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BIOLOGY AND MANAGEMENT OF ECONOMICALLY IMPORTANT LEPIDOPTERAN CEREAL STEM BORERS IN AFRICA

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■ **Abstract** Cereals (maize, sorghum, millet, rice) are extremely important crops grown in Africa for human consumption. Of the various insect pests attacking cereal crops in Africa, lepidopteran stem borers are by far the most injurious. All 21 economically important stem borers of cultivated grasses in Africa are indigenous except *Chilo partellus*, which invaded the continent from India, and *C. sacchariphagus*, which has recently been found in sugarcane in Mozambique. *C. partellus* is competitively displacing indigenous stem borers in East and southern Africa. A parasitoid, *Cotesia flavipes*, was introduced from Pakistan for biological control of *C. partellus* and caused a 32–55% decrease in stem borer densities. This article is an attempt to summarize the status of knowledge about economically important cereal stem borers in Africa with emphasis on their distribution, pest status and yield losses, diapause, natural enemies, cultural control, host plant resistance, and biological control. Special attention is given to *Busseola fusca* and *C. partellus*, the most important pests of maize and grain sorghum.

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INTRODUCTION

Cereals, especially maize and sorghum, are the most important field crops grown in Africa by commercial and resource-poor small-scale farmers (94, 167). Sugarcane is also an important cash crop grown in some areas. The crops are grown primarily for human consumption, but surpluses are used for feeding livestock (176). Among the insect pests attacking these crops in Africa, the lepidopteran stem borers are by far the most injurious (224). Because of their economic importance, stem borers have been the subjects of many studies, which resulted in an enormous amount of literature. This review summarizes the status of knowledge about cereal stem borers in Africa.

STEM BORERS AND THEIR DISTRIBUTION

Maes (105) listed 21 economically important lepidopteran stem borers of cultivated grasses in Africa, including 7 noctuids, 2 pyralids, and 12 crambids. Of these 21 species, 7 are primarily pests of rice, and one mainly attacks pearl millet in the Sahelian region. Among the noctuids, *Busseola fusca* and six *Sesamia* spp. are considered economically important. Two pyralids are serious pests: the rice borer, *Maliarpha separatella*, and *Eldana saccharina*, a pest of sugarcane and maize. The largest group (12 species) of injurious stem borers are crambids, with the majority (7 species) belonging to the genus *Chilo* Zincken. Within specific crops and geographic regions, fewer species are considered to be important pests (Table 1).

In South Africa, *B. fusca* and *Chilo partellus* are the only important stem borers of maize and sorghum (94), while in sugarcane in the same region, only *E. saccharina* is considered to be a serious pest (47). In East Africa, *C. partellus*, *Chilo orichalcociliellus*, *E. saccharina*, *B. fusca*, and *Sesamia calamistis* are mentioned as important and widely distributed stem borers of maize and sorghum (168). Major stem borers of maize and sorghum in West Africa include *B. fusca*, *S. calamistis*, and *E. saccharina* (34). In the Sahelian zone, where pearl millet is the most important cereal crop, *Coniesta ignefusalis* is the dominant stem borer (73).

TABLE 1 Important stemborer species in Africa and the Indian Ocean Islands, their distributions, and major cultivated host plants

Family	Species	Distribution	Host plants	Reference
Crambidae	*Chilo partellus*	eastern and southern	maize, sorghum	(71)
	Chilo orichalcociliellus	coastal eastern, Malawi, Madagascar; South Africa, Zimbabwe	maize, sorghum	(29)
	Chilo aleniellus	West and Central	rice, maize	(120)
	Chilo sacchariphagus	Indian Ocean Islands;	sugarcane	(222)
		Mozambique	sugarcane	(209)
	Chilo zacconius	West	rice	(105)
	Chilo diffusilineus	tropical Africa	rice	(105)
	Coniesta ignefusalis	Sahelian Africa	millet	(73)
	Scirpophaga spp.	West	rice	(40)
Pyralidae	*Eldana saccharina*	sub-Saharan	sugarcane, maize, rice	(23)
	Maliarpha separatella	sub-Saharan, Indian Ocean Islands	rice	(48)
Noctuidae	*Busseola fusca*	sub-Saharan	maize, sorghum	(72)
	Sesamia calamistis	sub-Saharan	maize, sorghum, rice	(187)
	Sesamia nonagrioides botanephaga	West, Sudan	maize, rice, sorghum, sugarcane	(187)
	Sesamia cretica	Northeast	sorghum, maize	(187)

Information on rice stem borers is primarily from West Africa and the Indian Ocean Islands, as these are areas where rice is an important food crop. *Chilo zacconius, M. separatella,* and *S. calamistis* are considered the most economically important stem borers of rice in West Africa (13, 37). *M. separatella* is the only rice borer that has a widespread distribution in sub-Saharan Africa, and it also occurs in the Comoro Islands and Madagascar (37). Other rice stem borers of secondary importance in West Africa include *Scirpophaga* spp., *Chilo diffusilineus,* and *Sesamia nonagriodes botanephaga* (37, 38). Additionally, *Chilo aleniellus* is reported to be a rice stem borer in Ivory Coast (189, 190).

Two of the economically important cereal stem borers in Africa are introduced species: *C. partellus* and *C. sacchariphagus. C. partellus* is an Asian species (29) that invaded Africa sometime before 1930 when it was first recorded in Malawi (186), but it was not reported again until some 20 years later in Tanzania (53). The distribution of *C. partellus* now includes Ethiopia, Sudan, Somalia, Kenya, Tanzania, Uganda, Mozambique, South Africa, Swaziland, Lesotho, Zimbabwe, Zambia, Malawi, and Botswana (41, 71, 79, 127). Using GIS tools, Overholt et al. (145) predicted the eventual distribution of *C. partellus* in Africa based on the climate at locations where it was known to occur and then extrapolating to other locations with similar climates. The prediction included several countries in southwestern and West Africa where *C. partellus* is not yet known to occur.

The other invasive species, *C. sacchariphagus*, is a serious pest of sugarcane in the Indian Ocean Islands. *C. sacchariphagus* may have been accidentally introduced into the islands either from Sri Lanka or Java with the introduction of sugarcane around 1850 (222). There are recent confirmed reports of *C. sacchariphagus* attacking sugarcane in Mozambique (209).

Some of the more important native species have restricted distributions, whereas others are found throughout sub-Saharan Africa. *C. orichalcociliellus*, a pest of maize and sorghum, occurs in coastal East Africa, Malawi, and Madagascar at altitudes below 600 m (51, 108, 127). *C. aleniellus* has been reported as a pest of rice in West and Central Africa and more recently as an important pest of maize in Ivory Coast (120). *C. ignefusalis* is the dominant stem borer of millet in the Sahelian zone of West Africa (69).

E. saccharina is widely distributed in Africa and has been reported from several grasses and sedges (23, 45, 61, 78). In southern Africa, *E. saccharina* is a major pest of sugarcane but rarely causes damage in maize (177). In contrast, *E. saccharina* is considered to be a pest of maize, sugarcane, and rice in West Africa (32, 64, 159, 174).

B. fusca and *Sesamia* spp. occur throughout subsaharan Africa (79). Of the *Sesamia* spp., *S. calamistis* is the most widely distributed and economically important species, but several others, including *S. cretica*, which occurs in Somalia, Sudan, and Ethiopia, and *S. nonagrioides botanephaga*, which is found in both East and West Africa, are also important. As with *E. saccharina*, the pest status of *B. fusca* varies by region. In East and southern Africa it is a pest at higher altitudes (>600 m) (127, 178), but in West Africa, *B. fusca* occurs from sea level to >2000 m (187) but is primarily a pest in the dry savanna zone (68).

DIAPAUSE

Many cereal stem borers have a resting period toward the end of the cropping season, which they spend as fully grown larvae in dry crop residues in the fields. In Kenya, *C. partellus*, *S. calamistis*, and *C. orichalcociliellus* enter diapause for several months in the dry season (130, 161, 163). However, *S. calamistis* was reported not to enter diapause in Uganda (78) or in Nigeria (68). In West Africa, *B. fusca* enters diapause during the dry season, and it takes up to six months to complete development. With the initiation of the rains, the larvae pupate within the stems, and 10–12 days later adult moths emerge (68). Similar observations were made on *C. ignefusalis*, which has a facultative diapause in dry millet stems (226).

In southern Africa, *B. fusca* and *C. partellus* pass winter in diapause, which is the cold dry season (April–September), in the lower parts of the dry stalks, where they are well protected from natural enemies and adverse climatic conditions (83–85). *B. fusca* diapauses throughout its distribution in Africa, whereas *C. partellus* does not diapause in the warm low-lying regions of the South African Provinces of Kwazulu-Natal (203) and Mpumalanga (R. Kfir, unpublished data), Swaziland

(218), and southern Mozambique (27). In regions where there is an abundance of host plants and the climate is warm, *C. partellus* normally develops continuously all-year round. In other regions with long dry periods in winter or in summer, the borer enters into a resting period. *C. partellus* was reported to diapause in the dry season in India (187) and on several islands off the coast of Africa (39, 51). However, populations without a resting period were reported from the Coast Province of Kenya (108) and Uganda (78). This explains the mixed populations of *C. partellus* found in the dry season on the Kenya Coast and at lower elevations in South Africa. In the coastal area of Kenya, in periods between cropping seasons, some stem borers diapause in maize stubble, whereas others remain actively feeding in wild grasses, such as Napier grass, in the proximity of cultivated areas (124).

An increase in carbohydrates and decrease in protein and water of the food plant are the main factors inducing diapause in *B. fusca* (193). Dry condition of the host plant (127) and the general deterioration of the nutritive environment (51, 160) induced diapause in larvae of *C. partellus* even when climatic conditions were favorable for development (161). Diapause could be artificially induced in nondiapause larvae introduced into aged maize stems.

During diapause, larvae of *B. fusca* and *C. partellus* progressively decreased in weight and had up to seven additional stationary molts. The longer time the larvae remained in diapause, the lighter in weight the emerging adults were, with fewer eggs and oocytes in their ovaries. After eight months in diapause, emerging adults weighed about half as much and had about half as many eggs and oocytes as adults that emerged from nondiapausing larvae (86).

Diapausing larvae of field-collected *B. fusca* in South Africa collected in winter emerged as adults in mid-October regardless of the date of collection and the length of time they were kept in the laboratory at 21°C and 60% relative humidity. Larvae of *C. partellus* collected in April–June emerged in November, whereas those collected in July emerged in October and those collected in August emerged in September. Regardless of the collection date, *C. partellus* started to emerge from diapause earlier, and the emergence period lasted up to twice as long as in *B. fusca*. Kfir (85) concluded that *B. fusca* had an obligatory diapause and *C. partellus* a facultative diapause. In the field, *C. partellus* starts to emerge from diapause in the second part of August, and it continues until the first week of November, a period of 12 weeks. In contrast, *B. fusca* pupates only during October–November (83, 85, 95). This difference in the pattern of emergence from diapause by the two borer species explains the distinct generations of *B. fusca* (54, 95, 106) and the overlapping generations of *C. partellus* (85, 205) occurring every year in South Africa.

Conditions of continuous moisture during the long rainy season in Kenya play a significant role in the termination of diapause by *B. fusca* (135, 137). Rainfall alone did not appear to be the main factor (192). Contact with water was a more significant factor in diapause termination than water uptake (136). Application of water or rainfall played an important role in promoting pupation during postdiapause dormancy of *B. fusca* in Ethiopia (59) and Ivory Coast (119). Delay in wetting larvae after diapause and access to water early in diapause had a deleterious effect on the larvae. The main factor enabling diapausing *B. fusca* larvae to survive adverse conditions appears to be efficient water conservation (194).

A combination of temperature and photoperiod played an important role in termination of diapause in *B. fusca* in South Africa, and water was important as a stimulus for morphogenesis following diapause (89). Long days accelerated termination of diapause in *C. partellus*, but under 16-h daylight, termination of diapause was faster than when under constant illumination. In contrast, temperature, relative humidity, and day length did not affect diapause of *C. partellus* and *C. orichalcociliellus* in Kenya (161). *C. partellus* collected in South Africa at 25°38′S, 27°47′E (90) is more affected by day length than the Kenyan population located near the equator. Kfir (89, 90) suggested that the right combination of day length and temperature could be used for breaking diapause to provide large numbers of insects for artificial infestations for plant-resistance trials. This requires only simple facilities and can save the large expense of keeping a continuous culture in the laboratory on artificial diet.

DISPLACEMENT OF NATIVE STEM BORERS BY *C. PARTELLUS*

The invasive stem borer, *C. partellus*, has proved to be a highly competitive colonizer in many of the areas it has invaded in eastern and southern Africa, often becoming the most injurious stem borer (93, 163) and displacing native species (92, 141). In coastal Kenya, there is evidence that *C. partellus* has partially displaced the indigenous stem borer, *C. orichalcociliellus* (130–132, 141). However, *C. orichalcociliellus* continues to be found at a relatively high frequency (10–30% of the borer complex), which suggests that the displacement of *C. orichalcociliellus* will not proceed to extirpation (228). Recent investigations have found that *C. orichalcociliellus* completed development in two native grasses, in which *C. partellus* could not develop (131), which may be one factor that allows their continued coexistence.

In addition to the work in the coastal area of Kenya, there is evidence of displacement of native stem borers in two other areas in Africa. In the Eastern Province of Kenya, *C. partellus* was present in the early 1980s but was less abundant than *B. fusca* (163). However, in the same area in the period 1996–1998, *B. fusca* was rare and *C. partellus* was dominant (183). Similarly, in the eastern Highveld region of South Africa, *C. partellus* partially displaced *B. fusca* over a period of seven years (92). The displacement was most evident in grain sorghum where the proportion of *C. partellus* in the total stem borer population increased from about 3% in 1986 to 91% in 1992.

Several factors have been investigated that may be responsible for the competitive superiority of *C. partellus* over some native stem borers. *C. partellus* completes a generation in less time than *C. orichalcociliellus* (101, 131), which may result in a higher population growth rate. Moreover, *C. partellus* terminates diapause more rapidly than *C. orichalcociliellus* (130) or *B. fusca* (92), which may allow *C. partellus* to colonize host plants before the two native species at the beginning of growing seasons. Kfir (92) speculated that *B. fusca* avoids plants already infested by *C. partellus*, using odors associated with host plant feeding. Ofomata (129) showed that when equal numbers of *C. partellus* and *C. orichalcociliellus* infest the same maize, sorghum, or wild-sorghum plant, more *C. partellus* successfully completed development, suggesting superiority during direct competition. Finally, more neonate *C. partellus* larvae dispersed from the plant where they hatched, and they dispersed greater distances than *C. orichalcociliellus*, which may allow *C. partellus* to colonize more plants than the native borer (129).

INDIGENOUS NATURAL ENEMIES

Parasitoids

The indigenous parasitoids associated with African cereal stem borers have been treated in Polaszek (150). All stem borer parasitoids belong to either the Hymenoptera or Diptera. Their effectiveness in keeping stem borer populations below acceptable thresholds has been doubted by several authors (93, 142). However, no studies are yet available that examine the effect of the absence of parasitoids on stem borer populations. Recent investigations (R. Kfir, manuscript submitted) into the effects of removal or partial removal of parasitoids from stem borer–infested crops by applying insecticides showed that borer populations would double.

Predators

There have been a number of studies of the effectiveness of indigenous predators on several borer species in the past decade (30, 31, 93, 103, 162). Virtually all studies have concluded that indigenous predators are not able to keep stem borer populations below economic injury levels (31, 162).

Nematodes and Pathogens

Available records of nematodes and pathogens infecting African cereal stem borers have been summarized recently (149). These authors also provided summaries for the study and identification of these agents. In doing so, they also concluded that in general nematodes and pathogens are not of great importance in regulating stem borer numbers.

Knowledge concerning viruses associated with African cereal stem borers has been reviewed (128). Iridoviruses, granulosis viruses, cytoplasmic viruses, and nuclear polyhedrosis viruses are known to attack and kill borer larvae in Africa, but no detailed studies have been conducted.

PEST STATUS AND YIELD LOSSES

Feeding and stem tunneling by borer larvae on plants results in crop losses as a consequence of destruction of the growing point, early leaf senescence, interference with translocation of metabolites, and nutrients that result in malformation of the grain, stem breakage, plant stunting, lodging, and direct damage to ears (18, 33, 36, 94). Infestations by stem borers increase the incidence and severity of stalk rots (33).

In South Africa, estimated yield losses from *B. fusca* damage ranges between 10% and total loss (24, 106, 109, 206). Yield loss in maize by *B. fusca* was significantly correlated with leaf damage, but a higher correlation was observed with stem-boring damage (24). The estimated yield losses due to *C. partellus* in maize and sorghum exceed 50% (153). A positive correlation between infestation level of *C. partellus* and yield loss was demonstrated (213). Trials in separate and mixed populations using artificial infestation on sorghum indicated that *C. partellus* was more injurious than *B. fusca* (200, 201). More damage by *C. partellus* was observed on long-season, grain-sorghum cultivars because of exposure over a longer period in the susceptible preflowering stages (199).

In Lesotho, seasonal variation in yield loss due to *B. fusca* damage on maize ranged between 0.4% and 36.6% (55). In Mozambique, larvae of third-generation *C. partellus,* the most important stem borer, were reported to infest 87% of cobs of late-planted maize and to severely damage 70% of grain (27). Infestations of up to 100% of plants, with considerable yield losses, have been recorded in the Maputo and Gaza Provinces (125), the Limpopo Valley (27), and in southern Mozambique (180).

In Zimbabwe, *C. partellus* caused yield loss of 50–60% in sorghum (178). In maize, borer infestations range from 30% to 70% in fields of resource–poor farmers but are less than 30% in commercial farms where insecticides are used (177). In Tanzania (215) and Kenya (216), loss of about 12% maize grain for every 10% plants infested by *B. fusca* were reported. In Kenya, 18% yield losses were attributed to *C. partellus* and *C. orichalcociliellus* in maize (217) and 88% in sorghum owing to *C. partellus* (165).

Maximum stalk damage in maize and up to 80% grain yield loss in sorghum by *C. partellus* were observed in Kenya on 20-day-old crops, whereas similar infestations gave statistically nonsignificant losses when plants were infested at 60 days after emergence (169, 170). Similar observations were made in Uganda (184). In Tanzania, Jepson (81) reported 40–100% sorghum plants infested by *B. fusca*, whereas in Ethiopia movement of *B. fusca* larvae into the base of the sorghum head resulted in undersized heads and grain loss of 15% (112).

Natural infestations by *E. saccharina* decreased maize yields by 16%, 15%, and 28% in the dry season and first and second rainy seasons, respectively (33). Infested plots had significantly lower grain weight, indicating that *E. saccharina* damage to the stems affects grain filling. In Ghana, a positive relationship between the number of *Sesamia* sp. larvae and the extent of damage to maize stems, and a negative relationship between damage to maize stems and maize yield were shown (64). The calculated yield loss caused by *Sesamia* sp. to maize in the rain forest coastal, derived, and Guinea ecological zones were 27%, 15%, 18%, and 14%, respectively (64). In Burundi, insecticides and exclusion-cage trials indicated maize yield reductions of 12–15% by *E. saccharina* and 30–50% by *B. fusca* (121). In Burkina Faso and Niger, yield loss in sorghum by *C. partellus* and in millet by *C. ignefusalis* was estimated by using carbofuran to protect the crops and by infesting the crops at different growth stages. The highest grain yield was obtained when the crop was protected between 15 and 30 days after emergence; artificial infestation at 15 days after emergence resulted in the greatest damage. The infestation in unprotected sorghum plots was 60–62% (188). Stem borer control in sorghum in the southern Guinea savanna of Nigeria, where *S. calamistis* predominates, improved yields by 16–19% (1), whereas in the northern Guinea savanna, where *B. fusca* predominates, yield losses of 49% in sorghum were reported (9). Yields of sprayed and unsprayed sorghum in 22 farmers' fields were studied in Nigeria, and a mean yield loss of 21% was determined (11). Yield loss in sorghum depends on the time of infestation (12). Sorghum infested by *B. fusca* before the booting stage suffered greater yield losses (110). Proportion of internodes bored in the lower part of the stalk had a more consistent negative correlation with grain yield than did proportion of stem tunneled (110). A recent study in Cameroon found that stem borers, primarily *B. fusca*, were responsible for a 9-g loss in grain yield per plant per borer and caused an 11% loss of plants owing to deadheart (43).

MANAGEMENT

Utilization of Synthetic Sex Pheromones

Pheromone-baited traps are useful devices for monitoring moth population levels of stem borers. Trap catches of male moths can provide useful information for the timing of insecticide applications (154, 208, 210). Campion & Nesbitt (42) reviewed the progress in the identification and the utilization of sex pheromones for stem borer monitoring and concluded that mass trapping is unlikely to provide satisfactory control but that mating disruption is more likely to be effective. Synthetic pheromone blends for *Chilo suppressalis*, *C. sacchariphagus*, *Chilo indicus*, *Chilo auricilius* and *C. zacconius* have shown satisfactory attractiveness to male moths in the field (25). Sex pheromones for *B. fusca*, *C. partellus*, *S. calamistis*, *S. cretica*, *S. nonagrioides* and *C. ignefusalis* have been identified and are available commercially (195, 225).

Several years of monitoring *B. fusca* using sex pheromone traps in South Africa (95, 96) revealed that the first flight resulting from moths emerging from hibernating borers peaked about the middle of November. The second flight, usually larger, peaked in the second half of February; a third flight, which occurred in

Mpumalanga Province, peaked around the middle of April. No catches of moths were recorded during winter (June–September). Larval peaks of *B. fusca* in the field lagged about 4–6 weeks behind the corresponding moth flight peaks (95, 96). Omni-directional traps were superior to delta traps for quantitative and qualitative estimation of *B. fusca* moth populations (95, 96, 207).

More research in trap design and correlations between moth catches and infestations in the field are required before trapping *C. partellus* can be used to determine economic threshold levels.

A slow-release pheromone formulation gave high levels of communication disruption in *B. fusca* when applied at 40 g a.i. ha^{-1} as 250 or 500 point sources ha^{-1} (49). This effect was observed to persist for at least 18 weeks and from release rate studies was predicted to last for 6 months. In field trials in Kenya, some reduction in damage levels was observed, indicating that mating disruption had occurred (49).

Cultural Control

Various methods of cultural control of stem borers in Africa have been reviewed (102, 113, 164, 166, 196). It is the most relevant and economic method of stem borer control available for resource-poor farmers in Africa. Other control options are often not relevant because pesticides are too expensive or not available, resistant cultivars are not widely available, and biological control of stem borers is only partially successful. Cultural control is among the oldest traditional practices and normally cannot be used as a tactical means of control (52). Cultural control is considered the first line of defense against pests and includes techniques such as destruction of crop residues, intercropping, crop rotation, manipulation of planting dates, and tillage methods (196). The latter three agronomic practices can directly affect crop yield (52). Many cultural control practices are labor intensive, but they have little adverse effects on the environment and are readily available without extra investment in equipment.

However, an understanding of stem borers' behavior and the relationships with their respective crops are important for the development of efficient management strategies. The differences in the behavior of *E. saccharina* in South and eastern Africa provide an example of the importance of understanding pest behavior in making control decisions. In South Africa, larvae of *E. saccharina* mainly infest lower parts of sugarcane stalks. It is recommended that farmers cut stalks low and leave the tops, which are then cut off and left in the field. In East Africa, on the other hand, recommendations are to not leave tops of plants in fields because *E. saccharina* larvae largely occur in upper-plant parts, and these residues would house the carryover population (196).

Although cultural control options for stem borer management appear promising, most African farmers have not adopted them (126). Cultural control is severely constrained by the lack of management capabilities of farmers, especially in areas where farming communities lack the support of an adequate extension service (70).

Intercropping and Habitat Management

Intercropping or mixed cropping has been widely practiced for centuries by small-scale farmers in Africa to reduce risk of crop failure, attain higher yields, and improve soil fertility (155, 196). Although some of these practices also lead to suppression of cereal stem borer populations, no studies have shown that farmers grow specific intercrops to exploit this effect. Many field studies have been conducted in Africa during the past two decades in an effort to identify the best crop combinations for reducing stem borer populations on cereal crops.

Studies in Kenya have concentrated both on the practice of intercropping cowpea with maize and sorghum and on the ways in which the developed systems could be adopted by small-scale farmers in eastern Africa (16, 138, 148, 162). Most concluded that intercropping reduced the incidence of stem borers. In West Africa, maize, millet, and sorghum intercropping were studied (3, 57, 82). Maize/cassava-intercropping systems in Nigeria reduced by half larval numbers of *E. saccharina*, *B. fusca*, and *S. calamistis* populations (82). Many of these intercropping studies did not seek to determine the underlying mechanisms behind the effect of intercropping on stem borer population levels. Intercropping maize with cowpea was an effective way of reducing damage caused by *C. partellus* larvae migrating from neighboring plants (146, 148). This finding was confirmed by the reports that 30% of *C. partellus* oviposition in maize/sorghum/cowpea-intercropping systems was on cowpea, and the number of larvae reaching host plants from cowpea decreased with distance (15, 16).

A recent study from Kenya has reported the effectiveness of intercropping maize with the nonhost molasses grass, *Melinis minutiflora* (98, 99). In field trials, molasses grass showed no colonization by stem borers, and when used as an intercrop with maize, it significantly reduced stem borer infestation of the main crop. A significant increase in parasitism of stem borers by the larval parasitoid *Cotesia sesamiae* was also observed. Volatile agents produced by the molasses grass repelled stem borers but attracted foraging *C. sesamiae*. Female *C. sesamiae* were attracted to (E)-4, 8-dimethyl-1,3,7-nonatriene, one of the volatile components released by intact molasses grass. Nonatriene has been implicated as an SOS signal for recruiting predators and parasitoids and is also produced by stem borer–damaged maize plants. Intact plants with an inherent ability to release such attractive stimuli could be used in new crop-protection strategies. As well as serving as an effective cover crop, the molasses grass provides good fodder for livestock. The grass is now being tested in on-farm trials in Kenya to control stem borers on maize (100).

Another useful diversionary tactic for stem borer control is planting an outer encircling row of some highly preferred host to act as a trap plant. Napier grass, *Pennisetum purpureum*, and Sudan grass, *Sorghum vulgare sudanense*, common fodder plants in Africa, were reported from Kenya to provide natural control to stem borers by acting as trap plants (99, 100). Although the stem borers oviposit heavily on the attractive Napier grass, only few larvae complete their life cycles (76). Napier grass has its own defense mechanism against crop borers. When the larvae enter the stem, the plant produces a gummy substance that causes the death of the pest (76). In on-farm trials in Kenya, planting Napier grass around maize fields significantly increases crop yields by reducing the stem borer population in maize. Sudan grass, also a fodder grass, provided natural control of stem borers by acting as a trap plant and as a reservoir for its natural enemies (99). In field trials conducted in Kenya, planting Sudan grass around maize fields decreased stem borer infestation on maize and thus increased crop yield (99). Planting Sudan grass around maize field also increased efficiency of natural enemies.

For the control of stem borers in resource-poor, maize farming systems in eastern Africa, novel habitat-management strategies have been developed using "push-pull" or stimulo-deterrent diversionary tactics (100). These strategies involve combined use of intercropping and trap crop systems. Stem borers are trapped on highly susceptible trap plants (pull) and are driven away from the maize crop by repellent intercrops (push). The plants, which are used as trap or repellent plants in a push-pull strategy, are Napier grass, Sudan grass, molasses grass, and silverleaf desmodium, *Desmodium uncinatum*. Napier grass and Sudan grass are used as trap plants, whereas molasses grass and silverleaf desmodium repel ovipositing stem borers. Molasses grass, when intercropped with maize, not only reduced infestation of the maize by stem borers but also increased stem borer parasitism by a natural enemy, *C. sesamiae* (98). All four plants are of economic importance to farmers in eastern Africa as livestock fodder.

The economic gain from the use of intercrops depends on the balance between a lowered cost of control of stem borers and the increased cost of maintaining an intercropped field, along with any decrease in yield of the main crop from greater plant competition. Net profit can be increased if the intercrop favorably changes the balance between income and costs. Economic data assessing the financial returns as well as the biological effects are therefore most useful in making decisions on the use of intercrops and trap plants for stem borer control.

Management of Crop Residues

Crop residues are important for carrying over stem borer larval populations from one growing season to the next. In Nigeria, larvae of *B. fusca*, *E. saccharina*, and *S. calamistis* were found in crop residues below the soil surface, and higher incidences of these borers were observed in no-tillage plots (82). In Kenya, *C. orichalcociliellus*, *C. partellus*, *E. saccharina*, and *S. calamistis* were observed in stalks after harvest (163, 217). In Ethiopia, a considerable proportion of *B. fusca* larvae survive in stubble (223). In Uganda, untreated crop residues were often used to mulch the next crop (115). Under these conditions, borers from the old stalks constantly infested the newly planted crops.

An effective control option would be to reduce the first generation of adult population by destroying the larvae in old stalks (78, 84, 97, 192). Ploughing in order to bury maize stubble was an effective control measure used early in the twentieth century in South Africa to control *B. fusca* (106). In Zimbabwe, it was observed that *B. fusca* moths emerging through 5 cm of soil were crippled and that deeper burial of the stalks under 10–15 cm of soil ensured that no adult moths emerged (115).

Tillage practices are viable options for *B. fusca* and *C. partellus* control in South Africa, where large areas of maize or sorghum are planted and between 90,000 and 226,000 larvae overwinter per hectare (84). Slashing maize and sorghum stubble destroyed 70% of *C. partellus* and *B. fusca* populations, and additional ploughing and disking destroyed a further 24% of the pest population in sorghum and 19% in maize (84, 97). Tillage may reduce borer populations through mechanical damage either by burying them deeply into the soil or by breaking the stems and exposing the larvae to adverse weather conditions (8, 68), as well as birds, rodents, ants, spiders, and other natural enemies (84, 87, 97, 167). For these cultural control measures to be effective, the cooperation of farmers in a region is required because moths emerging from untreated fields can infest adjacent crops (88). Currently this system is not widely practiced in South Africa because of the advent of minimum tillage and the importance of winter grazing of maize to beef farmers (88, 95).

In rural Africa, farmers often use dry stems of maize, sorghum, and millet for building houses and fences, as fuel, bedding for livestock, boundaries of terraces on slopes, and as stakes (68, 156, 161). Farmers normally stack dry stalks in the field where they are kept until commencement of rains before being taken to villages, thus creating a reservoir for infestation in the following season (196). To solve this problem, early cutting of stalks and horizontal placement on the soil surface has been recommended. This was observed to cause mortality of 97% of stem borers in maize and 100% in sorghum in Ethiopia (58) and to reduce the residual population of borers in millet from 16% in uncut stems to 3% (227). The high level of mortalities of *C. partellus*, *C. orichalcociliellus*, and *S. calamistis* in horizontally placed stalks was ascribed to the effects of sun and heat, more specifically, the reaching of the thermal threshold for survival (147). On the other hand, in Nigeria, the control of *S. calamistis*, *B. fusca*, *C. ignefusalis*, and *E. saccharina* on maize by removing stalks and stubble after harvest did not reduce stem borer populations significantly apparently because of migration of adults into the crops (2).

Control of *B. fusca* and *C. partellus* by burning old stalks and other crop residues immediately after harvest has been recommended (8, 68, 80, 192). In Tanzania, almost complete eradication of *C. partellus* on maize and sorghum was achieved by burning (53). About 95% of farmers in Nigeria kept sorghum stalks and did not follow the recommended practice of burning them after harvest (4). As a compromise, partial burning was recommended while the leaves are dry but the stalks are not (4, 8). Heat generated from the burning leaves kills up to 95% of larvae and at the same time cures the stalks, making them stronger as building materials and more resistant to termite attack (4, 12). Crop residues are the only organic matter added into soils in many small-scale African farms. Burning crop residues can create problems in farms where the organic content of soils is low and soil erosion from wind and rain is severe (196).

Manipulation of Sowing Dates and Densities

Growing crops when the pest is least abundant ensures that the most susceptible stage of crop growth does not coincide with periods of peak moth activity. In Kenya, an attempt to legislate this principle was made in order to control *B. fusca* on maize during the 1920s and 1930s (17, 221) with the objective to restrict planting maize to the February–May period, when infestation is normally low. There is no available information on the effectiveness of these measures, and the last implementation of this legislation was in 1937–1938 (72).

In West Africa, early planting reduced *B. fusca* and *S. calamistis* infestations (1). Several workers have reported more damage by stem borers to late-planted maize than to early plantings, e.g., in Benin (175), Burundi (121), Cameroon (22), Ghana (62, 64), Nigeria (5, 44, 68), and Zaire (77). Thus, in some areas of West Africa farmers do not plant maize during the second season because of severe infestations. This affects the borer populations in the rain forest zone where alternative wild host plants in the dry season are scarce (34). This strategy is also desirable in the semi-arid tropics, where rainfall is variable and unpredictable; late sowing is not desirable because the yield of late sown crops is low, even if free from stem borers (166).

In the Highveld region of South Africa, the second-generation population *B. fusca* is larger and can cause more damage than the first generation (211). The best strategy to reduce damage would be to plant early in the growing season. Similar observations were made in Lesotho (55), Zimbabwe (179), and Ethiopia where second-generation larvae caused crop losses of 22.5–100% compared with 0–22.6% by first generation (60).

In the lower elevations of South Africa, it is recommended that sorghum be planted after mid-October to avoid infestation from the first moth peak of *C. partellus* (204). In Tanzania, Swaine (185) found that maize planted early in the season was more infested by *B. fusca* than maize sown later. In Malawi, planting date influenced infestation levels of *B. fusca* and *C. partellus* on sorghum; however, the choice of optimum sowing date depends on the sorghum cultivar (111). In contrast, in the Sahelian region, manipulating the planting dates of millet is not a good method to reduce infestation by *C. ignefusalis* (227).

Sowing density may affect the crop and its pest population, as well as the behavior of the pest in searching for food or an oviposition site (102). Young *C. partellus* migrate from their hatching site to the funnel leaves or to other plants within the vicinity. During this migration, up to 100% mortality may occur (108). The lowest incidence of deadheart caused by *B. fusca* occurred at the lowest plant density in sorghum in South Africa (198) and maize in Nigeria (134). A reduction in row width increased the number of larvae able to reach adjacent plant rows through migration, and this in turn resulted in more damaged plants (211). *B. fusca* larvae migrate up to 2.4 m (68) and at a 0.9 m interrow spacing, which is common in commercial agriculture; they migrated over 4 rows from the hatching site (211). In Ivory Coast it was suggested that maize be grown with larger interrow spacing rather than with reduced plant number within the row to reduce *B. fusca* and *E. saccharina* damage (118). Studies on *C. partellus* in maize planted at different densities (56) and on *C. ignefusalis* in millet (57) showed no significant difference in oviposition or borer incidence.

In subsistence farming systems in Africa where farmers normally intercrop cereals with other crops and lack of water is a major constraint, manipulation of sowing dates and management of plant densities is not always practical as farmers often plant after first rains (196). Farmers' choice of sowing dates is affected by many constraints, and it is unlikely that a change in sowing date alone will result in higher sustainable yields (126).

Fertilizer

Fertilizing crops can increase infestation and survival of borers through an increase in the nitrogen content of plants (196). In Nigeria, damage to rice by *M. separatella* increased with the application of fertilizer (191), and in South Africa sorghum plants without fertilizers were less preferred for oviposition by *C. partellus* (197), but no differences were observed in oviposition by *B. fusca* (212). In South Africa, where *E. saccharina* is a problem on sugarcane, a reduction in nitrogen-fertilization rate from 50 kg per hectare to 30 kg per hectare is recommended (158). An increase in the survival of *S. calamistis* larvae and acceleration in larval development with increased nitrogen content of maize was observed, and this may result in an increase in the number of generations per year (171).

Nitrogen fertilization enhances borer development as well as the plant's tolerance to borer attack. Yield losses decreased linearly from 20% with no fertilizer to 11% with 120 kg of nitrogen per hectare (172). Ajayi (10) observed that time of nitrogen application influenced incidence of *C. ignefusalis* on millet and suggested that the manipulation of time of nitrogen application may achieve a compromise between using low levels of nitrogen for low stem borer infestation and using high levels for better yields.

Host Plant Resistance

Host plant resistance as an approach to pest management in gramineous crops confers many advantages (34). Resistant crop varieties provide an inherent control that involves no environmental problems, and they are generally compatible with other insect-control methods. The cultivation of resistant crop plants is not subject to the vagaries of weather as are chemical-control measures, and in certain circumstances it is the only effective means of control. Resistant varieties control even a low pest density, whereas insecticide use is justifiable only when the density reaches the economic injury level. Efforts are underway in Africa to identify sources of stem borer resistance in cereal crops, but high levels of resistance have not been found.

Breeding for Resistance

Efforts have been made to incorporate resistance of maize and sorghum to *C. partellus* into a good agronomic background during the past two decades (6, 7, 14), and many genotypes are already in national yield trials. Resistant lines/ hybrids with good general combining ability have been identified (167). Several hybrid sorghums bred in South Africa exhibited greatest tolerance to stem borer damage and therefore suffered low yield losses (202).

Biological Control

Over the past 60 years, there have been numerous attempts to introduce exotic parasitoids into Africa and the Indian Ocean Islands for biological control of exotic and native stem borers, but only a few species have established (Table 2). On the mainland, only *C. flavipes* has established.

In 1993, the gregarious larval endoparasitoid, *C. flavipes*, was introduced into Kenya from Pakistan for biological control of *C. partellus*. Releases were made in the southern coastal area of Kenya (144), and the parasitoid was recovered during the season of release from *C. partellus* and two native stem borers, *C. orichalcociliellus* and *S. calamistis* (143). In 1994 only one stem borer parasitized by *C. flavipes* was found despite intensive sampling. In 1995 and 1996 a few recoveries were made but parasitism remained low (143). In 1997 the number of recoveries increased dramatically and parasitism at 30 sites averaged about 6%. Parasitism continued to increase during the next two years with average parasitism of about 13% in 1999 (228). Surveys in other maize-growing areas of Kenya showed that *C. flavipes* was present in the Eastern Province (183) and in the area bordering Lake Victoria in western Kenya (139). In the Eastern Province, *C. flavipes* was found in low densities in 1996 and then released at three sites in 1997. Parasitism during the season following the releases was about 14% (183). *C. flavipes* was never intentionally released in western Kenya, but Omwega et al. (139) speculated that the establishment was the result of insects that escaped from a local laboratory colony in 1992. However, parasitism in western Kenya has not increased to the levels observed in coastal Kenya or the Eastern Province (133). In western Kenya, four stem borers are common in maize, *C. partellus, S. calamistis, B. fusca,* and *E. saccharina* (163), all of which are attractive and acceptable hosts for *C. flavipes*. Two of which, *B. fusca* and *E. saccharina*, are not suitable for its development (123, 143). Overholt (141) suggested that the presence of acceptable but unsuitable hosts in an area would create a sink for *C. flavipes* eggs and depress population growth.

The impact of *C. flavipes* on stem borer populations in coastal Kenya was recently investigated (228). A ratio-dependent, host-parasitoid model was used to estimate the stem borer density with and without the parasitoid. A reduction of 1.1–1.6 stem borers/plant, equivalent to a 32–55% decrease in the stem borer density,

TABLE 2 Exotic stem borer parasitoids established in mainland Africa and Indian Ocean Islands

Location	Host stage attacked	Species	Target host[a]/crop	Origin	Association (new/old)[b]	Years of release	Reference
MAINLAND							
Kenya	Larva	*Cotesia flavipes*	CP/maize	Pakistan/India	old	1993–1997	(139, 141, 183)
Mozambique	Larva	*Cotesia flavipes*	CP/maize	Pakistan/India	old	1996–1999	(50)
Uganda	Larva	*Cotesia flavipes*	CP/maize	Pakistan/India	old	1997–1999	(107)
Tanzania	Larva	*Cotesia flavipes*	CP/maize	??	old	not released	(140)
Ethiopia	Larva	*Cotesia flavipes*	CP/maize	??	old	not released	W.A. Overholt, unpublished data
ISLANDS							
Mauritius	Larva	*Cotesia flavipes*	CS/sugarcane	unknown[c]	old	unknown[b]	(222)
		Cotesia sesamiae	SC/maize, sugarcane	Kenya	old	1951–1952	(65)
		Bracon chinensis	CS/sugarcane	Sri Lanka	old?[d]	1939	(65)
	Pupa	*Xanthopimpla stemmator*	CS, SC/sugarcane, maize	Sri Lanka	old?[d]/new	1939	(117)
		Trichospilus diatraeae	CS/sugarcane	India	old?	1963	(65)
Reunion	Larva	*Cotesia flavipes*	CS/sugarcane	unknown[b]	old?[d]	unknown[b]	(65)
		Cotesia sesamiae	SC/maize, sugarcane	Mauritius	old	1953–1955	(65)
	Pupa	*Xanthopimpla stemmator*	CS, sugarcane, SC/maize, sugarcane	Mauritius	old?[d]	1953, 1960	(65)
Comores	Pupa	*Pediobius furvus*	SC/maize	Madagascar	old	1969–1971	(39)
Madagascar	Larva	*Cotesia flavipes*	CS/sugarcane	Mauitius	old?[d]	1961	(20)
		Cotesia sesamiae	SC/maize, sugarcane	Uganda	old	?	(39)
	Pupa	*Pediobius furvus*	SC, SB/maize	Uganda	old/new	1968	(19)

[a] CP, *Chilo partellus*; CS, *Chilo sacchariphagus*; SC, *Sesamia calamistis*; SB, *Sciomesa biluma*.

[b] Old/new is used when two stem borers were targets. The host listed first in the "target host" column is the old association host.

[c] There is confusion regarding the origin of the *C. flavipes* populations in Mauritius and Reunion. Appert (19) indicated that *C. flavipes* was introduced into Mauritius in 1917 and then later in Reunion, but provides no details or reference. Greathead (65) indicated that there was no record of the introduction, but he assumed that it was exotic. One possibility is that it arrived on the islands along with its host, *C. sacchariphagus*, around 1850.

[d] The determination of old vs. new associations with *C. sacchariphagus* is difficult because the origin and taxonomic status of the population of *C. sacchariphagus* in Mauritius is unclear. Williams (222) speculated that the borer either arrived in Mauritius from Sri Lanka in 1848, or from Java in 1850.

was shown. As there is not yet any evidence that the *C. flavipes* density has reached an equilibrium, it may continue to increase and provide greater suppression of stem borers in the future.

In addition to the work conducted in Kenya, a survey in 1995 in northern and central Tanzania recovered *C. flavipes* at two locations near Lake Victoria in an area bordering southwestern Kenya (140). Based on surveys conducted prior to 1994, and on electrophoretic evidence, it was concluded that the most likely explanation was that *C. flavipes* moved into Tanzania from Kenya (140).

Releases of *C. flavipes* were made in Mozambique in 1996 (50) and in Uganda and Somalia in 1997 (141). Recoveries in Mozambique in 1999 indicated that the parasitoid had established but parasitism was low. In Uganda, one year after the release of *C. flavipes*, it had become the most common parasitoid of a complex of four stem borers, and parasitism averaged about 20% (107). No postrelease surveys have been conducted in Somalia, but recoveries in neighboring Ethiopia, where the parasitoid was never released (W.A. Overholt, unpublished information), strongly suggest that the parasitoid established in Somalia and moved into Ethiopia. Releases in Zimbabwe, Zambia, Zanzibar, and Malawi were made in 1998–1999, but to date, establishment has not been confirmed (W.A. Overholt, unpublished information).

Examination of the failures and successes in establishing exotic parasitoids suggests several factors that may be related to establishment. The success rate on the Indian Ocean Islands has clearly been much higher than on mainland Africa, where the only confirmed establishment has been *C. flavipes*. The higher rate of establishment on islands is true not only for stem borer parasitoids but for natural enemies introduced against other pests as well. Greathead (65) reviewed classical biological control in Africa and suggested that the greater success on the Indian Ocean Islands could be explained by the theory of island biogeography (104). Species are packed more tightly and are more specialized on continents than on islands, and thus, specialist parasitoids encounter less resistance (competition) when colonizing islands.

The geographic factor of islands versus the mainland is confounded with a second, potentially influential factor. The major emphasis of the stem borer biological control activities on the Indian Ocean Islands was against *C. sacchariphagus* in a sugarcane ecosystem, whereas in mainland Africa the work has been directed mostly in maize and sugarcane, with lesser effort in rice. The only successes in maize have been the introductions of *Pediobius furvus* and *C. sesamiae* from mainland Africa to Indian Ocean Islands for control of *S. calamistis* and the recent establishment of *C. flavipes* in Kenya.

Ecological differences between sugarcane and maize ecosystems may influence establishment. Sugarcane is grown throughout the year and thus provides a fairly stable habitat. In contrast, the maize ecosystem is short-lived, providing a suitable habitat for stem borers and their natural enemies for only two or three months. Brenière et al. (39) suggested that a lack of habitat stability on the island of Ngazidja (Comores) was the reason for several failures of the establish parasitoids against

C. partellus in maize. A review of success rates in biological control programs in different categories of habitat stability supports the hypothesis that the chance of establishment increases with an increase in habitat stability (66). However, the lack of success in South Africa against *E. saccharina* in sugarcane, despite 15 years of intense effort (47), suggests that a semiperennial sugarcane habitat alone is not sufficient for the establishment of parasitoids. Conlong (47) points out that climate compatibility is also a major factor that influences establishment and suggests that the temperate climate of South Africa has not been conducive for the establishment of parasitoids from tropical and subtropical regions. Similar explanations have been given for the lack of success in biological control of *C. partellus* in South African maize (91, 181).

Old host/parasitoid associations more likely result in establishment than do new associations. All establishments on the Indian Ocean Islands and the only confirmed establishment on mainland Africa included at least one old-association relationship (see footnote c to Table 2). The behavioral and physiological compatibility of old-association parasitoids and their hosts are implicit, whereas in new associations compatibility cannot be assumed (220). The greater success of old associations supports the contention of several authors (66, 67, 214). However, as stem borers typically occur in complexes, at times including both exotic and native pests, introduced parasitoids will often encounter both old- and new-association hosts when colonizing a new area. The probability of establishment and the level of suppression of the stem borer complex may depend not only on the old host/parasitoid relationship(s) but also on the compatibility of the new relationships.

Finally, a notable aspect of the introduction of stem borer parasitoids into Africa has been the number of times *Cotesia* spp. have established as compared with other parasitoids. Worldwide, *C. flavipes* has been introduced into more than 40 countries in the tropics and subtropics for biological control of crambid stem borers, primarily those in the genera *Chilo* and *Diatraea* (151). In Mauritius, parasitism of 4–50% of larvae of the introduced stem borer, *Chilo sacchariphagous*, has been reported (152). In Madagascar, where *C. flavipes* was introduced in 1960, parasitism of 60% of *C. sacchariphagous* larvae was reported (28). The success of *C. sesamiae* is limited to its establishment on Mauritius, Reunion, and Madagascar (Table 2), where it was introduced against *S. calamistis*.

Several factors could be responsible for the success of the two *Cotesia* spp. In their areas of endemism, the *Cotesia* spp. parasitoids often attack more than one species of crambid and/or noctuid stem borers (26, 63, 114, 116, 122, 173). A parasitoid that exploits more than one of the hosts in the target habitat may better colonize a new area than a parasitoid with a narrow host range owing to a more constant availability of hosts and a lack of population growth depression due to wasting eggs in attractive but unsuitable hosts.

Another factor that may predispose *C. flavipes* and *C. sesamiae* to establish is gregarious reproduction. Hopper & Roush (75) suggested that an Allee effect might explain many failures to establish natural enemies for biological control.

They speculated that low densities, which may occur after the release of an arrhenotokus parasitoid, might decrease chances of mate finding, thus leading to possible extinction. However, *C. flavipes* and *C. sesamiae* mate with their siblings before dispersal (21, 144, 157), and thus Allee effects will not influence establishment.

A high host-searching ability has been suggested as a factor involved in the success of *C. flavipes*. Even at low host densities, *C. flavipes* successfully located stem borer hosts (219). The high host-searching success of *C. flavipes* may in part be due to its behavior of entering tunnels in plant stems to attack stem borer larvae (182). Many larval parasitoids of stem borers remain on the outside of the stem and attack their hosts by drilling, or locating breaches through the stem, with their ovipositor (182). This strategy may be effective for attacking stem borers in small-stemmed wild grasses, but in relatively larger-stemmed cultivated grasses, the length of the ovipositor may limit the number of hosts susceptible to attack (74).

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