
	Cyperus spp.		(2)/(2)		(4)/(2)		(2)/(2)		(0)/(1)
	Schoenoplectus confusus				(−)/(+)				
	Schoenoplectus maritimus		(−)/(+)						
	Scleria racemosa		(+)/(+)						
Poaceae	*Panicum maximum*		(+)/(+)		(−)/(+)		(+)/(+)		(+)/(+)
	Panicum spp.						(1)/(1)		(1)/(1)
	Pennisetum purpureum		(+)/(+)		(−)/(+)		(+)/(+)		(−)/(+)
	Pennisetum spp.		(1)/(2)		(0)/(3)				
	Setaria megaphylla		(+)/(+)						
	Setaria spp.				(0)/(1)		(1)/(1)		(0)/(1)
	Sorghum arundinaceum		(−)/(+)		(−)/(+)		(+)/(+)		(+)/(+)
	Sorghum bicolor	(+)/(+)		(+)/(+)		(+)/(+)		(−)/(+)	
	Zea mays	(+)/(+)		(+)/(+)		(+)/(+)		(+)/(+)	
	Other species		(1)/(6)		(2)/(2)		(4)/(4)		(4)/(5)
Typhacae	*Typha domingensis*		(+)/(+)		(−)/(+)		(+)/(+)		

[a] For 'Other species' the number of species (Species richness) was provided in parenthesis, whilst species abundance was provided without parenthesis.
[b] (−) or (+) indicated the absence or presence of a given host plant species, respectively.

Table 2
Stem borer and host plant ranges for *C. sesamiae* and *C. flavipes* in cultivated and natural habitats in four AEZs in Kenya.

Cotesia species	Locality	Habitat	Season	Host plant species	Stem borer species
C. sesamiae	Kakamega	Cultivated	Dry, rainy	*Sorghum bicolor*, *Zea mays*	*Busseola fusca*, *Busseola phaia*, *Sesamia calamistis*
		Natural	Rainy	*Panicum maximum*	*Busseola phaia*
	Suam	Cultivated	Dry, rainy	*Sorghum bicolor*, *Zea mays*	*Busseola fusca*, *Sesamia calamistis*
		Natural	Dry	*Sorghum arundinaceum*	*Busseola fusca*
C. flavipes	Muhaka	Cultivated	Dry, rainy	*Sorghum bicolor*, *Zea mays*	*Chilo partellus*, *Sesamia calamistis*
		Natural	Dry, rainy	*Sorghum arundinaceum*	*Chilo partellus*
	Mtito Andei	Cultivated	Dry, rainy	*Sorghum bicolor*, *Zea mays*	*Chilo partellus*, *Sesamia calamistis*
		Natural	Rainy	*Sorghum arundinaceum*	*Chilo partellus*

Table 3
Percentage parasitism by *C. sesamiae* and *C. flavipes* on different stem borers and host plants during dry and rainy seasons in cultivated and natural habitats during 2 years in four AEZs in Kenya.

Locality	Habitat	Species			Parasitism rates (%)	
		Host plant	Stem borer	*Cotesia*	Season	
					Dry	Rainy
Kakamega	Cultivated	*Zea mays*	*Busseola fusca*	*C. sesamiae*	6.4 (93)[a]	7.9 (265)
	Cultivated	*Zea mays*	*Sesamia calamistis*	*C. sesamiae*	2.2 (45)	7.4 (81)
	Cultivated	*Zea mays*	*Busseola phaia*	*C. sesamiae*	71.4 (7)	27.5 (189)
	Cultivated	*Sorghum bicolor*	*Busseola fusca*	*C. sesamiae*	–	3.7 (106)
	Natural	*Panicum maximum*	*Busseola phaia*	*C. sesamiae*	–	1.1 (89)
Suam	Cultivated	*Zea mays*	*Busseola fusca*	*C. sesamiae*	9.3 (161)	12.2 (441)
	Cultivated	*Zea mays*	*Sesamia calamistis*	*C. sesamiae*	–	25.0 (8)
	Cultivated	*Sorghum bicolor*	*Busseola fusca*	*C. sesamiae*	42.1 (19)	57.8 (19)
	Natural	*Sorghum arundinaceum*	*Busseola fusca*	*C. sesamiae*	14.2 (7)	–
Mtito Andei	Cultivated	*Zea mays*	*Chilo partellus*	*C. flavipes*	10.0 (60)	31.6 (278)
	Cultivated	*Zea mays*	*Sesamia calamistis*	*C. flavipes*	–	15.5 (45)
	Cultivated	*Sorghum bicolor*	*Chilo partellus*	*C. flavipes*	–	19.1 (47)
	Natural	*Sorghum arundinaceum*	*Chilo partellus*	*C. flavipes*	–	2.2 (44)
Muhaka	Cultivated	*Zea mays*	*Chilo partellus*	*C. flavipes*	17.9 (239)	4.3 (1670)
	Cultivated	*Zea mays*	*Sesamia calamistis*	*C. flavipes*	7.8 (140)	4.1 (144)
	Cultivated	*Sorghum bicolor*	*Chilo partellus*	*C. flavipes*	–	50.0 (8)
	Natural	*Sorghum arundinaceum*	*Chilo partellus*	*C. flavipes*	20.0 (15)	29.5 (44)
	Natural	*Panicum maximum*	*Chilo orichalcociliellus*	*C. flavipes*	0 (6)	0 (19)

[a] In parenthesis are *N* (parasitized and unparasitized stem borers) values for the percentages.

Table 4
Binomial regression analysis of stem borer parasitism (%) by *C. sesamiae* and *C. flavipes* between seasons on different host species in cultivated and natural habitats in four AEZs in Kenya.

Species		Number of cocoon masses									
Cotesia	Stem borer	Cultivated habitats Parameter estimate (SE)					Natural habitats Parameter estimate (SE)				
		Intercept	Dry vs. rainy season	*P*-Value	d.f.	Odds ratio	Intercept	Dry vs. rainy season	*P*-Value	d.f.	Odds ratio
Kakamega											
C. sesamiae	*Busseola fusca*	0.59 (0.03)	−1.06 (0.08)	0.0002	31	0.35[a]	–	–	–		–
	Sesamia calamistis	−1.29 (0.04)	−0.89 (0.08)	0.4058	7	0.41	NC[b]				
	Busseola phaia	1.37 (0.14)	−0.55 (0.08)	0.0013	57	0.58	NC				
Suam											
C. sesamiae	*Busseola fusca*	0.41 (0.02)	−0.26 (0.04)	0.2820	88	0.77	NC				
	Sesamia calamistis	0.25 (0.07)	0.08 (0.01)	0.5987	2	1.08	NC				
Mtito Andei											
C. flavipes	*Chilo partellus*	1.79 (0.03)	−0.51 (0.02)	0.0209	103	0.60	NC				
	Sesamia calamistis	0.15 (0.03)	−0.56 (0.09)	0.9999	7	0.57	NC				
Muhaka											
C. flavipes	*Chilo partellus*	−0.61 (0.11)	0.37 (0.09)	<0.0001	119	1.45	−1.47 (0.07)	−0.85 (0.04)	<0.0001	16	0.43
	Sesamia calamistis	−1.99 (0.07)	0.46 (0.05)	0.0004	17	1.58	NC				

[a] Odds ratio is a measure of the probability of the outcome of an event (Deeks, 1998; Conover, 1999; Sheskin, 2004). For significant (*P*-value) cases, higher odds ratio values indicate higher chances of the cocoon masses of either *Cotesia* species being significantly different across seasons on a particular stem borer host species, and vice versa.
[b] NC, not computed; due to insufficient data from natural habitats.

(Ngi-Song et al., 2001). In view of these considerations, there is need to further monitor whether increased temperatures will aid the spread of *C. partellus* and its biological 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.

The fact that *C. sesamiae* was not recovered in Muhaka suggests that it is becoming less common overtime in coastal Kenya, perhaps due to competitive displacement by *C. flavipes* (Zhou and Overholt, 2001; Sallam et al., 2001, 2002). Van Driesche (2008), for example, reported that in New England, *Cotesia glomerata* (L.) was displaced to trace levels by a Chinese strain of *Cotesia rubecula* (Marshall) imported for the biological control of the garden pest, *Pieris rapae* (L.). Earlier findings by Overholt et al. (1994b) had pointed out the need to import *C. flavipes* to the Kenya coast, as a result of the low abundance and inefficiency of *C. sesamiae* against *C. partellus*. Le Ru (Unpublished data), from field surveys in cultivated and natural habitats (33 and 11 localities in eastern and coastal Kenya, respectively [2001–2003]) recorded less than 4% of *C. sesamiae* amongst *Cotesia* species recovered from 25,000 stem borer larvae collected. The continuation of this study in natural habitats (43 and 15 localities in eastern and coastal Kenya, respectively [2003–2008]), likewise showed that *C. sesamiae* constituted less than 1% of both *C. sesamiae* and *C. flavipes* recovered from 5000 stem borer larvae collected.

4.2. Stem borer and host plant range

There was no sign of host specificity by *C. sesamiae* in either cultivated or natural habitats, as its stem borer and host plant range varied with both habitat type and locality. By contrast, *C. flavipes* was found restricted to a narrow range of stem borers and host plants, 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. Similarly, extensive surveys carried out in seven countries of eastern and southern Africa (2001–2008), confirmed that in natural habitats *C. sesamiae* had a much broader range of hosts (20 stem borer and nine wild host plant species) than *C. flavipes* that was more specific to *C. partellus* (with *C. partellus* being 100%, 100% and 94.44% of all stem borer species found on *Arundo donax* L., *Pennisetum purpureum* Schumach. and *S. arundinaceum*, respectively (Le Ru, Unpublished data). High host specificity of *C. flavipes* to *C. partellus* has been explained by the high physiological suitability of this host for its development (Ngi-Song et al., 1995; Sétamou et al., 2005). A major objective of classical biological control is the ability of an exotic natural enemy to achieve high specificity to its target host species with minimal or no impact on non-target hosts in the ecosystem (Howarth, 1991; Greathead, 1995). Our results suggest that *C. flavipes* is an efficient biological control agent against *C. partellus* in eastern Africa, with negligible effects on non-target stem borer hosts in both cultivated and natural habitats.

4.3. Parasitism and species perennation

These results show that both *C. sesamiae* and *C. flavipes* are important parasitoids of stem borers in their respective regions of occurrence. For both *Cotesia* species, parasitism varied with season, year and habitat type, with parasitism generally higher in cultivated habitats, and also during the rainy season. Though parasitism of *C. partellus* by *C. sesamiae* was never >3% on maize before the introduction of *C. flavipes* (Overholt et al., 1994b), this study showed that parasitism of *C. partellus* by *C. flavipes* now reaches 45.93% on maize and 50.00% on sorghum in cultivated habitats, and 60.00% on *S. arundinaceum* in natural habitats.

Our results further indicate that perennation of both *Cotesia* species across seasons occur 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 scarcity (Suam) and absence (Kakamega) of its suitable cereal stem borers on natural 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 *Sesamia calamistis* Hampson, feeding on maize and sorghum plants available in few crop fields. Seshu Reddy (1989) and Le Ru (Unpublished data), both, pointed out that *B. fusca* is capable of feeding actively throughout the year without any intervening diapause. In Suam, though rare, *C. sesamiae* was recovered from diapausing *B. fusca* larvae on maize during the earlier parts of the dry season, suggesting that *C. sesamiae* survives the severe dry period (that can persist for five months) in the field by parasitizing diapausing larvae prior to aestivation, to eventually assume a resting stage in diapaused larvae (Weseloh, 1973; Hoy, 1975). This is supported by the fact that *C. sesamiae* lacks the ability to locate diapaused larvae in dried maize stalks (Mbapila and Overholt, 1997). In a related study, Wahlberg et al. (2001), recovered *Cotesia melitaearum* (Wilkinson) (from *Melitaea cinxia* (L.) and *Euphydryas aurinia davidi* (Oberthür)) and *Cotesia acuminatus* (Reinhard) (from *Melitaea latonigena* Eversmann and *Melitaea phoebe* (Denis & Schiffermüller)) on post-diapaused larvae. Diapause, as a means of surviving unfavourable ecological conditions has been reported in *Cotesia* (=*Apanteles*) *melanoscelus* Ratzeburg (Weseloh, 1973; Hoy, 1975) and *Cotesia* (=*Apanteles*) *rubecula* (Nealis, 1985), but not in *C. sesamiae*. This should therefore be investigated in the future. 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 very few maize stems found in marshy areas. In 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. Additionally, several *C. flavipes* cocoons were recovered from diapausing *C. partellus* larvae in maize and sorghum stems during the dry season. Thus, suggesting that, as explained above for *C. sesamiae* in Suam, *C. flavipes* also survives the dry season by attacking diapausing *C. partellus* larvae, to assume a resting stage in diapaused host larvae.

In conclusion, the two *Cotesia* species were separated in their spatial distribution, as influenced by the suitability of local stem borer host community and temperature. Unlike *C. sesamiae* that had a broad range of stem borer and plant hosts, *C. flavipes* exhibited high specificity to its target host in different habitats, with little or negligible harmful effects on non-target stem borer hosts in eastern Africa. Perennation for both *Cotesia* species across seasons occurred mainly in cultivated habitats, and in addition, natural habitats served as refuges to *C. flavipes* only. Further, the stem borer and parasitoid community in eastern Africa constitute an important model with which to monitor the effects of global warming on farm land biodiversity in the cereal agroecosystem.

Acknowledgments

The authors thank Dr. F. Schulthess, Dr. D.E. Conlong and Dr. P.-A. Calatayud for critically reviewing earlier versions of the manuscript. Our thanks also go to Dr. J.-F. Silvain for financial assistance. We are also grateful to the entire members of the Noctuid Stem Borer Biodiversity Project (NSBB) and the Biosystematic Unit (BSU) of the International Centre of Insect Physiology and Ecology (ICIPE, Nairobi, Kenya) for assistance with field collections or laboratory work. This research was funded by the German Academic Exchange Service (DAAD) through the African Regional Postgraduate Programme in Insect Science (ARPPIS) at ICIPE in Kenya and the Institut de Recherche pour le Développement (IRD) in Kenya.

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