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Physiological suitability of six West African gramineous borers (Lepidoptera: Noctuidae, Pyralidae) for development of *Cotesia* species complex (Hymenoptera: Braconidae)

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Abstract. Three gregarious, endoparasitic braconids, a Kenyan strain of *Cotesia sesamiae*, and the exotic *Cotesia flavipes* and *Cotesia chilonis* were imported into Benin as candidates for biological control of stem- and cob borers of maize and stemborers of millet. Host acceptability and host suitability of six gramineous borers occurring in western Africa, the noctuids *Sesamia calamistis*, *Sesamia poephaga*, *Busseola fusca*, the crambid *Coniesta ignefusalis*, and the pyralids *Eldana saccharina* and *Mussidia nigrivenella*, to these parasitoids were evaluated to test the hypothesis that new associations were superior over old association parasitoid–host relationships. All hosts were accepted by all *Cotesia* spp., except *M. nigrivenella*, which was not attacked by *C. chilonis*. Parasitoid progeny developed successfully in *S. calamistis*, *S. poephaga* and *C. ignefusalis*. *S. calamistis* was the most suitable host in terms of duration of developmental time, brood size and mortality of parasitoid progeny. It was concluded that because of its host specificity, the old association parasitoid *C. sesamiae* would have the highest chance of establishment in cereal systems in West Africa.

Key words: *Cotesia*, stemborer, host acceptability, host suitability, encapsulation, biological control, new associations, maize, West Africa

Introduction

Economically important lepidopteran pests attacking cereal crops in West Africa include the stemboring noctuids *Sesamia calamistis* Hampson, *Sesamia poephaga* Tams and Bowden, *Busseola fusca* (Fuller), and the pyralids *Eldana saccharina* (Walker), *Coniesta ignefusalis* (Hampson) and the cob borer *Mussidia nigrivenella* Ragonot. With the exception of *C. ignefusalis,* which is a pest of pearl millet in the Sudano-Sahelian zone, and *M. nigrivenella*, which is a pest of maize cobs from the humid forest to the Northern Guinea Savanna, these borers cause economic damage to cultivated gramineous crops

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in the forest and forest–savanna transition zones only (Schulthess *et al.*, 1997; Sétamou *et al.*, 2000). Economic damage to cultivated gramineous crops in West Africa is restricted to the forest and forest–savanna transition zones, and the mid-altitude region (Schulthess *et al.*, 1997). Extensive surveys conducted in several western African countries showed that larval parasitization of stemborers was generally low and considered insufficient for stemborer suppression in agricultural crops (Gounou *et al.*, 1994; Bosque-Pérez *et al.*, 1995; Conlong, 2001; Ndemah *et al.*, 2001, 2007).

Biological control against lepidopterous stemborers native to Africa has been proposed since the 1970s (Greathead, 1971; Mohyuddin *et al.*, 1981; Mohyuddin, 1991). Schulthess *et al.* (1997) suggested expanding the range of indigenous natural enemies within Africa. Increased interest and research on the stemborers and their natural enemies across Africa have revealed that the complex of stemborers and their associated parasitoids, as well as their relative economic importance, differs throughout the continent. For example, *S. calamistis* is broadly distributed throughout sub-Saharan Africa, whereas most other *Sesamia* species have a more limited distribution and are only of local economic importance (Harris, 1962). Several reports have suggested the existence of biological strains of certain species of both stemborers and their natural enemies. For example, the braconid parasitoid *Cotesia sesamiae* Cameron successfully parasitized and developed in *B. fusca* in South Africa (Ullyett, 1935; Kfir and Bell, 1993; Kfir, 1995, 1998) and in East Africa, from where two biotypes are reported (Ngi-Song *et al.*, 1998; Mochiah *et al.*, 2001; Zhou *et al.*, 2003). A *C. sesamiae* biotype from inland Kenya successfully developed on *B. fusca* while the coastal strain was completely encapsulated by *B. fusca* (Ngi-Song *et al.*, 1998; Zhou *et al.*, 2003). A number of surveys have shown that *C. sesamiae* is rare in western Africa (Bosque-Pérez *et al.*, 1995; Conlong, 2001; Ndemah *et al.*, 2001, 2007), whereas in East and southern Africa, it is a common parasitoid of *S. calamistis* and *B. fusca* (Ingram, 1958; Kfir and Bell, 1993; Kfir, 1995, 1998).

The following study was part of a broader programme that addressed biological control of gramineous stemborers in sub-Saharan Africa. Thereby, the feasibility of using three species of palaeotropical *Cotesia*, namely the native *C. sesamiae* and the exotic *C. flavipes* Cameron and *Cotesia chilonis* (Matsumura), for control of West African stemborers was evaluated. Thus *C. sesamiae* reared on *S. calamistis*, and *C. flavipes* and *C. chilonis* reared on the crambid *Chilo partellus* (Swinhoe) at the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya, were introduced into the containment facilities of the International Institute of Tropical Agriculture (IITA), Benin. *C. sesamiae* is aboriginal to many regions of Africa where it attacks a wide range of stemborer hosts and shares a common evolutionary history with several African gramineous borers (Ullyett, 1935; Ingram, 1958; Mohyuddin, 1971; Walker, 1994). *Cotesia flavipes* and *C. chilonis* are Asian in origin (Polaszek and Walker, 1991) and thus share no common evolutionary relationship with native African stemborers.

Before releasing these parasitoids, host suitability and host acceptability of cob and stemborers inhabiting wild and crop plants in West Africa were investigated. For laboratory rearing, hosts were selected, which had an opportunity to co-adapt with the parasitoid (Smith *et al.*, 1993, Wiedenmann and Smith, 1997). In the present study, *S. calamistis* was considered a natural host for *C. sesamiae* and a new association host for *C. flavipes* and *C. chilonis*. New association hosts may be acceptable hosts for oviposition and may be completely, or partially suitable, or unsuitable for parasitoid development. Given the opportunity that West African gramineous stemborers have had an opportunity to co-adapt with *C. sesamiae*, we ask can host acceptability and host suitability differences be useful to quantify a physiological adaptation of these parasitoids to potential hosts in West Africa?

The objectives of the current experiment were to determine first whether *C. sesamiae*, *C. chilonis* and *C. flavipes* would attack and oviposit, and whether the subsequent progeny would complete development in the stemborers *E. saccharina*, *S. calamistis*, *S. poephaga*, *C. ignefusalis*, *B. fusca* and the cob borer *M. nigrivenella.* The data generated from these behavioural and physiological experiments would provide insight into the suitability of the different borers for *Cotesia* species development.

Materials and methods

Parasitoid and host culture

The *C. chilonis* laboratory culture originated from field collected *Chilo suppressalis* (Walker) on rice, *Oryza sativa* L., in Niigata, Japan via The Biological Control Facility, Texas A&M University, College Station (Oketch and Overholt, 1996). *C. flavipes* originated from *C. partellus* at Rawalpindi, Pakistan, from maize (Overholt *et al.*, 1994). *C. sesamiae* was reared from field collected *S. calamistis* from maize from the coastal zone of Kenya (Ngi-Song *et al.*, 1995). Laboratory cultures of *C. flavipes* and *C. chilonis* were maintained on *C. partellus*, and *C. sesamiae* on *S. calamistis* for several generations at *icipe*, Nairobi, Kenya, prior to shipment to Cotonou, Benin. Individuals from the Kenyan cultures were imported into the IITA-Benin laboratory in 1994,

and all three parasitoids were subsequently cultured using locally collected *S. calamistis* as the host. All laboratory experiments and stemborer and parasitoid cultures, unless otherwise specified, were maintained at 26 ± 2°C, a photoperiod of 12 h light-12 h dark and humidity of 50–90%. Adult parasitoids were fed with 20% honey–water solution before exposure of host larvae.

All hosts were reared on artificial diets developed by Bosque-Pérez and Dabrowski (1989), and Bolaji and Bosque-Pérez (1998).

Host exposure microhabitat

Larval feeding tunnels 4 cm long were constructed in 8 cm long maize or millet stems, or maize cobs by boring a 2 mm diameter tunnel longitudinally in the centre of each stem with a cork borer. This facilitated larval entry into the stem, and subsequent larval feeding and tunnelling. Using soft forceps, one fourth instar larva was introduced head first into each tunnel. The larva was left to feed and produce frass for at least 30 min. The arena for host exposure was a 165 ml clear plastic container tightly covered with a plastic top. Each top had a central hole of 2.5 cm diameter plugged with cotton wool. One infested stem or cob was placed in each arena.

Host acceptability

Fourth instar larvae were offered with their associated host plant material for parasitism to the parasitoid. Female parasitoids (6–8 h old) were gently transferred into each plastic container using a 1:1 parasitoid-to-host ratio. A cohort of 25 larvae for each host–parasitoid pairing was prepared; five larvae were left unexposed and the remaining 20 larvae were exposed to parasitoids. For each host–parasitoid pairing, six cohorts were used. After a 24 h exposure period, the larvae were removed from the plant material and 10 parasitized larvae were dissected to estimate the percentage of hosts accepted. The remaining ten larvae were placed on artificial diet and observed for parasitoid emergence.

Ten host larvae were longitudinally dissected in a 56.7 cm^2 Petri dish using pointed forceps. Water was flushed into the internal tissue and the Petri dish was gently shaken to distribute the contents evenly. Eggs were counted under a ×40 magnification. Several 0.053 cm^2 squares of a grid were thoroughly examined to determine the presence or absence of parasitoid eggs. Once the presence of parasitoid eggs was confirmed, ten fields of vision (which constituted 0.93% of the total area) were randomly inspected and eggs within each grid square were counted. The number of parasitoid eggs per 10 grid squares quantified the degree to which a given host species was accepted for oviposition. Acceptability was estimated from the sum of encapsulated and unencapsulated parasitoid eggs.

Host suitability

Host suitability was assessed for *S. calamistis*, *S. poephaga* and *C. ignefusalis*. *B. fusca*, *E. saccharina* and *M. nigrivenella* were not included because preliminary observations revealed that larvae exposed to the three *Cotesia* species did not produce parasitoid cocoons and were thus presumed unsuitable hosts. To assess the degree of host suitability, larvae exposed to parasitoids were placed on diet observed for three possible outcomes: (1) parasitoid cocoons produced, (2) the host pupated or (3) the host died. Parasitoid cocoons were transferred into 20 ml transparent plastic vials and held until adults emerged. For each *Cotesia* species, the duration of egg-larval, pupal total developmental time was recorded. Dividing the larval and pupal developmental time by the total development time estimated the proportion of larval and pupal period, respectively. Adult parasitoids were counted and sexed. The remaining cocoons in the brood were dissected to identify immature parasitoid mortality. The percentage of host larvae that died after exposure to parasitism by *Cotesia* species estimated parasitoid-induced host mortality. Intrinsic mortality of unparasitized hosts ($n = 30$) due to natural causes was subtracted from the percentage of hosts that died to prevent inflation of parasitoid host mortality using Abbott's formula (Abbott, 1925). Wiedenmann and Smith (1995) reported that the crambid *Diatraea saccharalis* (Fabricius) that encapsulated *C. flavipes* immature life stages remained at a 'terminal larval stage'. In the current study, if the host larval period exceeded three standard deviations from the mean larval period of unparasitized larvae, it was considered to be at terminal larval stage. The percentage of hosts that produced parasitoid cocoons was used to estimate successful parasitization. In the current study, an independent estimate of parasitization and parasitoid-induced host mortality was given. The sum of emergent adults plus adults that did not emerge from cocoons was used to estimate brood size.

Encapsulation

The presence of partially encapsulated parasitoid eggs (i.e. where parasitoid eggs were surrounded by haemocytes) or the presence of melanized tissue with conspicuous darkish pigmentation served as evidence of encapsulation. Hosts dissected at 24 h post-parasitism gave an estimate of encapsulation.

However, the dissections were made only after approximately 9% of the parasitoid larval development period had passed. By subtracting the percentage of hosts that successfully produced cocoons from the percentage that were accepted provided an overall encapsulation estimate that included a greater proportion of the developmental period. The estimates of host encapsulation were compared.

Suitability ranking

To determine the most suitable host species for parasitoid development, hosts were ranked by assigning scores for parameter values that differed significantly among hosts. The parameters used for suitability ranking were percentages of hosts parasitized, parasitoid-induced host mortality, and of adult parasitoids emergence, brood size, sex ratio as the percentage of female parasitoids and length of larval period. For percentage of hosts parasitized, brood size, sex ratio and percentage of emerged adults, the largest values were scored '3', intermediate values were scored '2' and smallest were scored '1'. For length of larval period and parasitoid-induced host mortality, the smallest values were scored '3', the intermediate values were scored '2' and the largest values were scored '1'. A perfect score for all attributes measured would have been 54. The host species that received the highest accumulative score was considered the most suitable.

Data analysis and reporting

The independent variables in this experiment were parasitoid and host species. The dependent variables were the percentage of accepted hosts, number of parasitoid egg counts per grid, percentages of hosts that encapsulated parasitoid eggs, percentage of parasitized hosts, hosts that died after an attack by a parasitoid, and of successful emergence of adult parasitoid, sex ratio, parasitoid brood size and parasitoid developmental time. The relationships between the independent and dependent variables were examined using one-way ANOVA (PROC GLM; SAS Institute, 1989). Means were separated using the Tukey test. All percentage data were arcsin transformed before analysis. In the tables, untransformed means (±SEM) are presented. The percentage of host species encapsulated (*y*-axis) was plotted against the different host species (*x*-axis) using Sigmaplot (1994). The normal distribution of parasitoid brood size was plotted using probabilities that were generated to fit the lognormal distribution (PROC CAPABILITY, SAS Institute, 1989).

Results

Host acceptability

All borer species were accepted for parasitism by all *Cotesia* species except for the *M. nigrivenella*–*C. chilonis* pairing (Table 1). Dissections revealed that all accepted hosts contained parasitoid eggs. The degree to which hosts were accepted for oviposition varied among host species. In general, parasitoids exhibited stronger host acceptance toward hosts that increased reproductive success.

Results from host acceptance studies indicated that *C. flavipes* accepted the greatest percentage of *B. fusca*, *M. nigrivenella* and *E. saccharina* ($P < 0.01$; Table 1). *C. sesamiae* and *C. flavipes* accepted a higher percentage of *S. poephaga* than *C. chilonis* ($P < 0.0001$), with no differences in the percentage of *S. calamistis* and *C. ignefusalis* accepted by the three parasitoid species ($P > 0.05$). Acceptance of a particular host by each of the three parasitoids showed that *S. calamistis*, *S. poephaga* and *C. ignefusalis* were readily accepted, *B. fusca* was less accepted, and *E. saccharina* and *M. nigrivenella* were the least accepted by the three parasitoids ($P < 0.05$, Table 1).

Estimates of clutch size for the same host and different parasitoids followed the general trends as host acceptance (Table 1). Clutch size estimate for *C. flavipes* was highest in *B. fusca*, *S. calamistis* and *S. poephaga* ($P < 0.0001$). The estimate of clutch size did not differ between *C. sesamiae* and *C. flavipes* when both species attacked *M. nigrivenella* and *E. saccharina* ($P > 0.05$). In most acceptable hosts, clutch size was significantly higher for *C. flavipes* than either of the other two *Cotesia* species. Observation of parasitoid eggs oviposited in larvae of *E. saccharina*, *B. fusca* and *M. nigrivenella* showed no sign of embryonic development.

Host suitability

Fate of parasitized larvae

Host larvae that produced parasitoid brood, pupated or died were compared across host and parasitoid (Table 2). Successful parasitization by *C. sesamiae* was higher on *S. calamistis* and *S. poephaga* than on *C. ignefusalis*. *C. flavipes* successfully parasitized a significantly higher percentage of *S. poephaga* than either *S. calamistis* or *C. ignefusalis*, and *C. chilonis* parasitized a higher percentage of *S. poephaga* and *C. ignefusalis* than *S. calamistis* larvae (Table 2). A similar trend for successful parasitization of a particular host by each parasitoid was evident when the suitability of hosts across parasitoids was estimated (Table 2). Parasitization of *S. calamistis* was highest by *C. sesamiae* ($P < 0.0001$). In contrast, parasitization

Table 1. Comparison of host acceptability and parasitoid clutch size among parasitoid and host species

	n	*Cotesia sesamiae*[1]	*n*	*Cotesia flavipes*[2]	*n*	*Cotesia chilonis*	*F*	*P*
Proportion of hosts accepted								
Sesamia calamistis	6	0.90aA	6	0.83abA	6	0.73aA	3.00	0.078
Sesamia poephaga	6	0.98aA	6	0.97aA	6	0.73aB	5.25	0.019
Busseola fusca	6	0.60bcB	6	0.78abA	6	0.48bcB	7.38	0.006
Coniesta ignefusalis	6	0.75abA	6	0.77abA	6	0.81aA	1.47	0.865
Eldana saccharina	6	0.12dB	6	0.48cA	6	0.33bAB	6.80	0.008
Mussidia nigrivenella	6	0.34cdB	6	0.70bcA	6	0.00dC	58.18	0.000
		$F = 20.38$		$F = 8.06$		$F = 27.9$		
		$P = 0.0001$		$P = 0.001$		$P = 0.0001$		
Number of parasitoid eggs/10 grids								
S. calamistis	6	0.90aA	6	0.76abB	6	0.67aB	5.00	0.022
S. poephaga	6	0.93aA	6	0.90aA	6	0.63aB	10.74	0.001
B. fusca	6	0.33bcB	6	0.61bcA	6	0.37bcB	7.11	0.007
C. ignefusalis	6	0.43bB	6	0.50cAB	6	0.57abA	0.66	0.532
E. saccharina	6	0.07dB	6	0.34dA	6	0.17bAB	5.21	0.019
M. nigrivenella	6	0.05cdB	6	0.30cdA	6	0.00dC	17.94	0.000
		$F = 69.31$		$F = 17.09$		$F = 23.06$		
		$P = 0.0001$		$P = 0.0001$		$P = 0.0001$		

Means within a row and observation followed by different capital letter, and means within a column followed by different lower case letter, are significantly different at $P < 0.05$ (Tukey test).
[1] Values presented for host acceptability and parasitoid clutch size are per cohort of 10 fourth-instar host larvae.
[2] Parasitoid eggs within an area of ten microscopic fields of vision under ×40 magnification (~0.93% of the total Petri dish surface) is used to generate clutch size estimate.

of *C. ignefusalis* by *C. chilonis* was significantly higher than by *C. sesamiae* ($P < 0.0001$). No significant differences were found in parasitism of *S. poephaga* among the three *Cotesia* species ($P > 0.05$).

The percentage of *C. ignefusalis* larvae exposed to *C. sesamiae*, which subsequently pupated, was higher than that of the two *Sesamia* species (Table 2). Also higher percentages of *S. calamistis* and *C. ignefusalis* than of *S. poephaga* larvae pupated when exposed to *C. flavipes*. Similarly, the percentage of *S. calamistis* larvae that pupated was higher than that of either *C. ignefusalis* or *S. poephaga* when exposed to *C. chilonis*.

Table 2. Percentage of hosts that produced parasitoid cocoon, pupated or died

	n	*Cotesia sesamiae*	*n*	*Cotesia flavipes*	*n*	*Cotesia chilonis*	*F*	*P*
Parasitized								
Sesamia calamistis	6	78.1 ± 4.7aA	6	52.1 ± 4.7bB	6	46.9 ± 4.5bB	9.26	0.001
Sesamia poephaga	6	74.7 ± 4.9aA	6	73.6 ± 4.7aA	6	64.8 ± 4.5aA	2.19	0.129
Coniesta ignefusalis	6	46.1 ± 4.5bB	6	54.4 ± 4.9bAB	6	72.2 ± 3.9aA	11.48	0.001
		$F = 16.32$		$F = 7.23$		$F = 8.17$		
		$P = 0.001$		$P = 0.003$		$P = 0.001$		
Pupated								
S. calamistis	6	19.4 ± 4.4bB	6	38.0 ± 4.4aA	6	48.1 ± 4.2aA	7.46	0.002
S. poephaga	6	13.0 ± 4.7bB	6	12.2 ± 4.4bB	6	22.6 ± 4.2bA	2.18	0.130
C. ignefusalis	6	41.0 ± 4.2aA	6	37.3 ± 4.7aAB	6	23.7 ± 3.7bB	7.50	0.002
		$F = 15.4$		$F = 12.5$		$F = 9.07$		
		$P = 0.001$		$P = 0.001$		$P = 0.001$		
Died								
S. calamistis	6	2.4 ± 2.1bB	6	10.0 ± 2.1aA	6	5.0 ± 2.0bAB	7.30	0.003
S. poephaga	6	12.2 ± 2.2aA	6	14.2 ± 2.1aA	6	12.6 ± 2.0aA	0.12	0.886
C. ignefusalis	6	13.0 ± 2.0aA	6	8.3 ± 2.2aAB	6	4.1 ± 1.7bB	7.84	0.002
		$F = 11.4$		$F = 1.13$		$F = 8.95$		
		$P = 0.001$		$P = 0.337$		$P = 0.001$		

Means within a row and observation followed by different capital letter, and means within a column followed by different lower case letter, are significantly different at $P < 0.05$ (Tukey test).

The percentage of *S. calamistis* larvae that pupated differed between *C. sesamiae* and the other two *Cotesia* species ($P < 0.05$). Also, there were significant differences among parasitoid species in the mean percentage of *S. poephaga* and *C. ignefusalis* larvae that pupated ($P < 0.05$). Host larvae that remained at the terminal larval stage varied for each parasitoid–host pairing. No terminal host larval stages were noted for *S. calamistis* larvae exposed to *C. sesamiae*, while 6% of the exposed hosts remained terminal when exposed to *C. flavipes* and *C. chilonis*. Six, 8 and 14% of *S. poephaga* larvae exposed for parasitism by *C. sesamiae*, *C. flavipes* and *C. chilonis*, respectively, remained in the terminal larval stage. Similarly, 8, 4 and 4% of the *C. ignefusalis* exposed to parasitism by *C. sesamiae*, *C. flavipes* and *C. chilonis*, respectively, remained in terminal larval stage.

Similarly, hosts that died after being exposed to parasitoids varied significantly among parasitoids ($P < 0.05$, Table 2). Host mortality was consistently highest in *S. poephaga* ($P < 0.05$). Hosts exposed for parasitism to *C. flavipes* showed a greater mortality when compared with hosts exposed to the other two *Cotesia* species ($P < 0.05$). No trends were found when combining the proportion of hosts that pupated with host death from unsuccessful parasitization.

Brood size, sex ratio, adult emergence and developmental time

Few significant differences were found in brood size, sex of brood and percentage of successfully emerged parasitoid adults (Table 3). Brood size and adult emergence of the three *Cotesia* spp. were consistently smaller when parasitizing *C. ignefusalis* compared with *Sesamia* spp. *C. chilonis* ranked lowest when compared among the three parasitoid species in terms of brood size, adult emergence and sex ratio except for sex ratio in *S. calamistis*. Brood size per host differed with host species (Fig. 1). *C. sesamiae* and *C. flavipes* exhibited a high plasticity in terms of brood size in the different host species. Brood size varied considerably in noctuid hosts (*S. calamistis* and *S. poephaga*) and to a much lesser extent in *C. ignefusalis*. Differences in developmental time among host and parasitoid species were observed (Table 3). For the same parasitoid, development time was longer with *S. poephaga* than *S. calamistis* or *C. ignefusalis* as the hosts (Table 3). Differences in the length of the larval period were more apparent. *C. chilonis* developed faster than the other two *Cotesia* when *C. ignefusalis* ($P < 0.001$) or *S. poephaga* was the host ($P < 0.001$). Similarly, *C. flavipes* developed faster than *C. sesamiae* with *S. poephaga* as the host ($P < 0.006$).

Table 3. Brood size, percentage of successfully emerged adults per total number of cocoons, proportion of female parasitoid progeny and number of days for parasitoid larva to emerge from host

	n	*Cotesia sesamiae*	*n*	*Cotesia flavipes*	*n*	*Cotesia chilonis*	*F*	*P*
Brood size								
Sesamia calamistis	49	90.6 ± 6.8aA	36	69.8 ± 6.4aB	33	49.4 ± 6.8aC	5.31	0.008
Sesamia poephaga	49	67.8 ± 4.1aA	43	65.6 ± 3.9aA	37	43.6 ± 4.2aB	8.57	0.001
Coniesta ignefusalis	33	41.2 ± 6.8bA	36	38.9 ± 4.6bA	46	31.7 ± 3.4bA	2.70	0.070
		$F = 8.76$		$F = 10.92$		$F = 7.76$		
		$P = 0.001$		$P = 0.001$		$P = 0.001$		
Emergent adults								
S. calamistis	49	88.2 ± 4.7abA	36	92.9 ± 4.5aA	33	68.6 ± 4.7abB	14.34	0.001
S. poephaga	49	93.6 ± 2.9aA	43	88.5 ± 2.7aA	37	75.1 ± 3.1aB	20.66	0.001
C. ignefusalis	33	77.1 ± 4.7bA	36	69.2 ± 4.4bA	46	62.8 ± 2.4bA	2.34	0.057
		$F = 8.2$		$F = 14.66$		$F = 4.02$		
		$P = 0.001$		$P = 0.001$		$P = 0.02$		
Female brood								
S. calamistis	49	61.8 ± 6.8aA	36	56.3 ± 6.5aA	33	56.1 ± 6.8aA	0.31	0.738
S. poephaga	49	59.6 ± 4.2aA	43	52.5 ± 4.1aA	37	31.5 ± 4.3bB	12.01	0.001
C. ignefusalis	33	53.9 ± 6.8aAB	36	62.5 ± 4.6aA	46	45.2 ± 3.5aB	4.08	0.019
		$F = 0.39$		$F = 1.34$		$F = 5.34$		
		$P = 0.677$		$P = 0.265$		$P = 0.006$		
Developmental time								
S. calamistis	49	11.8 ± 0.6bA	36	11.1 ± 0.5bA	33	11.2 ± 0.6aA	1.88	0.163
S. poephaga	49	15.9 ± 0.4aA	43	13.9 ± 0.3aB	37	12.5 ± 0.4aC	12.91	0.001
C. ignefusalis	33	12.4 ± 0.6bA	36	11.9 ± 0.6bA	46	11.3 ± 0.6aA	5.00	0.010
		$F = 15.29$		$F = 9.80$		$F = 12.47$		
		$P = 0.001$		$P = 0.001$		$P = 0.001$		

Means within a row and observation followed by different capital letter, and means within a column followed by different lower case letter, are significantly different at $P < 0.05$ (Tukey–Kramer test).

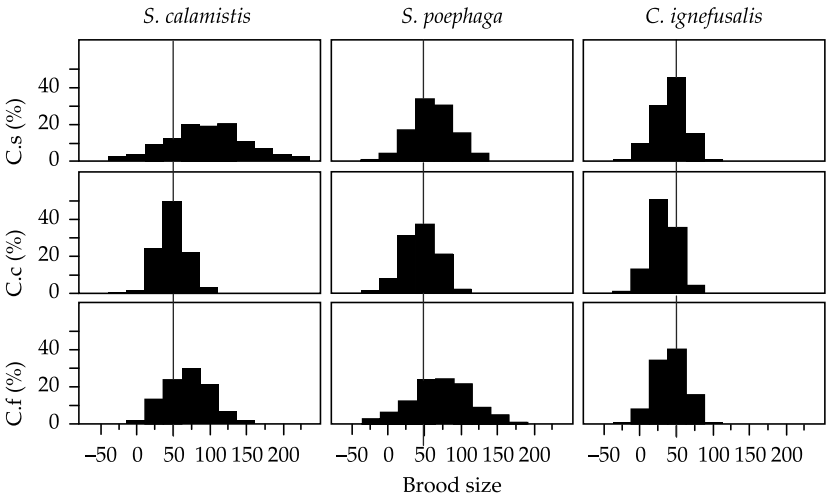

Fig. 1. Distribution of offspring brood by female *Cotesia sesamiae* (C.s), *Cotesia chilonis* (C.c) and *Cotesia flavipes* (C.f) in different host species (PROC CAPABILITY, SAS Institute, 1989). Parasitoid brood distribution across host species was tested under the assumption of equality of variance (HO: variances are equal *versus* HA: at least two variances are unequal) using Bartlett's test of homogeneity of variances (Sokal and Rohlf, 1995). *Cotesia sesamiae* ($\chi^2 = 21.2$, $P = 0.0001$), *C. flavipes* ($\chi^2 = 25.9$, $P = 0.0001$) and *C. chilonis* ($\chi^2 = 1.46$, $P = 0.45$).

Encapsulation

Parasitoid survival was quantified by estimating the percentage of the total accepted hosts that produced parasitoid cocoons. The remainder of the hosts that did not produce cocoons estimated percentage of hosts that encapsulated parasitoid life stages (Fig. 2). With *B. fusca*, *E. saccharina* and *M. nigrivenella* as the host, 100% of all parasitoids of all three species were encapsulated. By contrast, encapsulation was only 11.1% in *S. calamistis* for *C. sesamiae*, 27.7% in *S. poephaga* for *C. flavipes* and 10.9% in *C. ignefusalis* for *C. chilonis* (Fig. 2A–C).

Dividing the immature parasitoid development in two temporal periods (Fig. 2D–F) compared the rate of encapsulation in the different host species. The first period covered the first 24 h after host exposure and the second the time from host exposure until parasitoid larvae emergence. Early encapsulation of parasitoid eggs was most prevalent in those hosts that were unsuitable, i.e. *B. fusca*, *E. saccharina* and *M. nigrivenella*. With the exception of the *C. sesamiae*–*S. calamistis* pairing, all parasitoid–host pairings showed evidence of encapsulation during the first 24 h period. The percentage of suitable hosts (*S. calamistis*, *S. poephaga* and *C. ignefusalis*) that encapsulated parasitoid eggs were $<10\%$ for *C. sesamiae*, $<20\%$ for *C. flavipes* and $<9\%$ for *C. chilonis* during the first 24 h period (Fig. 2). By contrast, the percentage of non-suitable hosts (*B. fusca*, *E. saccharina* and *M. nigrivenella*) that encapsulated parasitoid eggs were $>40\%$ for *C. sesamiae*, $>20\%$ for *C. flavipes* and $>23\%$ for *C. chilonis*. With the exception of the *C. sesamiae*–*S. calamistis* pairing (0%), all other parasitoid–host pairings showed evidence of encapsulation during the first 24 h period.

Suitability ranking

Based on the ranking scores, *S. calamistis* was the most suitable host with a total score of 50 (92.6%), followed by *S. poephaga* with a total of 42 (77.8%), while *C. ignefusalis* with a total score of 38 (70.4%) was the least suitable.

Discussion

As also shown by Ngi-Song *et al.* (1995), *C. sesamiae* tended not to accept hosts when oviposition would not lead to a reproductive gain. By contrast, the exotic parasitoids *C. flavipes* and *C. chilonis* readily accepted both suitable and non-suitable hosts. *C. chilonis* was the only parasitoid that did not accept the cob boring *M. nigrivenella*. Suitability of indigenous and exotic gramineous borers in East Africa has been evaluated for the three parasitoids in the laboratory. Mohyuddin (1971) showed that *C. partellus* was the most preferred and *E. saccharina* the least preferred host for *C. sesamiae* and *C. flavipes*. Ngi-Song *et al.* (1995) and Oketch and Overholt (1996) reported that *C. sesamiae, C. flavipes* and *C. chilonis* successfully parasitized larvae of *C. partellus*, *C. orichalcociliellus* (Strand) and *S. calamistis*. In southern Africa, *C. sesamiae* is reported as an important mortality factor of *B. fusca* in the field (van Rensburg *et al.*, 1988; Kfir and Bell,

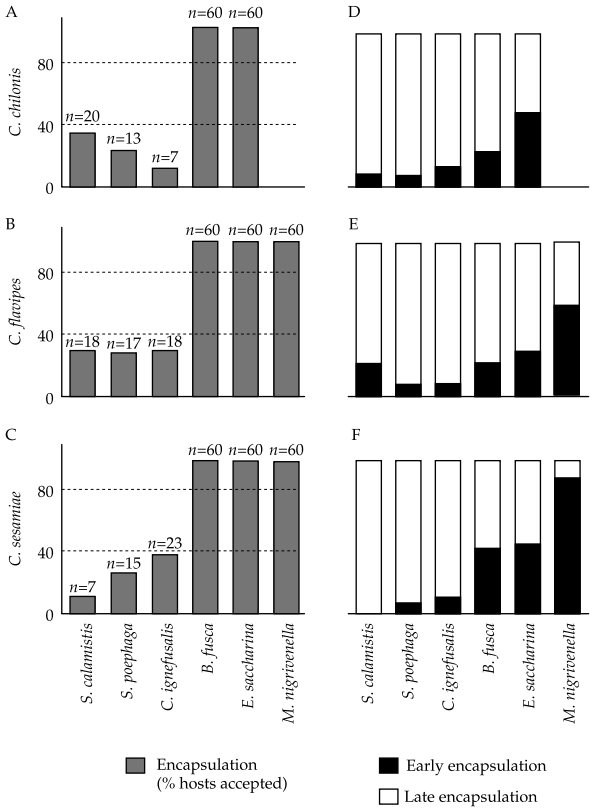

Fig. 2. Comparison of the rate of encapsulation of parasitoid life stages across different hosts. A–C Overall encapsulation rate values were estimated by subtracting the number of successfully parasitized hosts from the number, which were accepted for parasitism by *Cotesia* species. D–F Comparison between early (shaded) versus late encapsulation (blank) of parasitoid life stages. Parasitized hosts dissected as early as 2 h post-parasitism gave estimate of early encapsulation of parasitoid eggs and second estimate of late encapsulation that covers the period from 2 h post-parasitism up to prior to parasitoid larval emergence from the host.

1993). However, the *C. sesamiae* population in the present study originated from the Kenyan coast, which is encapsulated in *B. fusca*. Compatible *C. sesamiae*–*B. fusca* relationships have been observed in South Africa (Ullyett, 1935; van Rensburg *et al.*, 1988; Kfir and Bell, 1993; Kfir, 1995, 1998), Zimbabwe (Chinwada *et al.*, 2003), inland Kenya (Ngi-Song *et al.*, 1998), Uganda (Matama-Kauma *et al.*, 2001), Ethiopia (Getu *et al.*, 2001) and Tanzania (Nsami *et al.*, 2001). Apparently, *C. sesamiae* and *B. fusca* are compatible in much of southern and East Africa, but they are rare in western Africa (Schulthess *et al.*, 1997; Ndemah *et al.*, 2007).

Furthermore, for several stemborer species, various populations have been shown to exist in Africa. For example, a phylogenetic analysis by Sezonlin *et al.* (2006) separated *B. fusca* populations on maize in Africa into three mitochondrial clades: one from West Africa, and two from East, southern and Central Africa, which includes Cameroon. Likewise, for *E. saccharina* and *S. calamistis*, a South African and a West African clade and an Ethiopian clade were identified by Ong'amo *et al.* (2008) and Assefa *et al.* (2006), respectively. The stemborer populations vary in host range and climatic requirements, which may also affect the performance of the parasitoid. The present findings suggest, however, that differences in host populations play a minor role in their suitability to the three parasitoids.

A comparison with existing lists of aboriginal and new association host records for *C. sesamiae*, *C. flavipes* and *C. chilonis* (Gifford and Mann, 1967; Yasumatsu, 1967; Kajita and Drake, 1969; Mohyuddin, 1971; Nagaraja, 1971; Brénière and Bordat, 1982; Polaszek and Walker, 1991; Walker, 1994) shows that *S. poephaga* and *C. ignefusalis* constitute new host records for *C. flavipes* and *C. chilonis*, and *S. poephaga* for *C. sesamiae*.

The present study indicated differences in the suitability of host species for *Cotesia* development. *C. sesamiae* parasitized a greater percentage of *S. calamistis* than either *C. flavipes* or *C. chilonis*, but all three *Cotesia* species parasitized similar percentages of *S. poephaga*. Despite the absence of a co-evolutionary co-adaptive history, *C. chilonis* attacked a higher percentage of *C. ignefusalis* than either of the other two *Cotesia* species. In a laboratory study, Wiedenmann and Smith (1995) found that *C. chilonis* parasitized a higher percentage of the pyralid *D. saccharalis* (Fabricius), a New World stemborer, than *C. flavipes*. Neither parasitoid has an old association with the host. Mohyuddin (1971) considered *C. flavipes* as primarily a parasitoid of Pyralidae (including the stemboring genera *Chilo* and *Diatraea*), while *C. sesamiae* appears to have a wider host range including noctuids (*Sesamia* and *Busseola* species) and crambids (*Chilo* spp.).

In the present study, a large difference in the mortality among *S. calamistis*, *S. poephaga* and *C. ignefusalis* offered for parasitism to *C. sesamiae* was found. Ngi-Song *et al.* (1995) showed a similar trend with native stemborers in East Africa. The reasons for high mortalities observed in *S. poephaga* exposed to *Cotesia* species could be due to the relatively high encapsulation rates, which were higher than those of *S. calamistis* and *C. ignefusalis*. Moreover, development time was prolonged when *S. poephaga* was the host compared with *S. calamistis* or *C. ignefusalis*, suggesting unfavourable developmental conditions. In addition, the variation in the length of larval development was higher for *C. sesamiae* and *C. flavipes* than for *C. chilonis*. *C. chilonis* might benefit from having a relatively

short larval period as a means to escape from being successfully challenged by the host immune defence. Ngi-Song *et al.* (1995) reported that total development for *C. sesamiae* was longer on *C. partellus* than on *C. orichalcociliellus*; by contrast, *C. flavipes* required a shorter developmental duration on *C. partellus* than on *C. orichalcociliellus*.

Cotesia sesamiae and *C. flavipes* showed high plasticity compared with *C. chilonis* with respect to brood allocation in different host species. All three parasitoid species produced a larger brood size with *Sesamia* species than with *C. ignefusalis* as the host. In a preliminary experiment, we compared size differences between fourth instar *Coniesta* and *Sesamia* larvae, and found that the latter were heavier than the former. As host size increases, parasitoids are also expected to increase their brood size (Charnov and Skinner, 1985). The plasticity with respect to parasitoid brood allocation for *C. sesamiae* and *C. flavipes* could therefore be an adaptation to differences in host size. Thus we hypothesize that *C. sesamiae* and *C. flavipes* might have evolved under conditions, in which they interacted with hosts that varied in size. Evidence that might support this argument could be drawn from lists of host species of the three species (Polaszek and Walker, 1991; Walker, 1994). By contrast, the host range of *C. chilonis* is narrow.

The three *Cotesia* species exhibited a similar host range in the laboratory, with a few biological differences in host acceptance and host suitability. It was interesting to note that there were no differences in the number of suitable hosts among all parasitoids. All three parasitoids, regardless of their co-evolutionary history, successfully parasitized the noctuids *S. calamistis* and *S. poephaga* and the pyralid *C. ignefusalis*, and failed to parasitize the noctuid *B. fusca* and the pyralids *E. saccharina* and *M. nigrivenella*. In the current study, *E. saccharina* was the least accepted stemborer by *C. sesamiae* in comparison across host and parasitoid species. Thus *C. sesamiae* with the lowest acceptance of this pyralid should have the highest chance to establish in areas with chronic stemborer problems, where *E. saccharina* is often the most common borer species (Schulthess *et al.*, 1997). The three parasitoids were released in southern Benin, but only *C. sesamiae* permanently established supporting this assumption.

The contention that novel association biological control agents have a broader host range than old association biological control agents (Howarth, 1991; Lockwood, 1993) was not supported by the current data. Nor can we conclusively support the converse argument, which claims no difference in host range between novel and old association biological control agents (Hokkanen and Pimentel, 1984, 1989; Wiedenmann and Smith, 1997), due to insufficient data. As shown for East and southern Africa and Cameroon in Central Africa, various borer species that do not attack crops exist in the wild habitats (Le Rü *et al.*, 2006; Ndemah *et al.*, 2007). By contrast, little quantitative data exist on the diversity of borers on wild hosts in West Africa. Thus future studies should concentrate on the assessment of the relative importance of alternative borer hosts in wild habitats and their suitability for development of *Cotesia* spp. in order to establish their role in stabilizing pest–parasitoid relationships in cereal systems in West Africa.

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