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Intrinsic competition between two oligophagous parasitoids, *Sturmiopsis parasitica* and *Cotesia sesamiae*, attacking the same life stages of lepidopteran cereal stemborers

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Abstract

Host acceptability and suitability of four cereal stemborers (Lepidoptera) commonly occurring in eastern Africa, *Sesamia calamistis* Hampson, *Busseola fusca* (Fuller) (both Noctuidae), *Chilo partellus* Swinhoe (Crambidae), and *Eldana saccharina* Walker (Pyralidae), for a West African strain of *Sturmiopsis parasitica* (Curran) (Diptera: Tachinidae) were assessed. In addition, the outcome of multi-parasitism was studied using a local strain of the endoparasitic *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) as the competing parasitoid. Various parasitism sequences and time intervals between parasitism were chosen. Parasitism increased linearly with the number of planidia used per larvae and was 80% with eight planidia. All species were accepted for larviposition, but suitability varied greatly; parasitism was 75.2, 37.9, 34.8, and 23.8% with *S. calamistis*, *B. fusca*, *E. saccharina*, and *Ch. partellus*, respectively. *Sturmiopsis parasitica* outcompeted *Co. sesamiae* irrespective of the time interval between parasitism, and whether it was the first or second species to parasitize. This was mainly due to a longer egg-to-cocoon development time and a high cocoon-to-adult mortality in *Co. sesamiae*. The implications of these results for expanding the geographic range of the West African strain of the tachinid in Africa are discussed.

Introduction

In sub-Saharan Africa, the economically most important pests of cereals are lepidopteran stemborers belonging to the families Noctuidae, Pyralidae, and Crambidae (Polaszek, 1998). In East and southern Africa, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) is the predominant species at mid-altitudes and in highlands at >1 500 m a.s.l. (Kfir et al., 2002). In contrast, *B. fusca* is the predominant maize pest from 0 to >2000 m a.s.l. (Cardwell et al., 1997; Ndemah et al., 2001) in Cameroon, Central Africa. Indigenous parasitoids do not exert sufficient control on *B. fusca*. In East and southern Africa, the gregarious braconid larval parasitoid *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) is the most common parasitoid of *B. fusca*, but parasitism is usually below 5%, although in some localities, it can attain 75% (Kfir, 1995; Jiang et al., 2006; Songa et al., 2007). In Cameroon, larval and pupal parasitism is negligible, but *Telenomus* spec. (Hymenoptera: Scelionidae) egg parasitoids have shown to have a positive effect on maize yields (Ndemah et al., 2003).

Schulthess et al. (1997) proposed the exchange of natural enemies between African regions to control indigenous cereal stemborers. During country-wide surveys, Gounou et al. (1994), Bosque-Pérez et al. (1994), Ndemah et al. (2001), and Conlong (2001) found that several parasitoid species, common in other regions in Africa, were very scarce or absent in western Africa, and vice versa. For example, the tachinid fly *Sturmiopsis parasitica* (Curran) (Diptera: Tachinidae) is the most common larval parasitoid of *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Eldana saccharina* Walker (Lepidoptera: Pyralidae) in West Africa (Nagarkatti & Rao, 1975; Conlong, 2001). In Zimbabwe, *S. parasitica* is commonly obtained from *B. fusca*,

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but *S. calamistis* is an unsuitable host, as it encapsulates the planidial maggots (Chinwada & Overholt, 2001; Chinwada et al., 2004). In Kenya, *S. parasitica* is scarce (Zhou et al., 2003), and in South Africa it is completely absent on crops (Conlong, 2001), while in Cameroon *S. parasitica* was recovered from *B. fusca* on only one occasion (Ndemah et al., 2007). DNA sequences of cytochrome oxidase I by Dittrich et al. (2006) and morphological studies by Barraclough (2004) suggest that there are at least two distinct strains of *S. parasitica*, one occurring in East and southern Africa, and the other one in West Africa. *Cotesia sesamiae*, on the other hand, is exceedingly rare in western Africa, while in East and southern Africa, it is the most common larval parasitoid recovered from *B. fusca* and *S. calamistis*. In a recent survey in Cameroon, *Co. sesamiae* was obtained exclusively from *Poenoma serrata* Hampson and *Busseola quadrata* Bowden feeding on wild grasses (Ndemah et al., 2007). It is suggested that there are several strains of *Co. sesamiae* occurring in Africa that vary in their insect and plant host ranges. In Kenya, for example, *Co. sesamiae* exists as two biotypes that differ in their ability to parasitize *B. fusca*: *Co. sesamiae* from western Kenya completes development in *B. fusca* larvae, while in the coastal biotype the eggs that are oviposited are encapsulated by haemocytes in *B. fusca* larvae (Ngi-Song et al., 1998; Mochiah et al., 2002; Gitau et al., 2006). Releases of several western Kenyan strains of *Co. sesamiae* are presently being carried out in humid forest, and mid- and high-altitude zones of Cameroon by the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, and releases of *S. parasitica* from West Africa are also being considered.

In the cooler areas of Zimbabwe, *B. fusca* is the key pest of cereals. Unlike *S. calamistis* and *E. saccharina*, it diapauses in the larval stage during the off-season. *Sturmiopsis parasitica* survives this period of host scarcity by synchronizing its larval development with that of the diapausing host larvae (Chinwada & Overholt, 2001). As a result, active populations of *S. parasitica* on *B. fusca* in crops decline drastically, because suitable non-diapausing host species are scarce in the area. Thus, the question arises if a West African strain of *S. parasitica*, which develops successfully on *S. calamistis*, should be introduced into Zimbabwe and East and southern Africa in general.

It is hypothesized that the establishment of the West African strain of *S. parasitica* in either region depends on the availability of suitable host species during the off-season. Mixed populations of *B. fusca*, *S. calamistis*, and *E. saccharina* are commonly found on maize at the mid-altitudes of both regions and in the humid forest zone of Cameroon (Cardwell et al., 1997; Cugala & Omwega, 2001; Emana et al., 2001; Nsami et al., 2001; Zhou et al., 2001; Ong'amo et al., 2006). In addition, the invasive crambid *Chilo partellus* Swinhoe (Lepidoptera: Crambidae), which is the major pest in the lowland tropics, is increasingly invading the cooler zones of East and southern Africa (Kfir, 1997; Zhou et al., 2001; Wale et al., 2007). Conversely, suitable alternative hosts are very scarce in the highlands of Zimbabwe, while in the highlands of Cameroon they represent approximately 10–20% of the total borer population (Ndemah et al., 2001, 2007). Both *S. calamistis* and *E. saccharina* survive the off-season by feeding on wild host plants (Gounou & Schulthess, 2004).

Furthermore, it has been shown that the presence of a parasitoid in an area may prevent another from getting established, especially if alternative hosts are not available (Pijls & van Alphen, 1996). Parasitoid establishment may also be affected by competitive interactions among immatures of the different parasitoid species attacking the same host through direct physical attack (Salt, 1961; Clausen, 1962) or indirect physiological suppression of the inferior host (Mackauer, 1990; Quicke, 1997). *Sturmiopsis parasitica* and *Co. sesamiae* occupy the same niche: both are koinobionts and oligophagous, attacking medium to large larvae of noctuid, crambid, and pyralid cereal stemborers (Polaszek, 1998). While *Co. sesamiae* lays up to 70 eggs in one larva (Mochiah et al., 2001), in Zimbabwe, most borer larvae yield one or two *S. parasitica* puparia although it could be up to six (Smithers, 1960; Chinwada et al., 2004). In view of the relative large size of *S. parasitica* puparia compared to the size of the host larvae, and the small size of *Co. sesamiae* immatures, we hypothesize that the latter would outcompete the former when attacking the same host.

Thus, in a first step, we assessed the acceptability and suitability of stemborer species commonly occurring in prospective release areas to the West African strain of *S. parasitica*. Thereafter, the outcome of interspecific competition between *S. parasitica* and a Kenyan highland strain of *Co. sesamiae*, which successfully develops in *B. fusca*, was evaluated. The findings will help to predict the chances of establishment of an introduced parasitoid in a multi-stemborer multi-parasitoid situation in East and southern Africa and Cameroon, and help to decide if one or both parasitoids should be released in Cameroon.

Materials and methods

Inoculation method

Female *S. parasitica* larviposit mobile, planidial, first-instar maggots at the entrance to the tunnel made by stemborers. The larvae then search for the borer inside the tunnel (Smith et al., 1993). In the present bioassays, three *S. parasitica* females were dissected 14 days after mating and their planidia pooled. Inoculation was done by placing the planidia

on the ventral surface of the host larva using a fine camel hairbrush. *Sesamia calamistis* larvae were inoculated with two, four, or eight planidia in order to determine the optimal number of planidia per host. Twenty replications were done per treatment. The larvae were then reared on artificial diet in vials in an incubator set at 26 ± 1 °C, 65–80% r.h., and L12:D12 photoperiod and checked until parasitoid or moth emergence or death.

Insects

Busseola fusca, *S. calamistis*, *Ch. partellus*, and *E. saccharina* were used in the host suitability experiment. Testing the borers collected from fields in East Africa was necessary, although they were partly the same species as in West Africa, because several strains have been shown to exist for some of the species. For example, a phylogenetic analysis by Sezonlin et al. (2006) separated *B. fusca* populations on maize in Africa into three clades: one from West Africa, and two from East, southern, and Central Africa, which includes Cameroon. Likewise, for *E. saccharina* and *S. calamistis*, a southern African, an Ethiopian, and a West African clade were identified by Assefa et al. (2006) and Ong'amo et al. (2008), respectively. The populations varied in host range and climatic requirements, which in turn may also affect the performance of the parasitoid.

The borers were reared on artificial diet, which included maize and sorghum leaf powder, bean powder, brewers yeast, and vitamin E (Onyango & Ochieng-Odero, 1994). *Busseola fusca* was collected from maize fields in Kitale (1 875 m, 1°01′N, 35°00′E), Machakos (1 492 m, 01°30′S, 37°39′E), western Kenya (1 570 m, 0°14′N, 34°52′E), and the Mount Kenya region (1 759 m, 0°29′N, 36°58′E), and reared in the laboratory for eight generations before being used in the experiments. *Eldana saccharina* was collected from sorghum at Mbita, Lake Victoria region (1 146 m, 0°65′N, 34°45′E), and had been reared for 23–26 generations. *Sesamia calamistis* was collected from maize and sorghum in Kitale and reared for 2–5 generations, while *Ch. partellus* was obtained from maize in farms at the Kenyan coast (44 m, 04°16′S, 39°33′E) and from sorghum in Mbita and was reared for 65–70 generations. New insects collected from the field were added at least three times each year to rejuvenate the colonies. All laboratory experiments were carried out at 26 ± 1 °C, L12:D12, and 65–80% r.h.

A laboratory colony of *S. parasitica* was initiated with insects originating from southern Benin, where they were collected from *E. saccharina* and *S. calamistis* larvae feeding on maize. They were then introduced into the laboratories of the South Africa Sugar Research Institute, where they were maintained on *E. saccharina.* At ICIPE, *S. parasitica* was initially reared on *B. fusca* and then finally for five generations on *S. calamistis*, which was the best host for mass-rearing. Puparia were held singly in glass vials (2.5 × 7.5 cm) until adult parasitoid emergence. The parasitoids were fed with 50% (vol/vol) honey/water solution and kept in Perspex cages (12 × 12 × 8 cm). Three 3–4-day-old males together with newly emerged females were then exposed in a vial to bright artificial light (Nagarkatti & Rao, 1975). Fourteen days after mating, the females were dissected and their uteri ruptured into distilled water, liberating the planidia (Nagarkatti & Rao, 1975). A fine camel-hairbrush was used to transfer eight active planidia, which in the inoculation experiment has been shown to produce the highest parasitism, to the ventral surface of the host larva that had been wiped clean with cotton wool soaked in distilled water. The parasitized larvae were reared on artificial diet until formation of puparia.

Cotesia sesamiae cocoons were obtained in Kitale from *B. fusca* larvae sampled from maize and sorghum plants that exhibited signs of stemborer attack. On emergence, the parasitoid identity was confirmed via examination of the genitalia (Kimani-Njogu & Overholt, 1997). Colonies were initiated using *S. calamistis* as the host. For all hosts, the hand-stinging method described by Overholt et al. (1994) was used. Thereby, third and fourth instars held in a soft forceps were offered to a naïve 1-day-old mated female parasitoid in a sleeve cage. Stung larvae were placed individually on artificial diet in vials (2.5 × 7.5 cm). *Cotesia sesamiae* was reared for several generations before use in the experiments.

Host acceptance

To evaluate host acceptance, five larvae of each *B. fusca*, *Ch. partellus*, *E. saccharina*, and *S. calamistis* were exposed individually to *S. parasitica* in a maize stem in a no-choice situation. A 3-cm-long feeding tunnel was drilled in a 15-cm-long maize stem using a 3-mm-diameter cork borer. The larvae were introduced head first into the tunnel using a soft forceps. The tunnel opening was covered with Parafilm. The infested maize stem was supported vertically in a 1-l clear plastic jar covered with a plastic lid. Each lid had a central hole covered with netting material. The larvae were allowed to feed and produce frass overnight. The Parafilm was removed and the production of frass was confirmed prior to introduction of the parasitoid. A female *S. parasitica* that had mated 12–14 days previously was placed in each jar and observed for foraging/larviposition behavior, number of planidia larviposited, and the number of larvipositions. Upon observation of larviposition, the maize stem tunnel opening and the frass were immediately examined under a dissecting microscope and the planidia counted. Females that did not larviposit after 3 h were dissected to determine their fertility status.

Host preference

Host preference was assessed in dual choice tests using all combinations of *B. fusca*, *Ch. partellus*, *E. saccharina*, and *S. calamistis*. The larvae were offered in maize stems as described above, held vertically on a clay base 20 cm apart in a cage. A female *S. parasitica* that had mated 12–14 days earlier was released at a position equidistant between the maize stems and observed until it larviposited. Ten females were observed for each paired host combination. Preference was determined as percentage of females choosing and ovipositing on either host.

Host suitability

A total of 210 fourth instars of each stemborer species were each inoculated with eight planidia. The larvae were then reared individually on artificial diet until emergence of prepupae of the tachinid, death of larvae, or pupation. Parasitoid puparia were then held individually in glass vials (2.5×7.5 cm) until adult fly emergence. For each host, parasitoid development time from inoculation of the host larva until puparia formation and adult parasitoid emergence, total progeny, and number of females that emerged were recorded. The proportion of the host larvae that produced parasitoid puparia was determined. The potential growth index of *Co. sesamiae* was computed as the product of the percentage of stung larvae producing adult progeny, the mean number of adult progeny produced per host larva, and the sex ratio (proportion of females), divided by the immature period of the parasitoid, that is, the planidia/egg-to-adult emergence development time (Sétamou et al., 1999).

Interspecific competition

Thirty fourth-instar *S. calamistis* were each inoculated with eight planidia of *S. parasitica*; 0, 24, and 48 h thereafter, they were exposed individually to a mated 24-h-old *Co. sesamiae* female for oviposition using the hand-stinging method (Overholt et al., 1994). A second treatment consisted of offering the larvae first to *Co. sesamiae* and thereafter to *S. parasitica*. Another 30 larvae parasitized by *S. parasitica* or *Co. sesamiae* alone were used as control. The treatments will be referred to as Sp-Cs and Cs-Sp, and the controls as Sp and Cs, respectively.

After parasitization, the larvae were reared individually on artificial diet according to Onyango & Ochieng-Odero (1994). They were maintained in an incubator set at 26 ± 1 °C, 65–80% r.h., and an L12:D12 photoperiod. Host larvae were inspected daily. The percentage of females that produced puparia (for *S. parasitica*) and cocoons (for *Co. sesamiae*), time from inoculation or hand-stinging to puparia or cocoon formation and from puparia/cocoon formation to adult emergence, including associated immature mortality, numbers of puparia or cocoons per larva, the percentage of larvae that yielded both parasitoids, and sex ratio as the proportion of female offspring were recorded.

Data analysis

Percentages of host larvae from which parasitoids emerged, moth emergence, and death of larvae were compared using χ^2-test (Sokal & Rohlf, 1981). Development time, female progeny produced per stemborer host larva, total adult progeny, and mortality were compared between host species, parasitism sequence, and time interval between parasitization by analysis of variance (ANOVA) using the General Linear Procedure Proc GLM (SAS Institute, 2001). Percentage and ratio data were arcsin $\sqrt{x}$ transformed before ANOVA. Student–Newman–Keuls or Bonferroni tests were used for mean separation procedure when ANOVA yielded significant differences at $P<0.05$.

Results

Effect of inoculation method on parasitism

There were significant differences (ANOVA, followed by Student–Newman–Keuls test: $F_{2,59} = 7.8$, $P = 0.001$) in parasitism levels between all three inoculation treatments, with parasitism of 25, 40 and 80%, in the two, four, and eight planidia per larvae treatment, respectively.

Host acceptance and preference

All stemborer species were accepted for larviposition. In dual-choice tests, more than 70% of the *S. parasitica* females preferred *S. calamistis* over *B. fusca*, *Ch. partellus*, or *E. saccharina*, and there were no differences among the other species (Figure 1).

Host suitability

There were significant differences between host species in the percentage of larvae yielding *S. parasitica* puparia, with the lowest emergence occurring from *Ch. partellus* and the highest from *S. calamistis* (Table 1). The percentage of inoculated host larvae developing into the moth stage was the reverse, whereas larval death did not vary between host species, for unknown reasons (Table 1).

Development time for both male and female *S. parasitica* varied significantly between host species (Table 2); for both sexes, it was shortest with *Ch. partellus* but similar for the other host species. Sex ratio was between 0.55 and 0.64 and did not vary with host species ($F_{3,351} = 0.51$, $P = 0.67$). The highest potential growth index was obtained with *S. calamistis* as the host and the lowest with *Ch. partellus*.

Host species	Larvae yielding puparia	Moth emergence	Dead larvae
Busseola fusca	37.9b	55.5b	6.6
Chilo partellus	23.8c	68.1a	8.0
Eldana saccharina	34.8b	56.7b	8.6
Sesamia calamistis	75.2a	19.1c	5.7
χ^2	131.8	111.7	1.6
d.f.	3,5	3,5	3,5
P	<0.0001	<0.0001	0.6521

Means followed by the same letter within a column are not significantly different (χ^2-test: P<0.05).

Table 1 Percentage of larvae of four stemborers species parasitized by *Sturmiopsis parasitica* yielding puparia, that died, or from which moths emerged

Multi-parasitism

For all time intervals, the percentage of larvae yielding *S. parasitica* puparia was higher in the control than in the Cs-Sp and Sp-Cs sequences (ranges of χ^2 and P between time intervals were 0.52–5.1 and 0.0075–0.038, respectively; Figure 2), but differences among parasitism sequences were not significant. The same trend was observed for percentage of larvae producing *Co. sesamiae* cocoons (range of χ^2 between time intervals was 42.9–50.3 and P<0.0001). The percentage of larvae yielding both *S. parasitica* puparia and *Co. sesamiae* cocoons varied between 7.8 and 12.2 and there were no significant differences between parasitism sequences and time intervals ($F_{1,170}$ = 0.07–0.98, P>0.05 and $F_{2,269}$ = 0.05–0.33, P>0.05, respectively).

In the control, 100% of the *S. calamistis* larvae produced only one *S. parasitica* puparium, whereas 9.5–14.5% and 6.9–10.3% of the larvae produced two puparia in the Sp-Cs and Cs-Sp sequences, respectively. In the 0-h time interval, the mean number of puparia per larva did not vary between the control and the two sequences, while in the 24- and 48-h interval, it was higher in the Sp-Cs than in the Cs-Cp sequence and the control (Table 3). Conversely, the number of *Co. sesamiae* cocoons produced per larvae

Host species	Female	Male	PGI
Busseola fusca	31.8 ± 0.3a	29.0 ± 0.8a	0.71 ± 0.008
Chilo partellus	26.3 ± 0.4b	26.6 ± 0.6b	0.52 ± 0.006
Sesamia calamistis	29.9 ± 0.3a	27.6 ± 0.2a	1.45 ± 0.009
Eldana saccharina	28.6 ± 0.1a	29.6 ± 0.6a	0.68 ± 0.006
F	12.0	2.3	
d.f.	3,205	3,149	
P	<0.0001	0.0491	

Means followed by the same letter within a column are not significantly different (Student–Newman–Keuls test: P<0.05).

Table 2 Development time (days) and potential growth index (PGI) (mean ± SE) of female and male *Sturmiopsis parasitica* emerging from larvae of four stemborer hosts

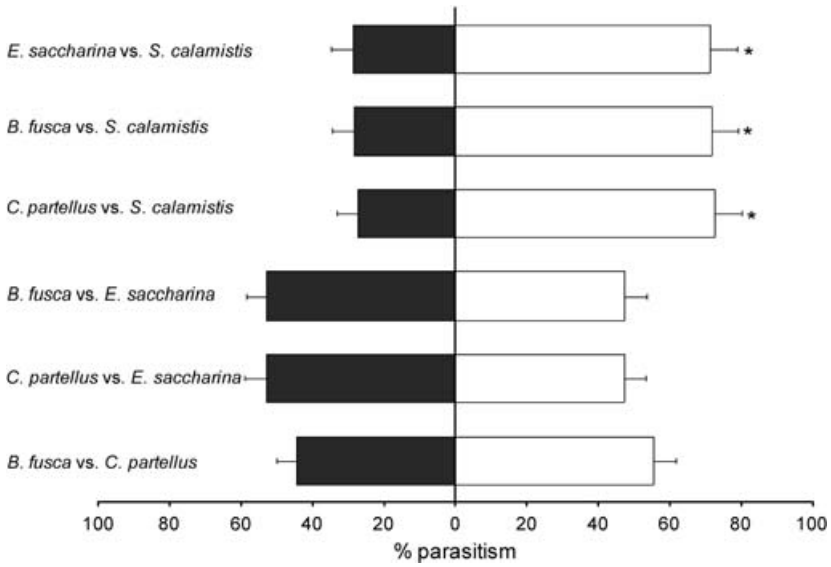

Figure 1 Dual-choice tests for preference (mean + SE % parasitism) of *Sturmiopsis parasitica* among four stemborer species. * indicates significant differences in parasitism between borer species (χ^2-test, P<0.05).

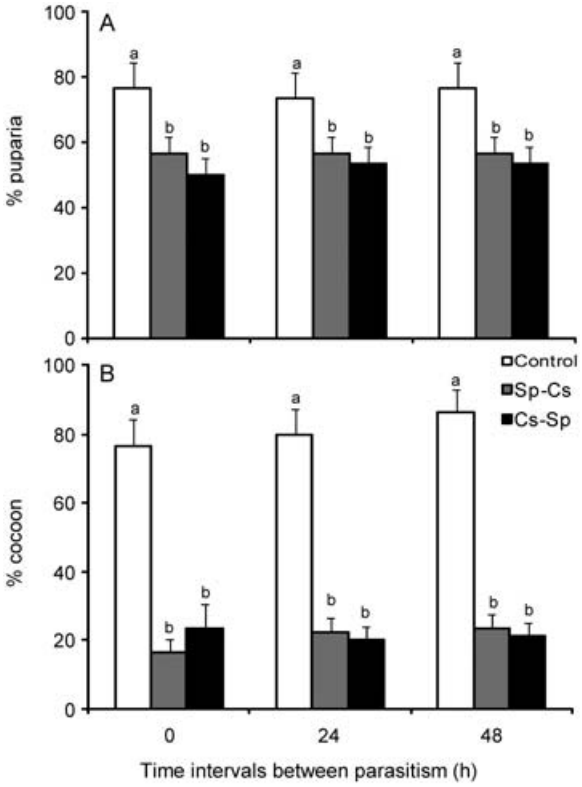

Figure 2 Percentage parasitized and multiparasitized host larvae yielding (A) *Sturmiopsis parasitica* or (B) *Cotesia sesamiae* at various time intervals between parasitism (0, 24, and 48 h). Within a time interval, columns capped with the same letter are not significantly different (χ^2-test: P>0.05). Sp and Cs indicate *S. parasitica* and *Co. sesamiae*, either parasitized alone (controls), or *S. parasitica* parasitized first followed by *Co. sesamiae* (Sp-Cs), or vice versa (Cs-Sp). [Correction added after online publication 27 November 2008 – legend amended]

was approximately 3–4 times higher in the control than in the multi-parasitized larvae, but there was no difference between time intervals and parasitism sequences, except at 24 h, when parasitism was lower in the Cs-Sp than in the Sp-Cs sequence (Table 3).

Planidia-to-puparia development time varied in the 0-h interval only, when it was shortest in the Sp-Cs sequence, and longest in the control (Table 4). For the same sequence, it was shortest in the 0-h interval and longest in the 48-h interval. *Cotesia sesamiae* egg-to-cocoon development time was significantly shorter in the controls than in multi-parasitized larvae at all three time intervals, and for both sequences, it was shorter in the 0-h intervals, compared to both other intervals. Puparia–adult development time was shortest in the controls, but similar in the parasitism sequences (Table 4). Cocoon–adult development time did not vary between parasitism sequence and the controls except for the Sp-Cs sequence, in which it was longest in the 0-h interval and shortest in the 48-h interval, and in the 0-h interval in which it was shorter in the control than in the two parasitism sequences (Table 4).

Puparia-to-adult mortality was lower in the control than in the two parasitism sequences in all three intervals (χ^2 = 0.3–5.4, P = 0.005–0.38; Figure 3). Also cocoon-to-adult mortality was always lowest in the controls (χ^2 = 12.8–14.8, P<0.0001; Figure 3) and similar in the two parasitism sequences. There were no significant differences in mortality between time intervals.

Sex ratios varied between 0.43 and 0.63 for *S. parasitica* and 0.44 and 0.56 for *Co. sesamiae* and there were no significant differences between parasitism sequences and the control or time intervals. Multi-parasitism reduced the potential growth index by 34% for *S. parasitica* and 96% for *Co. sesamiae*, when compared with the controls (Table 5).

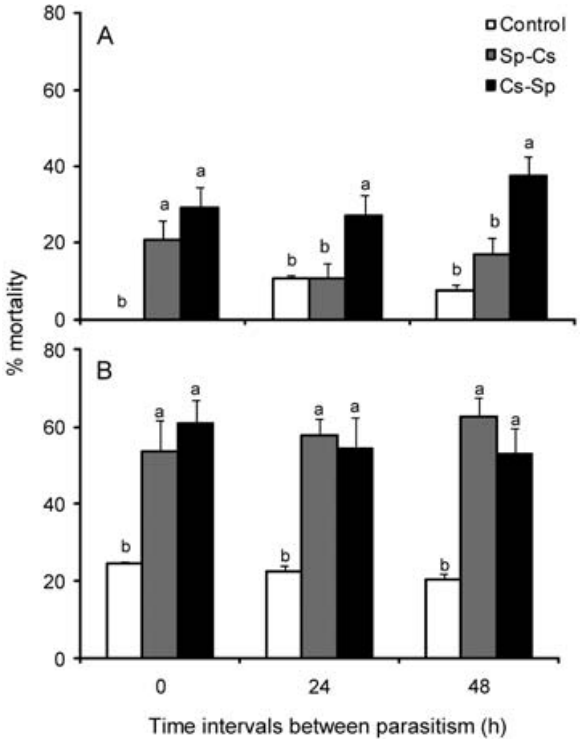

Figure 3 Mean mortality (% + SE) of (A) puparia and (B) cocoons at various time intervals between parasitism (0, 24, or 48 h). Within time interval, columns capped with the same letter are not significantly different (χ^2-test: P>0.05). Sp and Cs indicate *Sturmiopsis parasitica* and *Cotesia sesamiae*, either parasitized alone (controls), or *S. parasitica* parasitized first, followed by *Co. sesamiae* (Sp-Cs), or vice versa (Cs-Sp).

Table 3 Number of puparia or cocoons (mean ± SE) emerging from parasitized and multi-parasitized hosts at various time intervals (0, 24, or 48 h). Sp and Cs indicate *Sturmiopsis parasitica* and *Cotesia sesamiae*, either parasitizing alone (controls), or *S. parasitica* parasitizing first, followed by *Co. sesamiae* (Sp-Cs), or vice versa (Cs-Sp)

Sequence	0 h	24 h	48 h	F	d.f.	P
No. puparia per borer larva						
Sp	1.00 ± 0.0	1.00 ± 0.00a	1.00 ± 0.00a	0	2,82	0
Sp-Cs	1.09 ± 0.03	1.13 ± 0.04b	1.20 ± 0.04b	0.27	2,211	0.76
Cs-Sp	1.04 ± 0.02	1.03 ± 0.02a	1.03 ± 0.02a	0.15	2,207	0.86
F	2.01	4.78	3.47			
d.f.	2,171	2,170	2,159			
P	0.1377	0.0496	0.0436			
No. cocoons per borer larva						
Cs	70.1 ± 4.5a	59.2 ± 4.0a	63.0 ± 3.1a	0.79	2,72	0.46
Sp-Cs	22.6 ± 3.9b	17.8 ± 3.1c	22.6 ± 2.8b	1.43	2,56	0.25
Cs-Sp	23.2 ± 3.4b	29.4 ± 4.5b	28.1 ± 4.3b	0.77	2,47	0.47
F	20.89	25.92	26.39			
d.f.	2,55	2,57	2,63			
P	0.0001	0.0001	0.0001			

Means followed by the same letter within a column (puparia and cocoons separately) are not significantly different (Bonferroni test: P<0.05).

Table 4 Development time (mean ± SE) of *Sturmiopsis parasitica* and *Cotesia sesamiae* in (multi)parasitized hosts at various time intervals (0, 24, or 48 h). Sp and Cs indicate *S. parasitica* and *Co. sesamiae*, either parasitizing alone (controls), or *S. parasitica* parasitizing first, followed by *Co. sesamiae* (Sp-Cs), or vice versa (Cs-Sp)

Sequence	0 h	24 h	48 h	F	d.f.	P
S. parasitica planidia – puparia						
Sp	15.5 ± 0.4a	14.5 ± 0.3	14.5 ± 0.3	2.87	2,82	0.0626
Sp-Cs	12.9 ± 0.1cC	14.6 ± 0.2B	14.9 ± 0.2A	23.61	2,211	<0.0001
Cs-Sp	14.2 ± 0.1b	13.6 ± 0.28	14.3 ± 0.2	23.61	2,206	0.0544
F	36.55	2.39	1.59			
d.f.	2,168	2,170	2,161			
P	<0.0001	0.0945	0.2076			
Co. sesamiae egg – cocoon						
Cs	11.5 ± 0.1b	11.9 ± 0.1b	11.7 ± 0.1b	9.08	2,71	0.0503
Sp-Cs	12.3 ± 0.3aB	13.9 ± 0.2aA	13.9 ± 0.4aA	5.96	2,56	0.0046
Cs-Sp	13.4 ± 0.2aB	14.2 ± 0.2aA	14.8 ± 0.4aA	4.09	2,47	0.0233
F	6.52	35.80	25.27			
d.f.	2,55	2,57	2,62			
P	0.0029	<0.0001	<0.0001			
S. parasitica puparia – adult						
Sp	10.4 ± 0.5b	10.8 ± 0.5b	11.1 ± 0.5b	0.49	2,78	0.6160
Sp-Cs	14.8 ± 0.4aB	15.8 ± 0.5aA	15.9 ± 0.2aA	4.95	2,185	0.0081
Cs-Sp	15.1 ± 0.5aB	15.3 ± 0.3aB	16.4 ± 0.2aA	4.94	2,176	0.0082
F	24.38	44.79	71.16			
d.f.	2,146	2,152	2,141			
P	<0.0001	<0.0001	<0.0001			
Co. sesamiae cocoons – adult						
Cs	5.9 ± 0.2b	5.3 ± 0.3	6.3 ± 0.5	1.67	2,72	0.1951
Sp-Cs	8.8 ± 0.4aA	7.1 ± 0.3AB	6.8 ± 0.7B	3.95	2,47	0.0262
Cs-Sp	7.9 ± 1.5a	8.6 ± 0.6	6.3 ± 0.4	1.09	2,39	0.3460
F	3.28	2.58	1.74			
d.f.	2,50	2,52	2,56			
P	0.0461	0.0862	0.1849			

Means followed by the same lower case letter within a column (species and developmental phase kept apart) and means followed by the same upper case letter within a row are not significantly different (Bonferroni test: P<0.05).

Table 5 Potential growth index (± SE) for *Sturmiopsis parasitica* and *Cotesia sesamiae* after parasitizing fourth-instar *Sesamia calamistis* at various time intervals between parasitism (0–48 h). Sp and Cs indicate *S. parasitica* and *C. sesamiae*, either parasitizing alone (controls), or *S. parasitica* parasitizing first, followed by *Co. sesamiae* (Sp-Cs), or vice versa (Cs-Sp)

Sequence	0 h	24 h	48 h
S. parasitica			
Sp	1.87 ± 0.025	1.67 ± 0.012	1.89 ± 0.015
Cs-Sp	0.88 ± 0.015	1.30 ± 0.021	1.28 ± 0.016
Sp-Cs	1.00 ± 0.016	1.37 ± 0.019	1.10 ± 0.021
Co. sesamiae			
Cs	1.16 ± 0.015	1.21 ± 0.013	1.16 ± 0.010
Cs-Sp	0.04 ± 0.001	0.06 ± 0.001	0.06 ± 0.001
Sp-Cs	0.05 ± 0.001	0.04 ± 0.001	0.07 ± 0.001

Discussion

The present findings confirm the results from phylogenetic and morphological studies by Dittrich et al. (2006) and Barraclough (2004) that several strains of *S. parasitica* exist in Africa, which vary in host range. While being completely unsuitable for the East African strain due to maggot encapsulation (Chinwada et al., 2004), *S. calamistis* was the most suitable host for the West African strain. Also, in contrast to the Zimbabwean strain, which yielded up to six puparia per host (Chinwada & Overholt, 2004), the West African strain never produced more than one, except when multi-parasitized, but even then it never produced more than two per host. Furthermore, all host species used were suitable for development of the West African strain, indicating that the geographic race of the borer hosts (Assefa et al., 2006; Sezonlin et al., 2006) played no role or only a minor one.

The parasitoid was able to distinguish between a suitable and a less suitable host. Clement et al. (1985) and Stireman (2002) reported that kairomones in the frass and synomones produced by plants damaged by larvae (Dicke & Sabelis, 1988) may trigger larviposition activity by the tachinids. The West African strain of *S. parasitica* exhibited a strong preference for *S. calamistis*, but the differences among the other species were not significant. Thus, the cues produced by *S. calamistis* are host specific, possibly consisting of saliva or haemolymph (Nettles & Burks, 1975; Thompson et al., 1983).

The host range of the West African *S. parasitica* strain appeared to be greater than that of the Zimbabwean strain. According to Stireman & Singer (2004), relatively specialized tachinids tend to be associated with monophagous or narrowly oligophagous hosts. In West Africa, where *S. parasitica* was collected, the dominant noctuid borer species is *S. calamistis* and *B. fusca* is rare (Schulthess et al., 1997), while in Zimbabwe it is the reverse (Chinwada, 2003). As shown by Gounou & Schulthess (2004), Le Rü et al. (2006), and Ndemah et al. (2007), *B. fusca* is oligophagous, limited mostly to cultivated and wild sorghum species, while *S. calamistis* attacks a wide range of grass and sedge species.

It appears that the West African strain of *S. parasitica* is solitary, whereas the Zimbabwean strain is gregarious. In solitary species, normally only one larva completes its development to the adult stage in each host with supernumerary larvae being eliminated by some form of physiological suppression (King et al., 1976; Reitz, 1995) or by physical combat among larvae (Clausen, 1962; Mellini & Baronio, 1971; Quicke, 1997). Intraspecific competition among *S. parasitica* maggots may also have affected the performance of the competing parasitoid *Co. sesamiae*. As more than one puparium per host would lead to stronger interspecific competition for host resources, the Zimbabwean strain should affect *Co. sesamiae* to a greater extent than the West African one. On the other hand, the lower number of puparia per host suggests that the intraspecific competition for resources is fiercer in the West African than the Zimbabwean strain, which might also increase interspecific competition. Thus, although the mechanisms involved may vary with *S. parasitica* strain, it is suggested that both strains would reduce the fitness of *Co. sesamiae* when attacking the same host.

For the Zimbabwean strain, parasitism and the numbers of larvae yielding more than one puparium increased with the number of maggots used for inoculation (Chinwada et al., 2004). The same trend for parasitism was observed with the West African strain, but the final number of puparia never exceeded one, except when multi-parasitized. This suggests that the maggots had to overcome the immune system of the host and became increasingly successful as the number of maggots per larvae increased.

Of the multi-parasitized larvae, 7–14.5% yielded two puparia. The occurrence of two puparia per host may have been due to the combination of two factors. First, *Co. sesamiae* injects polyDNA viruses together with the eggs to induce immune suppression in the host in order to prevent encapsulation of the eggs (Gitau et al., 2006). This could have benefited both parasitoid species. For example, Ngi-Song et al. (2001) showed that *Cotesia flavipes* Cameron was only able to develop in *B. fusca* in cases of multi-parasitism, where *Co. sesamiae* had oviposited first and lowered the immune response of the host, thereby preventing encapsulation of *Co. flavipes* eggs. Second, in multi-parasitized larvae, interspecific competition caused

a drastic reduction in the number of *Co. sesamiae* successfully developing to pupae, but concomitantly it might have allowed the survival of supernumerary *S. parasitica* larvae as a result of reduced intraspecific competition among the fly maggots.

Multi-parasitism affected both parasitoids via reduced parasitism success and brood size, extended life cycle, and increased puparia/cocoon-to-adult mortality, but the effect was much more pronounced on *Co. sesamiae* than on *S. parasitica*, as shown by the drastic reductions in potential growth indices. Sétamou et al. (2005) and Jiang et al. (2004) showed that development time of *Co. flavipes* depended on the quality of their host *Ch. partellus* and it was longer in smaller hosts or hosts feeding on wild grasses, which affected host size. They attributed this to a lower rate of development due to lack of adequate food supply. In view of the differences in size of immatures of the two parasitoids, it is suggested that the extended development time and the low numbers of *Co. sesamiae* offspring in multiparasitized larvae were a result of increased inter- and intraspecific competition for host resources, which affected host quality. Host nutritional insufficiency in multi-parasitized hosts may also lead to pre-emergence mortality or unsuccessful emergence (House & Barlow, 1961; Wylie, 1963; Sétamou et al., 2005), which could explain the high cocoon-to-adult mortality of *Co. sesamiae* from multi-parasitized larvae.

The two parasitoids occupy similar niches in terms of host species and life stages attacked, and probably use the same cues to find the host (Ngi-Song & Overholt, 1997), but *S. parasitica* has considerably higher fecundity and adult longevity, and it is a much stronger flier than *Co. sesamiae* (Chinwada & Overholt, 2001; Mbapila & Overholt, 2001; Chinwada et al., 2004; Gitau et al., 2006). In addition, *C. sesamiae* belongs to the ingress-and-sting guild, while *S. parasitica* uses the planidial ingress strategy (Smith et al., 1993). Thus, *S. parasitica* has a developmental head start over *Co. sesamiae*, whose eggs require several days before they hatch.

Should the West African strain of *S. parasitica* be released in Zimbabwe and should both parasitoids or only one be released in Cameroon? The findings from the present experiments and the literature suggest that *S. parasitica* would outcompete *Co. sesamiae* in both extrinsic and intrinsic competition. Thus, the following outcomes are proposed. (1) In the highlands of East and southern Africa and of Cameroon, the West African *S. parasitica* and *C. sesamiae* will not be able to coexist, because together they would overexploit the reservoir of non-diapausing borers during the off-season, when *B. fusca* diapauses in the larval stage; in East and southern Africa, *P. parasitica* would not become established or it may cause local extinction of *Co. sesamiae*; in the humid forest zone of Cameroon, the release of both parasitoids would also affect populations of *Telenomus* spec. egg parasitoids, which have been shown to significantly reduce *B. fusca* infestations on maize (Ndemah et al., 2003). (2) In the mid-altitudes of both East and southern Africa and Cameroon, where mixed species populations of stemborers are common, the West African strain of *S. parasitica* would become established without affecting populations of *Co. sesamiae* or *Co. flavipes*, which were introduced to control *Co. partellus* and also successfully develop in *S. calamistis* (Chinwada et al., 2008). At the mid-altitude of Cameroon, both parasitoids would become established. Nonetheless, in Cameroon, *S. parasitica* should only be released if *Co. sesamiae* has not become established 2 years after its release.

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