ECOLOGICAL INTERACTIONS BETWEEN *Chilo orichalcociliellus* STRAND AND *Chilo partellus* (SWINHOE) (LEPIDOPTERA: PYRALIDAE) ON THE KENYA COAST

A Thesis
presented to the Department of Biological Sciences of the Faculty of Natural Sciences, Nnamdi Azikiwe University, Awka, Anambra State, Nigeria, in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Entomology

BY

VIVIAN CHINYERE OFOMATA

B.Sc. (PARASITOLOGY AND ENTOMOLOGY), ANAMBRA STATE UNIVERSITY OF TECHNOLOGY, ENUGU, NIGERIA.
M.Sc. (AGRICULTURAL BIOLOGY), UNIVERSITY OF IBADAN, IBADAN, OYO STATE, NIGERIA.

Department of Biological Sciences
Faculty of Natural Sciences
Nnamdi Azikiwe University
P. M. B. 5025, Awka
Anambra State, NIGERIA.

December 1997

CERTIFICATION

I hereby certify that the work herein now submitted as a thesis for the Degree of Doctor of Philosophy in Entomology is the result of my own investigations and has not been submitted for a similar degree in any other University.

VCOfomata

Vivian Chinyere Ofomata

We certify that the work herein was conducted under our supervision by Vivian Chinyere Ofomata.

Dr. W.A. Overholt

ICIPE Supervisor

Dr. S.A. Lux

ICIPE Supervisor

Professor R.I. Egwuatu

University Supervisor

DEDICATION

To my Parents
Hon. Justice Joseph N. Ofomata
and
Mrs Christy M. Ofomata

To my Brothers
Chudi, Obi, Arii, Ify and Iyke

To my Sisters
Adaeze, Chinwe and Ifeoma

To my Fiance
Chyke Osuji

whose tireless love, care, prayers and support greatly inspired me in achieving my life career

ACKNOWLEDGEMENTS

I am very grateful to the Vice Chancellor, Nnamdi Azikiwe University, Awka, Anambra State, Nigeria, Professor Festus Nwakor, for granting me a study leave to undertake this research. Fellowship for this research was from the German Academic Exchange Programme (DAAD) in collaboration with the International Centre of Insect Physiology and Ecology (ICIPE) and The Netherlands government under a collaborative project between ICIPE and Wageningen Agricultural University entitled "Biological Control of Tsetse and Crop Pests".

I thank the Director of ICIPE and the Coordinator of the African Regional Postgraduate Programme in Insect Science (ARPPIS) for giving me the opportunity to conduct my research in ICIPE.

I am most grateful to my supervisors, Dr. W.A. Overholt (Project Leader ICIPE/WAU project, ICIPE), DR. S.A. Lux (Senior Research Scientist, ICIPE), Professor R.I. Egwuatu (Director of Academic Planning, Nnamdi Azikiwe University, Awka) for their valuable discussions, suggestions, criticisms and encouragements throughout my research.

I very much appreciate the editorial assistance, contribution in the analysis and interpretation of various data and encouragements from Dr. A. Odulaja and Dr. A.J. Ngi-Song. The help of Mr. J.C. Mbapila in teaching me some graphical packages is greatly appreciated.

I deeply acknowledge the technical assistance of Mr. G. Okuku Ogolla of ICIPE/WAU project. I also thank all the other staff of the ICIPE/WAU project in Nairobi and Mombasa stations for their assistance, the Animal Rearing and Quarantine Unit (ARQU) for the supply of experimental insects, and those of the various units at ICIPE for their assistance.

I thank all my friends and relatives in the various ways they rendered their help throughout my stay in Kenya. My most sincere thanks go to the families of Dr. D.I. Okpala and Professor P. Kenya for their love, care and hospitality during my stay in Kenya. The sisterly love and care of Dr. A.J. Ngi-Song and the friendship of the family of Dr. N.K. Maniania are very much appreciated.

Finally, my sincere heartfelt gratitute and love go to my parents, Honourable Justice J.N. Ofomata and Mrs. C.M. Ofomata, my brothers, Chudi, Obi, Arii, Ify, Iyke, sisters, Adaeze, Chinwe, Ifeoma and my fiance, Chyke Osuji, for their immeasurable support.

ABSTRACT

Laboratory studies were conducted to determine the quantities of maize and sorghum stems consumed by larvae of *C. partellus* and *C. orichalcociliellus* as an indication of the amount of damage caused by these species to cereal crops. Results revealed that larvae of *C. partellus* consumed a greater quantity of maize than *C. orichalcociliellus* on a daily basis and throughout the larval lifetime. *C. partellus* also consumed more sorghum than *C. orichalcociliellus* on a daily basis, but both species consumed equal amounts of sorghum in their larval lifetimes despite the fact that *C. partellus* completed a larval generation in a shoter time than *C. orichalcociliellus* in both maize and sorghum. This suggests that even if the stem borer density at the coastal area of Kenya has not changed since the invasion of *C. partellus*, damage to cereal crops may be greater than when C. partellus has not invaded.

The extent of niche overlap and interspecific association between *C. partellus* and *C. orichalcociliellus* were investigated in cultivated and wild host plants. Results showed that *C. partellus* and *C. orichalcociliellus* overlapped to a great extent in their habitat, with a very weak positive association at the early larval instars but no association at the late larval instar and pupal stage. No negative association was found between the species suggesting that the species do not directly attack each other while in their habitat.

The role of indigenous parasitoids in the population regulation of *C. partellus* and *C. orichalcociliellus* was investigated. There was no evidence that indigenous parasitoids are involved in the displacement of *C. orichalcociliellus*.

Investigations on some bio-ecological and physiological aspects of *C. partellus* and *C. orichalcociliellus* revealed some superior attributes of *C. partellus* that may be giving this species a competitive advantage over *C. orichalcociliellus*. The fecundity, longevity and egg survival of these species were compared in the laboratory at different temperatures and relative humidities. The results showed that both species had similar longevities but *C. partellus* laid more eggs than *C. orichalcociliellus*. However, at high temperatures and relative humidities both species had similar fecundity. Higher numbers of *C. partellus* eggs survived to the first larval instar at all temperatures and relative humidities and this leaves *C. partellus* with more individuals reaching the reproductive stage.

The dispersing abilities of *C. partellus* and *C. orichalcociliellus* were compared in the laboratory using a wind tunnel. Higher percentages of *C. partellus* larvae dispersed from the experimental plants when compared to *C. orichalcociliellus* in both maize and sorghum plants. Also, *C. partellus* larvae dispersed over longer distances at a faster rate than *C. orichalcociliellus* in maize and sorghum plants.

Field experiments were conducted to determine the establishment successes of *C. partellus* and *C. orichalcociliellus* in maize, sorghum, napier grass and wild

sorghum plants. Equal numbers of first instar larvae of *C. partellus* and *C. orichalcociliellus* were recovered from all plants after 3 days of infestation. However, as the larvae developed, higher numbers of *C. partellus* larvae were recovered from all the plants except in napier grass, which had higher percentage establishment of *C. orichalcociliellus* at 10 and 21 days after infestation. *C. partellus* and *C. orichalcociliellus* successfully established and coexisted in the same plant at early larval instars, but competition and other mortality causing factors set in at the later instars resulting in the elimination of more *C. orichalcociliellus* compared to *C. partellus*.

Laboratory studies on the larval developmental times of *C. partellus* and *C. orichalcociliellus* in maize, sorghum, napier grass, wild sorghum and guinea grass revealed that *C. partellus* completed larval development in a shorter time than *C. orichalcociliellus* in maize, sorghum and wild sorghum, *C. partellus* did not complete development in napier and guinea grasses. On the other hand, *C. orichalcociliellus* completed development in all the plants. Development of both stem borer species was faster in maize, much slower in the wild grasses. Survival of both stem borer species was higher in maize, but very low in the wild grasses. The relatively faster development of *C. partellus* compared to *C. orichalcociliellus* in cultivated and wild grasses may be important in the displacement of *C. orichalcociliellus*. However, the ability of *C. orichalcociliellus* to complete development in two native grasses in which *C. partellus* did not survive may give this species an advantage over *C. partellus*. This differential survival in wild grasses may have allowed *C. orichalcociliellus* to escape extinction from the coast.

Investigations on the intensity of diapause and survival of diapausing larvae of *C. partellus* and *C. orichalcociliellus* revealed an earlier termination of diapause in *C. partellus* than in *C. orichalcociliellus*. *C. partellus* may be able to colonize crops before *C. orichacociliellus*, and thus might have an enhanced advantage over *C. orichalcociliellus*. Male and female moths of diapausing *C. partellus* larvae terminated diapause and adults emerged at the same time , whereas, differences were found in the diapause termination and emergence times of male and female diapausing *C. orichalcociliellus* larvae. This may facilitate immediate mating and production of viable eggs by *C. partellus,* while hindering mating of *C. orichalcociliellus* since the males may not be readily available to fertilize the eggs at the time of female emergence. These superior attributes of *C. partellus* may be implicated in the displacement of *C. orichalcociliellus*.

TABLE OF CONTENTS

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

CHAPTER SIX

CHAPTER SEVEN

CHAPTER EIGHT

CHAPTER NINE

CHAPTER TEN

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

CHAPTER ONE

1.0 General Introduction

Cereal crops, in particular rice, *Oryza sativa* L., maize, *Zea mays* L., sorghum, *Sorghum bicolor* (L.) Moench and millets, *Pennisetum* species, are extremely important sources of human nutrition (Seshu Reddy, 1990). These crops are of relatively low cash value, and are grown by a large proportion of the world's poorest peoples (Seshu Reddy, 1990). In sub-Saharan Africa , maize and sorghum are the staple food crops for the majority of people (Hill, 1983). They are also grown as feed for poultry and livestock in the form of grain, forage and fodder. In Kenya alone, nearly 1,500,000 hectares are under maize cultivation (FAO, 1991).

In the tropics, the yield of maize and sorghum is low. One of the major constraints to increasing the production of maize and sorghum is damage by phytophagous insects. Over 150 species of insects are known to damage these crops (Ingram, 1958; Mohyuddin and Greathead, 1970; Young and Teetes, 1977; Seshu Reddy and Davies, 1979; Hill, 1983; Seshu Reddy, 1991). Lepidopterous stem borers are among the most damaging pests of cereal crops worldwide (Jepson, 1954; Ingram, 1958; Nye, 1960; Harris, 1962; Youdeowei, 1989; Seshu Reddy, 1991). In Africa, several species of noctuid and pyralid stem borers occur. The most injurious are *Chilo partellus* (Swinhoe), *Chilo orichalcociliellus* Strand, *Sesamia calamistis*

Hampson, *Sesamia crecita* Lederer, *Busseola fusca* (Fuller), *Eldana saccharina* Walker and *Coniesta ignefusalis* (Walker) (Nye, 1960; Seshu Reddy, 1983a, b; Youdeowei, 1989; Seshu Reddy, 1991; Overholt *et al.*, 1994a). With the exception of *C. partellus,* which is an Asian species, all other species are thought to be indigenous to Africa. Plant damage is caused by larval feeding in the plant whorl and later through stem tunnelling. Infested plants have poor growth and reduced yield and are more susceptible to secondary infection and wind damage. Heavy infestations at the early stages of plant growth may cause 'dead heart' and sometimes lead to total crop failure. Youdeowei (1989) and Seshu Reddy and Walker (1990) gave estimates of yield losses due to stem borers in the neighbourhood of 20-40% of the potential yield.

Population dynamics of *C. partellus* and *C. orichalcociliellus* have been investigated in some African countries, including South Africa (Kfir, 1994), Madagascar (Delobel, 1975a), and Kenya (Mathez, 1972; Warui and Kuria, 1983; Overholt *et al.*, 1994a). There is evidence that the introduced stem borer, *C. partellus*, is an efficient colonizer in many of the areas it has invaded, often becoming the predominant and most economically important stem borer in maize and sorghum (Delobel, 1975a; Kfir, 1994; Overholt, *et al.*, 1994a) at elevations below 1500m (Seshu Reddy, 1983a, b).

In Kenya, studies have been conducted on the species composition of stem borers. For example, studies conducted in the mid 1960s on the Kenya coast revealed that *C. orichalcociliellus* was the predominant stem borer species on maize, followed by *C. partellus* and *S. calamistis* (Mathez,1972). The same study revealed that there were two peaks of larval populations of *C. partellus* and *C. orichalcociliellus* at 50 and 100 days after planting, respectively. The infestation started very early and 100% of the larvae were found in the funnel base at 20 days after planting. The percentage of larvae in the whorl decreased regularly as the stem elongated, to about half of the original value 30 days later, and eventually to zero at tasselling. The highest number of larvae per plant was 98 for *C. orichalcociliellus*, 43 for *S. calamistis*, and 28 for *C. partellus*.

A later study at the Kenya coast from 1978-1981 reported two population peaks of *C. orichalcociliellus* and *C. partellus* during the short and long rains, but these two peaks were more prominent in the short rains than in the long rains (Warui and Kuria, 1983). There were more *C. orichalcociliellus* than *C. partellus* during the long rains, whereas *C. orichalcociliellus* and *C. partellus* were equally abundant during the short rains (Warui and Kuria,1983). Warui and Kuria (1983) also reported that in a maize/sorghum intercrop, *C. partellus* larvae were 2.25 times more abundant than *C. orichalcociliellus* on sorghum. However, *C. orichalcociliellus* was 1.46 times more abundant than *C. partellus* on maize, suggesting that *C. partellus* was more attracted to sorghum than to maize, and that the tillering of sorghum seemed to increase the population of stem borers which consisted mainly of *C. partellus*.

Recent investigations by Overholt *et al* (1994a) on the distribution and sampling of *C. partellus* on maize and sorghum on the Kenya coast from 1990-1993, indicated that *C. partellus* was the most abundant stem borer species in all the fields, accounting for more than 80% of total stem borers, while *C. orichalcociliellus* and *S. calamistis* accounted for less than 10% of the total population of stem borers. The reports of Overholt *et al.* (1994a), compared with those of Mathez (1972) and Warui and Kuria (1983), indicate a decrease in the absolute numbers of *C. orichalcociliellus* on the Kenya coast since the invasion of *C. partellus* in the early 1960s. This shift in species abundance over a period of 30 years suggests that the introduced *C. partellus* may be gradually displacing the indigenous *C. orichalcociliellus* in Kenya.

Invasions may add species to a community, which may result in local displacement or local extinction. Changes in the composition of the biotic environment may also include displacement and extinction. Consequently, there have been reports of shifts in distribution and abundance of previously established species of several insects following the arrival of new ones. For example, *Aedes albopictus* became less common in several Southeast Asian cities after the invasion of *A. aegypti* (Sartees, 1966; Gilotra *et a*l., 1967). Also the recent invasion by *A. albopictus* into the southeastern United States has been accompanied by a parallel decrease in the abundance of *A. aegypti* (Hawley, 1988; Peacock *et al.*, 1988; Black *et al.*, 1989; Hobbes *et al.*, 1991; McHugh, 1991) and of *A. triseriatus* in Florida (O'

Meara *et al*., 1992; 1993).

The distributional shifts and changes in species abundance can be explained through non-interactive and interactive processes. Non-interactive processes refer to situations in which ecological factors affect the populations of the previously established species independently of the new arrival (Chan *et al*., 1971; Black *et al*., 1989). There may be no displacement of one species by another, but an increase in habitat availability for one of the species, most often the invading species. For example, Chan *et al*., (1971) proposed that there has been no displacement of *Aedes albopictus* in Singapore City, but that the potential habitat for *A. aegypti* has increased through urbanization. His explanation was based on the assumption that these species of *Aedes* differ in the habitat preference of the adults. Overholt *et al* (1994b) noted that it could possibly be argued that *C. partellus* populations are simply expanding into a partially empty ecological niche rather than displacing indigenous stem borer species, but available information does not seem to support this because stem borer populations have remained more or less constant over the years, whereas *C. orichalcociliellus* populations have decreased in absolute numbers. Kfir (unpublished data) noted that *C. partellus* simply expanded its distribution into a partially empty ecological niche in the lower elevations of southern Africa where low populations of *S. calamistis* and *B. fusca* occurred.

Interactive processes refer to situations in which the invaders are thought to depress the population of the established species. Researchers have attempted to explain the processes involved in the population declines of previously established species by invading species (Debach and Sundby, 1963; Debach, 1966; Delobel, 1975b; Debach *et al*., 1978). A number of factors are implicated, but in some cases the obvious explanations have been found untenable (Debach *et al*., 1978). Among other factors, interspecific competition is an important aspect in the interaction between species (Schoener, 1983; Settle and Wilson, 1990), that plays a key role in the distribution, abundance and community structure of species (MacArthur, 1972; Ricklefs, 1973; Schoener, 1974; Cody and Diamond, 1975; Pianka, 1976; Hutchinson, 1978). Simberloff (1981) implicated competition amongst predation and habitat change , as a factor involved in species extinction after the introduction of new species. However, the importance of competition in the structuring of species communities is a matter of controversy in ecology (Diamond, 1975; White, 1978; Connor and Simberloff, 1979; Grant and Abbott, 1980; Lawton and Strong, 1981; Strong, 1983; Strong *et al.*, 1984; White, 1984; Belovsky, 1986; Belovsky and Shade, 1992). Wiens (1977) and Diamond (1978) published articles in total disagreement as to the importance of interspecific competition in nature. Wiens (1977) argued that the importance of interspecific competition as an agent of natural selection may be very minimal, since substantial competition between many species is intermittent, perhaps even rare. Diamond (1978) argued that competition is often a major driving force of natural selection. The role of competition in structuring phytophagous insect communities was challenged severely in the early 1980s. The challenge was first as a result of criticism from the work of Hairston *et al.*, (1960) who argued that predators, parasites, and pathogens were largely responsible for maintaining herbivore densities below competitive levels, rather than competition for resources. He supported his argument by stating that food limitation for herbivores must be rare, since defoliation is a very rare event. The second avenue of criticism stemmed from analyses of phytophagous insect distributions and co-occurrences, which revealed, positive interspecific associations, the failure to find repulsed distributions (Strong, 1981; 1982; Lawton, 1982; Bultman and Faeth, 1985) and the presence of vacant niches and unsaturated communities (Lawton, 1982). However, in the era of these challenges, there were very few experimental field studies of competition in phytophagous insects. Also, the insect studies responsible for both the rejection and acceptance of interspecific competition were mainly observational and pattern, rather than process orientated. In the mid 1980s more experimental investigations of competition between insect herbivores were conducted and these provided sufficient evidence for the existence of competition in herbivorous insects (Faeth, 1987; 1988; Strauss, 1988; Damman, 1993).

In a review of 193 pair-wise interspecific interactions between phytophagous insects, Denno *et al.*, (1995) included experimental demonstrations of competition (McClure, 1980; Karban, 1986; Denno and Roderick, 1992), displacement or exclusion of a species following the introduction of a competitor (Huffaker and Kennett, 1969; Messenger, 1975; McClure, 1989; 1990; 1991; Settle and Wilson, 1990), and mortality or niche shift (Paine *et al.*, 1981; Stiling and Strong, 1984; Akimoto, 1988), as direct evidences of competition. They scored the consequences of competitive interactions as competitive exclusion on the geographic or habitat scale, local displacement from the feeding or oviposition site on a plant, fitness reduction or population change. These could be as a result of overt killing, niche preemption, niche shifting, avoidance, emigration, adverse effects on survival, developmental time, fecundity, body size, and from changes in population size in the presence or absence of a competitor. Of the 193 pair-wise interactions, the consequences were as follows: competitive exclusion (12), local displacement (86) and fitness reduction/population change (95). Out of the 86 cases of displacement, 13 were stemborer species.

The mechanisms of competition include interference (Connell, 1961), exploitation (MacArthur and Levins, 1967) or both. Exploitative competition occurs when individuals, by using resources, deprive others of benefits to be gained from those resources (Schoener, 1983; 1988). Interference competition results when individuals harm one another directly by fighting or killing or indirectly by the aggressive maintenance of territory or the production of chemicals that deter other individuals (Schoener, 1983). In all cases, the deprivation or harm decreases the victims' population size by decreasing their survival, reproduction or both. Some good examples of immediate displacement by aggressive behaviour have been observed among vertebrates, between chipmunk species (Brown, 1971), among voles (Koplin and Hoffman, 1966), and other rodents (Grant, 1972), and between fish species on coral reefs (Sale and Dybdahl, 1978). Interspecies displacement in vertebrates might also be affected by resource depletion. Connell (1961) attributed the displacement of one species of intertidal barnacle by another to interference competition. In phytophagous insects, 57 cases showed exploitative competition while 52 showed interference competition. Exploitative and interference competition were shown in 38 cases (Denno *et al.*, 1995). The local displacements in 13 interactions involving stemborers were attributed to interference competition. Exploitative and interference competition in phytophagous insect species can be mediated through a number of factors, including host plants, natural enemies, physical factors, and intraspecific competition. Some ecological differences between species which may influence the outcome of competitive interactions in natural conditions have been noted (Sturtevant, 1929; Morgan, 1929; Patterson, 1943; Spieth and Hsu, 1950). These include, climatic factors, rate of development, food preferences, fertilization of females a few hours after emergence, differences in courtship pattern and equal insemination of females in both light and dark. Denno *et al.*, (1995) reviewed certain life history traits including fecundity, body size, voltinism, and dispersal ability that may contribute to the competitive success of a species.

The success of *C. partellus* in colonizing new areas, reaching economically important densities and displacing indigenous stem borers, is not well understood.

Several attempts have been made to explain the competitive advantage of *C. partellus* over indigenous stemborers. Delobel (1975b) studied the biologies of *C. partellus* and *C. orichalcociliellus* in Madagascar and concluded that the two species have approximately the same biotic potential. The author was unable to explain the greater abundance of *C. partellus*. Kioko *et al.*, (1995) conducted a comparative laboratory investigation on the developmental periods of *C. partellus* and *C. orichalcociliellus* on an artificial diet. They reported that *C. partellus* completes a generation in less time than *C. orichalcociliellus*. Mbapila (1997) compared the developmental times of *C. partellus* and *C. orichalcociliellus* on maize and found that *C. partellus* completed a generation in less time than *C. orichalcociliellus* at 22 and 28^{0}C. In laboratory life table studies at 22, 25, 28 and 31^{0}C, Mbapila (1997) reported that *C. partellus* had a higher intrinsic rate of increase than *C. orichalcociliellus* at all temperatures except 31^{0}C. The higher rate of population growth was due primarily to the shorter life cycle of *C. partellus*. The findings of Kioko *et al.*, (1995) and Mbapila (1997) suggest that the relatively shorter developmental time of *C. partellus*, resulting in a higher intrinsic rate of increase, may be a factor in the displacement process. Kfir (unpublished data) attributed the competitive success of *C. partellus* over *B. fusca* in some areas of the western highveld region of South Africa to its higher potential rate of increase and its facultative diapause as opposed to the obligatory diapause in *B. fusca*. *Chilo partellus* and *C. orichalcociliellus* occur sympatrically at the Kenya coast. The two species are presumed to be equally vulnerable to the same physical and natural mortality factors. They do encounter each other in their habitat since they have similar ecological niches. Therefore, they may not remain sympatric in time or space. There are many similarities in their biologies, but in order to understand the competitive advantage of *C. partellus*, the differences have to be appraised.

The displacement of one species by another on economically important crops is of major concern both economically and ecologically. Unfortunately, changes in species composition are seldomly noticed, and consequently, there is hardly any documentation on such gradual changes of species composition, and on the mechanisms involved. Only rarely is the displacement of one species by another detected early enough to allow a study of the process and the mechanisms (Brown *et al.*, 1995). Overholt *et al.*, (1994a) provided distributional evidence indicating that a gradual competitive displacement of *C. orichalcociliellus* is occurring at the Kenya coast. This study investigates the interaction between *C. partellus* and *C. orichalcociliellus* at the Kenya coast. It provides some hypotheses on the possible mechanisms involved in the displacement of *C. orichalcociliellus* by *C. partellus*. Comparative laboratory and field investigations were conducted on some ecological and physiological aspects of *C. partellus* and *C. orichalcociliellus*.

1.1 Statement of the problem and justification of the project

Three studies during the past 30 years on the composition of stem borer species in Kenya strongly suggest that an introduced species, *C. partellus*, which was first reported in Africa from Malawi in 1930 (Tams, 1932), and not reported in Kenya until 1960 (Nye,1960), is gradually displacing the indigenous species, *C. orichalcociliellus*, on the Kenya coast. Ecological homologues, however closely related, exhibit some level of differences in their biophysiological attributes which favour one species over the other in any given situation. The effect of such a displacement is unknown. One implication is that the exotic stemborer species may completely displace the indigenous species and result in greater crop damage. Secondly, the displacement might after some time lead to complete extinction of the indigenous stemborer species which is a serious threat to biodiversity. There is very little information on the factors involved in the displacement process. There is a need, therefore, to conduct comparative laboratory and field investigations on *C. partellus* and *C. orichalcociliellus* to determine the factors that may be contributing to the superior competitiveness of *C. partellus* over *C. orichalcociliellus*. An increased knowledge of how indigenous species are displaced may be useful in understanding general declines in biodiversity in the tropics. In addition, understanding these factors may lead to new strategies for managing *C. partellus*, *C. orichalcociliellus* and other stemborer species.

1.2 Hypotheses

C. partellus and *C. orichalcociliellus* occupy the same niches, are equally affected by the same physical and natural mortality factors. The ability of *C. partellus* to competitively displace *C. orichalcociliellus* is believed to be due to intrinsic and extrinsic superiorities of *C. partellus* over *C. orichalcociliellus*. For the purpose of this study, the working hypotheses are as follows:

1. The population of *C. orichalcociliellus* is decreasing on the Kenya coast.
2. The decrease in the population of *C. orichalcociliellus* is due to competition with *C. partellus*.
3. Food consumed by *C. partellus* is more than that of *C. orichalcociliellus*.
4. *C. partellus* and *C. orichalcociliellus* are parasitized differentially by indigenous parasitoids.
5. *C. partellus* and *C. orichalcociliellus* have overlapping niches and both species associate within their niche.
6. There is higher fecundity and egg survival in *C. partellus* than in *C. orichalcociliellus*.
7. *C. partellus* has a greater dispersing capability than *C. orichalcociliellus*.
8. *C. partellus* has a higher colonization success than *C. orichalcociliellus* in cultivated and wild host plants.

9. The developmental time of *C. partellus* is less than *C. orichalcociliellus* in cultivated and wild host plants.
10. The diapause in *C. orichalcociliellus* is more intense than in *C. partellus* and survival of diapausing larvae of *C. partellus* is more than in *C. orichalcociliellus*.

1.3 Objectives

The main objective of this project is to investigate the interaction between *C. orichalcociliellus* and *C. partellus* and identify the mechanisms of displacement of *C. orichalcociliellus* by *C. partellus* at the Kenya Coast. The specific objectives were the following.

1. To estimate the food consumption by *C. partellus* and *C. orichalcociliellus*.
2. To determine the degree of niche overlap and association between *C. partellus* and *C. orichalcociliellus*.
3. To determine parasitism levels of *C. partellus* and *C. orichalcociliellus* by indigenous parasitoids.
4. To compare the fecundity, longevity, egg fertility and hatchability of *C. partellus* and *C. orichalcociliellus*.
5. To estimate the dispersing capabilities of *C. partellus* and *C.*

orichalcociliellus.

6. To determine the colonization successes of *C. partellus* and *C. orichalcociliellus* in cultivated and wild host plants.
7. To compare the developmental times of *C. partellus* and *C. orichalcociliellus* in cultivated and wild host plants.
8. To compare the intensity of diapause and survival of diapausing larvae of *C. partellus* and *C. orichalcociliellus*.

CHAPTER TWO

2.0 Literature Review

2.1 Biology of *C. partellus* and *C. orichalcociliellus*

The biology of *C. partellus* (Khan, 1970; Goncalves, 1970; Mathez, 1972; Girling, 1978; Nur, 1978; Neupane *et al.*, 1985; Berger, 1989a) and *C. orichalcociliellus* (Delobel, 1975b) has been studied in different parts of the world. The general life cycle of *Chilo* spp. is summarized in Fig. 2.1 The adult moths (Plates 2.1 and 2.2) are nocturnal and live for approximately one week (Alghali, 1988; Unnithan and Paye, 1991). In both species oviposition begins on the night of emergence and continues for two nights (Delobel, 1975b; Berger, 1989a). Eggs are deposited in masses (Plate 2.3) on the undersurface of leaf blades (Neupane *et al.*, 1985). The fecundity of the two species is approximately equal with *C. partellus* ovipositing a mean of 434 eggs (Berger, 1989a) and *C. orichalcociliellus* ovipositing a mean of 475 eggs (Delobel, 1975b). The egg developmental period for *C. partellus* is 4 to 5 days at 26-28^{0}C (Berger, 1989a) and 5 to 6 days for *C. orichalcociliellus* at 28^{0}C (Delobel, 1975b). Eggs hatch early in the morning (Delobel, 1975; Chapman *et al.*, 1983b; Neupane *et al.*, 1985). On hatching larvae crawl to the tips of the leaves where they either suspend themselves on fine silken threads and are blown away to infest neighbouring plants (Roome, 1980; Chapman *et al.*, 1983a; Neupane *et al.*, 1985; Ampofo, 1986a; Berger, 1989b; Berger, 1992) or crawl towards the leaf whorls or sheaths depending on the stage of the plant (Neupane *et al.*, 1985). Young larvae feed actively on tender leaves, but bore into the stems as they increase in size. The larval stage lasts for 16 to 41 days at 24-33^{0}C for *C. partellus* on a natural diet (Neupane *et al.*, 1985) and 23 to 36 days for *C. orichalcociliellus* on an artificial diet (Delobel, 1975b). There are 5 to 6 larval moults for *C. partellus* (Neupane *et al.*, 1985) and 5 to 7 for *C. orichalcociliellus* (Delobel, 1975b). When larvae are fully grown (Plate 2.4) they start preparing for pupation by cutting exit holes in the stem to enable the emerging moths to escape. The pupal stage (Plate 2.5) lasts 4 to 8 days for *C. partellus* (Neupane *et al.*, 1985) and 6 to 9 days for *C. orichalcociliellus* (Delobel, 1975b). The life cycle may be continuous where favourable conditions for host plant growth exist throughout the year. However, the cycle is usually interrupted by a cold or dry season, during which host plants are not available or unsuitable for growth and development of the stem borers. The mature larvae then enter diapause inside old stems or stubbles (Scheltes, 1978) and pupate on return of favourable conditions. Diapausing larvae of *C. partellus* and *C. orichalcociliellus* (Plate 2.6) lose their cuticular pigments, cease to feed and become resistant to dessication (Delobel, 1975b; Scheltes, 1978). Diapause is broken with the onset of favourable conditions (Scheltes, 1978). There is large variation in the duration of the larval stage (Mathez, 1972; van Hamburg, 1980) and the period spent in facultative larval diapause (Scheltes, 1978; Kfir, 1991). Consequently, overlapping generations occur (van Hamburg, 1979, 1980).

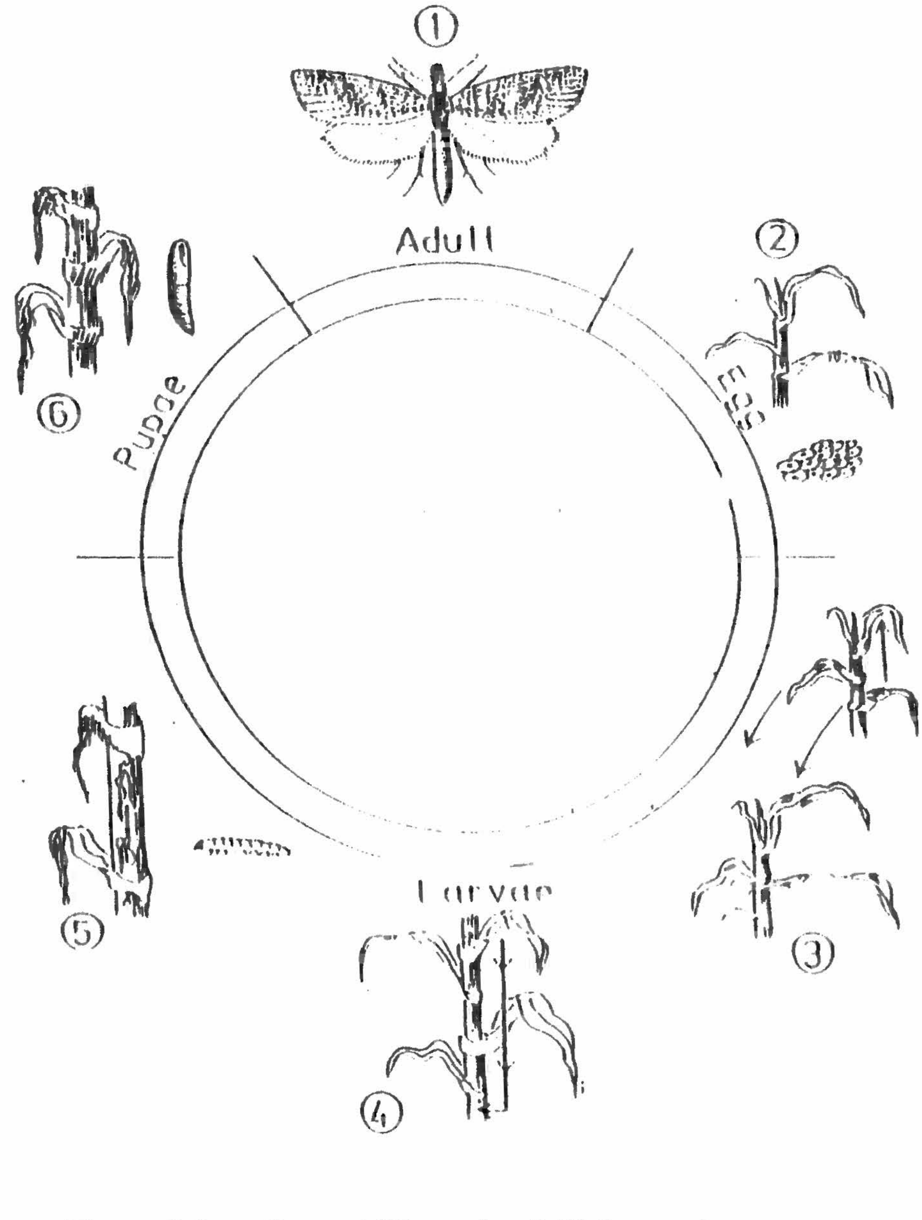

Figure 2.1 General life cycle of *Chilo* species

1. Adult of *Chilo* species 2. Egg batch laid on leaf surface

5. Mature larva found in stem 6. Pupa of *Chilo* species

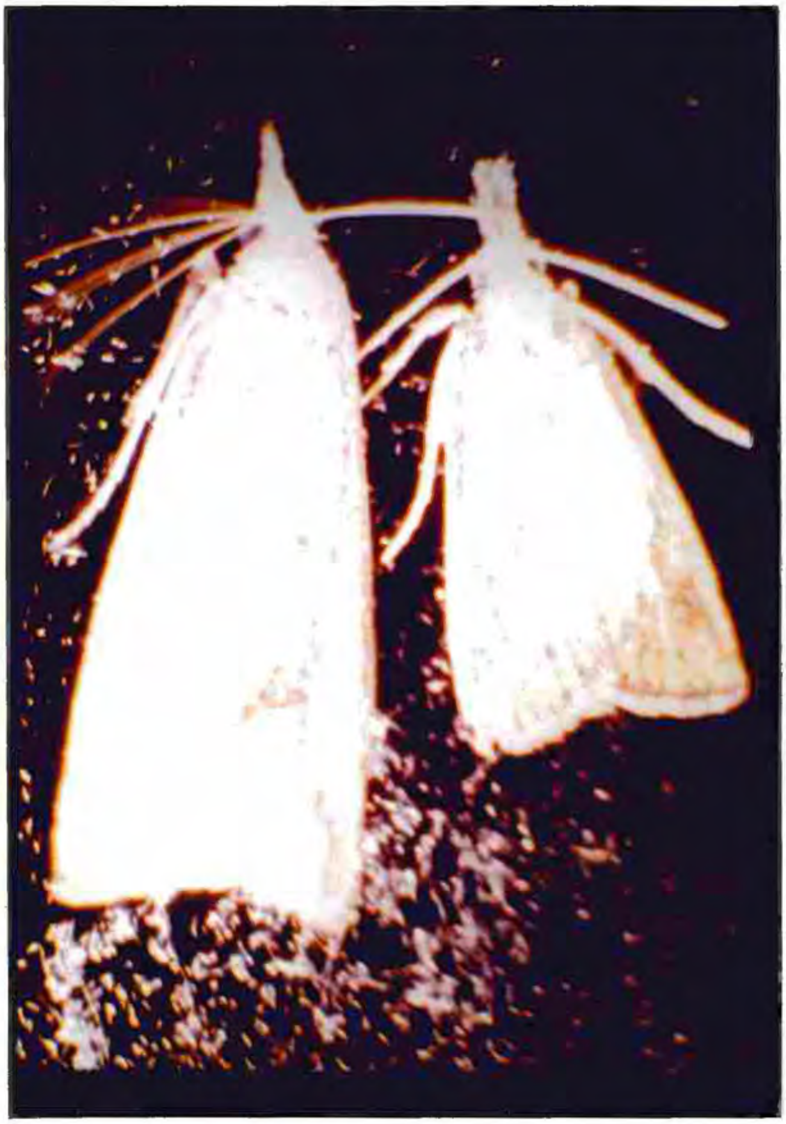

Plate 2.1 Adult male (a) and female (b) of *C. partellus*

Plate 2.2 Adult male (a) and female (b) of *C. orichalcociliellus*

Plate 2.3 Egg batch of *Chilo* species

Plate 2.4 Non diapausing larva of *Chilo partellus*

Plate 2.5 Pupa of *Chilo partellus*

Plate 2.6 Diapausing larva of *Chilo* species

2.2 Distribution and economic importance of *C. partellus* and *C. orichalcociliellus*

The global distribution of *Chilo* species has been reported by many researchers, including, Bleszynski (1970), Hachiya (1979), Gu and Li (1983), Akinsola and Agyen (1984), Tayabi and Azizi (1984), Li (1985), and Chundurwar (1989). The coastal stalk borer, *C. orichalcociliellus*, is indigenous to Africa. It has been recorded from Kenya, Tanzania, Zaire, South Africa, Madagascar, Nigeria and Malawi (Nye, 1960; Bleszynski, 1970; Delobel, 1975a; Medler, 1980). However, Mohyuddin and Greathead (1970) suggest that *C. orichalcociliellus* may have been confused with *C. thyrsis* Bleszynski in some earlier records. There is a suspicion that the reference from Nigeria (Medler, 1980) was confused with *C. aleniellus* (Strand) which is a West African species that is morphologically similar to *C. orichalcociliellus* (Meijerman and Ulenberg, 1996). In Kenya and other African countries, *C. orichalcociliellus* occurs at altitudes below 600 metres (Nye, 1960; Mathez, 1972; Delobel, 1975a) (Fig. 2.2).

The spotted stem borer, *C. partellus* (Bleszynski, 1970), is indigenous to Asia. Its distribution in its aboriginal home includes Afghanistan, Bangladesh, Cambodia, India, Indonesia, Laos, Nepal, Pakistan, Sri lanka, Thailand and Vietnam (Bleszynski, 1970; Neupane *et al.*, 1985; Harris 1990). It was accidentally introduced to Africa earlier this century and was first reported in Malawi in the early 1930s (Tams, 1932). The African distribution of *C. partellus* now includes Malawi (Tams, 1932), Tanzania (Duerdon, 1953), Uganda (Ingram, 1958), Kenya (Nye, 1960), Ethiopia, Mozambique, Sudan, Zambia, Somalia (CAB, 1977) and South Africa (CAB, 1977; Kfir, 1994). Sithole (1989) gave additional records of this pest from Botswana, Swaziland and Zimbabwe. It has also been reported from Burundi, Comoros, Djibouti, Rwanda, Cameroon and Togo (IAPSC, 1985; Harris, 1990; Minja, 1990). However, as with *C. orichalcociliellus,* the West African reports are questionable since *C. partellus* has not been recorded in recent extensive surveys in West Africa (Bosque-Perez and Mareck, 1990; Schulthess *et al.*, 1991; Moyal and Tran, 1989). In most African countries, including Kenya (Fig. 2.2) *C. partellus,* is generally considered to be the most economically important insect pest of maize and sorghum at elevations below 1500 metres (Ingram, 1958; Skoroszewski and van Hamburg, 1987; Greathead, 1990; Seshu Reddy, 1991).

C. partellus and *C. orichalcociliellus* are pests on maize and sorghum in Asia and Africa. They cause serious damage to these crops sometimes leading to total crop failure and consequently tremendous reductions in yield. The yield losses caused by *C. partellus* and *C. orichalcociliellus* to maize and sorghum, the country where the study has been made and references are given in Table 2.1.

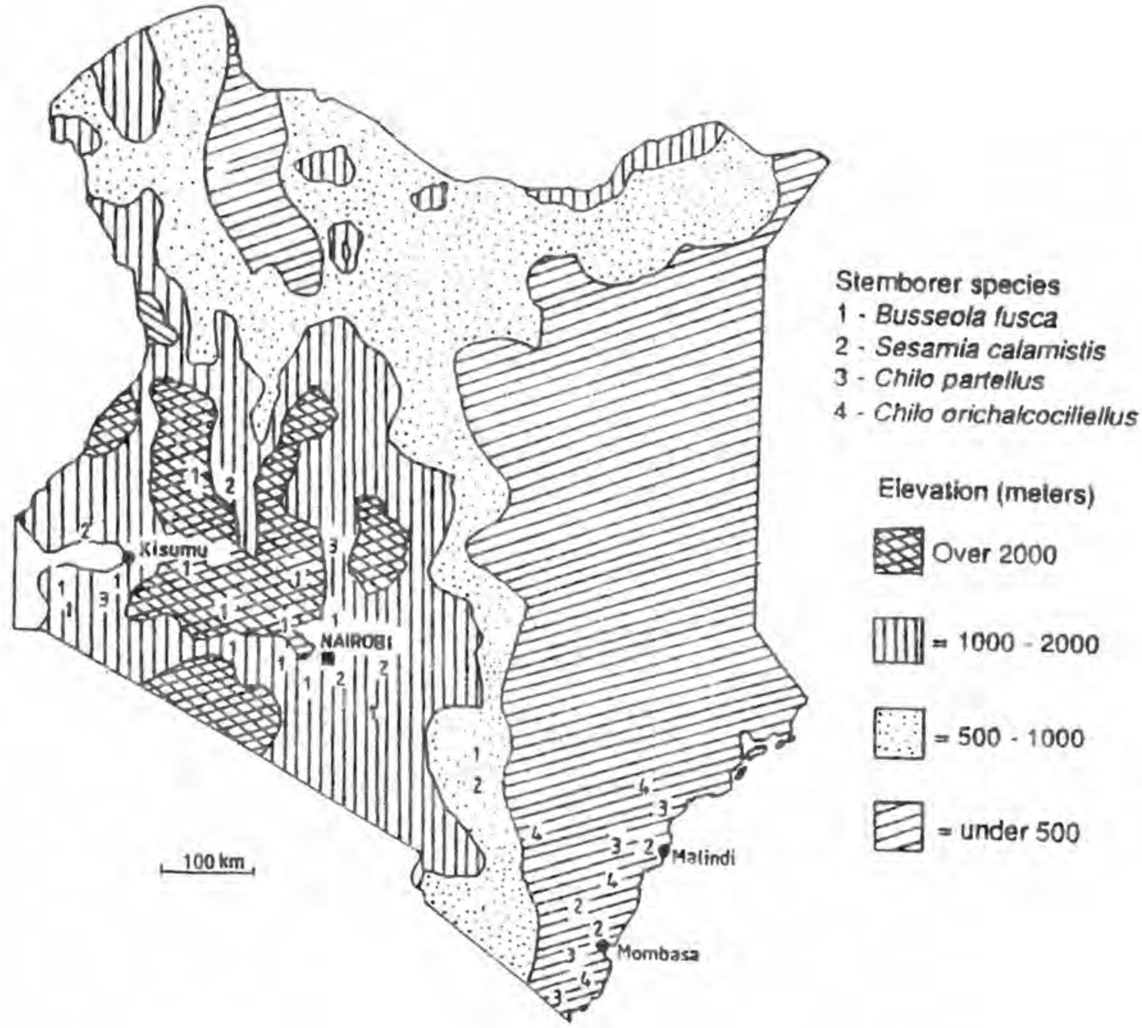

Figure 2.2 Distribution of four major stem borer species in Kenya (Nye, 1960)

Table 2.1 Yield losses caused by *C. partellus* and *C. orichalcociliellus* to crops.

Crop	Species	% losses	Country	References
Maize	*C. partellus*	23-53	Kenya	Wheatley (1961)
		24.3-36.3	India	Chatterji *et al.* (1969)
		37.0	Uganda	Starks (1969)
		11.4	India	Singh *et al.* (1971)
		57-97	India	Sarup *et al.* (1971)
		43.7	Pakistan	Mohyuddin and Attique (1978)
		50.3	India	Sharma and Sharma (1987)
		4, 26, 73	Kenya	Ampofo (1986)
	C. partellus and *C. orichalcociliellus*	20.0	Kenya	Warui and Kuria (1983)
Sorghum	*C. partellus*	2.7-15	India	Pradhan and Prasad (1955)
		56.0	Uganda	Starks (1969)
		55-83 (grain)	India	Jotwani *et al.* (1971)
		57.0 (fodder)	India	Jotwani *et al.* (1971)
		36.5	South Africa	Van Rensburg and van Hamburg (1975)
		13-42	India	Kulkarni and Jotwani (1976)
		20.0	India	Davies and Seshu Reddy (1980)
		80.6	India	Sachan and Rathore (1983)
		56.6-70.8	India	Taneja and Nwanze (1989)
		13.3-86.1	India	Taneja and Nwanze (1989)
		2-88	Kenya	Seshu Reddy (1988)

Information from Seshu Reddy and Walker (1990).

2.3 Control measures for *C. partellus* and *C. orichalcociliellus*

Stem borers, including *Chilo* spp. are difficult to control largely because of the cryptic and nocturnal habits of adult moths and the protection afforded by the stem of the host plant to the larval and pupal stages. Several methods, including chemical control, cultural practices, host plant resistance and biological control have been used or recommended for stem borers management (Mohyuddin and Greathead, 1970; Seshu Reddy, 1983; Unnithan and Seshu Reddy, 1986; Betheder-Matibet, 1989; Seshu Reddy 1990).

Attempts have been made to control young stem borer larvae using insecticidal dusts has been reported (Swaine, 1957; Walker, 1960; Assefa, 1981). However, this method has often proved unsuccessful because firstly, many of the larvae are in the stem and thus, are well protected from the effect of insecticides (Swaine, 1957; Walker, 1960; Assefa, 1981). Secondly, insecticides are expensive and may not be economically feasible on subsistence farms (Swaine, 1957; Walker, 1960). Other drawbacks to chemical control include danger of environmental pollution, the potential of pest resistance, post-control pest resurgence and hazards to the user, non-target/beneficial insects.

Several cultural practices have a profound influence on insects' survival, their persistence in a particular environment and damage to a crop. The effect of various crop management practices on the population of cereal stem borers has been reviewed (Lawani, 1982; Seshu Reddy, 1985; Sharma, 1985; Verma and Singh, 1989). Some cultural practices have been reported to disrupt or slow-down the population build-up of *Chilo* spp. on cereal crops.

Soil tillage may reduce insect populations by burying them so deeply that they cannot emerge, or by bringing them to the surface where they may be exposed to adverse weather factors such as high temperature and low humidity, birds or other natural enemies. Tillage after harvest of the preceding crop and before planting the succeeding crop is known to destroy the stubble, weeds, and alternate hosts which otherwise may habour stem borers (Gahukar and Jotwani, 1980; Lawani, 1982).

Removal or destruction of stubbles, stalks of cereal crops and alternate host plants is highly effective in reducing the carry-over populations of stem borers during winter, dry and noncropping seasons. In Tanzania, nearly complete eradication of *C. partellus* on maize and sorghum was achieved by burning stubbles and residues (Duerden, 1953). Similarly, Ingram (1958) and Nye (1960) advocated the destruction of all crop residues and wild species of sorghum.

Time of planting follows the principle of growing the crop when the pest is not present or planting at such a time that the most susceptible stage of crop development coincides with the time when the pest is less abundant. Warui and Kuria (1983) worked with *C. partellus* and *C. orichalcociliellus* and found that early planted maize had a lower number of borers per plant (0.6 borers per plant) and the number increased with late sowing to nearly 1.6 borers per plant when planting was done eight weeks after the onset of rains. Thus, early planted maize will have passed the susceptible growth stage by the time *C. partellus* and *C. orichalcociliellus* reach high populations in the field. However, adjusting the sowing dates to escape damaging populations of stem borers is of limited use because rainfall is unreliable in most areas and therefore, farmers tend to have varying sowing dates, thus, making it impossible to effect area-wide synchronization of sowing dates.

Spacing may affect the relative rate of development of a plant and its pest population as well as the behaviour of the pest in searching for food or oviposition site (Lawani, 1982). *C. partellus* first instar larvae are known to migrate from hatching site to the funnel of the plant on which they hatched or to other plants within the vicinity (Ampofo, 1986b). During this process as high as 100% mortality occurs (Mathez, 1972). Increasing the spacing between adjacent plants would decrease the chances of the migrating larvae coming in contact with neighbouring plants. Consequently, fewer larvae would survive than if the plants were closely spaced.

Intercropping is the most widespread traditional agricultural system in many areas of Asia, Africa and Central America (Seshu Reddy, 1990). In intercropping, the modification of the crop micro-environment and differences in nutrient uptake by the intercrops are likely to influence plant infestation, development and spread of pests and their natural enemies (Seshu Reddy, 1990). Reports on the reduction of pest populations by increasing the diversity of an agro-ecosystem have been given (Smith, 1970; Solomon, 1973). Intercropping sorghum with cowpea (Omolo and Seshu Reddy, 1985a; Mahadevan and Chelliah, 1986;), lablab bean (Sadakatulla and Mani, 1978; Mahadevan and Chelliah, 1986) and simsim (Kato *et al*., 1982) reduced *C. partellus* damage on sorghum. Similarly, Chand and Sharma (1977) found that growing maize in association with various legumes significantly reduced *C. partellus* damage on maize. Also, Gyawali (1986) reported that intercropping maize with soyabeans gave a 13% reduction in *C. partellus* incidence on maize and a 9.2% increase in grain weight per plant. Amoako *et al*., (1983) reported a significant delay in *C. partellus* colonization and establishment until 42 days after germination on cereals in different cowpea, maize and sorghum intercropping combinations, compared with maize and sorghum monocrops or maize and sorghum dicrop where borer infestation was recorded from 14 days after germination. At the International Centre of Insect Physiology and Ecology (ICIPE), encouraging results have been obtained in studies assessing the effect of intercropping on *Chilo* spp. population levels (Minja, 1990). Minja (1990) showed that planting sorghum and cowpea simultaneously or planting sorghum 2 weeks after cowpea, significantly delayed *C. partellus* larval population build-up compared with that under monocrop sorghum. These results demonstrate the potentiality of intercropping host and nonhost crops as a cultural method of controlling *Chilo* spp. Notwithstanding the many cases of the success of intercropping in pest management, there are cases where intercropping has proved unsuccessful. For example, Minja (1990) reported no difference in *C. partellus* larval population between an intercrop of sorghum sown 2 weeks before cowpea and a sorghum monocrop. Intercropping maize and sorghum is a common practice in farmers' fields in many parts of eastern Africa and Ogwaro (1983) observed that intercropping the two cereals resulted in a higher borer infestation than in monocrops. Southwood and Way (1970) cautioned that the right kind of crop combinations have to be selected for intercropping to be successful in any given situation. Also, Omolo and Seshu Reddy (1985b) observed that results of intercropping may vary depending on the crop combination, location, season and cropping pattern.

The use of resistant and tolerant crop cultivars forms one of the important management methods for stem borers (Brader, 1979; Minja, 1990; Saxena *et al*., 1992). Maize cultivars with varying levels of resistance to *C. partellus* have been identified by different workers (Chatterji *et al*., 1971; Sarup *et al*., 1978; Ampofo *et al*., 1986; Kumar, 1988a). Sorghum varieties resistant to *C. partellus* were reported by Starks and Dogget (1970) and Gebrekidan (1981). Omolo (1983) and Omolo and Sesshu Reddy (1985a) identified sources of stem borer resistance from local and exotic maize lines which offered a wide scope in multiple resistance to stem borers. Ampofo *et al.*, (1986) further evaluated these lines against *C. partellus* oviposition and establishment and concluded that some of them formed a good source of material for selection for resistance to *C. partellus*. Research at ICIPE has concentrated on the screening of maize and sorghum lines, out of which some have shown good levels of resistance/tolerance to stem borer attack (Dabrowski and Kidiavai, 1983; Omolo, 1983; Seshu Reddy, 1983c; 1985a; Ampofo *et al.*, 1986). Dabrowski and Kidiavai (1983) found 100 promising sorghum lines showing six levels of relationship affecting *C. partellus* plant colonization and damage. Seshu Reddy (1983c; 1985a) evaluated these lines further and selected 20 that may act as multiple sources of resistance to the stem borer complex of eastern Africa. However, the long term advantages of resistant cultivars in suppressing insect pests have been threatened by the emergence of insect biotypes (Painter, 1951, 1958; Sogawa, 1982). Secondly, agronomically acceptable varieties with adequate levels of stem borer resistance are not yet available (Leuschner *et al.*, 1985; Nwanze and Youm, 1994).

Biological control of cereal stem borers using parasitoids, predators, and pathogens, has been attempted in different parts of the world with some success (Betbeder-Matibet, 1971; Betbeder-Matibet, 1989). In different parts of eastern Africa, naturally occurring biocontrol agents have been reported for different growth stages of stem borers. Mathez (1972) reported that up to 90% of borer eggs could be killed by *Trichogramma* spp., while larval and pupal mortality was usually below 10% and was mainly due to unidentified bacteria, fungi and virus diseases on the larvae and *P. furvus* parasitism on the pupae. *Cotesia sesamiae* (Cam.) and *Psilochalsis sudanensis* Stef. were reported to parasitize *C. partellus* larvae and pupae, respectively (Ingram, 1958), while *Pheidole* spp. and other formicids were reported to prey on stem borer eggs (Mohyuddin and Greathead, 1970). *Dentichasmias busseolae* Heinr. also parasitized *C. partellus* pupae (Mohyuddin 1972).

Augmentation biological control using pathogens has also been reported. At ICIPE, the potential use of the microsporidian protozoan, *Nosema* spp. has been demonstrated. An 80% increase in yield was reported when field plots infested with *C. partellus* were treated with this protozoan (Odindo, 1991). In glass house experiments, yields of sorghum protected with a spray of a local isolate of *Bacillus thuringiensis* Beliner were five to seven times higher than those of unprotected sorghum (Brownbridge, 1991). In laboratory experiments, eggs of *C. partellus* were reported to be susceptible to some ICIPE isolates of *Beauveria bassiana* Vuillemin, *Metarhizium anisopliae* Sorokin and *Paecilomyces fumosoroseus* Brown and Smith (Maniania, 1991).

Classical biological control utilizes exotic natural enemies to suppress exotic pest populations (Debach and Rosen, 1991). This method is generally accepted as the first choice to combat exotic pests in many countries (Betbeder-

Matibet and Malinge, 1968; Appert *et al.*, 1969; Greathead, 1971; Bordat, 1983; Betbeder-Matibet, 1989; Kfir, 1994; Overholt, 1994b). A classical biological control attempt against *C. partellus* using a larval parasitoid, introduced from Pakistan, *Cotesia flavipes* Cameron, was initiated on the Kenya Coast in 1991. Successful establishment of *C. flavipes* has been achieved at the coastal and other parts of Kenya (Overholt *et al.*, 1997).

2.4 Host plants of *C. partellus* and *C. orichalcociliellus*

Larvae of stem borers, including *C. partellus* and *C. orichalcociliellus,* feed on communities of wild and cultivated grasses whose stems are large enough to accommodate stem borer feeding tunnels (Harris, 1990). In addition to grasses, sedges (Cyperaceae) and cat-tails (Typhaceae) are important wild hosts for some stem borers (Jepson, 1954; Seshu Reddy, 1989; Conlong, 1990). Prior to the introduction of maize into Africa (Purseglove, 1972), native grasses, sedges, and cat-tails were presumably the aboriginal host plants for the indigenous stem borers in Africa. However, stem borer densities in wild grasses are far lower than levels observed in cultivated crops (Mathez, 1972). *C. partellus* is an important pest of maize, sorghum and pearl millet in Asia and Africa. It also attacks wheat, sugar cane, rice, foxtail, finger millets (Harris, 1990) and various grasses, including several species of wild sorghum, *Sorghum* *halepense* (L) Pers., *S. verticilliflorum*, *S. arundinaceum* (Desv.) Stapf, napier grass, *Pennisetum purpureum* L. and guinea grass, *Panicum maximum* (Jacq). Hill (1983) listed the host range of *C. orichalcociliellus* to include maize, sorghum, finger millet, and sugar cane as the main crop hosts and various grasses, including *Panicum*, *Pennisetum* and *Sorghum* species as alternative hosts. At ICIPE, several species of wild grasses listed in Table 2.2 have been identified as hosts of both *C. partellus* and *C. orichalcociliellus* (Khan *et al.*, 1997).

Table 2.2 Wild hosts of cereal stem borers recorded from various parts of Kenya

Plant species		Stem borer species				
Family	Species	CL	BF	SC	ES	UN
Poaceae	*Andropogon gayanus*	-	-	++	-	-
	Cenchrus ciliaris	++	-	++	-	-
	Coix lacryma-jobi	++	-	++	-	-
	Dactylocterium bogdanii	++	-	-	-	-
	Echinochloa pyrmidalis	++	++	++	-	++
	Hyparrhenia cymbaria	-	++	-	-	-
	Hyparrhenia filipendula	++	-	++	-	-
	Hyparrhenia pilgerana	++	++	-	-	-
	Hyparrhenia rufa	++	++	++	-	-
	Panicum deustum	++	++	-	-	-
	Panicum maximum	++	++	++	++	++
	Pennisetum macrourum	-	-	-	-	++
	Pennisetum procerum	-	-	-	-	++
	Pennisetum purpureum	++	++	++	++	++
	Pennisetum trachyphillum	++	++	-	-	-
	Phragmites sp.	++	-	++	++	++
	Rottboellia cochinchinensis	++	++	-	++	-
	Setaria incrassata	++	++	-	-	-
	Setaria sphacelata	-	++	++	-	-
	Sorghum arundinaceum	++	++	++	++	-
	Sorghum versicolor	++	++	++	++	-
	Sporobolus pyramidalis	-	++	-	-	-
	Tripsacum laxum	-	++	++	-	-
	Vossia spp.	-	-	++	-	-
Cyperaceae	*Cyperus immensis*	-	-	++	++	++
	Cyperus maculatus	-	-	-	++	++
	Cyperus papyrus	-	-	++	++	++
Typhaceae	*Typha domingensis*	-	++	++	-	-

Information from Khan (1997)

++, recorded as a host -, not recorded as a host

CL, *Chilo* species BF, *Busseola fusca* SC, *Sesamia calamistis*

ES, *Eldana saccharina* UN, Unidentified borer species.

2.5 The concept of competitive displacement.

All organisms have certain habitable zones delimited by physical parameters beyond which they cannot persist for long. Within these zones, populations of all long established species exhibit an average density which fluctuates within limits. A very large proportion of population studies have been concerned with the mechanisms which regulate relative abundance of a species within the habitable or tolerable zones, but little emphasis has been placed on the important fact that some species do not occur within zones or habitats which are perfectly suitable for them as far as physical conditions are concerned, even though they may reach these habitats from time to time in suitable numbers. Sometimes species have become extinct in such habitats and sometimes they are unable to invade successfully from adjacent habitats. The reasons for their absence must involve some sort of interaction between species because the physical environment is suitable. Thus, absence of a species from a habitat may be due to unsuitability of physical factors, lack of physical or biological requisites, geographical isolation or interspecific interactions (Debach, 1966).

Competitive displacement between ecological homologues is a unique and special type of interaction between species where one species brings about the extirpation or displacement of another ecologically homologous species, or prevents a second such species from successfully colonizing all or a part of its habitat. Obviously, this would limit the range of distribution of certain species. Strictly, one species wins and the other dies out. There is no neutral balance for the loser in a classical case. However, in nature, various degrees of coexistence or displacement are observed (Debach, 1966). Cases involving insects will be emphasized in this review, but reference to other organisms will be made whenever necessary.

2.6 Competitive displacement principle and definitions.

2.6.1 Principle

Hutchinson and Deevey (1949) referred to the competitive exclusion principle as perhaps the most important theoretical development in general ecology and is one of the chief foundations in modern ecology. The competitive displacement principle may be defined as follows: different species having identical ecological niches cannot coexist for long in the same habitat (Debach and Sundby, 1963). The principle includes the implicit understanding that all species differ biologically no matter how closely related they are or however similar they may be in habits (Hardin 1960). Even though they may be ecological homologues, their inherent biophysiological differences will favour one species over the other in a particular situation.

2.6.2 Definitions.

The definitions of the following terms are as given in Debach and Sundby (1963), Debach (1966) and Debach *et al.* (1978).

Habitat- the environment of a species natural population unit. The essential physical and biotic factors in a locality where individuals of that population normally live and reproduce.

Role- is what an animal does to obtain its particular requisites for survival and reproduction in a particular habitat.

Ecological niche- the role played by an animal based on its precise food, spatial and habitudinal requirements in a particular habitat. Ecological niche, which has to do with function, should therefore not be confused with the spatial niche of an animal, which has to do with location.

Ecological homologues- two different species having identical ecological niches.

Coexist- live together in an identical habitat. This means habitation of identical ranges.

Competition- the attempted or actual utilization of common resources or requisites by two organisms involves competition even if one does not directly harm the other in the process. Cole (1960) defined competition as that which eliminates one of two sympatric species occupying the same niche.

Competitive displacement- the elimination, in a given habitat, of one species by another species where one has the identical ecological niche of the other.

Effective progeny production (R)- the number of female progeny produced per parental female which are themselves capable of producing progeny, thus excluding males and sterile females.

2.7 The importance of competitive displacement.

Competitive displacement may be rather uncommon. This is because most species do not have ecological homologues. Most cases of competitive displacement are rarely observed by man. Thus, the occurrence of competitive displacement between ecological homologues, although not common, is undoubtedly thought to be more rare in nature and of less significance than it actually is. Competitive displacement is of much importance in explaining the failure of a species establishing in areas where the climate should be ideal for it and where it has colonized in large numbers in many sites with abundant food (hosts) present. It would be difficult explaining the distribution of species based on presumed effects from meteorological factors alone. Each species can exist throughout an area alone. However, different species can be found with more or less distinct areas of distribution and with little or no evidence of competition between them except where they overlap. Having missed the process of competitive displacement, it would be difficult to correctly explain the current distribution of the different species. Competitive displacement is an important part in the evolutionary processes of adaptation and speciation. Just as there are expressed differences in environmentally modified R values (effective progeny production) between ecological homologues, there is expressed genetic variability within specific populations. The hypothesis is of considerable importance in biological control work where multiple species of natural enemies are frequently introduced in attempts to obtain efficient regulation of insect pest populations. In cases where more than one species of natural enemy is known to attack precisely the same host stage, one would suspect them to be ecological homologues and not to be able to coexist in the same habitat if their ranges completely or nearly completely overlap. In a classical biological control attempt, if one species is already established on a given host, the imported species should either displace the previously established one or itself be excluded. If it displaces the originally established species, it is an indication that it probably leaves more progeny. This should result in better population regulation of the host.

2.8 The basic mechanism of competitive displacement

Competitive displacement between ecological homologues has been reported in the laboratory and field (Gause, 1934; Lack, 1944; Crombie, 1945; Park, 1954; Andrewartha and Birch, 1954; Elton and Miller, 1954; Elton, 1958; Darwin, 1959; Connell, 1961; Debach and Sundby, 1963; Debach, 1966; Debach *et al*., 1978). The ultimate winner in any case of competition between ecological homologues is one which leaves the most female progeny (R) that survive to reproductive stage. Hardin (1959) noted that no matter how small the difference may be, in the efficiency of competing species to produce offsprings, one species will eventually displace the other. Many factors aside from the intrinsic fecundity of a species will influence the production of progeny and their survival to reproductive adulthood. Such factors as active interference between species, cannibalism, disease, predation, parasitism, genetic drift or changes in physical conditions may complicate the process of competitive displacement by affecting the progeny production of one species relative to the other (Debach, 1966). Obviously, environmental factors do not have equal effect on the R of both populations, and the relative effect may differ in different habitats. One species may, therefore, have greater R in one habitat, and the other species a greater R in a different habitat. Thus, the species with the greatest R value after moderation by environmental conditions, will gain a larger proportion of each successive generation and thus, will increase at the expense of the competing species, regardless of the relative abundance or scarcity of food and space. However, none of these processes alone or in combination would result in competitive displacement except through their modifying influence on progeny production. The displacement is dependent on the relative differential between the Rs of the two species. Actual cases of competitive displacement, particularly in the laboratory, have far fewer than 100 generations before complete displacement takes place. However, in cases where ecological homologues have similar R rates, the time required could be very lengthy (Debach, 1966).

2.9 Cases and mechanisms involved in competitive displacement between species.

Cases of actual or apparent competitive displacement have been reported between ecological homologues. However, most of the cases of competitive displacement in nature are based upon circumstantial, distributional evidence, and only a few, including that of Connell (1961) have been derived from extensive experimental work in the field and describe mechanisms by which exclusion is effected. Many of the observed cases of competitive exclusion in nature occur between species of highly mobile vertebrates where the mechanisms of exclusion must be very different. Debach (1965; 1966) discussed competitive displacement of ecological homologues and implicated temperature, humidity, natural enemies, disease, type or condition of the food source among other factors to account for displacement. He noted that displacement could occur in the presence of surplus food.

2.9.1 Previous laboratory studies.

A large proportion of studies on competitive displacement between ecologically homologous insects have been carried out in the laboratory with species of *Tribolium*, *Rhizopertha*, *Calandra*, *Sitotroga*, *Latheticus*, *Oryzaephilus*, or *Callosobruchus* inhabiting grains or flour or with *Drosophila* species. Few studies have involved insect parasitoids. Gause (1934) was the first to focus the attention of ecologists on the competitive displacement hypothesis. He studied mixed populations of two species of protozoans, *Paramecium caudatum* Ehrenberg and *P. aurelia* Ehrenberg. He concluded that in competition for food in a uniform habitat one species will always replace the other, but the winner may be different in different conditions. He stated the hypothesis of competitive displacement or its converse as follows: "As a result of competition, two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain peculiar kinds of food and modes of life in which it has an advantage over its competitor". However, both species survive indefinitely only when they occupy different niches in the microcosm in which they have an advantage over their competitors. Following Gause's work, contributions were made by Park (1948; 1954; 1955a, b and 1957). His work was primarily with the flour beetles, *Tribolium confusum* Daval and *T. castaneum* (Herbst), competing for the same food in the same habitat. Park found that one species always displaces the other. The winner, however, was not always the same species but depended on such characteristics of the habitat as temperature and natural enemies. Crombie (1945; 1946) studied competition between different species of graminivorous insects in the same habitat and found that when specific pairs of individuals of different species competed, *Rhizopertha* sp. eliminated *Sitotroga* sp. because their larvae had the same needs and habits. Utida (1953) reported that when two species of the genus *Callosobruchus* competed in the same laboratory universe, *C. quadrimaculatus* (Fab.) completely eliminated *C. chinensis* (L.) by the fifth generation. Polnik (1960) worked with *T. confusum* and *Latheticus oryzae* Watech. He obtained the same types of results and made a general statement that laboratory experiments have shown that the end result of such interspecies competition is extinction for all but one species which becomes established.

The elimination of one parasitoid by another under laboratory conditions has been demonstrated. The female of *Aphytis lingnanensis* Compere mutilated the pre pupae and pupae of *Encarsia lounsburyi* (Berlese and Paoli) (Flanders, 1951). Similarly, in laboratory culture with black scale as host, *Cocophagus pulvinariae* Compere displaced *C. cowperei* Girault. However, in the field both were able to co-exist because the host preferences of the females were not exactly the same (Compere, 1940). In laboratory studies, whenever any two of three species (*Aphytis fisheri* Debach, *A. melinus* (Debach) and *A. lingnanensis* were cultured together, one species was eventually eliminated. The species surviving was influenced by the temperature and humidity regimes of the particular experiment. Even in the abundance of hosts *A. lingnanensis* eliminated *A. fisheri* after 9 generations.

2.9.2 Previous field studies.

Field studies or observations on competitive displacement between ecological homologues were viewed in two basic ways (Debach, 1966). One involves the process in action; the other, the result after its completion. The first type, competitive displacement proper, occurs when an ecological homologue of an already established species, accidentally or through purposeful action of man, invades the habitat of an established species and eliminates it from all or part of the habitat. The second type of competitive displacement involves established populations in stable equilibrium. Such cases have been termed by Elton (1958) "mutually exclusive distribution" and by Miller (1964) "contiguous allopatry" and usually involve closely related allopatric species. In most cases, the distribution of the two species is completely separate except for a narrow band of overlap. Various authors have cited examples of an invading species displacing another, often closely related species in the field. Clark (1931) reported the disappearance in North America of the native cabbage butterflies, *Pieris oleracea* Harris and *P. protodice* Boisduval and LeConte, following the accidental introduction of the European cabbage butterfly, *P. rapae* (Linnaeus), into North America. Andrewartha and Birch (1954) reported the replacement of the Mediterranean fruit fly, *Ceratitis capitata* (Weidemann), around Sydney, Australia by the Queensland fruit fly, *Dacus tryoni* (Froggatt), which invaded from the north. In Hawaii a similar phenomenon occurred when the invading Oriental fruit fly, *Dacus dorsalis* Hendel, largely displaced the established *C. capitata* from littoral areas and *C. capitata* is now restricted almost entirely to cool climates at higher elevations (Christenson and Foote, 1960). Elton (1958) reported the case of two species of wheat stem sawflies, both of which developed in the wheat stem and invaded the northeastern United States in the 1880's. In eastern Pennsylvania, the European wheat stem sawfly gradually displaced the invading black grain stem sawfly. Today they have adjacent ranges with only a narrow band of overlap. The California red scale, *Aonidiella aurantii* (Mask.) has completely replaced the yellow scale, *A. citrina* (Coquillett), in the presence of abundant food in all areas where they occurred together for many years in southern California (Debach *et al*., 1978). Blakley and Dingle (1978) reported the exclusion of seed-feeding milkweed bugs, *Oncopeltus spp*., from the island of Barbados by monarch butterflies, *Danaus plexippus*.

Competitive displacement of native and introduced parasitoids of pests has been reported. Flanders (1966) discussed species replacement among parasitic hymenoptera and provided several examples of an introduced parasitoid of a pest displacing another parasitoid, but he did not cite any examples of displacement of native parasitoids of pests. On the other hand, Bennett (1993) noted that several native or previously introduced parasitoids of exotic pest species have become scarce or have disappeared completely following the introduction of more natural enemies. He reviewed cases where an introduced parasitoid eliminated its host, where at least partial displacement of a native parasitoid of a native host by an introduced parasitoid occurred, and where introduced parasitoids were displaced by subsequent introductions. Howarth (1991), while reviewing the negative impacts of classical biological control, cited examples where extinction of the non target as well as the target species have been reported. Subsequent to the introduction of the tachinid, *Trichopoda pilipes* (F.) and the scelionid, *Trissolcus basalis* (Wollaston) in 1962 for the control of the immigrant southern green stink bug, *Nezara viridula* (L.) another immigrant pentatomid, *Murgantia histrionica* (Hahn), as well as its deliberately introduced parasitoid, *Trissolcus murgantiae* (Ashmead), became extinct in Hawaii. Additionally the disappearance of at least 15 species of the larger native moths of Hawaii was attributed to the direct or indirect impact of biological control introductions (Howarth, 1991).

Competitive suppression of native parasitoids by introduced parasitoids have been reported. In Isreal, the introduction of the parasitoid, *Clausenia purpurea* Ishii, against the mealybug, *Pseudococcus citriculus* Green, resulted in a gradual disappearance of the previously established parasitoids, *Leptomastix flavus* Mercet and *Anagyrus bivuensis* Compere (Rivany, 1964). Selhime *et al.* (1969) reported that the introduced *Aphytis holoxanthus* Debach, a parasitoid of the Florida red scale, *Chrysomphalus aonidum* L., completely displaced *Pseudhomalopoda prima* Girault which used to be the main control agent of the Florida red scale. However, *P. prima* is still the most important parasitoid on at least one of its native hosts. In Brazil, *C. flavipes* is now the dominant parasitoid on *Diatraea saccharalis* (F.), while the native tachinid parasitoids, *Metagonistylum minense* Townsend and *Paratheresia claripalpis* Walp, have become scarce (Botelho, 1992).

Displacement of introduced parasitoids subsequent to the introduction of other parasitoids has been reported. In Florida, *Anagyrus antoninae* Timberlake, which initially established readily and showed promise as an efficient control agent for the Rhodesgrass mealybug, *Antonina graminis* (Maskell), was completely displaced by *Neodusmetia sangwani* (Subbo Rao), another encytid parasitoid of the Rhodesgrass mealybug introduced into Florida from Texas (Bennett, 1993). Bennett (1993) reported that another encytid, *Pseudectroma* sp., might also have been a contributory factor to the disappearance of *A. antoninae*. Schuster and Dean (1976) reported the competitive displacement of

A. antoninae by *N. sangwani* in Texas and suggested that the lack of competitiveness of *A. antoninae* was as a result of its inability to develop at high vapour deficits and at high seasonal temperatures prevailing during the summer months. The introduced parasitoids of oriental fruitfly, *D. dorsalis*, showed displacements in Hawaii. Three of several braconid parasitoids introduced in succession became established. Initially, *Biosteres longicaudatus* (Ashmead) became widely established, but eventually *B. vandenboschi* Fullaway and finally *B. arisanus* (Sonan) became dominant to the extent that the other two species have been relegated to the status of rare species in some of the islands (van den Bosch *et al.*, 1982). *B. arisanus* accounts for 74 to 92% of all parasitoids reared from *D. dorsalis* and *C. capitata* in both tropical and temperate zones in Hawaii (Ramadan *et al.*, 1992). Perhaps the most conclusive evidence for competitive displacement and likelihood of extinction over large areas is the extensive studies on *Aphytis* spp. by Debach and Sundby (1963). *Aphytis chrysomphali* was eliminated from nearly all of its range in southern California within 10 years of the introduction of *A. lingnanensis* which in turn was displaced over much of its range within 4 years by *A. melinus* from India. However, *A. lingnanensis* precluded the establishment of *A. melinus* in the milder climatic areas of San Diego County. In some areas, host scarcity was not a limiting factor.

There are reports of competitive displacement between stem borer species. For example, *C. partellus*, first recorded in Madagascar in 1972 was considered to be the most damaging stem borer on maize and sorghum by 1975, being more important than the indigenous *C. orichalcociliellus* (Delobel, 1975a). Yearly sampling of stem borer populations in the western Transvaal highveld area of South Africa, since 1985 indicated that *C. partellus* populations have continuously increased to a point that it is the dominant stem borer, surpassing the populations of *B. fusca* which formerly was the only stem borer found in the area (Kfir, unpublished data).

CHAPTER THREE

3.0 Food consumption by *C. partellus* and *C. orichalcociliellus.*

3.1 Introduction

Most stem borers of maize and sorghum, including *C. partellus* and *C. orichalcociliellus*, are generally polyphagous attacking several graminaecous crops and other wild hosts in addition to more than one cultivated crop. Adult females of *C. partellus* and *C. orichalcociliellus* oviposit on the lower leaves of host plants, but the newly emerged larvae climb up to the leaf whorl where they settle and initiate feeding. From the third instar, larvae move from the folded leaves to attack stems of the host plant. These stem borers may attack at different phenological stages of the crop. Consequently, serious crop and yield losses resulting from leaf, stem and ear damage caused by the larvae have been reported.

Prior to the invasion of *C. partellus* into Kenya in the early 1960s, *C. orichalcociliellus* was considered to be of importance to cereal crops (Mathez, 1972; Warui and Kuria, 1983). However, since the invasion of *C. partellus*, this species has successfully established and has become the most abundant and economically important stem borer species in Kenya. Three studies over the past

30 years (Mathez, 1972; Warui and Kuria, 1983; Overholt *et al.*, 1994a) have shown that in absolute numbers, *C. orichalcociliellus* densities appear to be decreasing over time at the Kenya Coast, while total stem borer numbers have remained more or less constant. Although total stem borer densities may not have changed dramatically since the introduction of *C. partellus*, the displacement of the indigenous *C. orichalcociliellus* by *C. partellus* may have influenced crop damage. Much of the information on feeding responses and habits of these stem borers have been concentrated on *C. partellus* (Alghali and Saxena, 1988; Torto *et al.*, 1990; Torto and Saxena, 1991; Torto *et al.*, 1991). With the exception of the report by Warui and Kuria (1983), on the loss of maize caused by both *C. partellus* and *C. orichalcociliellus*, there are no other reports on the feeding habits and amount of damage caused by *C. orichalcociliellus* to cereal crops. In this study, the quantities of maize and sorghum stems consumed by larvae of *C. partellus* and *C. orichalcociliellus* on a daily basis and throughout the larval lifetime are reported.

3.2 Materials and Methods

First instar larvae of *C. partellus* and *C. orichalcociliellus* were fed individually on tender stems of maize and sorghum seedlings. From the third instar until pupation, larvae were fed with pieces of fresh maize and sorghum stems. The pieces of stems were washed in a 2% solution of commercially available bleach (0.05% sodium hypochlorite) to kill any microbial contaminant originating from the field and then dried. A preweighed piece of stem was offered to a larva in a glass vial (7.5 by 2.5 cm) plugged with cotton wool. Larvae were allowed to feed for 4 days before replacing old stems with fresh ones. The injured stem was weighed after the frass was carefully removed. Control pieces of stems were kept in separate vials alongside the experimental stems to determine the weight loss from evaporation. The difference between the initial and final weights of stem after adjustment for weight loss from evaporation indicated stem feeding by the larvae. The number of days taken for each larva to reach the pupal stage was recorded. Larvae which died or escaped before pupation were not included in the analysis. Experiments were conducted at 28°C. Data were subjected to an analysis of variance (ANOVA) to detect any differences in the mean quantities of maize and sorghum consumed by *C. partellus* and *C. orichalcociliellus* on a daily basis and in a larval lifetime. Differences in the quantity of maize and sorghum consumed by *C. partellus* and *C. orichalcociliellus* in a four-day interval was detected using a t-test.

3.3 Results

Larvae of *C. partellus* consumed significantly more maize stem tissue between the first and the fifth instars than *C. orichalcociliellus* (Figure 3.1). However, *C. partellus* larvae of later instars consumed less maize tissue (Figure 3.1). The maize consumed by *C. partellus* on a daily basis was higher, being 0.18±0.10grams while, *C. orichalcociliellus* consumed 0.11±0.04grams (Figure 3.3). In maize, the developmental time for *C. partellus* (26.7±7.70 days) was shorter than that of *C. orichalcociliellus* (29.9±13.10 days) (Figure 3.4). In this shorter developmental time, *C. partellus* consumed more maize stem than *C. orichalcociliellus* (Figure 3.5).

Larvae of *C. partellus* fed more on sorghum than *C. orichalcociliellus* in a four-day interval (Figure 3.2). Feeding of both stem borer species was reduced towards the end of the larval instars being about equal for the two species. As in maize, *C. partellus* consumed more sorghum than *C. orichalcociliellus* on a daily basis (Figure 3.3). Although *C. partellus* had a shorter developmental time than *C. orichalcociliellus* in sorghum (Figure 3.4), this species still consumed equal amounts of sorghum as *C. orichalcociliellus* in a larval lifetime (Figure 3.5)

Comparisons of the quantities of maize and sorghum stems consumed by each stem borer species revealed that *C. partellus* consumed more maize than sorghum both on a daily basis (F = 42.96; Df = 1, 138; P = 0.0001) and throughout the larval lifetime (F = 11.83; Df = 1, 138; P = 0.0008). *C. orichalcociliellus* also consumed more maize than sorghum on a daily basis (F = 34.69; Df = 1, 119; P = 0.0001), but the quantities of maize and sorghum consumed by *C. orichalcociliellus* in a larval lifetime were not different (F = 1.19; Df = 1, 119; P = 0.2775).

3.4 Discussion

The present study and the studies on the larval developmental times of *C. partellus* and *C. orichalcociliellus* on an artificial diet (Kioko *et al*., 1995), maize (Mbapila,1997), and on maize, sorghum and wild sorghum (Chapter 9) all showed that *C. partellus* completed larval development in less time than *C. orichalcociliellus*. In its shorter developmental time, *C. partellus* larvae consumed more maize than *C. orichalcociliellus* on a daily basis and throughout the larval lifetime. This suggests that *C. partellus* may be causing more injury to maize than *C. orichalcociliellus*, although *C. orichalcociliellus,* having a longer larval lifetime, will continue feeding even after *C. partellus* has stopped feeding and pupated. *C. partellus* consumed more sorghum than *C. orichalcociliellus* on a daily basis but, both species consumed the same amount of sorghum in their larval lifetime. The above results suggest that *C. partellus*, an introduced species into Africa, may be a more voracious feeder compared to *C. orichalcociliellus*.

Yield losses of cereals resulting from stem and whorl damage caused by lepidopterous stem borers have been reported by Sampson (1982), Sampson and Kumar (1985), Seshu Reddy and Walker (1990), van den Berg and van Rensburg

(1991) and Kumar (1992). One implication of the invasion and spread of *C. partellus* in Kenya is that it may be causing greater damage to crops than native stem borers with which it is often found in mixed populations.

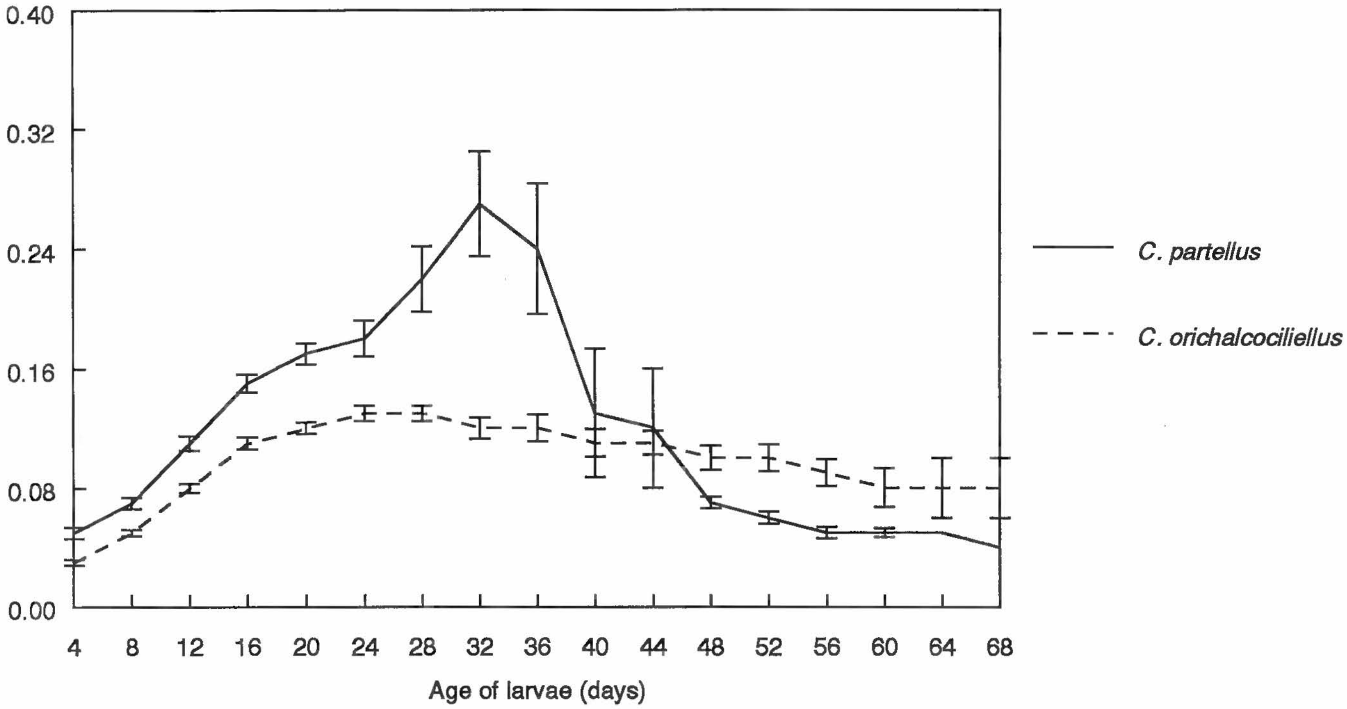

Figure 3.1 Quantities of maize stems consumed by larvae of *C. partellus* and *C. orichalcociliellus* on a four-day interval. (Vertical lines represent the standard error values).

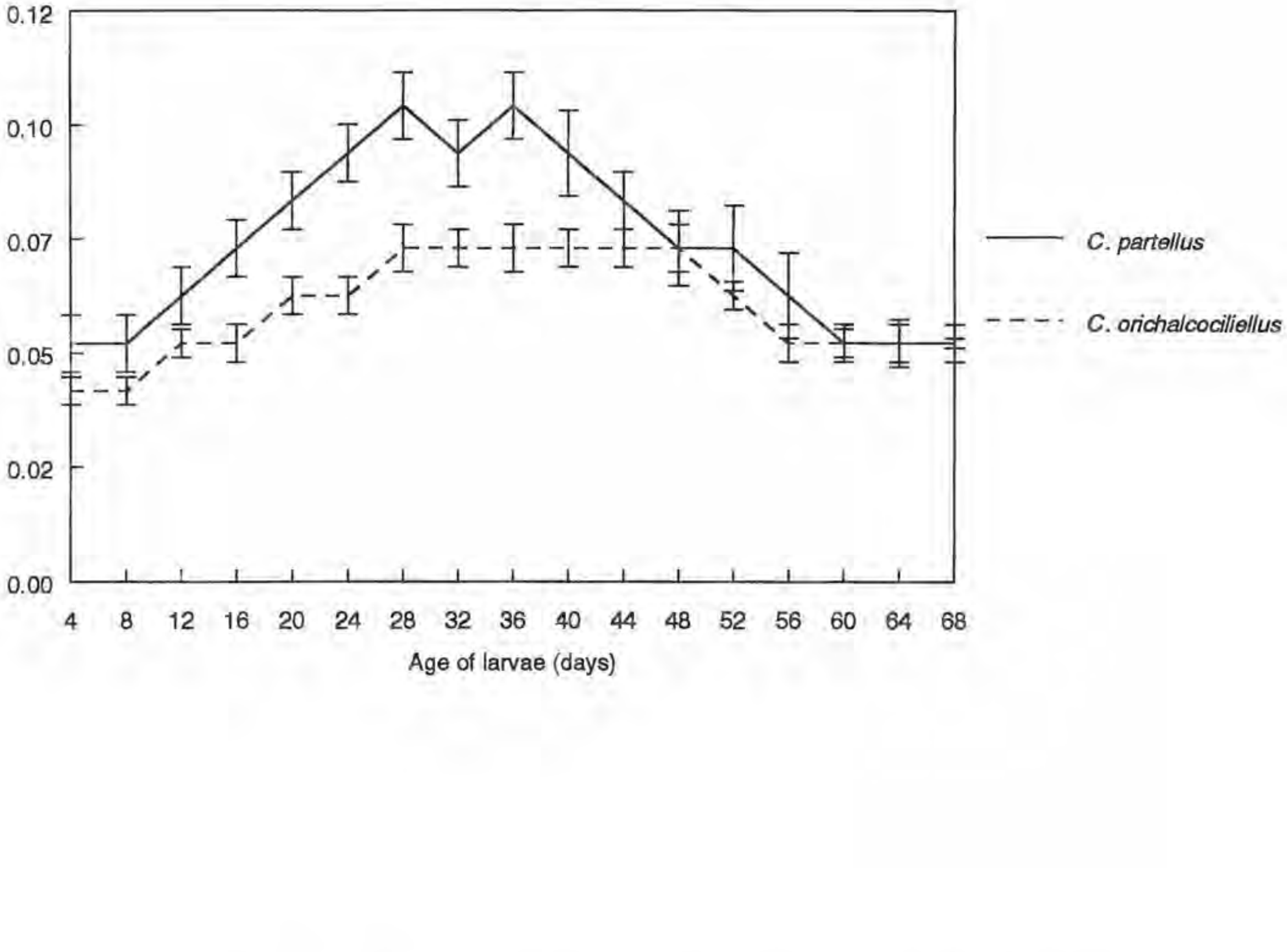

Figure 3.2 Quantities of sorghum stems consumed by larvae of *C. partellus* and *C. orichalcociliellus* on a four-day interval. (Vertical lines represent the standard error values).

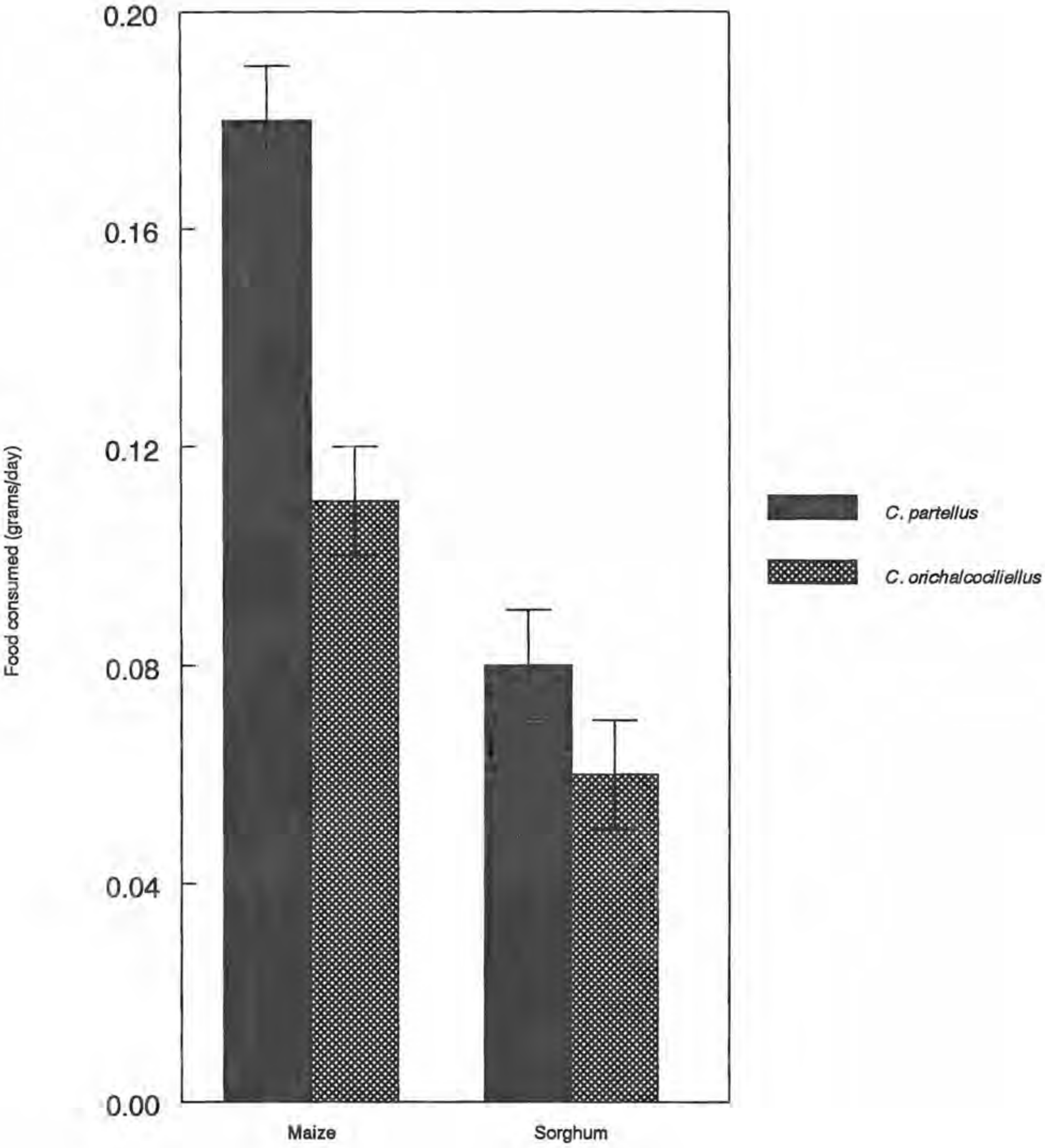

Figure 3.3 Quantities of maize and sorghum stems consumed by larvae of *C. partellus* and *C. orichalcociliellus* on a daily basis. (Vertical lines represent the standard error values).

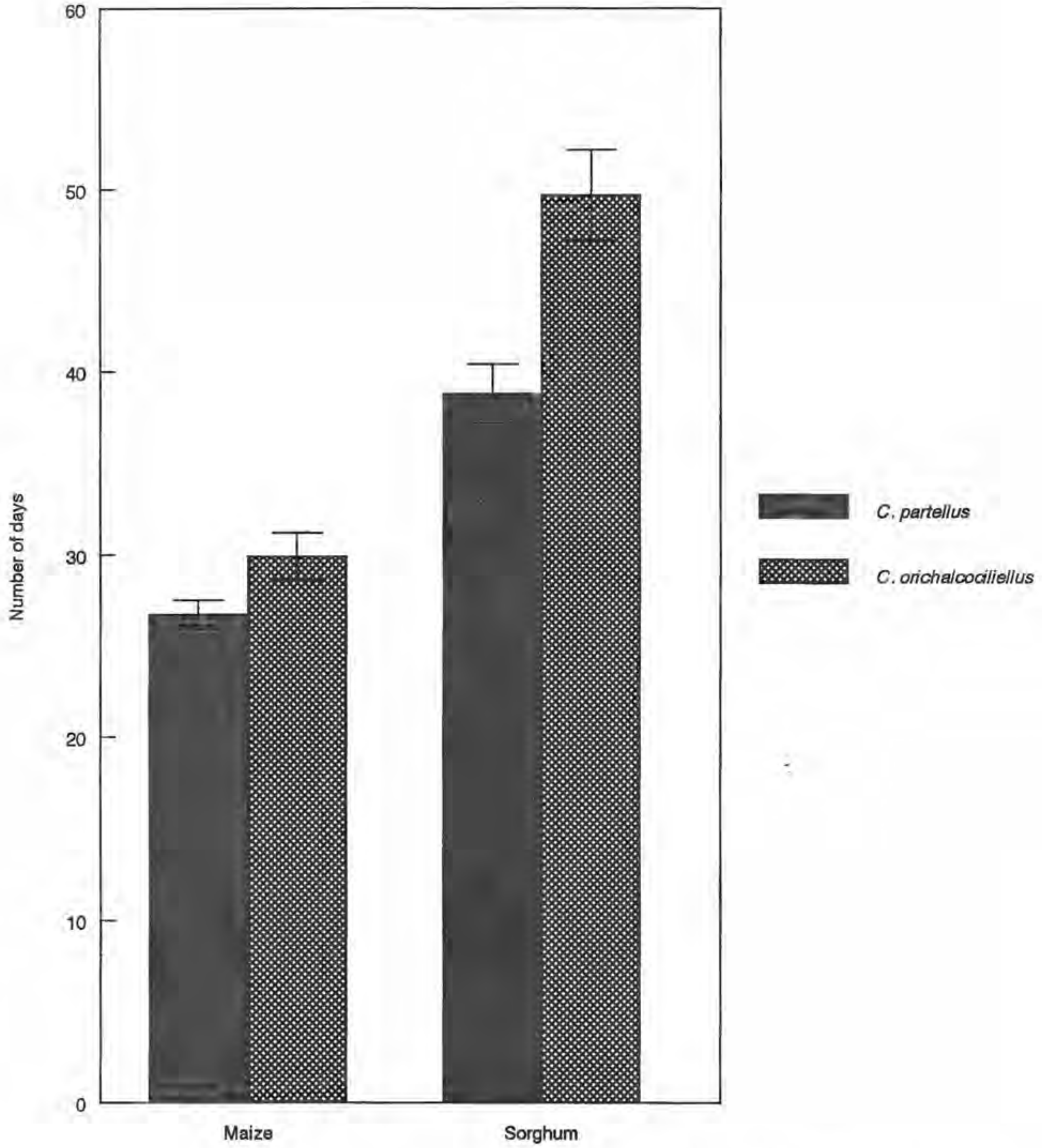

Figure 3.4 Number of days taken by *C. partellus* and *C. orichalcociliellus* to complete larval development in maize and sorghum stems. (Vertical lines represent the standard error values).

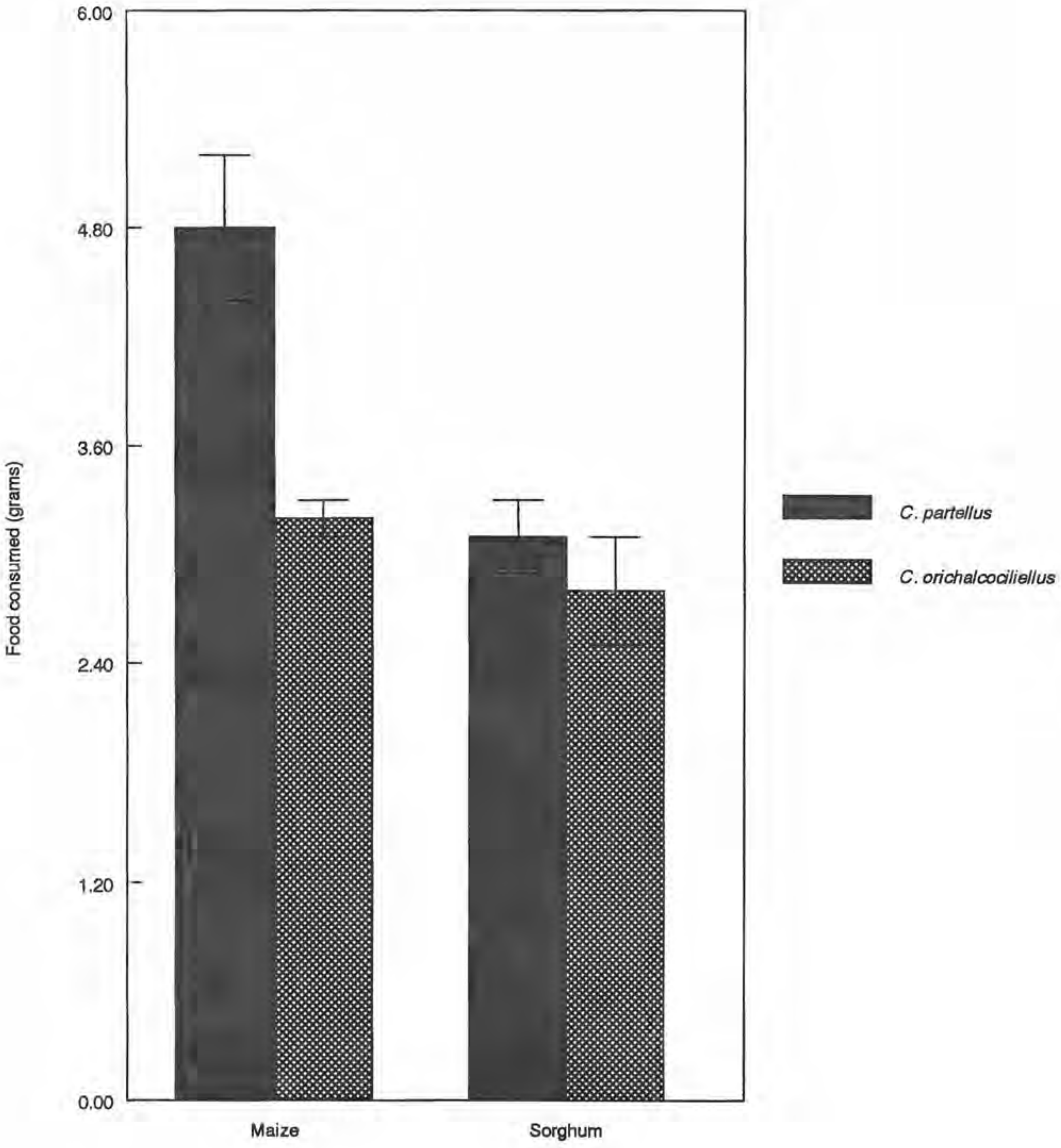

Figure 3.5 Quantities of maize and sorghum stems consumed by *C. partellus* and *C. orichalcociliellus* in a larval lifetime. (Vertical lines represent the standard error values).

CHAPTER FOUR

4.0 Niche overlap, interspecific association and parasitisation of *C. partellus* and *C. orichalcociliellus* by indigenous parasitoids.

4.1 Introduction

Niche overlap measures are designed to measure the degree to which two species share a set of common resources or utilize the same part of the environment. They are commonly based on kinds of food items consumed, micro habitats occupied, or times of activity. Many different measures of overlap have been proposed (Hurlbert, 1978), but with the exception of that by Hurlbert (1978), all are scaled from zero to unity. Zero overlap indicates two species that are completely dissimilar, and a value of unity indicates complete overlap. A clear understanding of the extent of overlap between *C. partellus* and *C. orichalcociliellus* may be useful in explaining their abundance, population dynamics and function in their habitats. Species with overlapping niches are expected to interact in many different ways.. The measurement of interspecific association is of importance in detecting interactions between species (Cole, 1949). These measurements may be based on the presence or absence, or the relative abundance of species (Cole, 1949; Hulbert, 1969). Interspecific association may result from species interaction, food chain co-action, or similarity in adaptation and response to the environment (Smith, 1980). A positive association occurs when two species have overlapping habitat requirements or interact in such a way as to favour mutual presence (Cole, 1949). A negative association occurs when two species have different habitat requirements or interact in such a way that is detrimental to one or both species, i.e interspecific competition (Smith, 1980).

Insect populations can be regulated by a number of biotic and abiotic factors, including competition with other species for the same resources, physical conditions and natural mortality factors. Species differ in the extent to which they respond to mortality-causing factors. A superior species will have a higher survival rate than an inferior species. In Kenya, the role of natural enemies including predators, pathogens and parasitoids in the regulation of the population of stem borer species have been reported by some workers (Mathez, 1972; Warui and Kuria, 1983; Oloo, 1989 and Overholt *et al*., 1994a, b). Oloo (1989) gave a list of the parasitoids and potential predators encountered in the field while evaluating the role of indigenous natural enemies in population dynamics of *C. partellus*. Overholt (Unpublished data) recorded *Cotesia sesamiae* (Cam.), *Pediobius furvus* (Gah.) and *Goniozus indicus*. to be the most common parasitoids recovered from stem borer species at the Kenya Coast.

C. partellus and *C. orichalcociliellus* have overlapping niches, and may occur together within a plant, with some degree of association. Quantitative studies on interspecific association have been shown to elucidate ecological relationships between species and can shed some light on species abundance and population dynamics (Reilly and Sterling, 1983; Bultman and Faeth, 1985; Fritz *et al.*, 1987; Nyrop, 1988). No information exists on the extent of overlap and nature of association between *C. partellus* and *C. orichalcociliellus*. *C. partellus* and *C. orichalcociliellus* are vulnerable to the same natural enemies, but little information exists on the degree of parasitism of these stem borer species (Overholt *et al.*, 1994a, b). *C. orichalcociliellus* having co-evolved with African natural enemies may be more affected than *C. partellus*. In this study, the extent of habitat overlap, interspecific association and degree of parasitism of *C. partellus* and *C. orichalcociliellus* by indigenous parasitoids, in relation to the success of *C. partellus* and the population decline of *C. orichalcociliellus* at the Kenya Coast are reported.

4.2 Materials and Methods

4.2.1 Niche overlap between *C. partellus* and *C. orichalcociliellus*.

Niche overlap between *C. partellus* and *C. orichalcociliellus* was determined using data collected on counts of different stem borer species between December 1991 and December 1993 sampled in various cultivated and wild grasses at three locations (Kilifi, Mtwapa and Kwale) in the coastal area of Kenya. Maize plants from farmers fields and wild host plants of *Chilo* spp. were sampled every 2 weeks. Forty randomly selected plants per crop were excised and carefully dissected to locate stem borer larvae and pupae. All stem borers collected were held individually in glass vials on maize stems and reared at room temperature for identification. Overlap between *C. partellus* and *C. orichalcociliellus* was determined in maize, napier grass, wild sorghum and guinea grass. Niche overlap was calculated using Morisita's index of similarity formulated for counts of individuals (Morisita, 1959), and is calculated from the formula:

$$C=\frac{2\Sigma P_{ij}P_{ik}}{\Sigma^{n}P_{ij}[(n_{ij}-1)/(N_{j}-1)]+\Sigma^{n}P_{ik}[(n_{ik}-1)/(N_{k}-1)]}$$

where

C = Morisita's index of niche overlap between species j and k.

P_{ij} = Proportion resource i is of the total resources used by j.

P_{ik} = Proportion resource i is of the total resources used by k.

n_{ij} = Number of individuals of species j that use resource category i.

n_{ik} = Number of individuals of species k that use resource category i.

N_j N_k =Total number of individuals of each species in sample ($\Sigma n_{ij} = N_j$;

$\Sigma n_{ik} = N_k$).

Percentage overlap between the species was calculated using the method proposed by Renkonen (1938). This method is given by the equation:

$$P_{jk}=[\Sigma(minimumP_{ij}P_{ik})]100$$

where

P_{jk} = Percentage overlap between species j and species k.

P_{ij} P_{ik} = Proportions resource i is of the total resources used by species j and species k.

n = Total number of resource states.

Interspecific association between *C. partellus* and *C. orichalcociliellus.*

Interspecific association between *C. partellus* and *C. orichalcociliellus* was determined using data accumulated for a period of four years (1992-1995) by the International Centre of Insect Physiology and Ecology/Wageningen Agricultural University (ICIPE/WAU) project, on stem borer population dynamics and the impact of indigenous and introduced parasitoids on stem borer populations in the coastal area of Kenya in cultivated and wild grasses. Densities of stem borers were estimated in maize and sorghum at different locations on the

Kenya coast. Weekly samples of 40-120 randomly selected plants were excised from each field and carefully dissected to locate larval and pupal stages of stem borers. Larvae were divided into three size categories: small, medium and large, which approximately corresponded to first and second instars, third and fourth instars, and fifth and sixth instars, respectively. All collected stem borers were reared in maize or sorghum stems for identification. The number of uninfested plants, the number of plants in which only *C. partellus* or *C. orichalcociliellus* were present and the number of plants in which both stem borer species were present were determined in all fields for different borer stages (small-sized, medium-sized, large-sized larvae and pupa) and pooled by growing season (long and short rains) and plant species (maize and sorghum) for each year. The interspecific association between *C. partellus* and *C. orichalcociliellus* was measured using the method described by Southwood (1978). This measure is based on the presence or absence of borers in the same plant and employs a 2 x 2 contingency table as its principal analytical tool. Only contingency tables where both borer species were present were used in the analysis. These contingency tables were tested by a χ^2 test of independence at a 5% level of significance to determine whether the hypothesis of independence should be accepted or rejected. Hurlbert's coefficient of interspecific association (C_8) was used to measure the strength of association and to determine whether the association was positive or negative. Values of C_8 range from -1 to 1 for perfect negative and positive association, respectively. The formula is as follows:

$$C_8 = \frac{ad-bc}{|ad-bc|} \left| \sqrt{\frac{OBS\chi^2 - MIN\chi^2}{MAX\chi^2 - MIN\chi^2}} \right|$$

where

a, b, c, and d = The four cells of a 2 x 2 contingency table.

Obs χ^2 = The value of χ^2 associated with the observed values of a, b, c, and d.

Max χ^2 = The value of χ^2 when a is as large (If ad $\geq$ bc) or as small (if ad $<$ bc) as the marginal totals of the 2 x 2 table permit.

Min χ^2 = The value of χ^2 when the observed value of a differs from the expected value of a by less than 100.

4.2.3 Parasitisation of *C. partellus* and *C. orichalcociliellus* by indigenous parasitoids.

This study was also conducted using data accumulated for a period of four years (1992-1995) by the ICIPE/WAU project The parasitism levels of *C. partellus* and *C.orichalcociliellus* by the three most common indigenous parasitoids, *C. sesamiae*, *P. furvus* and *Goniozus indicus*, at the coastal area of Kenya was evaluated in maize and sorghum plants. For *C. sesamiae* and

Goniozus indicus., which are larval endo-parasitoid and ecto-parasitoid, respectively, analysis was on medium and large sized larval instars, the susceptible stages for parasitoid attack. For *P. furvus*, which is a pupal parasitoid, analysis was on the pupal stage. Data from each field and plant species for each year were analysed separately and the number of plants infested with each of the stem borer species recorded. The number of each of the stem borer species parasitized by the different parasitoids was also recorded. Data from all fields for all the year and growing seasons (long and short rains) were then pooled by plant species. A χ^2 test of independence was performed to detect any differences in the degrees of parasitism of the stem borer species for each parasitoid species.

4.3 Results

4.3.1 Niche overlap between *C. partellus* and *C. orichalcociliellus*.

Simultaneous occurrence of *C. partellus* and *C. orichalcociliellus* in the same plant was evident in maize, napier grass, wild sorghum and guinea grass. Niche overlap as calculated from Morisita's (1959) formula was 0.97 giving an overlap according to Schoener (1970) of 83.7%.

4.3.2 Interspecific association between *C. partellus* and *C. orichalcociliellus.*

A weak positive association was detected between small, medium and large sized larvae of *C. partellus* and *C. orichalcociliellus* in both maize and sorghum plants throughout the long and short rains of 1992-1995 (Tables 4.1and 4.2). The strength of the association decreased as borers developed, with almost no evidence of association between the two stem borer species in maize and sorghum at the pupal stage (Tables 4.1 and 4.2).

4.3.3 Parasitisation of *C. partellus* and *C. orichalcociliellus* by indigenous parasitoids.

The degree of parasitism of *C. partellus* and *C. orichalcociliellus* by the three parasitoid species was similar and below 2% in maize and sorghum (Table 4.3). The highest parasitism of *C. partellus* and *C. orichalcociliellus* was caused by *C. sesamiae* and lowest by *Goniozus indicus*. In sorghum plants, no parasitism of either stem borer species by *Goniozus indicus* was recorded (Table 4.3).

4.4 Discussion

This study revealed a very high degree of niche overlap between *C. partellus* and *C. orichalcociliellus* in the resources examined. In gramineous plants, the presence of multiple stem borer species has been reported by several authors (Girling, 1978; Hughes *et al*, 1982; Kaufmann, 1983; Sampson and Kumar, 1983; Seshu Reddy, 1983b and Youm, 1984) indicating that stem borer species have overlapping niches, irrespective of the type of association between them. Previous attempts have been made to analyse the nature of association between insect species including stem borers (Girling, 1978; Rodriguez-Del-Bosque *et al*, 1990). Girling (1978) investigated interspecific association between *E. saccharina*, *C. partellus*, *B. fusca* and *S. calamistis* in maize, sorghum and sugar cane. He reported that the coefficient of interspecific association for pairs of species was in the region of -0.9, which reflects a very marked lack of association between the species. However, a contrary report was given by Rodriguez-Del-Bosque *et al.* (1990), who found a weak positive interspecific association between three species of neotropical stem borers, *Diatraea lineolata* (Walker), *D. saccharalis* (F.) and *Eoreuma loftini* (Dyar) in sugar cane. In the present study a weak positive association was found between small and medium sized larvae of *C. partellus* and *C. orichalcociliellus*. Positive associations may occur when species have overlapping niches or interact in a manner that favours mutual occurrence (Cole, 1949; Reilly and Sterling, 1983). Association between *C. partellus* and *C. orichalcociliellus* may have been derived from a mutual preference of the adults to oviposit on the same host plants. Bultman and Faeth (1985) and Fritz *et al.* (1987) noted that positive association between potential competitors may result from both species responding similarly to host plant variation for feeding or oviposition. Antolin and Addicott (1988) reported that for some phytophagous insects, feeding and oviposition sites are not chosen on the basis of the presence or absence of a competing species. Moth oviposition has been directly correlated with plant leaf area. Plants with a larger leaf area received more eggs than those with smaller leaf area (Stewart and Walton, 1964).

No significant association was found between large sized larvae and pupae of *C. partellus* and *C. orichalcociliellus*. A probable explanation may be that some of the larvae die in the process of development, thus, reducing the number of larvae getting to the later larval and pupal stages in the plant. Like most lepidopterous pests, gramineous stalk borers suffer from high early larval mortality (Mohyuddin and Greathead, 1970; Mathez, 1972; Girling, 1978; van Hamburg, 1980; van Hamburg and Hassel, 1984) in response to strong density dependent activity. van Hamburg (1980) demonstrated density dependence establishment of early larval *C. partellus* on sorghum. He showed that losses primarily due to dispersal increased with increasing levels of infestation. He also noted that the tendency for the second and third instar larvae to move from the funnels to the leaf sheaths may also result in some mortality with fewer numbers of larvae surviving to later stages. A negative association occurs when two species have different habitat requirements or interact in a way that is detrimental to one or both species (Smith, 1980). No negative association was observed in the present study indicating that *C. partellus* and *C. orichalcociliellus* occupy the same niches but do not directly harm each other in their habitat. Thus, the gradual displacement of *C. orichalcociliellus* by *C. partellus* over the last 30 years may not be attributed to direct attack of *C. orichalcociliellus* by *C. partellus*, but may be due to some superior competitive attributes of *C. partellus* that indirectly affect the survival of *C. orichalcociliellus*.

Parasitism levels of stem borer species by indigenous natural enemies had previously been reported by researchers in Kenya. Mathez (1972) reported up to 90% egg mortality of stem borers due to *Trichogramma* spp., while larval and pupal mortality was usually below 10% and was mainly due to unidentified bacteria, fungi and virus diseases on larvae and *P. furvus* parasitism on pupae. Oloo (1989) reported up to 97.6% real mortality of *C. partellus* occurring in the age interval from egg to early instar larvae and he attributed this to losses or mortality due to predation and other unidentified factors. He reported that parasitoids and insect pathogens contributed less than 1% to generation mortality at various life stages of *C. partellus*. Overholt *et al.* (1994b) reported that parasitism of *C. partellus* by *C. sesamiae* in maize for a period of two years was never more than 3% and was typically less than 0.5%. In the present study, parasitism of *C. partellus* and *C. orichalcociliellus* by *C. sesamiae*, *P. furvus* and *Goniozus indicus* was very low, with no differences in the degrees of parasitism of *C. partellus* and *C. orichalcociliellus*. These results and those of previous studies, suggest that natural enemies are probably not involved in the displacement of *C. orichalcociliellus*.

Table 4.1 Interspecific association between different life stages of *C. partellus* and *C. orichalcociliellus* in maize during the long and short rains of 1992-1995.

Season/year	Stem borer stage	Number of Larvae	Cell frequencies (%)				χ^2 (df = 1)	C_8
			Cp+ Co+	Cp+ Co-	Cp- Co+	Cp- Co-		
Lr	Small larvae	3500	0.6	3.1	0.4	95.7	271.91*	0.14
1992	Medium larvae	3627	0.4	6.2	0.8	92.6	56.77*	0.05
	Large larvae	3754	0.3	9.4	0.9	89.4	9.29*	0.02
	Pupae	3411	0.0	1.3	0.3	98.4	5.27*	0.00
Sr	Small larvae	1250	4.5	10.9	1.3	83.4	223.89*	0.25
1992	Medium larvae	1335	2.8	17.3	1.8	78.1	65.74*	0.10
	Large larvae	1439	2.5	22.4	2.7	72.4	21.35*	0.05
	Pupae	1147	0.3	7.7	1.2	90.8	1.08	0.01
Lr	Small larvae	5099	0.8	5.8	1.5	91.9	156.01*	0.10
1993	Medium larvae	5445	1.2	10.9	1.8	86.1	121.28*	0.07
	Large larvae	5892	0.8	17.5	2.1	79.6	11.21*	0.02
	Pupae	4902	0.1	3.3	1.0	95.6	1.73	0.01
Sr	Small larvae	1698	1.7	13.3	3.6	81.4	20.86*	0.06
1993	Medium larvae	1947	2.6	22.3	4.1	71.0	13.03*	0.04
	Large larvae	1950	2.0	23.4	3.7	70.9	5.37*	0.02
	Pupae	1610	0.5	12.3	1.3	85.9	4.52*	0.02
Lr	Small larvae	3366	2.1	17.6	2.6	77.7	63.08*	0.06
1994	Medium larvae	3528	2.4	20.8	2.6	74.2	62.88*	0.06
	Large larvae	3866	2.0	27.8	2.5	67.7	18.39*	0.02
	Pupae	3234	0.9	14.0	4.2	80.9	0.52	0.01
Sr	Small larvae	1080	66.0	9.8	1.3	82.9	277.02*	0.33
1994	Medium larvae	1192	2.5	19.5	2.9	75.1	22.71*	0.06
	Large larvae	1437	3.3	32.1	2.4	62.3	18.27*	0.04
	Pupae	1133	1.1	17.3	2.6	79.0	3.71	0.02
Lr	Small larvae	3200	0	0	0	100.0	-	-
1995	Medium larvae	3328	0.4	3.3	0.2	96.2	208.83*	0.10
	Large larvae	3426	0.3	5.9	0.5	93.4	34.00*	0.03
	Pupae	3360	0.1	4.0	0.7	95.2	2.05	0.01

*, $P \leq 0.05$

Cp, *C. partellus*; Co, *C. orichalcociliellus*

Lr, Long rains; Sr, Short rains

An invalid chisquare is indicated by a dash

Table 4.2 Interspecific association between different life stages of *C. partellus* and *C. orichalcociliellus* in sorghum during the long and short rains of 1992-1995.

Season/year	Stem borer stage	Number of Larvae	Cell frequencies (%) Cp+ Co+	 Cp+ Co-	 Cp- Co+	 Cp- Co-	χ^2 (df = 1)	C_8
Lr	Small larvae	4339	0.2	3.8	0.3	95.7	91.36*	0.05
1992	Medium larvae	4720	0.3	10.9	0.9	87.9	7.15*	0.01
	Large larvae	5114	0.5	17.2	1.1	81.2	8.83*	0.01
	Pupae	4235	0.0	1.7	0.3	98.0	2.55	0.00
Sr	Small larvae	1165	4.2	13.7	1.2	80.9	157.72*	0.19
1992	Medium larvae	1281	2.0	23.3	1.2	73.5	26.80*	0.05
	Large larvae	1522	3.4	33.6	1.1	61.9	43.95*	0.05
	Pupae	1108	0.3	13.5	1.2	85.0	0.33	0.00
Lr	Small larvae	3777	0.5	8.7	0.6	90.2	59.44*	0.04
1993	Medium larvae	4263	0.8	18.3	1.0	79.9	29.27*	0.02
	Large larvae	4884	0.9	28.8	0.6	69.7	30.53*	0.02
	Pupae	3534	0.0	3.2	0.4	96.3	0.56	0.00
Sr	Small larvae	1773	1.6	12.0	2.1	84.3	51.10*	0.08
1993	Medium larvae	2048	4.2	20.2	2.6	73.0	113.73*	0.11
	Large larvae	2072	2.4	22.9	2.6	72.2	28.13*	0.05
	Pupae	1773	0.3	14.4	0.9	84.3	1.85	0.01

*, $P \leq 0.05$

Cp, *C. partellus*; Co, *C.orichalcociliellus*

Lr, Long rains; Sr, Short rains

Table 4.3 Percentages and number of larvae ( ) of *C. partellus* and *C. orichalcociliellus* parasitized by indigenous parasitoids in maize and sorghum during the long and short rains of 1992-1995.

Plant species	Parasitoid species	Stem borer species		χ^2
		C. partellus	*C. orichalcociliellus*	(df = 1)
Maize	*Cotesia sesamiae*	2.0 (233)	1.5 (28)	2.37
	Pediobius furvus	1.0 (17)	1.5 (6)	0.00
	Goniozus indicus	0.1 (13)	0.1 (2)	0.01
Sorghum	*Cotesia sesamiae*	1.9 (250)	1.5 (17)	0.83
	Pediobius furvus	0.5 (7)	1.1 (3)	1.41
	Goniozus indicus	0.0 (0)	0.0 (0)	-

An invalid χ^2 is represented by a dash.

CHAPTER FIVE

5.0 Fecundity, longevity, egg fertility and hatchability of *C. partellus* and *C. orichalcociliellus.*

5.1 Introduction

Ecological homologues exhibit varying degrees of biological differences which may influence the outcome of competitive interactions in any given condition. For instance, differences occur in their fecundity and longevity. The outcome of competitive displacement between ecological homologues hinges on which of the competing species has the highest effective progeny production under given conditions. The effective progeny production, i.e, the relative rate of production per parental female of female progeny that survive to reproduce (R) (Debach and Sundby, 1963; Debach, 1966) is based on total fecundity, sex ratio, survival to reproduction, effective reproductive period and time required for development to reproductive maturity (Debach *et al.*, 1978). All these parameters may be modified by a variety of environmental conditions such as temperature, humidity, food quality or quantity and interspecific competition. Debach and Sundby (1963) evaluated the biological characteristics of three ecological homologues, *Aphytis chrysomphali*, *A. lingnanensis* and *A. melinus*, and showed the species with the greatest number of F1 progeny to be the winner in any paired interspecific competition. They implicated the inherent fecundity of the species to be the factor of most consequence to the actual progeny production. The fecundity of *C. partellus* ovipositing a mean of 434 eggs (Berger, 1989a) was reported to be equal with *C. orichalcociliellus* ovipositing a mean of 475 eggs (Delobel, 1975b). Mbapila (1997) rearing both stem borer species on maize reported the fecundity and egg viability of *C. partellus* to be higher than that of *C. orichalcociliellus* at different temperatures except that of 31^{0}C. In this study, the fecundity, longevity, egg fertility and hatchability of *C. partellus* and *C. orichalcociliellus* reared on an artificial diet (Ochieng *et al.*, 1985) were compared under constant temperatures of 25, 28 and 31^{0}C and relative humidities of 75, 84 and 96%.

5.2 Materials and Methods

Fresh pupae of *C. partellus* and *C. orichalcociliellus* originating from larvae reared on an artificial diet (Ochieng *et al.*, 1985) were obtained from the ICIPE insectary. The pupae were weighed and kept singly in glass vials until adult emergence.

5.2.1 Fecundity and longevity of *C. partellus* and *C. orichalcociliellus.*

Newly emerged male and female pairs of the different moth species were held singly in square-shaped, wire mesh oviposition cages. The insides of the cages were lined with crumpled waxed paper as a removable oviposition substrate. *C. partellus* and *C. orichalcociliellus* are known to oviposit readily on this substrate (Delobel, 1975b; Kumar and Saxena, 1985a). Experiments were conducted in incubators under three constant temperatures of 25, 28 and 31^{0}C and relative humidities of 75, 84 and 96% with a L:D 12:12 photoperiod. Each treatment included 100 pairs of *C. partellus* and *C. orichalcociliellus* except for all temperatures in the 75% relative humidity treatment in which only 50 pairs of *C. orichalcociliellus* were used due to an inadequate supply. Each pair of moths was provided with a cotton ball saturated with a 20% sugar-water solution to provide nourishment for the moths. Waxed papers were removed and examined daily for eggs until death of the female. Egg batches from each female were cut from the waxed papers the day after they were laid, counted and kept under the same controlled environments in 7.5 x 2.5 cm glass vials. Total fecundity and adult longevity were compared between temperatures and relative humidities using the generalized linear model (GLM) and mean separation was carried out using the Student-Newman-Keul (SNK) multiple range test (SAS Institute, 1987).

5.2.2 Egg fertility and hatchability of *C. partellus* and *C. orichalcociliellus.*

Individual egg batches kept in glass vials under the same controlled environments were examined daily until the black-head stage when the number of fertile eggs could be determined. The number of larvae hatching from eggs was recorded. Data were converted to an arcsine transformation and analysis was done using the general linear model (GLM) to determine differences in percentage egg fertility and hatchability. Means were separated using the Student-Newman-Keul (SNK) multiple range test (SAS Institute, 1987).

5.3 Results

Adult females of *C. partellus* and *C. orichalcociliellus* have equal longevities at all temperatures and relative humidities (Table 5.1). The mean number of eggs laid by *C. partellus* was always greater than that of *C. orichalcociliellus* at 25 and 28^{0}C at the different relative humidities, but at a higher temperature of 31^{0}C, no difference was found in the mean number of eggs laid by *C. partellus* and *C. orichalcociliellus* irrespective of the relative humidity (Table 5.2). In most cases, higher numbers of *C. partellus* eggs were fertile and hatched to first instar larvae compared to *C. orichalcociliellus* eggs (Tables 5.3 and 5.4). In as much as the mean number of eggs laid by *C. partellus* and *C.*

orichalcociliellus were the same at 31^{0}C, *C. partellus* still had an advantage over *C. orichalcociliellus* in having higher number of eggs surviving to the first instar larvae compared to *C. orichalcociliellus* (Tables 5.3 and 5.4).

5.4 Discussion

The longevity of adult female of *C. partellus* and *C. orichalcociliellus* was the same at all temperatures and relative humidities. Delobel (1975b) reported that *C. partellus* and *C. orichalcociliellus* adults live for approximately the same number of days. He also reported equal fecundities for *C. partellus* and *C. orichalcociliellus* reared on an artificial diet. The results of this study showed that at lower temperatures, *C. partellus* laid more eggs compared to *C. orichalcociliellus*. However, at higher temperatures, the mean number of eggs laid by the two species was equal, indicating that in areas with high temperatures and relative humidities, *C. orichalcociliellus* may have an equal reproductive potential as *C. partellus*. However, in this study the mean number of eggs laid by both species was low compared to earlier reports by Berger (1989b) for *C. partellus* and Delobel (1975a) for *C. orichalcociliellus*. A possible explanation for these differences may be the different artificial diets used in the various experiments, which may have had an affect on the reproductive capacity of the females reared as larvae on these diets. Egg fertility and hatchability of *C.*

partellus was higher than that of *C. orichalcociliellus* especially at high temperatures and relative humidities. *C. partellus* may thus have more individuals in a generation surviving to reproductive stage compared to *C. orichalcociliellus*. Mbapila (1997) reported higher egg viability of *C. partellus* compared to *C. orichalcociliellus* at low temperatures, and suggested that low temperatures may have reduced the reproductive success of *C. orichalcociliellus*. Debach (1963) reported that the winner in any competitive displacement process is the species that has the greatest effective progeny production under any given conditions.

Table 5.1 Mean longevity (±std) of *C. partellus* and *C. orichalcociliellus* adult females under different temperatures and relative humidities

	Stem borer longevity (days±std)											
Temp	Relative humidity (%)											
(^{0}C)	75				85				96			
	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co
25	98	7.0±1.95a	50	6.5±2.06a	100	5.8±2.14a	100	5.6±1.28a	100	6.1±2.46a	100	5.5±2.28a
28	100	5.2±1.45a	50	5.7±2.48a	98	4.9±1.97a	99	5.1±2.05a	100	4.8±1.60a	100	4.9±2.07a
31	100	5.3±1.58a	50	5.6±1.43a	100	4.9±1.71a	100	4.7±1.35a	100	4.9±1.79a	100	4.5±1.45a

For each relative humidity, means in the same row with the same letter are not significantly different (P > 0.05).

Cp, *Chilo partellus* Co *Chilo orichalcociliellus*

Table 5.2 Mean fecundity (±std) of *C. partellus* and *C. orichalcociliellus* under different temperatures and relative humidities

Temp (^{0}C)	Mean number of eggs											
	Relative humidity (%)											
	75				85				96			
	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co
25	100	99.9±123.92a	50	53.7±100.17b	100	126.0±108.02a	100	73.9±96.40b	100	150.7±124.85a	100	112.7±129.47b
28	100	153.1±136.85a	50	69.4±97.64b	100	165.7±140.81a	100	121.2±107.59b	100	144.4±113.10a	100	101.3±114.04b
31	100	128.9±133.12a	50	101.3±125.47a	100	126.0±142.22a	100	105.2±150.87a	100	113.8±132.02a	100	135.3±171.05a

For each relative humidity, means in the same row with different letters are significantly different P ≤ 0.05.

Cp, *Chilo partellus* Co, *Chilo orichalcociliellus*

Table 5.3 Percentage egg fertility (±std) of *C. partellus* and *C. orichalcociliellus* under different temperatures and relative humidities

Temp (°C)	Percentage fertility Relative humidity (%)											
	75				85				96			
	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co
25	65	43.2±40.88a	24	33.6±30.39a	77	72.0±33.06a	68	47.9±41.36b	77	63.7±38.45a	73	38.0±40.61b
28	86	70.9±35.21a	22	55.8±35.27a	76	70.3±32.67a	82	34.2±37.53b	84	74.3±34.80a	57	59.7±39.06b
31	68	59.8±39.12a	28	35.3±35.51b	67	67.6±36.30a	72	30.6±34.49b	77	70.6±36.63a	63	30.0±37.40b

For each relative humidity, means in the same row with different letters are significantly different P ≤ 0.05.

Cp, *Chilo partellus*   Co, *Chilo orichalcociliellus*

Table 5.4 Percentage egg hatchability (±std) of *C. partellus* and *C. orichalcociliellus* at different temperatures and relative humidities

Temp	Percentage hatchability Relative humidity (%)											
(°C)	75				85				96			
	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co
25	65	34.1±36.64a	24	22.9±27.93a	77	61.7±33.38a	68	36.9±35.46b	77	52.2±35.59a	73	32.5±36.90b
28	86	57.6±33.30a	22	42.6±29.96a	76	58.0±31.97a	82	25.9±29.89b	84	62.9±36.25a	57	50.5±35.79b
31	68	50.5±36.27a	28	30.2±30.44b	67	58.0±34.00a	72	20.9±25.19b	77	59.8±38.37a	63	20.1±29.06b

For each relative humidity, means in the same row with different letters are significantly different P ≤ 0.05.

Cp, *Chilo partellus* Co, *Chilo orichalcociliellus*

CHAPTER SIX

6.0 Dispersal of newly hatched larvae of *C. partellus* and *C. orichalcociliellus* from maize and sorghum plants.

6.1 Introduction

Dispersal is a very vulnerable stage in the life history of many insects (Roome, 1980). For most stem borer species, female moths fly actively to locate and oviposit on larval food source. The eggs are laid in batches containing a few to more than a hundred eggs on leaf surfaces. Immediately after the eggs hatch, some larvae move from the egg batch, but still stay on the oviposition plant, establishing themselves behind the upper leaf sheath or leaf whorl (Bernays *et al.*, 1983, 1985; Berger, 1989a). Once established in the whorl or behind a leaf sheath, young larvae are reasonably protected from adverse physical and natural mortality factors. They later change the feeding site and migrate down the outside of the stem which they may penetrate, or they may enter other plant tissues. However, one plant can only sustain a limited number of larvae (van Hamburg, 1980; Chapman *et al.*, 1983). A sorghum plant can support only about four to five larvae to full term (van Hamburg, 1980) and a maize plant up to 24 larvae (Berger, 1992). This means that many of the eggs laid on a single plant will not be able to develop on their oviposition plant. Thus, the need arises for individuals from a newly hatched egg batch, particularly a large batch, to leave the plant (van Hamburg, 1980; Chapman *et al*., 1983; Ampofo and Kidiavai, 1987; Leuschner, 1989) and migrate to other hosts to avoid competition.

Larvae of most insects have a complicated pattern of different kinds of dispersal. Berger (1992) described the major phases of dispersal in the larval life cycle of *C. partellus*. Of these, ballooning on silk threads is an important behaviour of first instar larvae which makes it possible for them to be transported by wind from one plant to another (van Hamburg, 1980; Roome, 1980; Chapman *et al*., 1983; Ampofo, 1986a; Berger, 1989a). The rate of ballooning is highly variable in *C. partellus* (Berger, 1989a) as well as in other Lepidoptera species (Leonard, 1970; McManus, 1973; Capinera and Barbosa, 1976; Futuyama *et al*., 1984; Ramachandran, 1987). Among the factors which influence the ballooning behaviour of Lepidoptera are host plant and larval quality. Host plant quality has been shown to influence the ballooning behaviour of *C. partellus* in different varieties of maize and sorghum (Chapman *et al*., 1983; Ampofo, 1986a; Woodhead and Taneja, 1987). The influence of larval quality on ballooning has been observed in first instar larvae of the gypsy moth, *Lymantria dispar* (L.) (Leonard, 1970; McManus, 1973) and in the fall cankerworm, *Alsophila pometaria* (Harris) (Futuyama *et al*., 1984). Genetic variation in *A. pometaria* has also been found to influence ballooning behaviour of the larvae.

During this wandering stage,larvae are clearly susceptible to adverse environmental factors. Thus, mortality may occur if larvae do not find a new host, are exposed to adverse weather conditions, or are attacked by natural enemies. Hence the ability of the young larvae to successfully disperse to adjacent suitable host plants is crucial for their further development and survival. The dispersal of a number of lepidoptera species including *C. partellus* has been studied using, among other plants, maize and sorghum (Chapman *et al.*, 1983; Bernays *et al.*, 1983, 1985; Ampofo, 1986a; Woodhead and Taneja, 1987; Berger, 1989a, 1992; Ross and Ostile, 1990). Information on the dispersing ability of *C. orichalcociliellus* is lacking. This study compares the dispersing abilities of newly hatched larvae of *C. partellus* and *C. orichalcociliellus* in maize and sorghum plants using a wind tunnel.

6.2 Materials and Methods

Newly hatched larvae of *C. partellus* and *C. orichalcociliellus* were obtained from colonies maintained on artificial diet (Ochieng *et al.*, 1985) at the ICIPE insectary. Experiments were conducted between 8.00-12.00 hours when the larvae were still active. The ballooning experiments were carried out in a wind tunnel (Plate 6.1) at room temperature. Three week old potted maize and sorghum plants (with 6-7 leaves) were placed inside the wind tunnel. The base of the wind tunnel was covered with white papers to facilitate observation of the larvae. Plants were infested with 10 larvae each, on the uppermost leaf. A wind speed of 0.2-0.3 metres per second was directed towards the plant. A plant was placed 50 cm away from the experimental plant. Observations were made on whether a larva dispersed from or stayed on the experimental plants. The larvae that dispersed were counted and removed. The number of larvae that remained on the experimental plants was also recorded. Experiments for each stem borer and plant species were conducted separately, replicated 32 times and terminated after one hour when most of the larvae were assumed to have entered the plant whorl or left the plant on silken thread. A goodness of fit test was carried out on each stem borer and plant species using a G-test to detect any difference in the number of larvae dispersing from each plant. Analysis of variance (ANOVA) was performed using the GLM procedure (SAS Institute, 1987) to determine the mean dispersal distance, which indicates the average distance that larvae moved and the mean dispersal rate, which provides a measure of overall dispersal rate for a specific time period.

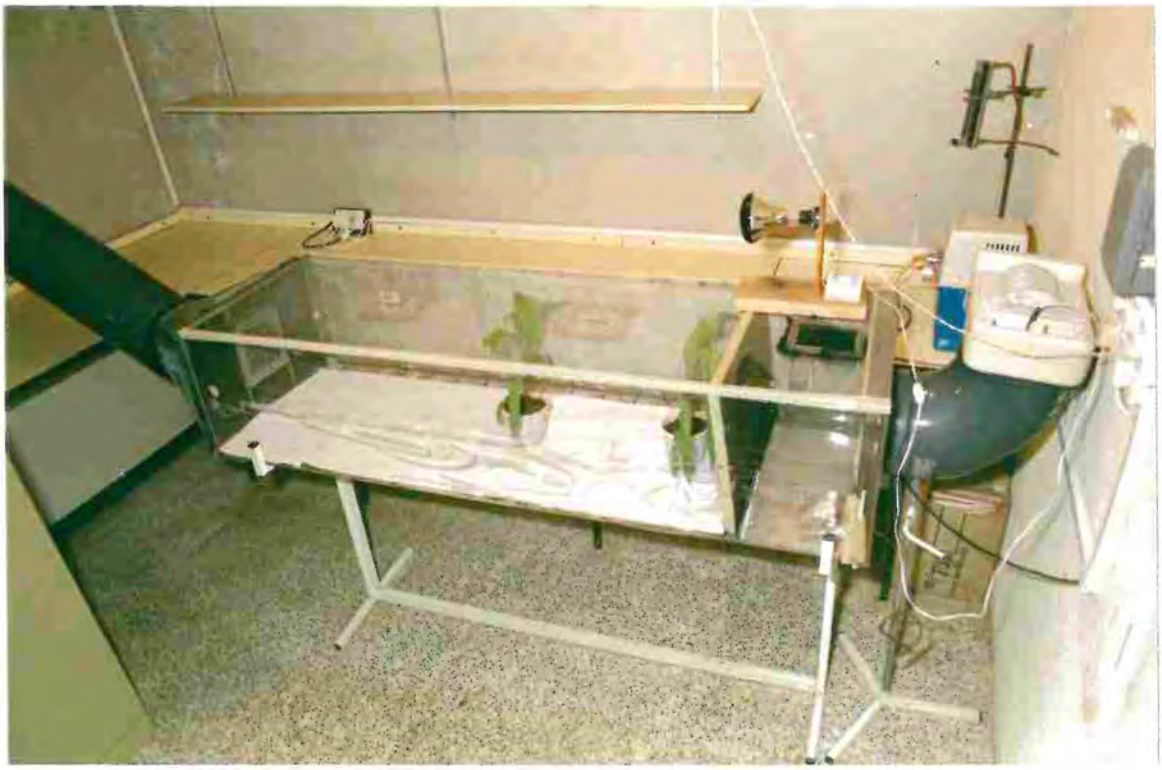

Plate 6.1 Picture showing a wind tunnel

6.3 Results

A significantly higher percentage of newly hatched larvae of *C.partellus* compared to *C. orichalcociliellus* dispersed from the experimental plants in both maize and sorghum, with a significant difference in the percentage of *C. partellus* dispersing from maize compared to sorghum (Figure 6.1). The percentages of *C. orichalcociliellus* larvae dispersing from maize and sorghum plants were not different. *C. partellus* larvae dispersed over greater distances compared to *C. orichalcociliellus* in both maize and sorghum plants (Figure 6.2). Also, *C. partellus* dispersed over greater distances in maize than in sorghum, whereas, distances covered by *C. orichalcociliellus* in maize and sorghum plants were not different.

Results on the rates of dispersal of *C. partellus* and *C. orichalcociliellus* revealed that *C. partellus* moved at a faster rate than *C. orichalcociliellus* in maize and sorghum plants (Figure 6.3). The rate of dispersal of *C. partellus* was faster in maize compared to sorghum, whereas no significant difference was found in the rate of dispersal *C. orichalcociliellus* larvae in maize and sorghum plants. More of *C. orichalcociliellus* larvae failed to leave the experimental plants (distance = 0 cm) compared to *C. partellus* in maize, while the numbers of *C. partellus* and *C. orichalcociliellus* larvae that failed to disperse from sorghum plants were the same (Figures 6.4 and 6.5). Significantly higher numbers of *C.*

partellus larvae reached and dispersed beyond (distance ≥ 50 cm) the control plant compared to *C. orichalcociliellus* in maize and sorghum (Figures 6.4 and 6.5). Maximum distances covered by *C. partellus* in maize and sorghum were beyond 100 and 80 cm, respectively, whereas, *C. orichalcociliellus* did not disperse beyond a distance of 60 cm in maize and sorghum.

6.4 Discussion

Dispersal in insects has been traditionally viewed from an essentially evolutionary perspective with different phases involved (McManus, 1973; Capinera and Barbosa, 1976; Berger, 1992). To ensure a homogenous distribution of the insect population, thus minimizing competition between young individuals, and to colonize new areas (Gadgil, 1971; Hamilton and May, 1977) first instar larvae of most insects are expected to successfully undergo an initial dispersal irrespective of the host plant they encounter. In the gypsy moth, *L. dispar*, the first instars have been reported to undergo at least one initial dispersal while the subsequent dispersals have been suggested to be influenced by the host plants that they encounter and the proportion of dispersers in the population (McManus, 1973; Capinera and Barbosa, 1976). In the present study, newly emerged first instar larvae of *C. partellus* and *C. orichalcociliellus* were observed dispersing from maize and sorghum plants within one hour of the start of an experiment, indicating the presence of an obligate dispersal phase in these *Chilo* spp. when they are less receptive to cues associated with food and are predisposed to dispersal. However, in some insects this dispersal phase does not take place. Ramachandran (1987) noted that this obligatory dispersal phase is not a feature of the behaviour of the geometrid moth, *Ectropic excursaria* (Guenée).

Observations in this study have shown that higher percentages of newly hatched larvae of *C. partellus* were able to disperse from the experimental plants, covering greater distances at a faster rate compared to *C. orichalcociliellus*. Thus, in the natural ecosystem of these stem borer species, *C. partellus* may be a more efficient dispersant than *C. orichalcociliellus*. Hence, the newly hatched larvae of *C. partellus* may have a higher chance of being able to escape the adverse effects of physical and natural mortality factors by dispersing in great numbers at a fast rate to locate adjacent host plants suitable for their establishment for further feeding and development. On the other hand, *C. orichalcociliellus*, a less efficient dispersant is likely to be more prone to adverse mortality factors on failing to reach other host plants in which it gets established for further feeding and development.

Newly hatched first instar larvae of *C. partellus* and *C. orichalcociliellus* exhibited differences in dispersal depending on the host plant. Similar reports by other workers have shown that subsequent dispersals of the larvae of most insects are influenced by, among other factors, the host plant related characteristics. Robinson *et al*. (1978) investigated the dispersal of the European corn borer, O*strinia nubilalis* (Hübner), in maize and demonstrated that dispersal differed according to the maize cultivar. More larvae were observed dispersing from resistant maize hybrids and this was related to the content of the resistance factor DIMBOA, since this chemical requires biting of the plant and subsequent hydrolysis to be effective. This implies that corn borer larvae feed before dispersal. Ramachandran (1987) evaluated the influence of host plant on the wind dispersal and survival of first instar larvae of *E. excursaria* and concluded that the dispersal differed in different host plants. He related the host-influenced dispersal of *E. excursaria* to the suitability of the plants/plant parts for the insect's establishment and survival. Host plant nutritional quality does not seem to be an influential factor in the initial host-plant dispersal of newly hatched first instar larve of *C. partellus* and *C. orichalcociliellus*, which agrees with a previous finding that *Chilo* larvae do not feed before leaving the plant (COPR/ICRISAT, 1977) or establishing inside the plant (Berger, 1989a). The host plant differential dispersal of larvae of *C. partellus* and *C. orichalcociliellus* may have been effected by surface characters of the host plants and probably inherent characteristics of the stem borer species.

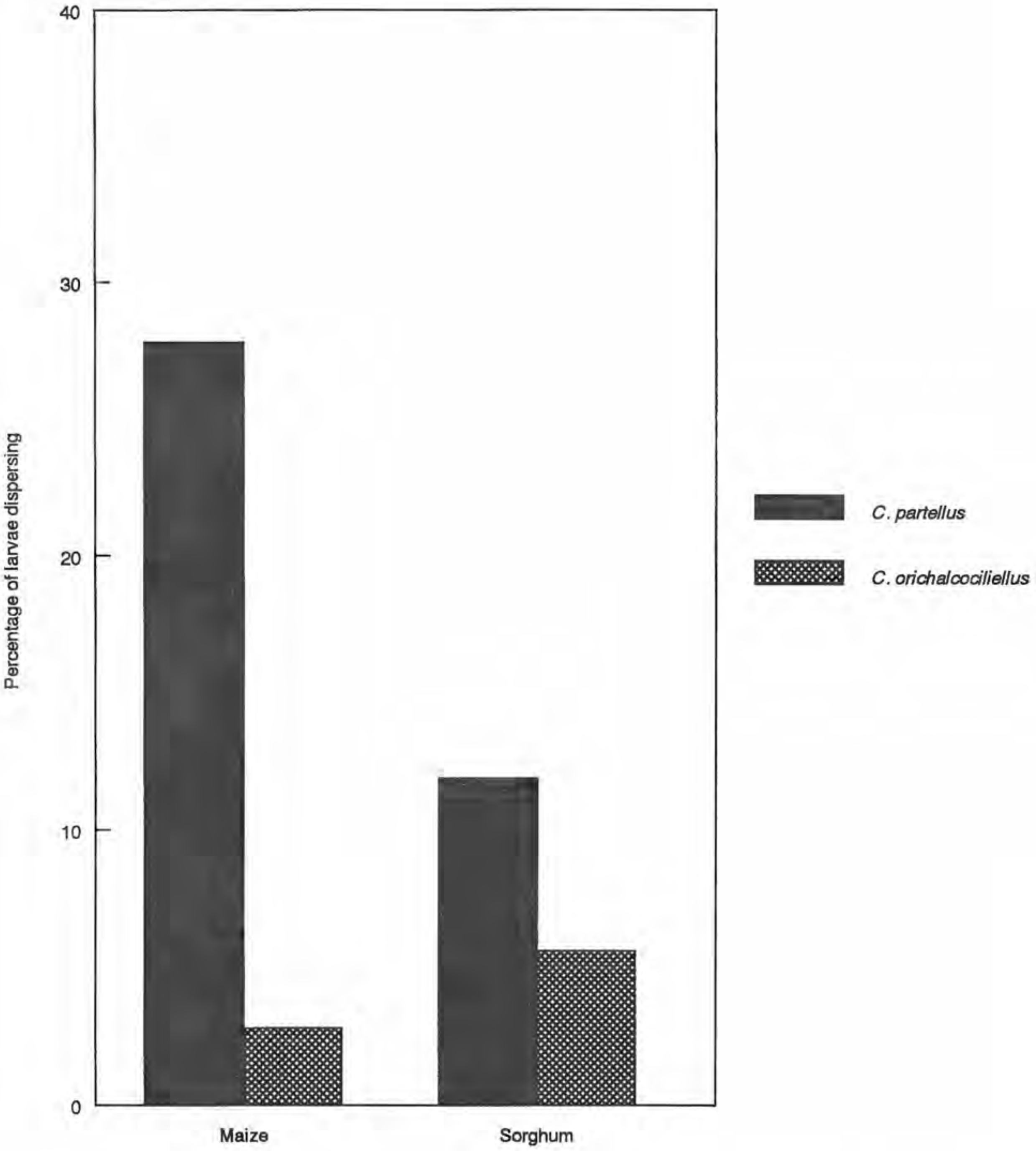

Figure 6.1 Percentages of newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from maize and sorghum plants.

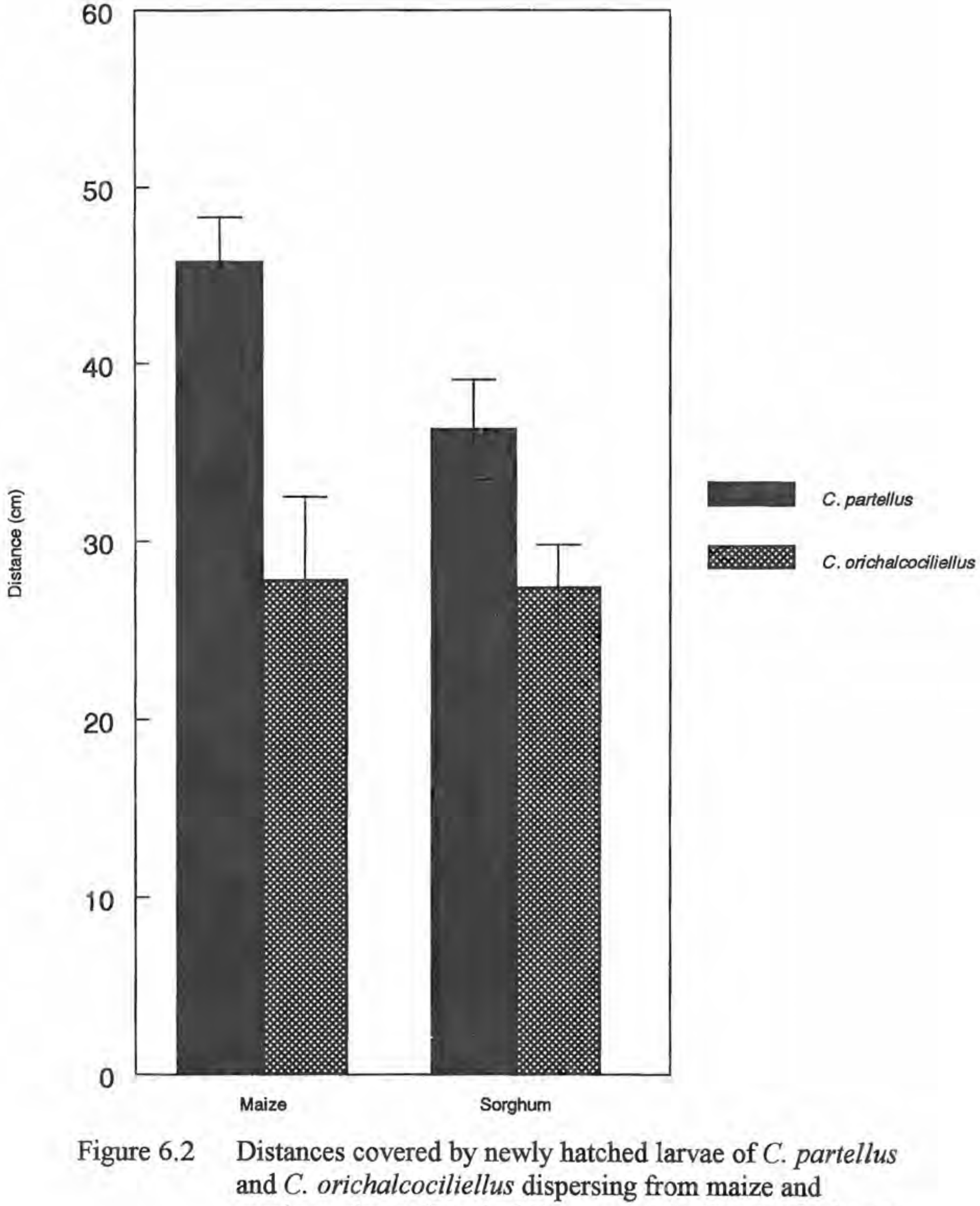

Figure 6.2 Distances covered by newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from maize and sorghum plants. (Vertical lines represent the standard error values).

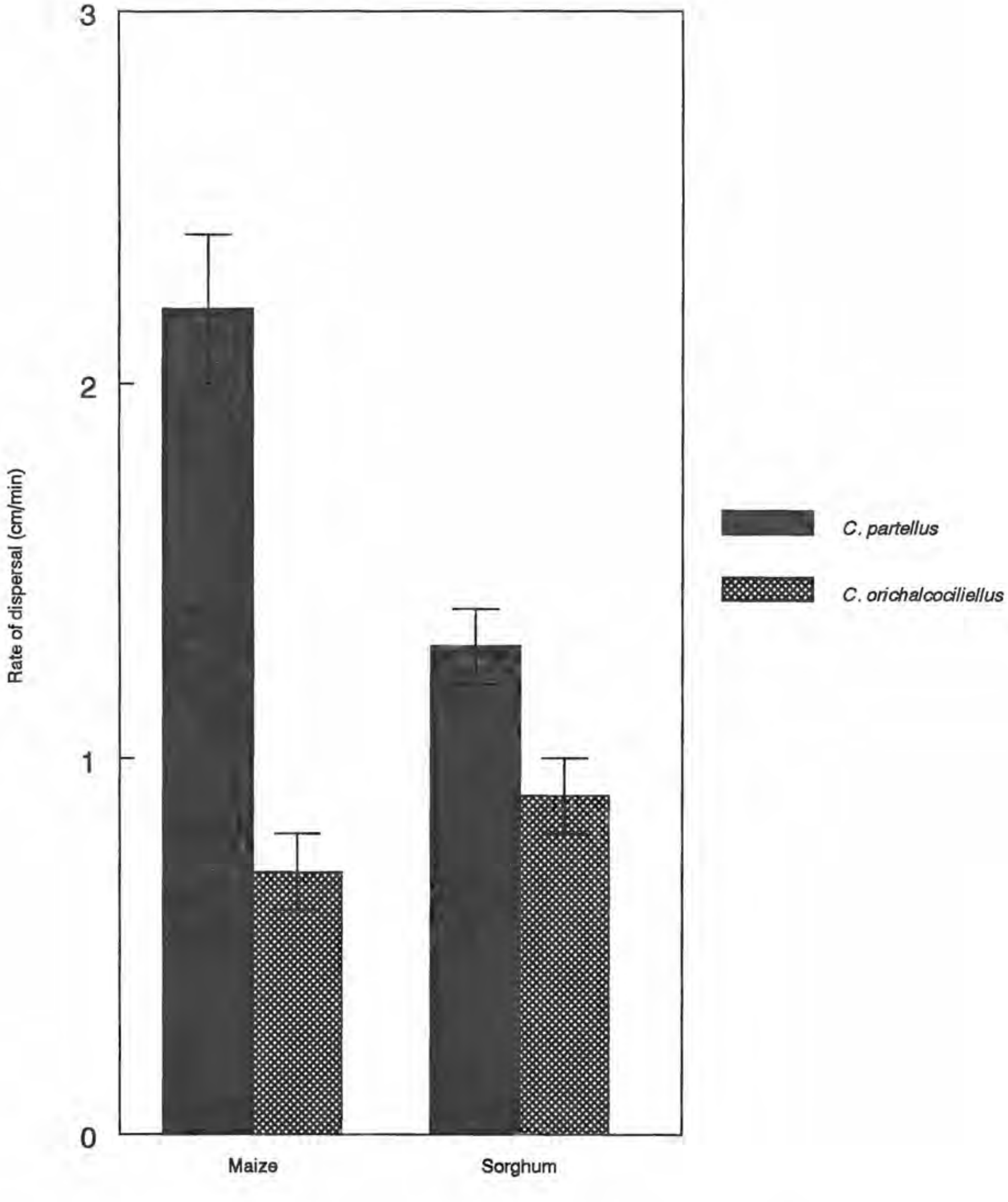

Figure 6.3 Rate of dispersal of newly hatched larvae of *C. partellus* and *C. orichalcociliellus* from maize and sorghum plants. (Vertical lines represent the standard error values).

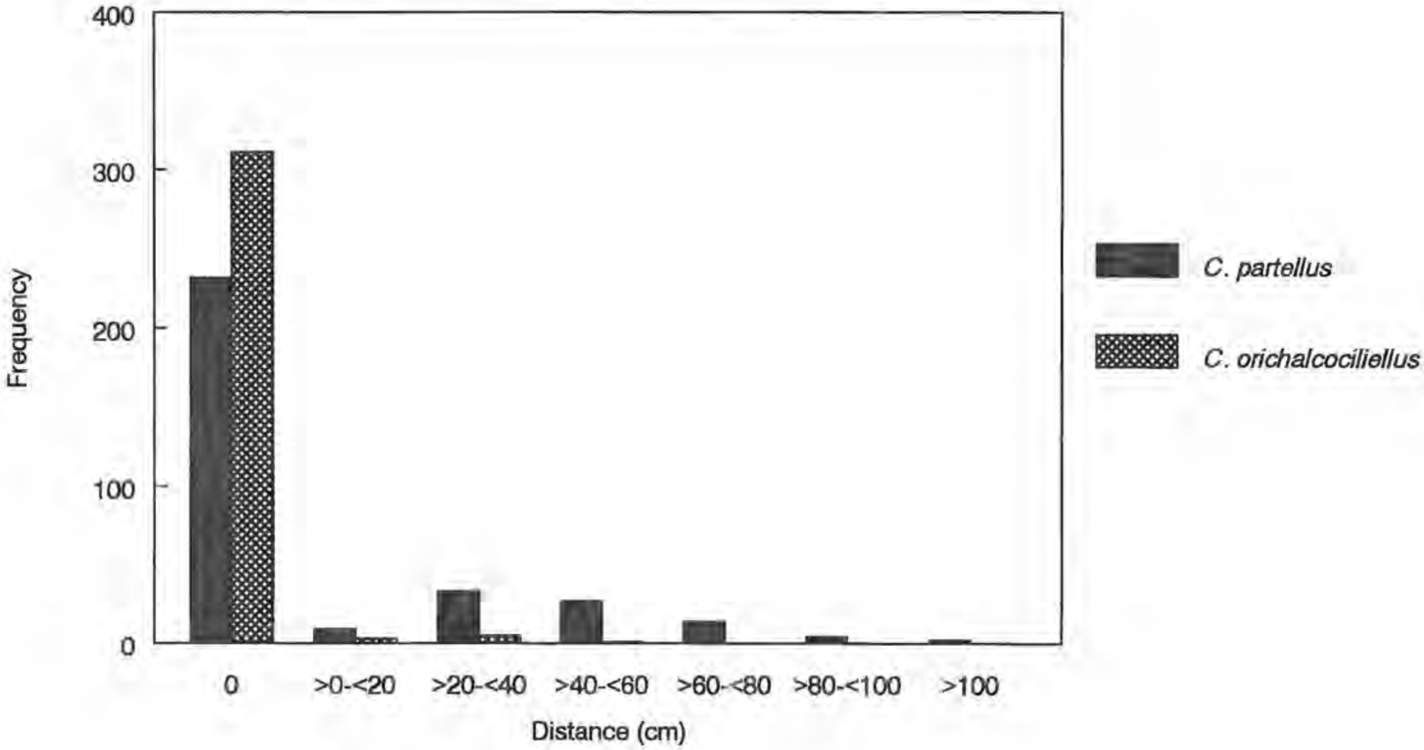

Figure 6.4 Frequency distribution of distances covered by newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from maize plants.

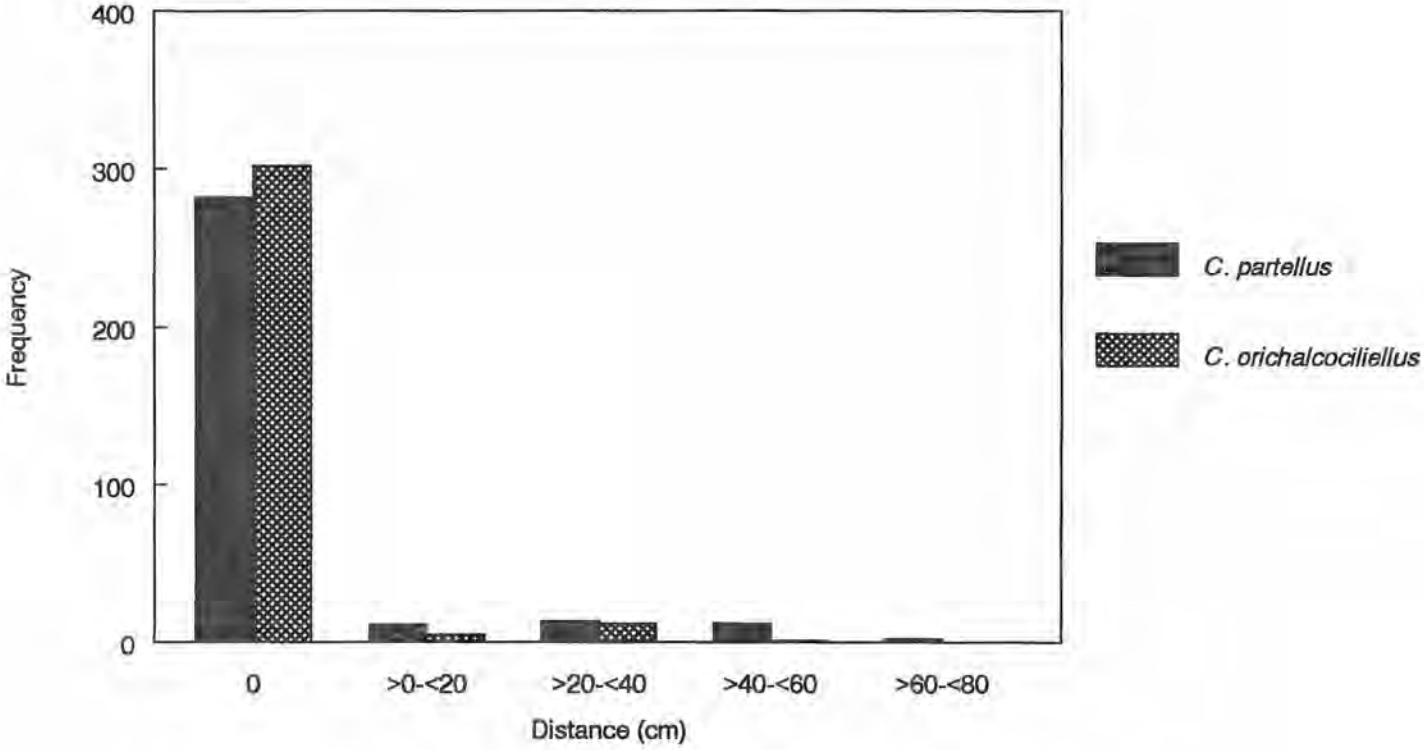

Figure 6.5 Frequency distribution of distances covered by newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from sorghum plants.

CHAPTER SEVEN

7.0 Colonization successes of *C. partellus* and *C. orichalcociliellus* in cultivated and wild host plants.

7.1 Introduction

Host plants may vary in their acceptability and suitability to an oligophagous insect (Hough and Pimentel, 1978; Barbosa and Greenblatt, 1979). Thus, individuals of an oligophagous insect may be expected to show a certain degree of selectivity in the choice of food plants. To this effect, the survival of many insects, including stem borers, depends to a large extent on the ability of the adult females to locate and select suitable host plants for oviposition. Subsequently, this will lead to successful establishment of the young individuals in the host plants for further feeding and development.

C. partellus and *C. orichalcociliellus* are major pests of maize and sorghum, which are transient crops grown in a permanent mosaic of native wild grasses. During non-cropping seasons, these stem borers may enter diapause in crop residues (Wheatly, 1961; Delobel, 1975a; Scheltes, 1978; Warui and Kuria, 1983; Kfir, 1991a, b; Kfir, 1993a, b). Some of them however, continue their life cycle in alternative wild grasses. Different graminaecous plants have been reported to influence the colonization responses of many stem borer species, including adult orientation and oviposition, larval arrest, establishment, feeding, development and survival (Ampofo, 1985). Preferential oviposition by stem borers has been reported in different host plants (Alghali, 1988; Khan, unpublished data) and in different cultivars of a plant (Sharma and Chatterji, 1971; Kumar, 1988a b; Alghali, 1988; Kumar *et al*, 1993). Variations also occur in relation to plant phenology (Ampofo, 1985). Oviposition and larval behaviour of the stem borer, *C. partellus*, on different varieties of maize have been studied by several workers (Sharma and Chatterji, 1971; Singh and Sandhu, 1978; Kumar, 1986). The ovipositional responses of *C. partellus* to sorghum plants have been reported (Lal and Pant, 1980; Dabrowski and Kidiavai, 1983; Singh and Rana, 1984) though inadequately. Ovipositional response studies of *C. partellus* have been conducted on susceptible and resistant maize and sorghum genotypes and cultivars (Durbey and Sarup, 1982; Ampofo, 1985; Kumar, 1988a, b; Alghali, 1988). The colonization responses of *C. partellus* with reference to adult oviposition, larval arrest and establishment, larval feeding and development have been studied under the screenhouse and field conditions in various resistant cultivars of maize with varying results (Kumar *et al*., 1993).

The ability of an insect species to locate and select suitable host plants for oviposition and for the young individuals to successfully establish in the plants, is essential for the future development and survival of that particular insect species. The present study investigates the colonization successes of *C. partellus* and *C. orichalcociliellus* with reference to their larval establishing abilities in cultivated and wild host plants.

7.2 Materials and Methods

The experiments were conducted at the International Centre of Insect Physiology and Ecology (ICIPE) field station at Muhaka, Kenya (40 m above sea level, Lat. 4^0S, Long. 39^0E). The insects used in the study were obtained from cultures of *C. partellus* and *C. orichalcociliellus* maintained on artificial diet (Ochieng *et al*, 1985) at the ICIPE insectary. Two cultivated host plants, maize, *Z. mays*, and sorghum, *S. bicolor*, one cultivated wild host, napier grass, *P. purpureum*, and another wild host, wild sorghum, *S. arundinaceum*, were used in this experiment. Early maturing varieties, Coast Composite and Serena were used for maize and sorghum respectively. For maize, sorghum and wild sorghum plants, the seeds were sown. For napier grass, plants were propagated through young seedings. Each plant species was grown in three plots. Plot sizes were 3.0 by 3.0 metres, with five rows (two guard rows and three inner rows) and ten plants on a row. Plants were grown 30 cm apart within rows and 75 cm between rows. Plots were covered with 2.5 metres metal frame cages, made of 400 micron diameter nylon mesh, to avoid infestation of plants from natural populations. The plots were manually kept free of weeds and were irrigated when necessary using an overhead sprinkler.

Four weeks after plant emergence, all plants (a total of thirty plants) in the three inner rows of each cage were infested with 10 neonate larvae. Plants aged 3-4 weeks after germination have been reported to be preferred by *C. partellus* for oviposition than other age groups (Singh and Sandhu, 1978; Dabrowski and Nyangiri, 1983). *C. orichalcociliellus* also prefers 3-4 week old plants for oviposition (Personal observation). To infest the plants, 10 neonate larvae was placed in the inner whorl leaf where they settle for subsequent establishment in the plant. For each plant species, there were three treatments; each infested plant in a plot receiving five *C. partellus* and five *C. orichalcociliellus* larvae, ten *C. partellus* or ten *C. orichalcociliellus* larvae. Ten plants from each plot were systematically selected at 3, 10, and 21 days after the infestation, removed, and carefully dissected. The number of larvae recovered from each plant on each sampling date was recorded. All the stem borers recovered on each sampling date were later identified and the stem borer species noted. The number of larvae recovered were converted to a percentage of the number infested and subjected to arcsine transformation. A t-test was performed to detect any difference in the percentage establishment of *C. partellus* and *C. orichalcociliellus* in the different host plants. Data were also subjected to an analysis of variance using the General Linear Model (GLM) procedure to determine the percentage establishment of each species in the different host plants. Means were separated using the Student-Newman-Keul (SNK) multiple range test at 5% level of significance.

7.3 Results

First instar larvae of *C. partellus* and *C. orichalcociliellus* infested on the leaf whorl of maize, sorghum, napier grass and wild sorghum plants established themselves in the plant within three days after infestation. Comparisons of the establishing successes of *C. partellus* and *C. orichalcociliellus* while colonizing these plants alone showed that the percentage of larvae of *C. partellus* and *C. orichalcociliellus* recovered three days after infestation was the same in all plants except in wild sorghum plants where *C. partellus* had a higher establishing ability than *C. orichalcociliellus* (Table 7.1). In sorghum plants, the percentages of *C. partellus* and *C. orichalcociliellus* larvae recovered after 10 and 21 days of infestation were not significantly different whereas, in maize, napier grass and wild sorghum plants, differences were found in the percentages of *C. partellus* and *C. orichalcociliellus* larvae recovered with *C. partellus* having a higher establishing ability in all the plants except in napier grass, where a higher percentage of *C. orichalcociliellus* was recovered (Table 7.1).

In cases where first instar larvae of *C. partellus* and *C. orichalcociliellus* were infested in the same plant and allowed to establish, higher percentages of *C. partellus* compared to *C. orichalcociliellus* larvae were recovered on most of the sampling dates, for all the plants except napier grass which had a higher recovery of *C. orichalcociliellus* larvae (Table 7.2). However, in sorghum and napier grass, no difference was found in the percentage recovery of the species on the third day after infestation. When *C. partellus* and *C. orichalcociliellus* were allowed to establish in the same plant, lower percentages of each of the species were recovered in all plants within recovery days compared to when they were colonizing the plants alone.

Examination of the percentage of larvae of *C. partellus* and *C. orichalcociliellus* recovered in different host plants showed that for each stem borer species, the trend of establishment in the different plants was similar irrespective of whether the species was colonizing the plants alone or in combination with another species. For *C. partellus*, the percentage of larvae recovered on the different dates was always highest in maize plants. In most cases, establishment of *C. partellus* larvae in sorghum and wild sorghum were equal. Lowest recoveries of *C. partellus* larvae were in napier grass (Tables 7.3a and b). For *C. orichalcociliellus* the percentage recovery was also highest in maize, although in some cases the percentage recovery of *C. orichalcociliellus* larvae was the same in maize, sorghum and wild sorghum. The establishment of *C.orichalcociliellus* larvae in napier grass plants was comparable to its

establishment in sorghum and wild sorghum plants (Tables 7.4a and b).

7.4 Discussion

The results of this study showed clear differences in the establishing abilities of *C. partellus* and *C. orichalcociliellus* in all the plants. *C. partellus* had an advantage over *C. orichalcociliellus*, having greater establishing ability in maize, sorghum and wild sorghum. To this effect, more *C. partellus* larvae may have been able to escape the adverse physical and natural mortality factors than *C. orichalcociliellus*. These results suggest that in the next generation of these stem borers, *C. partellus* population density may be higher than the population of *C. orichalcociliellus*, if all other mortality factors occurring in later stages are equal. In napier grass, however, *C. orichalcociliellus* had a higher establishing ability than *C. partellus*. The results of this study are in agreement with that of Overholt (Unpublished data) who recorded higher population densities of *C. partellus* compared to *C. orichalcociliellus* in all plants except napier grass, during sampling at the coastal areas of Kenya.

All plants used in this experiment have been reported to habour *C. partellus* and *C. orichalcociliellus*. All the same, the observations presented above show differences among the host plants investigated with respect to the extent of establishment of *C. partellus* and *C. orichalcociliellus*. Establishment of both stem borer species was highest on maize, reflecting the high suitability of this plant. Results on the developmental times of *C. partellus* and *C. orichalcociliellus* reared on cultivated and wild host plants showed that *C. partellus* and *C. orichalcociliellus* developed faster and survived more on maize compared to sorghum, wild sorghum, napier and guinea grasses (Chapter 8). Ampofo (1985) reported that ovipositional preference and larval establishment are responsible for determining the susceptibility and resistance of various varieties of maize to *C. partellus*. According to Saxena (1990), low levels of larval arrest on a plant reflect an insect's non-preference for that particular plant and this hampers colonization of the plant. The present study revealed a low level of establishment of *C. partellus* and *C. orichalcociliellus* in napier grass, suggesting the relative non-suitability of this host. Non-preference reduces an insect's three major behavioural responses; these are, oviposition, orientation and feeding, which are involved in the initial three stages of colonization of a plant (Saxena, 1985).

In maize and wild sorghum *C. partellus* was recovered in higher numbers than *C. orichalcociliellus* from 3 days after infestation. In the other plants, the lack of difference at 3 days after infestation may be attributed to equal mortalities of larvae of both species in these plants. The lower establishment of *C. partellus* compared to *C. orichalcociliellus* in napier grass at 10 and 21 days after infestation, suggests that napier grass is a more suitable host for *C.*

orichalcociliellus. Developmental studies showed that *C. orichalcociliellus* completed development on napier grass, although survival was very low, whereas, *C. partellus* did not succeed in completing development in napier grass.

Table 7.1 Larval establishment (±std) of *C. partellus* and *C. orichalcociliellus* in different host plants.

Days after infestation		Percentage of larvae recovered															
		Host plants															
		Maize				Sorghum				Napier grass				Wild sorghum			
	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co
3	50	76.4± 22.5a	30	71.3± 20.8a	50	68.4± 20.5a	10	66.0± 21.2a	50	36.2± 15.1a	20	53.0± 13.4a	30	71.3± 28.0a	20	62.0± 11.1b
10	50	60.2± 13.9a	30	53.0± 22.9b	50	42.4± 12.7a	10	43.0± 10.6a	50	25.6± 13.0b	20	32.5± 17.8a	30	49.7± 21.4a	20	47.0± 10.0b
21	50	50.4± 16.7a	30	49.3± 22.6b	50	32.4± 13.8a	10	25.0± 15.8a	50	19.4± 9.1b	20	27.0± 12.2a	30	36.3± 14.7a	20	35.5± 9.4b

For each host plant, means in the same row with different letters are significantly different P≤ 0.05.

Cp, *Chilo partellus* Co, *Chilo orichalcociliellus*

Table 7.2 Larval establishment (±std) of *C. partellus* and *C. orichalcociliellus* colonizing the same plant in different host plants.

	Percentage of larvae recovered															
Days after infestation	Host plants															
	Maize				Sorghum				Napier grass				Wild sorghum			
	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co	N	Cp	N	Co
3	30	66.7± 31.2a	30	64.7± 10.1b	50	51.2± 17.7a	50	48.8± 16.2a	30	31.3± 12.5a	30	41.3± 14.8a	30	41.3± 21.6a	30	38.7± 12.8b
10	30	54.7± 34.4a	30	34.0± 16.7b	50	41.0± 11.0a	50	28.0± 22.5b	30	19.3± 3.7b	30	29.3± 10.1a	30	36.7± 16.7a	30	20.7± 8.3b
21	30	36.7± 15.8a	30	24.0± 10.0b	50	28.8± 11.5a	50	18.0± 21.9b	30	18.0± 6.1b	30	26.7± 13.2a	30	26.7± 14.2a	30	12.7± 10.0b

For each host plant, means in the same row with different letters are significantly different P ≤ 0.05.

Cp, *Chilo partellus* Co, *Chilo orichalcociliellus*

Table 7.3a Larval establishment (±std) of *C. partellus* while alone in different host plants.

Host plants	Percentage of larvae recovered Number of days after infestation 3	 10	 21
Maize	76.4±22.5a	60.2±13.9a	50.4±16.7a
Sorghum	68.4±20.5a	42.4±12.7c	32.4±13.8b
Napier grass	36.2±15.1b	25.6±13.0d	19.4±9.1c
Wild sorghum	71.3±28.0a	49.7±21.4b	36.3±14.7b
F-value	27.89	38.01	33.18
Pr > F	0.0001	0.0001	0.0001

Means in the same column with different letters are significantly different P ≤ 0.05.

Table 7.3b Larval establishment (±std) of *C. partellus* while with *C. orichalcociliellus* in different host plants.

Host plants	Percentage of larvae recovered Number of days after infestation 3	 10	 21
Maize	66.7±31.2a	54.7±34.4a	36.7±15.8a
Sorghum	51.2±17.7b	41.2±11.0b	28.8±11.5b
Napier grass	31.3±12.5c	19.3±3.6c	18.0±6.1c
Wild sorghum	41.3±21.6bc	36.7±16.7b	26.7±14.2b
F-value	18.82	17.23	11.62
Pr > F	0.0001	0.0001	0.0001

Means in the same column with different letters are significantly different P ≤ 0.05.

Table 7.4a Larval establishment (±std) of *C. orichalcociliellus* while alone in different host plants.

Host plants	Percentage of larvae recovered Number of days after infestation 3	 10	 21
Maize	71.3±20.8a	53.0±22.9a	49.3±22.6a
Sorghum	66.0±21.2ab	43.0±10.6ab	25.0±15.8b
Napier grass	53.0±13.4b	32.5±17.7b	27.0±12.2b
Wild sorghum	62.0±11.1ab	47.0±10.0a	35.5±9.4b
F-value	5.13	4.99	8.60
Pr > F	0.0028	0.0033	0.0001

Means in the same column with different letters are significantly different P ≤ 0.05.

Table 7.4b Larval establishment (±std) of *C. orichalcociliellus* while with *C. partellus* in different host plants.

Host plants	Percentage of larvae recovered Number of days after infestation 3	 10	 21
Maize	64.7±10.1a	34.0±16.7a	24.0±10.0a
Sorghum	48.8±16.2b	28.0±22.5ab	18.0±21.9ab
Napier grass	41.3±14.8c	29.3±10.1ab	26.7±13.2a
Wild sorghum	38.7±12.8c	20.7±8.3b	12.7±10.0b
F-value	21.32	2.72	3.29
Pr > F	0.0001	0.0471	0.0226

Means in the same column with different letters are significantly different P ≤ 0.05.

CHAPTER EIGHT

8.0 Larval development of *C. partellus* and *C. orichalcociliellus* in cultivated and wild host plants.

8.1 Introduction

Competitive displacement is considered in relation to the growth rates and generation times of the competing species, as well as to the rate at which environmental conditions relevant to the species fluctuate. The development of phytophagous insects depends to a large extent on the nutritional quality of the host plant (Schulthess *et al.*, 1993). The effect of host plant quality on growth, development and reproduction of phytophagous insects is not always predictable. Highly variable results have been obtained for different insects and host plants, with respect to the effect of various nutritional conditions (Schulthess *et al.*, 1993). In addition to maize and sorghum, it has been reported that a number of alternative cultivated and wild grasses provide habitats for *C. partellus* and *C. orichalcociliellus* during the dry season when maize and sorghum are not availablle (Seshu Reddy, 1989; Shanower *et al.*, 1993; Khan, unpublished data). However, the quality and quantity of these crops available as food for stem borer development and survival vary greatly owing to differences in the morphology, physiology and biochemistry of these plants. Consequently, variations have been reported regarding the rate of development and survival of stem borers in the different host plants, which in turn affect the overall abundance of the stem borer species.

Comparative laboratory investigations on the development of *C. partellus* and *C. orichalcociliellus* on an artificial diet revealed that *C. partellus* completed a generation in a shorter time than *C. orichalcociliellus* (Kioko *et al*, 1995). Mbapila (1997) compared the developmental times of *C. partellus* and *C. orichalcociliellus* in maize and found that *C. partellus* completed a generation in a shorter time than *C. orichalcociliellus* at 31^{0}C. He reported a higher intrinsic rate of increase for *C. partellus*, which was primarily due to its shorter developmental time. Information on the development of *C. partellus* and *C. orichacociliellus* on other host plants may be useful in explaining recent changes in the population densities of these stem borer species. The present study, thus, compared the developmental times and survival of *C. partellus* and *C. orichalcociliellus* in cultivated and wild host plants under laboratory conditions.

8.2 Materials and Methods

Larvae used in this experiment originated from colonies maintained on artificial diet (Ochieng *et al*., 1985) at the ICIPE insectary. Three cultivated grass hosts, maize, *Z. mays*, sorghum, *S. bicolor*, and napier grass, *P. purpureum*., and two wild grass hosts, wild sorghum, *S. arundinaceum*, and guinea grass, *P. maximum*, were infested with neonate larvae. First instar larvae of each of the borer species were placed individually in glass vials on leaf whorls. From the third instar, larvae were reared on pieces of fresh stems until death or pupation. Larvae were maintained at different temperatures of 25, 28 and 31^{0}C and a photoperiod of L12:D12. Larvae were inspected every other day for signs of ecdysis and to change the diet. The number of larvae surviving to pupation was recorded for each plant. Pupae were weighed and placed in a clean, dry vial for adult emergence. Developmental time of the various larval stadia, pupa and adult were recorded. Larvae that died at the first larval instar were not included in the analysis. Analysis of variance (ANOVA) was performed to compare the larval developmental period and survival between borer species for each host plant, and between host plants for each borer species. Mean separation was carried out using the Student-Newman-Keul (SNK) multiple range test. A G-test of independence was performed to detect any differences in the number of larvae of *C. partellus* and *C. orichalcociliellus* surviving in the different host plants.

8.3 Results

8.3.1 Host plant and stem borer development.

The developmental periods of *C. partellus* and *C. orichalcociliellus* varied depending on the host plant on which they were reared. The mean time taken by *C. partellus* and *C. orichalcociliellus* to complete different larval stadia showed similar trends in the different host plants. For both stem borer species, the mean time taken to complete different larval stadia was similar in maize and sorghum plants except in a few larval stadia (Tables 8.1 and 8.2). There was a significant difference in time taken to complete different larval stadia for each stem borer species between maize, sorghum and the wild grasses. The time taken was longer in the wild grasses, especially in napier grass and wild sorghum compared to maize and sorghum (Tables 8.1 and 8.2). Comparison of the larval to adult developmental times of *C. partellus* and *C. orichalcociliellus* in the different host plants showed that *C. partellus* completed larval development in a shorter time than *C. orichalcociliellus* when reared on maize, sorghum and wild sorghum plants (Table 8.3). The larval to adult developmental time of the stem borer species could not be compared in napier and guinea grasses since *C. partellus* did not survive to the pupal stage on these grasses. For both *C. partellus* and *C. orichalcociliellus*, larval development was faster in maize than the other host plants (Table 8.3). The mean number of moults for *C. orichalcociliellus* in maize, sorghum and wild sorghum was higher compared to *C. partellus* (Table 8.4). *C. partellus* completed a maximum of seven moults in maize and sorghum but moulting in the wild grasses was rarely beyond the sixth larval instar (Table 8.1). *C. orichalcociliellus* completed a maximum of eight larval instars in maize and guinea grass and ten instars in sorghum. In napier grass, moulting continued until the eleventh instar in some individuals with a mean developmental period of 83.5 days (Table 8.2).

8.3.2 Host plant and stem borer survival.

Survival of *C. partellus* and *C. orichalcociliellus* was higher in maize than the other host plants (Table 8.5). Percentage pupation in maize and sorghum was about the same for the two stem borer species. Larval survival in napier and guinea grasses was low for both species. *C. partellus* larvae did not survive to the pupal stage in napier and guinea grasses and 13.5% pupated in wild sorghum. No significant difference was found in the survival of *C. partellus* and *C. orichalcociliellus* in all the plants except in napier grass, where only *C. orichalcociliellus* survived (Table 8.5).

8.4 Discussion

The host plants tested in this experiment differed in their suitability for borer development and survival. Larval development was faster in maize than in sorghum, napier grass, wild sorghum and guinea grass. Shanower *et al.* (1993) reported similar larval periods for two different stem borers, *S. calamistis* and *E. saccharina* on maize and wild grasses, but noted that larval development was 50% faster on artificial diet. Maize was the best host for both borer development and survival. When larvae were reared on sorghum and wild grasses, larval survival was lower than when reared on maize. Shanower *et al.* (1993) compared life table parameters of *S. calamistis* and *E. saccharina* feeding on maize, wild grasses and artificial diet. They reported that larval survival was higher on artificial diet compared to maize and wild grasses. However, maize was a better host for stem borer survival than the wild grasses. They reported that mortality on wild hosts varied between 94 and 99% compared to 70% on maize. Results of the present study on the survival of *C. partellus* and *C. orichalcociliellus* in maize and wild grasses are similar to the results obtained by Shanower *et al.* (1993). Maize is an exotic plant in Africa which has only recently been widely cultivated in East Africa (Purseglove, 1972; Dowswell *et al.*, 1996). It appears that the introduction of this plant, which has no evolutionary history with Old World stem borers, has provided a highly nutritional resource for stem borers, and is likely to have resulted in increased stem borer densities.

Differences in growth and development of Lepidoptera larvae reared on different plant species have been reported. For example, it was demonstrated that leaves of the beet are superior for growth of the cabbage armyworm, *Mamestra brassicae* L., than leaves of sweet potato (Hirano and Noguchi, 1963). Similarly, plants may differ intraspecifically according to variety, conditions for growth and age. *C. partellus* (Kalode and Pant, 1966), *Ostrinia nubilalis* (Hbn.) (Bottger, 1951) and several rice borers, including *Chilo plejadellus* Zincken (Oliver and Gifford, 1975) and *Chilo suppressalis* Walker (Das, 1976) have performed differently on different species of Graminae. In this study *C. partellus* and *C. orichalcociliellus* developed fastest and survival was highest in maize. When reared on wild grasses, *C. partellus* performed better on wild sorghum, while napier grass was a better host for *C. orichalcociliellus*. Survival of both stem borers was low on guinea grass.

Wild grass hosts of stem borers may be of less nutritional quality than the cultivated hosts. McNaughton *et al.* (1985) reported a higher silica content in natural grass hosts of stem borers and a low content in maize. Silica has been shown to play an important role in strengthening the cell walls of plants (Painter, 1951) and in enhancing resistance of the plant to pests and diseases. High larval mortality of *C. suppressalis* has been reported on rice varieties with high silica content (Djamin and Pathak, 1967). Larvae of the yellow rice borer, *Scirpophaga incertulas* (Walker), were unable to attack resistant rice plants because of the high silica content of their stems (Panda *et al.*, 1975). The poor quality of the grasses may have contributed to the prolonged development and low survival of *C. partellus* and *C. orichalcociliellus*. Usua (1973) reported that the nutritionally inadequate food condition provided by developing maize stems was thought to lengthen the larval development of *B. fusca*. Hill (1983) reported slower development of *C. partellus* larvae on plants of poor quality.

C. orichalcociliellus moulted more often over longer periods in all the plants than *C. partellus*. This may have prolonged its total generation time compared to *C. partellus*. Kioko *et al.* (1995) reported that the difference in the larval developmental periods between the two species on an artificial diet would result in an overall shorter generation time for *C. partellus* if the egg, pupal and preovipositional periods of *C. partellus* and *C. orichalcociliellus* were the same, which appeared to be the case (Berger, 1989a; Delobel, 1975b; Neupane *et al*, 1985). The results of the present study indicating a shorter larval developmental time of *C. partellus* compared to *C. orichalcociliellus* in maize, sorghum and wild sorghum confirm previous studies by Kioko *et al.* (1995) and Mbapila (1997) on artificial diet and maize, respectively. Intrinsic rate of increase is an important factor in the ability of one species to exclude or displace another. Mbapila (1997) reported that *C. partellus* had a higher intrinsic rate of increase than C. *orichalcociliellus* at all temperatures except 31°C. The higher rate of population growth was due primarily to the shorter life cycle of *C. partellus*. The relatively faster development of *C. partellus* compared to *C. orichalcociliellus* in cultivated and wild grasses may be an important factor in the displacement process. However, the ability of *C. orichalcociliellus* to complete development in two native grasses in which *C. partellus* did not survive, may give this species an advantage over *C. partellus*. Debach *et al*. (1978) noted that if the reproductively inferior ecological homologue in a given habitat had an alternate host or a spatial refuge suitable only to itself, it would survive and apparently coexist because of these differences. The differential survival in wild grasses may therefore be an important factor that has allowed *C. orichalcociliellus* to escape extirpation from the Kenya coast.

Table 8.1 The developmental time (mean±std) of *C. partellus* to reach various larval stadia, pupa and adult in different host plants.

				Mean time in days				
Host plants	L2	L3	L4	L5	L6	L7	Pupa	Adult
Maize	4.9d± 1.46	9.1d± 2.57	13.2b± 3.24	17.4b± 3.76	20.1c± 3.14	24.3a± 6.18	25.1b± 5.40	31.9b± 5.91
Sorghum	5.2cd± 1.73	9.8cd± 2.86	14.7b± 3.86	20.0b± 4.00	24.7b± 3.36	31.5a± 0.71	31.5a± 5.48	39.3a± 6.35
Napier grass	5.9b± 1.96	11.8b± 3.53	18.7a± 5.30	24.6a± 11.07	38.7a± 12.01	- -	- -	- -
Wild sorghum	6.4a± 2.18	14.4a± 4.15	18.4a± 3.02	26.7a± 5.03	- -	- -	32.0a± 7.81	39.7a± 7.37
Guinea grass	5.6bc± 1.41	11.1bc± 4.54	19.0a± 6.68	- -	- -	- -	- -	- -
F-value	12.67	18.17	17.42	11.73	40.97	2.43	11.16	11.43
Pr > F	0.0001	0.0001	0.0001	0.0001	0.0001	0.1939	0.0001	0.0001

Means in the same column with different letters are significantly different $P \leq 0.05$

Table 8.2 The developmental time (mean±std) of *C. orichalcociliellus* to reach various larval stadia, pupa and adult in different host plants

				Mean time in days								
Host plants	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	Pupa	Adult
Maize	5.4c±	9.7c±	14.5d±	19.1c±	22.7b±	34.6a±	46.0a±	-	-	-	31.4b±	38.8b±
	1.44	2.52	3.31	4.44	6.07	9.80	8.49	-	-	-	9.79	10.47
Sorghum	6.0bc±	12.4b±	16.8cd±	22.8b±	32.1b±	41.2a±	48.0a±	56.3a±	64.5a±	-	39.6ab±	47.3b±
	2.06	3.75	4.19	5.24	13.37	3.43	5.20	5.51	3.54	-	12.20	12.08
Napier grass	6.3b±	12.4b±	18.8bc±	26.7b±	32.9b±	42.4a±	50.0a±	55.3a±	64.0a±	83.5±	56.8a±	70.0a±
	1.87	3.13	4.10	4.46	4.42	5.84	6.60	6.95	8.83	0.71	14.77	7.81
Wild sorghum	7.1a±	14.9a±	22.1a±	35.6a±	47.0a±	-	-	-	-	-	54.0a±	61.7ab±
	2.33	5.02	6.87	10.83	0.00	-	-	-	-	-	11.27	10.79
Guinea grass	5.6c±	12.5b±	19.9ab±	25.4b±	31.3b±	37.0a±	56.0a±	-	-	-	34.0b±	46.0b±
	2.06	4.33	8.01	5.96	4.57	5.66	0.00	-	-	-	0.00	0.00
F-value	13.90	24.80	21.54	33.28	16.97	2.85	0.59	0.05	0.01	-	10.47	10.45
Pr > F	0.0001	0.0001	0.0001	0.0001	0.0001	0.0521	0.6351	0.8357	0.9437	-	0.0001	0.0001

Means in the same column with different letters are significantly different P ≤ 0.05

Table 8.3 Larval to adult developmental times (mean±std) of *C. partellus* and *C. orichalcociliellus* reared on different host plants.

		Mean time in days				
Host plants		Stem borer species			F-value	Pr > F
	N	*C. partellus*	N	*C. orichalcociliellus*	(row-wise)	(row-wise)
Maize	84	31.9±5.91Bb	88	38.8±10.47Ba	28.20	0.0001
Sorghum	15	39.3±6.35Ab	12	47.3±12.08Ba	4.89	0.0363
Napier grass	0	-	3	70.0±7.81A	-	-
Wild sorghum	3	39.7±7.37Ab	3	61.7±10.79Ba	8.51	0.0434
Guinea grass	0	-	1	46.0±0.00B	-	-
F-value (column-wise)		11.43		10.45		
Pr > F (column-wise)		0.0001		0.0001		

1 Means followed by different upper case letters in the same column are significantly different P ≤ 0.05.

2 Means followed by different lower case letters in the same row are significantly different P ≤ 0.05.

Table 8.4 Number of instars (mean±std) of *C. partellus* and *C. orichalcociliellus* reared on different host plants

	Mean number of instars					
Host plant	Stem borer species				F-value	Pr > F
	N	*C. partellus*	N	*C. orichalcociliellus*	(row wise)	(row wise)
Maize	115	4.7±1.42Ab	114	5.3±0.90Ba	14.13	0.0002
sorghum	15	5.7±0.59Ab	12	6.7±1.74ABa	4.28	0.0494
Napier grass	0	-	4	7.8±1.71A	-	-
Wild sorghum	3	4.7±0.58Ab	3	6.0±0.00ABa	16.00	.0161
Guinea grass	0	-	1	5.0±0.00B	-	-
F-value (Column wise)		3.61		19.73		
Pr > F (Column wise)		0.0299		0,0001		

Means followed by different upper case letters in the same column are significantly different P ≤ 0.05.

Means followed by different lower case letters in the same row are significantly different P ≤ 0.05

Table 8.5 Percentage survival of *C. partellus* and *C. orichalcociliellus* reared on different host plants.

		Percentage survival			
Host plant		Stem borer species			G-test
	N	*C. partellus*	N	*C. orichalcociliellus*	(row-wise)
Maize	316	32.9a	305	34.9a	0.113
Sorghum	170	6.6b	126	7.3b	0.042
Napier grass	121	-	159	1.9b	4.050*
Wild sorghum	32	13.5b	48	7.4b	1.728
Guinea grass	80	-	111	1.1b	0.775
F-value		29.21		29.84	
Pr > F		0.0001		0.0001	

1 Statistical analysis was done using squareroot arcsine transformed data.

2 Percentages in the same column with different letters are significantly different $P \leq 0.05$

3 A significant difference ($P \leq 0.05$) in the number of borers surviving in each plant is indicated by an asterisk

CHAPTER NINE

9.0 Intensity of diapause of *C. partellus* and *C. orichalcociliellus.*

9.1 Introduction

Diapause is a crucial link in the life cycle of many insects, enabling them to overcome unfavourable conditions . It has been reviewed among insects of the temperate and tropical zones (Beck and Hanec, 1960; Evert, 1960; Danilevskii, 1961; Adkisson *et al.*, 1963; Lees, 1968; Beck, 1968; Bell, 1982; Briers *et al.*, 1982; Denlinger, 1986). Diapause of stem borers, including *C. partellus* and *C. orichalcociliellus*, has been widely studied (Usua, 1970, 1973, 1974; Scheltes, 1978; Fuchs *et al.*, 1979; Taley and Thakare, 1976; 1980; Singh *et al.*, 1985; Chaudhary and Sharma, 1988; Unnithan and Seshu Reddy, 1989; Kfir, 1988, 1991a, b, 1993a, b).

In Kenya, the seasonal abundance of stem borer species, including *C. partellus* and *C. orichalcociliellus*, has been described (Mathez, 1972; Warui and Kuria, 1983; Unnithan and Seshu Reddy, 1989; Overholt *et al*, 1994a). During off seasons, these stem borers survive in alternative hosts and wild grasses, although carry-over populations occur in crop residues left in the field (Wheatly, 1961; Scheltes, 1978). *C. partellus* and *C. orichalcociliellus* enter diapause as mature larvae soon after the start of a period of prolonged drought from February to March. Diapausing larvae are typically found in the lower part of the dry stalks where they are well protected from natural enemies and adverse climatic conditions (Nye, 1960; Mathez, 1972; Scheltes, 1978). Diapause in *C. partellus* (Scheltes, 1978: Kfir, 1991a) and *C. orichalcociliellus* (Delobel, 1975a; Scheltes, 1978) were considered to be facultative. Senescence of the host plant (Nye, 1960) and the general deterioration of the nutritive environment (Delobel, 1975a: Scheltes, 1978) were found to induce diapause in larvae of *C. partellus* and *C. orichalcociliellus*. A number of factors, including temperature, photoperiod and water influence diapause termination in *C. partellus* (Scheltes, 1978: Kfir, 1991a) and in *C. orichalcociliellus* (Scheltes, 1978). The duration and termination of diapause of several stem borers, including *C. partellus,* has been studied in several countries (Usua, 1970, 1973; Fuchs *et al*., 1979; Singh *et al*., 1985; Chaudhary and Sharma, 1988; Rodriguez-del-Bosque *et al*., 1990; Kfir, 1988; 1991a, b; 1993a, b). Some aspects of diapause of *C. partellus* and *C. orichalcociliellus* have been studied in Kenya (Scheltes, 1978), but the intensity of diapause of these borer species in Kenya is unknown. This study compared the intensity of diapause of *C. partellus* and *C. orichalcociliellus*.

9.2 Materials and Methods

During the dry season of 1995/96 (February-March) senescent stalks of maize were collected weekly from different fields in the coastal area of Kenya. The plants were dissected in the laboratory and healthy diapausing *Chilo* spp. were collected. *C. partellus* and *C. orichalcociliellus* larvae are morphologically indistinguishable when in diapause (Mathez, 1972; Scheltes, 1978). To ensure that all larvae used in the experiment were in diapause, immaculate white larvae were further examined under the microscope for absence of the asetose tubercle, which is an indication of diapause (Mathez, 1972). Larvae and fresh pieces of maize stems were washed in 100 and 50 parts per million of 0.05% sodium hypochlorite solution respectively, to minimize contamination by micro-organisms from the field. Larvae were provided with the washed pieces of stems and kept singly in glass vials (10 by 2.5cm) plugged with wet cotton wool. Larvae were held at 28±0.05^{0}C and a 12:12 L:D photoperiod. The larvae usually bored into the stems or were in close contact with the wet cotton wool. Scheltes (1978) demonstrated that moist conditions induced a rapid decrease in juvenile hormone content in the haemolymph of diapausing *C. partellus* larvae which stimulated the termination of diapause. Larvae were examined every other day to record mortality, moults and pupation. Pupae were kept singly in dry glass vials and examined every day for moth emergence. Adult moths were identified and their sexes recorded. Pupae which failed to metamorphose were identified before being discarded. Larvae that died before pupation or escaped were disregarded in the analysis. Time to pupation and adult emergence were analyzed using the generalized linear model (GLM), and means separated using Student-Newman Keul's (SNK) test (SAS Institute, 1987).

9.3 Results

Diapause termination was faster in *C. partellus* than *C. orichalcociliellus*. The number of days taken to terminate diapause while larvae were subjected to diapause terminating conditions was 9.7±4.45 and 14.4±9.86 days for *C. partellus* and *C. orichalcociliellus*, respectively (Figure 9.1). Male and female moths of diapausing *C. partellus* larvae emerged at the same time (Figure 9.2), while temporal differences were found in the emergence of male and female diapausing *C. orichalcociliellus* larvae (Figure 9.3). Of the 1806 diapausing larvae collected, 550 of *C. partellus* and 197 of *C. orichalcociliellus*, survived to pupation.

9.4 Discussion

Diapause termination of *C. partellus* was more rapid than *C.*

orichalcociliellus. This may allow *C. partellus* to complete more generations per year than *C. orichalcociliellus*. Denno *et al*. (1995) compared the voltinism of some groups of phytophagous insects as a factor contributing to the superior competitiveness of one species over the other. They noted that one might hypothesize that multivoltinism could contribute to rapid population growth and competitive superiority, especially for species that interact exploitatively. A more rapid diapause termination may also enable *C. partellus* colonize crops before *C. orichalcociliellus*. Early arrival at a resource, which can result either from advanced seasonal emergence (Waloff, 1968; Huffaker and Kennett, 1969) or rapid colonization (Fitt, 1984) allows some species to gain the numerical, and consequently, the competitive edge (Huffaker and kennett, 1969; Fitt, 1984; Edson, 1985). Early arrival tends to confer competitive superiority when coupled with rapid population growth and/or the preemption of resources that results from physical exclusion (Waloff, 1968) or chemical deterrence (Fitt, 1984). McClure (1980) reported that when the advantage of early arrival was experimentally removed, the scale insect, *Fiorinia externa* Ferris (Homoptera:Diaspididae), lost its competitive superiority.

Studies have shown that a number of *Chilo* spp. start mating on the night of eclosion (Bughio *et al*., 1977; Kumar and Saxena, 1985a; Unnithan, 1988; Päts, 1991). The synchrony in diapause termination and eclosion times of males and females of *C. partellus* may enable the moths to copulate immediately after eclosion, resulting in the production of viable eggs. Males of *C. orichalcociliellus* emerged long before the females. This phenomenon, known as protandry, has been reported by many researchers in butterflies and many other insects (Ford, 1945; Petersen, 1947; Forster, 1954; Newman, 1968). The explanation of the functional significance of protandry includes, among others, prevention of inbreeding and mating of females by the fittest, longest surviving males. Adult moths of *C. partellus* live for approximately one week (Alghali, 1988; Unnithan and Paye, 1991; Chapter 5). Delobel (1975a) reported that adult females of *C. orichalcociliellus* lived longer than the males with adult longevity averaging 135 and 114 hours, respectively. Thus, the difference in the diapause termination and emergence times of males and females of *C. orichalcociliellus* may result in some females not being mated, as the males may not be readily present at the time of female emergence. Wiklund and Fagerstrom (1977) suggested that protandry in butterflies is a reproductive strategy of males, resulting from competition for mates, and should occur in species maintaining female monogamy or in which sperm from males mating with virgin females on the average fertilizes a larger number of eggs than sperm from males mating with already mated females. They noted that protandry could also evolve in species in which the females mate more than once, provided that males which mate with virgin females are reproductively favoured. This phenomenon might be true for *C. orichalcociliellus*. *C. partellus* females are reported to seldom mate more than once, although males are known to mate repeatedly (Unnithan and Paye, 1991). Similar studies on mating frequency have not been conducted on *C. orichalcociliellus*. It would be interesting to determine whether the reproductive behaviour of *C. orichalcociliellus* differs from that of *C. partellus*, and if so, whether these differences support the current speculation regarding protandry in this species.

Additionally, the longer period in diapause of *C. orichalcociliellus* may adversely affect the fecundity of this species, as a strong correlation exists between body mass of female moths and the number of eggs and oocytes in their ovaries (Southwood, 1978; Kfir, 1991a). Kfir (1991a) reported that the body mass of females of *B. fusca* and *C. partellus* and the number of eggs and oocytes in their ovaries were adversely affected by long periods of larval diapause.

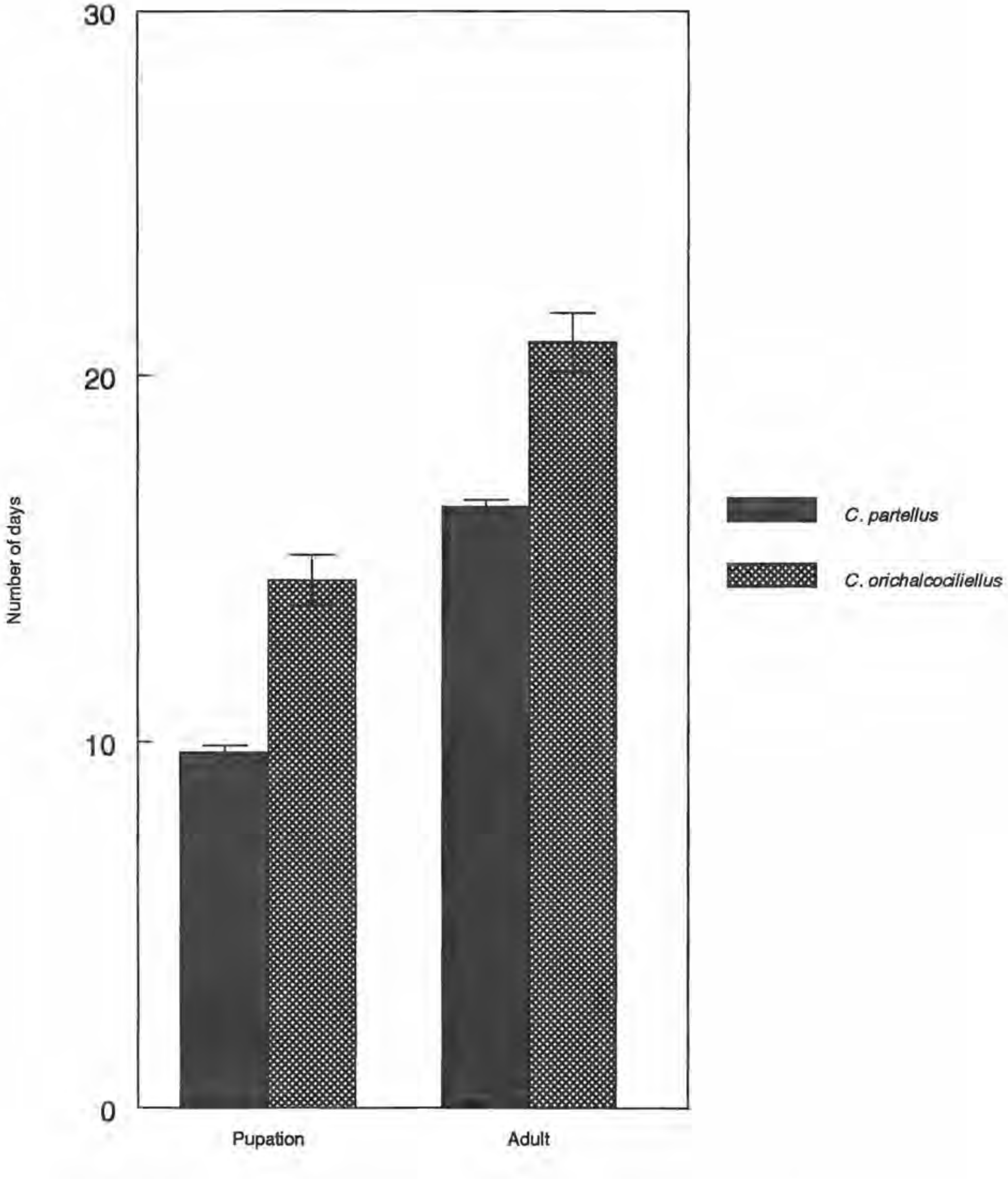

Figure 9.1 Cummulative time to diapause termination of field collected diapausing larvae of *C. partellus* and *C. orichalcociliellus*. (Vertical lines represent the standard error values).

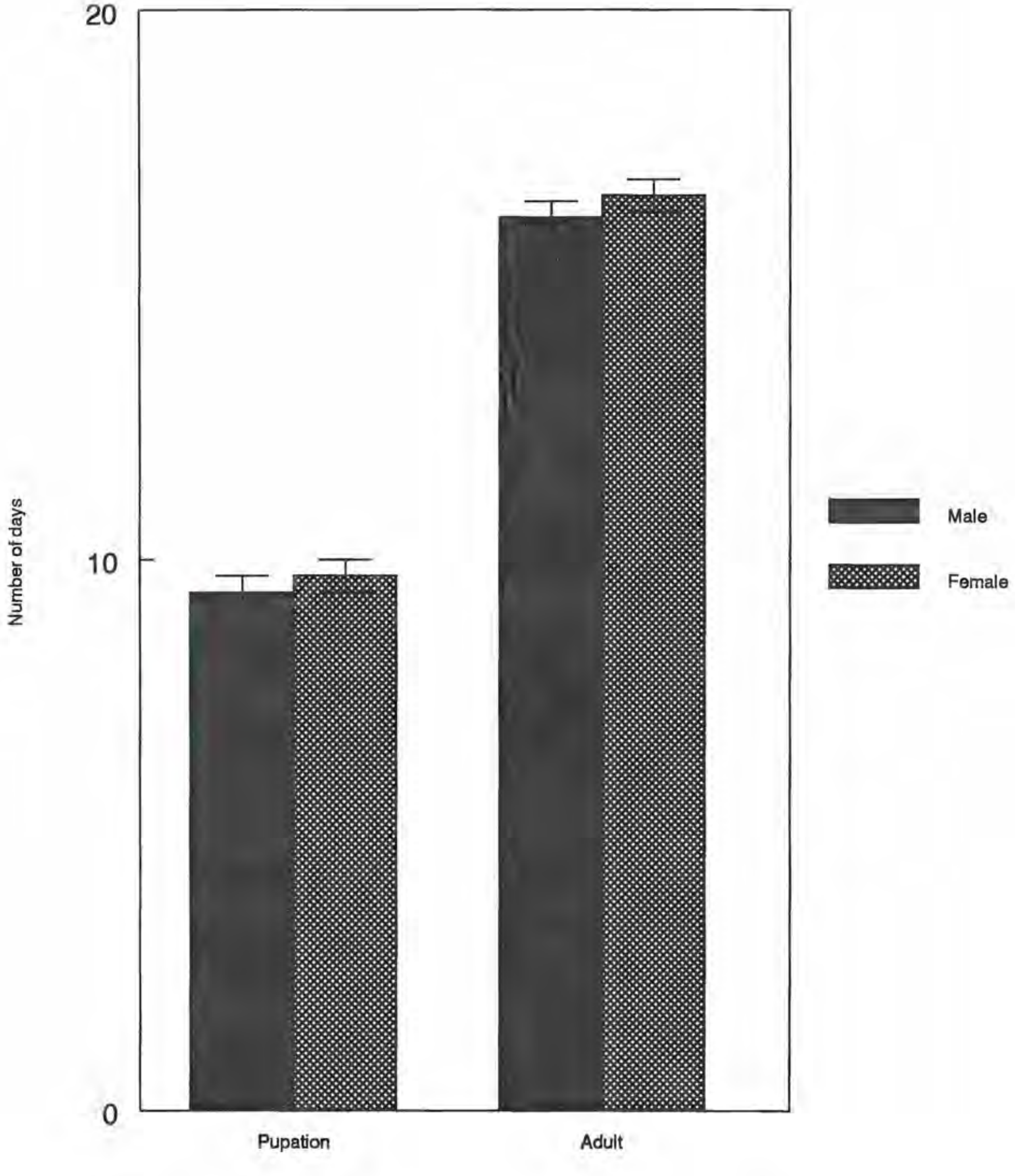

Figure 9.2 Cummulative time to diapause termination of field collected male and female diapausing larvae of *C. partellus*. (Vertical lines represent the standard error values).

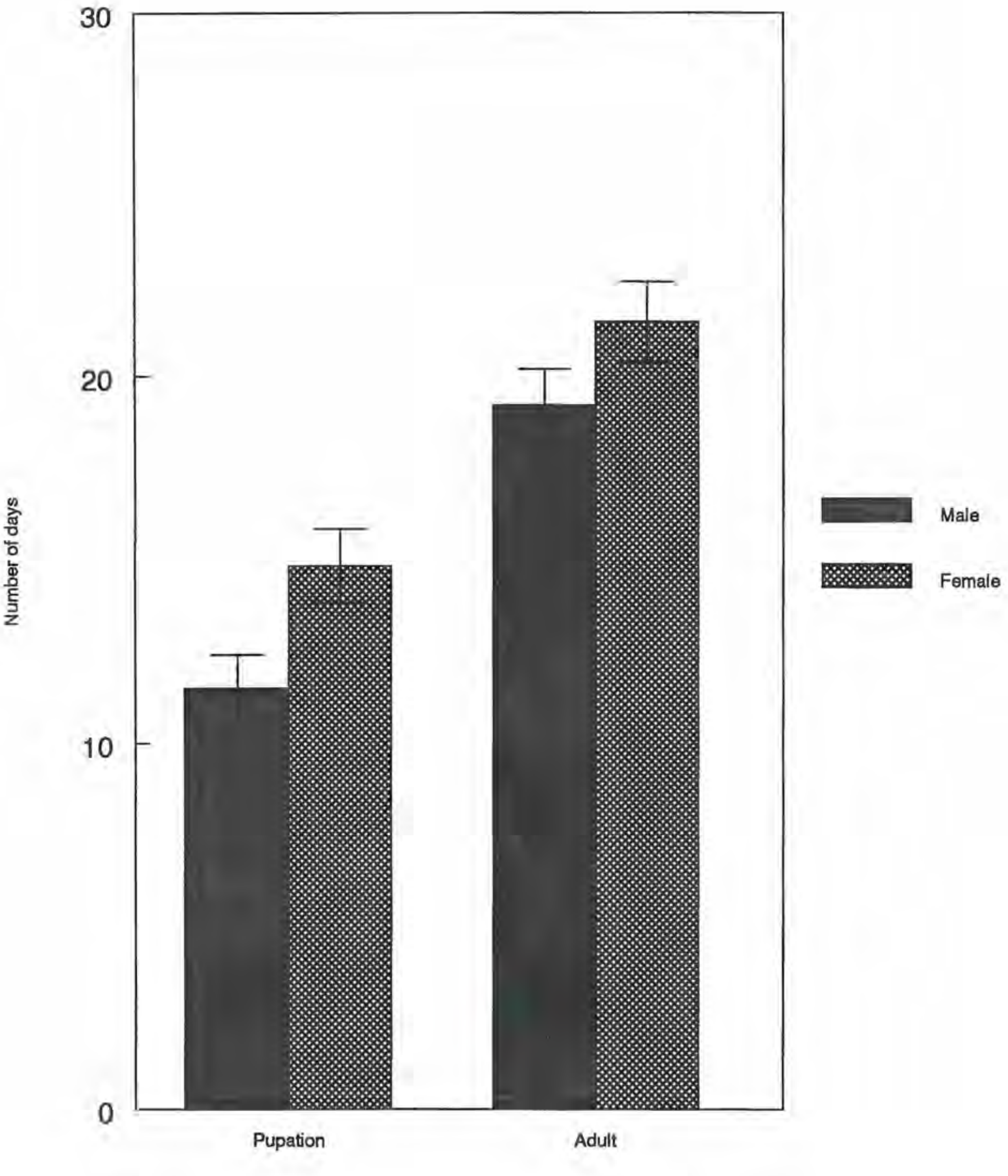

Figure 9.3 Cummulative time to diapause termination of field collected male and female diapausing larvae of *C. orichalcociliellus*. (Vertical lines represent the standard error values).

CHAPTER TEN

10.0 Summary and conclusions

10.1 Summary

C. partellus and *C. orichalcociliellus* are pests of maize and sorghum in Kenya. Both species occur sympatrically at the coastal area of Kenya. The two stem borer species have overlapping niches and thus, are considered to be ecological homologues. Previous laboratory and field experiments on ecological homologues have shown that competitive displacement of one species by the other usually occurs. The winner, however, is not always the same. When physical or biological characteristics undergo change, the expected winner may be displaced. Field observations involving a few species of animals have indicated that competitive displacement does occur in nature. Usually, however, the mechanism of displacement has not been demonstrated nor was it certain that competing species are ecological homologues. Studies reported here have examined the implication of such a displacement on crop damage, extent of niche overlap, interspecific association and the role of indigenous parasitoids in the population regulation of *C. partellus* and *C. orichalcociliellus*. More importantly, some bio-ecological and physiological characteristics of *C. partellus* and *C. orichalcociliellus* were examined, aimed at identifying superior attributes of *C. partellus* as mechanisms involved in its displacement of *C. orichalcociliellus*.

Laboratory studies showed that *C. partellus* consumed more maize than *C. orichalcociliellus*, on a daily basis and throughout their larval lifetime. Consequently, damage to crops may be greater since the invasion of *C. partellus* into Kenya.

C. orichalcociliellus became displaced in areas where it occurs sympatrically with *C. partellus* for an appreciable number of years. The hypothesis was examined that the two species were ecological homologues and that competitive displacement was responsible for the population decline of *C. orichalcociliellus*. *C. partellus* and *C. orichalcociliellus* were observed to be ecological homologues in the field with very close overlap in their niches. Examination of the degree of interspecific association between *C. partellus* and *C. orichalcociliellus* in their niches gave an indication of the coexistence of early larval instar of *C. partellus* and *C. orichalcociliellus* without obvious harmful effects. As larvae developed to the later instars and the pupal stage, no association was found. There was no evidence that the stem borers were involved in any kind of direct interference or aggression.

In order to determine the effect, if any, of different indigenous parasitoids on displacement, parasitism levels of *C. partellus* and *C. orichalcociliellus* by the three most common parasitoids at the coastal area of Kenya were examined. Results showed no significant differences in parasitism levels of these species. This may be an important factor that has allowed the apparent coexistence of *C. partellus* and *C. orichalcociliellus* at the coast of Kenya. Flanders (1956) reported the long coexistence of yellow and California red scales on citrus in Southeast China based on the effect of evenly balanced natural enemy activity.

Laboratory and field experiments helped to explain why *C. partellus* partially displaced *C. orichalcociliellus* at the coastal areas of Kenya. Basic reproduction data such as fecundity per female at controlled temperatures of 25, 28 and 31^{0}C and relative humidities of 75, 85 and 96% showed a reproductive superiority of *C. partellus* compared to *C. orichalcociliellus* at all temperatures except 31^{0}C, where fecundity was not different. In addition to this advantage, more *C. partellus* eggs survived to the first instar larvae at all temperatures and relative humidities. *C. partellus* apparently has a wider range of climatic conditions favourable to its survival and development. Past studies have shown that *C. partellus* occurs at elevations below 1500 metres (Mathez, 1972; Warui and Kuria, 1983; Skoroszewski and van Hamburg, 1987; Greathead, 1990; Seshu Reddy, 1991; Overholt *et al.*, 1994a), while *C. orichalcociliellus* occupies only the low, warm and humid areas at altitudes below 600 metres (Delobel, 1975a; Mathez, 1972; Warui and Kuria, 1983; Overholt *et al.*, 1994a). Previous studies on competitive displacement between three *Aphytis* spp. was partially explained by the differences in relative fecundity and survival of immature stages (Debach and Sundby, 1963). The species with the highest number of F_1 progeny was always the winner in any paired interspecific competition.

It was shown that greater numbers of neonate larvae of *C. partellus* dispersed over greater distances at a faster rate compared to *C. orichalcociliellus*. Thus, *C. partellus* has an advantage over *C. orichalcociliellus* because higher numbers of newly hatched larvae of *C. partellus* may be better able to leave the oviposition plants, and because they move faster, they will escape adverse mortality factors, and locate neghbouring plants for further infestation. Differences in the ability to move and take refuge in other plants is an important part of the interaction between species. Relative searching ability is a highly important biological characteristic under field conditions (Nicholson, 1933). Although a species may have a high intrinsic fecundity, its poor searching ability will result in a decreased progeny production as food becomes scarce. Hence, species with low intrinsic fecundity, but with a high searching ability have an advantage over species with high intrinsic fecundity and poor searching ability.

Field experiments showed *C. partellus* to have a greater establishing success than *C. orichalcociliellus*. In all plants but napier grass, *C. partellus* dominated and by the end of the experiments after 21 days, *C. partellus* was always recovered in higher numbers. *C. partellus* may be more able to resist or cope with the adverse conditions of the host plants compared to *C.*

orichalcociliellus.

Comparison of the developmental times of *C. partellus* and *C. orichalcociliellus* in cultivated and wild host plants revealed that *C. partellus* completed larval development in a shorter time than *C. orichalcociliellus*. This study confirmed the larval developmental studies of *C. partellus* and *C. orichalcociliellus* by Kioko *et al.* (1995) and Mbapila (1997) on artificial diet and maize, respectively. However, *C. orichalcociliellus* was able to complete development and survived in two native wild grasses in which *C. partellus* did not survive. Extirpation of *C. orichalcociliellus* from the Kenya Coast may have been precluded by its ability to survive in these grasses and escape competition from *C. partellus*. Generally, the development of both stem borer species was slower and survival was lower on wild grasses than on cultivated hosts. Wild grasses may provide new strategies for the management of stem borers. Recently, the potentials of several cultivated and wild grasses for the management of cereal stem borers has been demonstrated with some success (Khan, *et al.*, 1997).

Laboratory experiments showed a more rapid diapause termination of diapausing larvae of *C. partellus* than *C. orichalcociliellus*. This may allow *C. partellus* to complete more generations in a year as well as give this species more individuals that first colonize crops at the onset of favourable conditions, thus displacing *C. orichalcociliellus* from most of their habitats.

This study has demonstrated several clear biological differences between

C. partellus and *C. orichalcociliellus* that may be involved in the partial displacement of *C. orichalcociliellus* by *C. partellus*. With the exception of survival in two native grasses, *C. partellus* appeared to have a competitive advantage over *C. orichalcociliellus*. The ability of *C. orichalcociliellus* to develop in *P. purpureum* and *P. maximum* may be an important factor that has allowed its continued existence in the coastal environment. It may be interesting to periodically revisit the coast in the future to see whether both species continue to coexist.

10.2 Conclusions

1. Since the invasion of *C. partellus* into Kenya, crop damage has become greater due to the higher consumption of *C. partellus* as compared to *C. orichalcociliellus*.
2. It is reaffirmed that *C. partellus* and *C. orichalcociliellus* are ecological homologues, with close overlap in their niches.
3. No evidence of direct interference or aggression is implicated in the displacement of *C. orichalcociliellus* by *C. partellus*.
4. Indigenous parasitoids are not important factors in the displacement of *C. orichalcociliellus*.
5. Competitive displacement of *C. orichalcociliellus* appears to be due to

superior characteristics of *C. partellus* which give this species a competitive advantage over *C. orichalcociliellus*.

6. *C. partellus* is reproductively superior to *C. orichalcociliellus* in total fecundity and egg survival.
7. *C. partellus* is a more efficient dispersant with a higher host plant establishing success compared to *C. orichalcociliellus*.
8. The relatively faster development of *C. partellus* compared to *C. orichalcociliellus* in cultivated and wild grasses may be an important factor in the competitive displacement of *C. orichalcociliellus*.
9. The survival of *C. orichalcociliellus* in native wild grasses may have allowed the coexistence of *C. partellus* and *C. orichalcociliellus* at the coastal area of Kenya.
10. Native wild grasses serve as refuges for reinfestation of other crops by these stem borers.
11. Since the development of these stem borers in wild grasses is slower and survival is low compared to the cultivated hosts, wild grasses may have value as trap crops for stem borers.
12. Earlier termination of diapause in *C. partellus* compared to *C. orichalcociliellus* may allow *C. partellus* to complete more generations in a year, giving this species more individuals to colonize crops after the onset of rains and, thus, displace *C. orichalcociliellus* from their habitats.

REFERENCES

Adkisson, P.L., Bell, R.A. and Wellso, S.G. (1963). Environmental factors controlling the induction of diapause in the pink bollworm *Pectinophora gossypiella* (Saunders). *J. Insect Physiol.* 9: 299-310.

Akimoto, S. (1988). Competition and niche relationships among Eriosoma aphids occurring on the Japanese elm. *Aecologia* 75: 44-53.

Akinsola, E.A. and Agyen-Sampong, M. (1984). The ecology, bionomics and control of rice stem borers in West Africa. *Insect Sci. Applic.* 5: 69-77.

Alghali, A.M. (1988). Oviposition on sorghum by the stem borer, *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae). *Journal of Plant Protection in the Tropics* 5: 45-50.

Alghali, A.M. and Saxena, K.N. (1988). Larval movement, feeding and development of *Chilo partellus* Swinhoe (Lepidoptera:Pyralidae) on two sorghum cultivars. *Insect Sci. Applic.* 9(1): 7-11.

Amoako-Atta, B., Omolo, E.O., and Kidega, E.K. (1983). Influence of maize, cowpea and sorghum intercropping systems on stem-/pod-borer infestations. *Insect Sci. Applic.* 4(1-2): 47-57.

Ampofo, J.K.O. (1985). *Chilo partellus* (Swinhoe) oviposition on susceptible and resistant maize genotypes. *Insect Sci. Applic.* 6: 323-30.

Ampofo, J.K.O. (1986a). Effect of the resistant maize cultivars on larval dispersal and establishment of *Chilo partellus* (Lepidoptera:Pyralidae). *Insect Sci. Applic.* 7(1): 103-106.

Ampofo, J.K.O. (1986b). Maize stalk borer (Lepidoptera:Pyralidae) damage and plant resistance. *Environ. Entomol.* 15: 1124-1129.

Ampofo, J.K.O. and E.L. Kidiavai (1987). *Chilo partellus* (Swinhoe) (Lep.:Pyralidae) larval movement and growth on maize plants in relation to plant age and resistance or susceptibility. *J. Appl. Entomol.* 103: 483-488.

Ampofo, J.K.O., K.N. Saxena, J.G. Kibuka and E.O. Nyangiri (1986). Evaluation of some maize cultivars for resistance to the stem borer *Chilo partellus* (Swinhoe) in western Kenya. *Maydica* 31: 379-389.

Andrewartha, H.G., and Birch, L.C. (1954). *The distribution and abundance of animals*. The University of Chicago Press, Chicago Illinois. 732 pp.

Antolin, M.F. and Addicott, J.F. (1988). Habitat selection and colony survival of *Macrosiphum valeriani* Clarke (Homoptera:Aphididae). *Ann. Entomol. Soc. Am.* 81: 245-251.

Appert, J.M., M. Betheder-Matibet, and H. Ranaivosa (1969). Vingt annees de lutte biologique a Madagascar. *Agronomie Tropicale* 24: 555-572.

Assefa, G.A. (1981). Some preliminary studies on maize stalk borer *Busseola* *fusca* (Fuller) in Ethiopia. M.Sc thesis Addis Ababa University, Nazareth, Addis Ababa Ethiopia.

Barbosa, P. and J. Greenblatt (1979). Suitability, digestibility and assimilation of various host-plants of gypsy moth, *Lymantria dispar* (L.) *Oecologia* 43: 111-119.

Beck, S.D. (1968). *Insect photoperiodism*. Academic Press, New York, 288 pp.

Beck, S.D. and Hamec, W. (1960). Diapause in the European corn borer, *Pyrausta nubilalis* (Hubn). *J. Insect Physiol.* 4: 304-318.

Bell, C.H. (1982). Observation on the intensity of diapause and cold tolerance in larvae from twelve populations and two reciprocal crosses of the Indian meal moth, *Plodia interpunctella. Physiological Entomology* 7:371-377

Belovsky, G.E. (1986). Generalist herbivore foraging and its role in competitive interactions. *Am. Zool.* 26: 51-69.

Belovsky, G.E. and J.B. Shade (1992). Survival in some grasshoppers: relationships among weather, food abundance and interspecific competition. *Ecology* (in press).

Bennett, F.D. (1993). Do introduced parasitoids displace native ones? *Florida Entomologist* 76(1): 54-63.

Berger, A. (1989a). Ballooning activity of *Chilo partellus* larvae in relation to size of mother, egg batches, eggs and larvae and age of mother.

Entomologia Experimentalis et Applicata 50: 125-132.

Berger, A. (1989b). Egg weight, batch size and fecundity of the spotted stalk borer, *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in ralation to weight of females and time of oviposition. *Entomologia Experimentalis et Applicata* 50: 199-207.

Berger, A. (1992). Larval movement of *Chilo partellus* (Lepidoptera:Pyralidae) within and between plants: timing, density response and survival. *Bull. ent. Res.* 82: 441-448.

Bernays, E.A., Chapman, R.F., and Woodhead, S. (1983). Behaviour of newly hatched larvae of *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) associated with their establishment in the host plant, sorghum. *Bull. ent. Res.* 73: 75-83.

Bernays, E.A., Woodhead, S., and Haines, L. (1985). Climbing by newly hatched larvae of the spotted stalk borer *Chilo partellus* to the top of sorghum plants. *Entomologia Experimentalis et Applicata* 39: 73-79.

Betheder-Matiber M. (1971). Biological control of *Chilo sacchariphagus*, the spotted borer of sugar-cane in Madagascar. *Agronomie Tropicale* 26(3): 332-336.

Betheder-Matibet, M. (1989). Biological control of sorghum stem borers. ICRISAT International workshop on sorghum stem borers. 17-20 Nov

1987.

Betheder-Matibet, M., and P. Malinge (1968). Un succes de la lutte biologique controle de *Proceras sacchariphagus* Boj. Borer ponctue de la canne a sucre a Madagascar par un parasite introduit: *Apanteles flavipes* Cam. *Agronomie Tropicale* 22: 1196-1220.

Black, W.C., Rai, K.S., Turco, B.J. and Arroyo, D.C. (1989). Laboratory study of competition between United States strains of *Aedes albopictus* (Diptera:Culicidae). *Journal of Medical Entomology* 26: 839-850.

Blakley, N. and Dingle, H. (1978). Butterflies eliminate milkweed bugs from a Caribbean island. *Oecologia* 37: 133-136.

Bleszynski, S. (1970). A revision of the world species of *Chilo zinchen* (Lepidoptera:Pyralidae). *Bulletin of the British Museum of Natural History Entomology* 25: 101-195.

Bordat, D. (1983). *Mise au point de l'elevage de masse d'Apanteles chilonis Matsumura, 1912 et d'Apanteles flavipes (Cameron 1891) (Hymenopteres:Braconidae) sur trois lepidopteres Pyralidae foreurs des graminees (Chilo zacconius Bleszynski, 1970; Chilo partellus (Swinhoe,1884) et Diatraea saccharalis (Fabricius, 1794) dans un objectif de lutte.* These Universite des Sciences et Technique du Languedoc; Academie de Montpellier.

Bosque-Perez, N.A. and Mareck, J.H. (1990). Distribution and composition of lepidopterous maize borers in southern Nigeria. *Bull. ent. Res.* 80: 363-368.

Botelho, P.S.M. (1992). Quinze anos de controle biologico da *Diatraea saccharalis* utilizando parasitoides. *Pesquisa Agropecuria Brasileira* 27(S/N): 255-262.

Bottger, G.T. (1951). Sugars and protein in the corn plant as related to nutrition of the European corn borer. *J. econ. Ent.* 44: 40-44.

Brader, L. (1979). Integrated pest control in the developing world. *Ann. Rev. Entomol.* 24: 225-254.

Briers, T.; Peferoen, M. and De Loof, A. (1982). Ecdysteroids and adult diapause in the Colorado potato beetle, *Leptinotarsa decemlineata*. *Physiological Entomology* 7: 379-386.

Brown, J.H. (1971). Mechanisms of competitive exclusion between two species of chipmunks. *Ecology* 52: 305-311.

Brown, M.W., H.W. Hogmire and J.J. Schmitt (1995). Competitive displacement of apple aphid by spirea aphid (Homoptera:Aphididae) on apple as mediated by human activities. *Environ, Entomol.* 24: 1581-1591.

Brownbridge, M. (1991). Natural *Bacillus thuringiensis* isolates for the management of Lepidopteran cereal pests. *Insect Sci. Applic.* 12: 57-61.

Bughio, A.R., Akbar, S.S. and Qureshi, Z.A. (1977). Rearing and biology of maize borer, *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae). *Pakistan Journal of Zoology* 9: 145-156.

Bultman, T.L. and S.H. Faeth (1985). Patterns of intra and interspecific association in leaf-mining insects on three oak host species. *Ecol. Entomol.* 10: 121-129.

Commonwealth Agricultural Bureau (1977). *Chilo partellus* (Swinh). Distribution maps of pests No 194 (revised) Commonwealth Agricultural Bureaux, Commonwealth Institute of Entomology, London.

Capinera, J.L. and P. Barbosa (1976). Dispersal of first instar gypsy moth larvae in relation to pupulation quality. *Oecologia* 26: 53-64.

Capinera, J.L.; P. Barbosa and H.H. Hagedorn (1977). Yolk and yolk depletion of gypsy moth eggs: implications for population quality. *Ann Ent. Soc. Am.* 70: 40-42.

Centre for Overseas Pest Research, International Crops Research Institute for the Semi Arid Tropics (1977). COPR/ICRISAT collaborative project on sorghum stem borer ecology and behaviour. Report on the first field study period, July-November 1976. London.

Chan, K.L., Ho, B.C. and Chan, Y.C. (1971). *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) in Singapore City. 2. Larval habitats. *Bulletin of the*

World Health Organization 44: 629-633.

Chand, P. and Sharma, N.N. (1977). Influence of crop association on insect pest incidence. *Proc. Indian Nat. Sci. Acad.* 43: 108-114.

Chapman, R.F., S. Woodhead and E.A. Bernays (1983a). Survival and dispersal of young larvae of *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) in two cultivars of sorghum. *Bull. ent. Res.* 73: 65-74.

Chapman, R.F.; Bernays, E.A.; Woodhead, S.; Padgham,D.E. and Simpson, S.J. (1983b). Control of hatching time of eggs of *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) *Bull. ent. Res.* 73: 667-677.

Chatterji, S.M., Young, W.R., Sharma, G.C., Sayi, I.V., Chahal, B.S., Khare, B.P., Rathore, Y.S., Panwar, V.P.S. and Siddiqui, K.H. (1969). Estimation of loss in yield of maize due to insect pests with special reference to borers. Indian J. Entomol. 31: 109-115.

Chatterji, S.M., Bamburkar, M.W., Marwaha, K.K., Panwar, V.D.S., Siddiqui, K.H. and Young, W.K. (1971). Relative susceptibility of some promising exotic maize material to *Chilo zonellus* Swinhoe under aritificial infestation. *Indian J. Entomol.* 33: 209-213.

Chaudhary, R.N. and V.K. Sharma (1988). Induction and termination of diapause in maize stalk borer, *Chilo partellus* Swinhoe. *Indian J. Entomol.*

50(4): 523-529.

Christenson, L.D. and Foote, R.H. (1960). Biology of fruit flies. *Ann. Rev. Entomol.* 5: 171-192.

Chundurwar, R.D. (1989). Sorghum stem borers in India and Southest Asia. In Proc. Int. Workshop on Sorghum Stem Borers 7-20 November 1987. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, AP 502324, India. pp. 19-25.

Clark, A.H. (1931). The extirpation of one butterfly by another. *Sci. Monthly* 33(2): 173-174.

Cody, M.L. and Diamond, J.M. (1975). *Ecology and evolution of communities*. Cambridge, Mass Harvard Univeristy Press.

Cole, L.C. (1949). The measurement of interspecific association. *Ecology* 30: 411-424.

Cole, L.C. (1960). Competitive exclusion. *Science* 132(3423): 348-349.

Compere, H. (1940). Parasites of the black scale, *Saissetia oleae*, in Africa. *Hilgardia* 13: 387-425.

Conlong, D.E. (1990). A study of pest-parasitoid relationships in natural habitats: an aid towards the biological control of *Eldana saccharina* (Lepidoptera:Pyralidae) in sugarcane. Proceedings of the South African Sugar Technologists' Association 64: 111-115.

Connell, J.H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle, *Chthamalus stellatus*. *Ecology* 42(4): 710-723.

Connor, E.F. and Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140.

Crombie, A.C. (1945). On competition between different species of graminivorous insects. *Roy. Soc. London, Ser.* B(132): 362-395.

Crombie, A.C. (1946). Further experiments on insect competition. *Roy. Soc. London, Proc. Ser.* B(133): 76-109.

Crombie, A.C. (1947). Interspecific competition. *J. Animal Ecol.* 16: 44-73.

Dabrowshki, Z.T. and Kidiavai, E.L. (1983). Resistance of some sorghum lines to the spotted stalk-borer, *Chilo partellus*, under western Kenya conditions. *Insect Sci. Applic.* 4(1-2): 119-126.

Dabrowshki, Z.T. and Nyangiri, E.O. (1983). Some field and screenhouse experiments on maize resistance to *Chilo partellus* under western Kenya conditions. *Insect Sci. Applic.* 4: 109-118.

Danilevskii, A.S. (1961). *Photoperiodism and seasonal development of insects.* English translation 1965. Oliver and Boyd, Edinburgh.

Damman, H. (1993). *Patterns of herbivore interaction among herbivore species. In Caterpillars: Ecological and Evolutionary Constraints of Foraging,* ed.

NE Stamp, TM Casey, pp. 132-69. New York: Chapman and Hall.

Darwin, C. (1959). *On the origin of species*. Reprinted 1909. Caswell and Co Ltd, London. 430 p.

Das, Y.T. (1976). Some factors of resistance to *Chilo suppressalis* in rice varieties (lep.:Pyralidae). *Entomologia Experimentalis et Applicata* 20: 131-134.

Davies, J.C. and Seshu Reddy, K.V. (1980). Insect pests of sorghum and pearl millet and assessment of insect numbers and losses. *In Proc. of the Workshop on Assessment of Crop Losses due to Pests and Diseases*, 19-30 September 1971, University of Agricultural Science, Hebbal, Bangalore, India. pp. 232-239.

Debach, P. (1965). Some biological and ecological phenomena associated with colonizing entomophagous insects. In H.G. Baker and G.L. Stebbins (eds.). *The genetics of colonizing species*. Academic Press, New York. pp. 287-306.

Debach, P. (1966). The competitive displacement and coexistence principles. *Ann. Rev. Entomol.* 11: 183-212.

Debach, P. and Sundby, L.A. (1963). Competitive displacement between ecological homologues. *Hilgardia* 34(5): 105-166.

Debach, P. and Rosen D. (1991). *Biological control by natural enemies*.

Cambridge University Press.

Debach, P., Hendrickson, R.M. Jr and Rose, M. (1978). Competitive Displacement: Extinction of the Yellow Scale, *Aonidiella citrina* (Coq.) (Homoptera:Diaspididae), by its Ecological Homologue, the California Red Scale, *Aonidiella aurantii* (Mask.) in Southern California. *Hilgardia* 46(1): 1-35.

Delinger, D.L. (1986). Dormancy in tropical insects. *Ann. Rev. Entomol.* 31: 230-264.

Delobel, A. (1975a). *Chilo orichalcociliellus* Strand (Lepidoptera::Pyralidae) Foreur des tiges du sorgho et du mais a Madagascar 11. Premeres donnees biologique. *ORSTOM Series Biologie* 10: 11-16.

Delobel, A. (1975b). Une population hivernante de *Chilo partellus* (Lepidoptera:Pyralidae) sur la cote ouest de Madagascar. *ORSTOM Series, Biologie* 10: 17-23.

Denlinger, D.L. (1986). Dormancy in tropical insects. *Ann. Rev. Entomol.* 31:230-264.

Denno, R.F. and Roderick, G.K. (1992). Density-related dispersal in planthoppers; effects of interspecific crowding. *Ecology* 73: 1323-1334.

Denno, R.F., McClure, M.S. and Ott, J.R. (1995). Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Ann. Rev.*

Entomol. 40: 297-311.

Diamond, J.M. (1975). Assemby of species communities. *Ecology and Evolution of communities* (M.L. Cody and J.M. Diamond ed.), pp. 342-444, Belknap, Harvard.

Diamond, J.M. (1978). Niche shifts and the rediscovery of interspecific competition. *Am. Sci.* 66: 322-331.

Djamin, A. and Pathak, M.D. (1967). Role of silica in resistance to Asiatic rice bore, *Chilo suppressalis* Walker in rice varieties. *J. econ. Ent.* 60: 347-351.

Doggett, H. (1988). *The origin of the sorghum crop. In Sorghum.* Second edition, Tropical agriculture series. Longman. pp. 40-43.

Dowswell, C.R., Paliwal, R.L. and Cantrell, R.P. (1996). *Maize in the third world.* Colorado, Westview Press. U.S.A.

Duerdon, J.C. (1953). Stem borers of cereal crops at Kongwa, Tanganyika, 1950-52. *East African Agricultural and Forestry Journal* 19: 105-119.

Durbey, S.L. and P. Sarup (1982). Morphological characters-development and density of trichomes on varied maize germplasms in relation to preferential oviposition by the stalk borer *Chilo partellus*. *J. ent. Res.* 6: 187-196.

Edson, J.L. (1985). The influences of predation and resource subdivision on the coexistence of goldenrod aphids. *Ecology* 66: 1736-1743.

Elton, C.S. (1958). *The ecology of invasions by animals and plants*. Methuen and Co London 181 p.

Elton, C.S. and R.S. Miller (1954). The ecological survey of animal communities with a practical system of classifying habitats by structural characters. *J. Ecol.* 42: 460-496.

Evert, I.S. (1960). Diapause and secondary parasites nullify the effectiveness of Rose-aphid parasites in Riverside, California, 1957-1958. *J. econ. Ent.* 53(1): 151-154.

Faeth, S. (1987). Community structure and folivorous insect outbreaks: the role of vertical and horizontal interactions. In *Insect Outbreaks*, ed. P. Barbosa, J.C. Schultz, pp. 135-71. New York: Academic.

Faeth, S. (1988). Plant-mediated interactions between seasonal herbivores: enough for evolution or coevolution? In *Chemical Mediation of Coevolution*, ed. K.C Spencer, pp. 391-414. New York: Academic.

Food and Agricultural Organization (1991). Yearbook vol. 45.

Fitt, G.P. (1984). Oviposition behavior of two tephritid fruit flies, *Dacus tryoni* and *Dacus jarvisi*, as influenced by the presence of larvae in the host fruit. *Oecologia* 62: 37-46.

Flanders, S.E. (1951). Mass culture of California red scale and its golden chalcid parasites. *Hilgardia* 21: 1-42.

Flanders, S.E. (1956). Struggle for existence between red and yellow scales on citrus. *Citrus leaves* 36(8): 6, 7, 22, 26, 31.

Flanders, S.E. (1958). *Moranila californica* as a usurped parasite of *Saissetia oleae*. *J. econ. Ent.* 50(2): 247-248.

Flanders, S.E. (1959). The biological control of the nigra scale, *Saissetia nigra* (Nietn.)in California. *J. econ. Ent.* 52: 596-600.

Flanders, S.E. (1966). The circumstances of species replacement among parasitic hymenoptera *Canadian Ent.* 98: 1009-1024.

Ford, E.B. (1945). *Butterflies*, London: Collins.

Forster, W.,(1954). Biologie der Schmentterlinge, pp. 138-139 Stuttgart: Franck'sche Verlagshandlung.

Fritz, R.S., Gaud, W.S., Sacchi, C.F. and Price, P.W. (1987). Patterns of intra and interspecific association of gall-forming sawflies in relation to shoot size on their willow host plant. *Oecologia* 73: 159-169.

Fuchs, T.W., Harding, J.A. and Smith J.W. Jr. (1979). Induction and termination of diapause in the sugarcane borer. *Ann Entomol. Soc. Am.* 72: 271-274.

Futuyama, D.J., P.S. Robin and I. van Noordwijk (1984). Adaptation to host plants in the fall cankerworm (*Alsophila pometaria*) and its bearing on the evolution of affiliation in phytophagous insects. *Am. Nat.* 123: 287-296.

Gadgil, M. (1971). Dispersal: Population consequences and evolution. *Ecology* 52: 253-261.

Gahukar, R.T. and Jotwani, M.G. (1980). Present status of field pests of sorghum and millets in India. *Trop. Pest Manage.* 26: 128-131.

Gause, G.F. (1934). *The struggle for existence.* Williams and Wilkins Co., Baltimore 163 p.

Gebrekidan, B. (1981). Ethiopian Sorghum Improvement Project Report No. 9. Addis Ababa University and Institute of Agricultural research, Nazareth, Ethiopia.

Gilotra, S.K., Rozeboom, L.E. and Battacharya, N.C. (1967). Observatios on possible competitive displacement between populations of *Aedes aegypti* Linneaeus and *Aedes albopictus* Skuse in Calcutta. *Bulletin of the World Health Organization.* 37: 437-446.

Girling, D.J. (1978). The distribution and biology of *Eldana saccharina* Walker (Lepidoptera:Pyralidae) and its relationship to other stemborers in Uganda. *Bull. ent.. Res.* 68: 471-488.

Goncalves, L. (1970). The corn borer, *Chilo partellus* Swinhoe (Lepidoptera:Crambidae) in Mozambique. Contribution for its study. *Agron. Mozambicana* 4: 193-246.

Gounou, S., Schulthess, F., Shanawer, T., Hammond, W.N.O., Braima, H., Cudjoe, A., Radjakloe, R., Antwi, K.K. and Olalaye, I. (1993). Plant Health Management Research Monograph. No. 3 International Institute of Tropical Agriculture. Ibadan, Nigeria. 31 pp.

Grant, P.R. (1972). Interspecific competition among rodents. *Ann. Rev. Ecol.* 3: 79-106.

Grant, P.R. and Abbott, I. (1980). Interspecific competition, island biogeography and null hypotheses. *Evolution* 34: 332-341.

Greathead, D.J. (1971). A review of biological control in the Ethiopian region. *Tech. Commun. Commonw. Inst. Biol. Control*, No 5, pp 168.

Greathead, I.A. (1990). Utilization of natural enemies of *Chilo* spp. for management in Africa. *Insect Sci. Applic.* 11: 749-755.

Gu, C.Y. and Li, C.X. (1983). Biology and control of *Chilo panici* (in Chinese). *Insect Knowl.* (Kunchong Zhishi) 20: 104-105.

Gyawali, B.K. (1986). Influence of soyabean on infestation of corn and rice borers. *Q. Newsl. Asia and Pacific Plant Prot. Commun.* 29: 39-44.

Hachiya, K. (1979). Seasonal prevalence of stem borers of the genus *Chilo* (Lepidoptera:Pyralidae) in Hokkaido and its importance in studying by light trap. *Bull. Hokkaido Prefect. Agric. Exp. Stn.* 42: 43-53

Hairston, N.F., Smith, F.E. and Slobodkin, L.B. (1960). Community structure, population control, and competition. *Am. Nat.* 44: 421-425.

Hamilton, W.D. and R.M. May (1977). Dispersal in stable habitats. *Nature* 269: 578-581.

Hardin, G. (1960). The competitive exclusion principle. *Science* 131(3409): 1292-1298.

Harris, K.M. (1962). Lepidopterous stem borers of cereals in Nigeria. *Bull. ent. Res.* 53: 139-171.

Harris, K.M. (1990). Bioecology of *Chilo* species. *Insect Sci. Applic.* 11: 467-477.

Hawley, W.A. (1988). The biology of *Aedes albopictus*. *Journal of the American Mosquito Control Association.* 4(1): 1-39.

Hill, D.S. (1983). *Agricultural insect pests of the tropics and their control.* Cambridge University press. p 281-381.

Hirano, C. and Noguchi, H. (1963). Food utilization by the last instar of the cabbage armyworm, *Memestra brassicae* L., fed on plant leaves of different food values. *Jap. J. appl. Ent. Zool.* 7: 311-315.

Hobbes, J.H., Hughes, E.A. and Eichold, B.H.II. (1991). Replacement of *Aedes aegypti* by *Aedes albopictus* in Mobile, Alabama, *Journal of the American Mosquito Control Association.* 7: 488-489.

Hough, J.A. and D. Pimental (1978). Influence of host foliage on development, survival and fecundity of the gypsy moth. *Environ. Entomol.* 7: 97-102.

Howarth, F.G. (1991). Environmental impacts of classical biological control. *Ann. Rev. Entomol.* 36: 485-509.

Huffaker, C.B, and Kennett, C.E. (1969). Some aspects of assessing efficiency of natural enemies. *Canadian Ent.* 101: 125 147.

Hughes, G; P.S. Hammond and W.G. des Vignes (1982). Population cycles of the small moth-borers of sugar cane, *Diatraea*, and their primary and secondary parasitoids in Trinidad, West Indies. *Agro-Ecosystems* 8: 13-25.

Hurlbert, S.H. (1969). A coefficient of interspecific association. *Ecology* 50(1): 1-9.

Hurlbert, S.H. (1978). The measurement of niche overlap and some relatives. *Ecology* 59: 67-77.

Hutchinson, G.E. (1978). *An introduction to population ecology*. Yale University Press, New Haven, Connecticut, USA.

Hutchinson, G.E. and Deevey, E.S. Jr. (1949). *Ecological studies on populations, 325-359 in Survey of Biological Progress*, Academic Press, New York. pp. 396.

Inter-African Phytosanitary Council. (1985). *Chilo partellus* (Swinhoe) Distribution maps of major crop pests and diseases in Africa No 199 Yaounde, Cameroon.

Ingram, W.R. (1958). The lepidopterous stalk borer associated with Gramineae in Uganda. *Bull. ent. Res.* 49: 367-383.

Jepson, W.F. (1954). *A critical review of the world literature on the lepidopterous stalk borers of tropical graminaceous crops.* Commonw. Inst. Entomol. London.

Jotwani, M.G., Dinesa Chandra, Young, W.R, Sukhani, T.R. and Saxena, P.N. (1971). Estimation of avoidable loss caused by the insect complex on sorghum hybrid CSH-1 and percentage increase in yield over untreated control. *Indian J. Entomol.* 33: 375-383.

Kalode, M.B. and Pant, N.C. (1966). Studies on the susceptibility of different varieties of sorghum, maize and bajra to *Chilo zonellus* (Swinhoe) under field and cage conditions and the methods of determining it. *Indian J. Ent.* 28: 448-464.

Karban, R. (1986). Interspecific competition between folivorous insects on *Erigeron glaucus. Ecology* 67: 1063-1072.

Kato, D., Karel, A.K. and Ndunguru, B.J. (1982). Effect of insecticide spray on insect pests and yield of sorghum and simsim in pure stand and in intercropping-summary. In *Proc. of the Second Symposium on Intercropping in Semi-Arid Areas, Morogoro, Tanzania, 4-7 August 1980. Ottawa, Ontario, IDRC-186e.* pp. 117-118.

Kaufmann, T. (1983). Behavioural biology, feeding habits, and ecology of three species of maize stem-borers: *Eldana saccharina* (Lepidoptera:Pyralidae), *Sesamia calamistis* and *Busscola fusca* (Lepidoptera:Noctuidae) in Ibadan, Nigeria, West Africa. *Journal of the Georgia Entomological Society* 18: 259-272.

Kfir, R. (1988). Hibernation by the lepidopteran stalk borers *Busseola fusca* and *Chilo partellus* on grain sorghum. *Entomologia experimentalis et applicata* 48: 31-36.

Kfir, R. (1991a). Effect of diapause on development and reproduction of the stem borers *Busseola fusca* (Lepidoptera:Noctuidae) and *Chilo partellus* (Lepidoptera:Pyralidae). *J. econ. Ent.* 84(6): 1677-1680.

Kfir, R. (1991b). Duration of diapause in the stem borers, *Busseola fusca* and *Chilo partellus*. *Entomologia Experimentalis et applicata* 61: 265-270.

Kfir, R. (1993a). Diapause termination in the spotted stem borer, *Chilo partellus* (Lepidoptera:Pyralidae) in the laboratory. *Ann. Appl. Biol.* 123: 1-7.

Kfir, R. (1993b). Diapause termination in *Busseola fusca* (Lepidoptera:Noctuidae) in the laboratory. *Ann. Entomol. Soc. Am.* 86(3): 273-277.

Kfir, R. (1994). Attempts at biological control of the stem borer *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) in South Africa. *African Entomology* 2:

67-68.

Khan, B.M. (1970). Biology and control of maize stem borer (*Chilo partellus* (Swinhoe) and other related species, if any, in Peshwar valley. *J. agric. Res.* 8: 329-331.

Khan, Z.R., Chiliswa, P, Ampong-Nyarko, K., Smart, L.E., Polaszek, A., Wandera, J. and Mulaa, M.A. (1997). Utilization of wild gramineous plants for management of cereal stemborers in Africa. *Insect Sci. Applic.* 17(1): 143-150.

Kioko, E.N.; Overholt, W.A. and Mueke, J.M. (1995). Larval development in *Chilo orichalcociliellus* and *Chilo partellus*: A comparative study in the laboratory. In *Proc of the African Association of Insect Scientists*.pp. 191-198.

Koplin, J.R., and R.S. Hoffman (1966). Habitat overlap and competitive exclusion in voles (*Microtus*). *Am. Midl. Nat.* 80: 494-507.

Kulkarni, K.A. and Jotwani, M.G. (1976). Chemical control of sorghum stem borer, *Chilo partellus* (Swinhoe). *J. Karnataka Univ. Sci.* 21: 286-292.

Kumar, H. (1986). Enhancement of oviposition by *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) on maize plants by larval infestation. *Applied Entomology and Zoology* 21: 539-545.

Kumar, H. (1988a). Effects of stalk damage on growth and yield of certain maize cultivars by the maize stalk borer *Chilo partellus*. *Entomologia Experimentalis et Applicata* 46: 149-153.

Kumar, H. (1988b). Oviposition and larval behaviour of stalk-borer (*Chilo partellus*) on susceptible and resistant varieties of maize (*Zea mays*). *Ind. J. agric. Sci.* 58(12): 918-921.

Kumar, H. (1992). Patterns of stem borer incidence and damage to two cultivars of maize in the field. *Insect Sci. Applic.* 13(2): pp. 211-216.

Kumar, H. and Saxena, K.N. (1985a). Oviposition by *Chilo partellus* (Swinhoe) in relation to its mating, diurnal cycle and certain non-plant surfaces. *Appl, Ent. Zool.* 20: 18-21.

Kumar, H.; E.M.O. Nyangiri and G.O. Asino (1993). Colonization responses and damage by *Chilo partellus* (Lepidoptera:Pyralidae) to four variably resistant cultivars of maize. *J. econ. Ent.* 86(3): 739-746.

Lack, D. (1944). Ecological aspects of species formation in passerine birds. *Ibis* 86: 260-286.

Lal, G. and J.C. Pant (1980). Laboratory and field testing for resistance in maize and sorghum varieties to *Chilo partellus* (Swinhoe). *Ind. J. Ent.* 42: 606-610.

Lawani, S.M. (1982). A review of the effects of various agronomic pracitces on cereal stem borer poupulations. *Trop. Pest Manage.* 28: 266-276.

Lawton, J.H. (1982). Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *J. Anim. Eco.* 51: 573-595.

Lawton, J.H. and Strong, D.R. (1981). Community patterns and competition in folivorous insects. *Am. Nat.* 118: 317-338.

Lees, A.D. (1968). Photoperiodism in insects. *Photophysiology* 4: 67-138.

Leonard, D.E. (1970). Air-borne dispersal of larvae of the gypsy moth and its influence on concepts of control. *J. econ. Ent.* 64: 638-641.

Leuschner, K. (1989). A review of sorghum stem borer screening procedures. In International workshop on sorghum stem borers. ICRISAT, Patancheru, India. 17-20 November 1987. pp. 129-135.

Leuschner, K.; S.L. Tanaja and H.C. Sharma (1985). The role of host plant resistance in pest management in sorghum in India. *Insect Sci. Applic.* 6: 453-460.

Li, C.S. (1985). Sugar-cane insect pests with special reference to the moth borers in the Markham Valley, Papua New Guinea. *Moshi* 50: 3-18.

MacArthur, R.H. (1972). *Geographical ecology*. New York: Harper and Row.

MacArthur, R.H. and R. Levins (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101: 377-385.

Mahadevan, N.R. and Chelliah, S. (1986). Influence of intercropping legumes with sorghum on the infestation of the stem borer, *Chilo partellus* (Swinhoe) in Tamil Nadu. *Trop. Pest Manage.* 32: 162-163.

Maniania, N.K. (1991). Potential of some fungal pathogens for the control of pests in the tropics. *Insect Sci. Applic.* 12: 63-70.

Mathez, F.C. (1972). *Chilo partellus* Swinh., *C. orichalcociliellus* Strand (Lep. Crambidae) and *Sesamia calamistis* Hamps. (Lep. Noctuidae) on maize in the Coast Province Kenya. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 45: 267-289.

Mbapila, J.C. (1997). *Comparative seasonal adaptation of Cotesia flavipes Cameron and Cotesia sesamiae (Cameron) (Hymenoptera:braconidae) to Chilo partellus Swinhoe (Lepidoptera:Pyralidae) on the Kenya coast.* Ph.D Thesis. University of Dar-Es-Salaam, Tanzania. pp 145.

McClure, M.S. (1980). Competition between exotic species: scale insects on hemlock. *Ecology* 61: 1391-1401.

McClure, M.S. (1981). Effects of voltinism, interspecific competition and parasitism on the population dynamics of the hemlock scales, *Fiorinia externa* and *Tsugaspidiotus isugane* (Homoptera: Diaspididae). *Ecol. Entomol.* 6: 47-54.

McClure, M.S. (1989). Biology, population trends, and damage of *Pineus* *boerneri* and *P. coloradensis* (Homoptera: Adelgidae on red pine. *Environ. Entomol.* 18: 1066-1073.

McClure, M.S. (1990). Cohabitation and host species effects on the population growth of *Matsucoccus resinosae* (Homoptera: Margarodidae) and *Pineus boerneri* (Homoptera: Adelgidae) on red pine. *Environ. Entomol.* 19: 672-676.

McClure, M.S. (1991). Adelgid and scale insect guilds on hemlock and pine. In Forest Insect Guilds: Patterns of Interaction with Host Trees. Gen. Tech. Report NE-153, ed. Y.N. Baranchikov, W.J. Mattson, F.P. Hain, T.L. Payne. Broomall, PA: US Dept. Agric. For. Serv. Northeast For. Exp. Stn. pp. 256-270.

McHugh, C.P. (1991). Distributional records from the U.S. Air Force ovitrapping program, 1990. *Journal of the American Mosquito Control Association* 7: 499-501.

McManus, M.L. (1973). The role of behaviour in the dispersal of newly hatched gypsy moth larvae. USDA Forest Service Research Paper NE-267.

McNaughton, S.J. Tarrants, J.L. McNaughton, M.M. and Davis, R.H. (1985). Silica as a defence against herbivory and a growth promotor in African grasses. *Ecology* 66: 528-535.

Medler, J.T. (1980). *Insects of Nigeria- check list and bibliography.* Memoirs, American Entomological Institute No 30 Michigan; Ann Arbor, p 919.

Meijerman, L. and Ulenberg, S.A. (1996). Identification of African stem borer larvae (Lepidoptera:Noctuidae, Pyralidae) based on morphology. *Bull. ent. Res.* 86: 567-578.

Messenger, P.S. (1975). Parasites, predators and population dynamics. In *Insects, Science and Society*, ed. D. Pimintel. New York: Academic. pp. 201-223.

Miller, R.S. (1964). Ecology and distribution of pocket gophers in Colorado. *Ecology* 45(2): 256-272.

Minja, E.M. (1990). Management of *Chilo* spp. infesting cereals in Eastern Africa. *Insect Sci. Applic.* 11(4/5): 489-500.

Mohyuddin, A.I. (1972). Distribution, biology and ecology of *Dentichasmias busseolae* Heinr. (Hym:Ichneumonidae) a pupal parasite of graminaceous stem borers (Lepidoptera:Pyralidae). *Bull. Ent. Res.* 62: 161-168.

Mohyuddin, A.I. and Greathead, D.J. (1970). An annotated list of the parasites of graminaceous stem borers in East Africa with a discussion of their potential in biological control. *Entomophaga* 15: 241-274.

Mohyuddin, A.J. and Attique, M.R. (1978). An assessment of loss caused by *Chilo partellus* to maize in Pakistan. *PANS* 24: 111-113.

Morgan, T.H. (1929). Experiments with *Drosophila. Carnegie Inst. Wash. Pub.* 399: 203-222.

Morisita, M. (1959). Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science of Kyushu University Series E Biology* 3: 65 -80.

Moyal, P. and Tran, M. (1989). Etude morphologique des stades pre-imaginaux delepidopteres foreurs du mais en zone des savanes de Cote D'Ivoire. *Annales de la Societe Entomologique de France* 25: 461-472.

Neupane, F.P.; Coppel, H.C. and Chapman, R.K. (1985). Bionomics of the maize borer, *Chilo partellus* (Swinhoe) in Nepal. *Insect Sci. Applic.* 6: 547-553.

Newman, L.H. (1968). *The complete British butterflies in colour*. London: Ebury Press and Michael Joseph p 13.

Nicholson, A.J. (1933). The balance of animal populations. *J. Animal Ecol.* 2(1): 132-178.

Nur, A.F. (1978). *Biology and control of the spotted stalk borer, Chilo partellus (Swinhoe) in Somalia.* M.Sc. Thesis University of Wyoming, Laramie, Wyoming, USA.

Nwanze, K.F. and O. Youm (1994). Integrated pest management of sorghum and pearl millet. *Proceedings of the Third International Conference on*

Tropical Entomology, 30th October-4th November 1994, Nairobi, Kenya.

Nye, I.W.B. (1960). *The insect pests of graminaceous crops in East Africa.* Colonial Research Study No. 31 London, Her Majesty's Stationary Office p 48.

Nyrop, J.P. (1988). Spatial dynamics of an acarine predator-prey system: *Typhlodromus pyri* (Acari:Phytoseiidae) preying on *Panonychus ulmi* (Acari:Tetranychidae). *Environ. Entomol.* 17: 1019-1031.

Ochieng, R.S.; F.O. Onyango and M.D.O. Bungu (1985). Improvement of techniques for mass culture of *Chilo partellus* (Swinhoe). *Insect Sci. Applic.* 6: 425-428.

Odindo, M.O. (1991). Management of cereals stemborers, especially *Chilo partellus* using Microsporidia. *Insect Sci. Applic.* 12: 51-55.

Ogwaro, K. (1983). Intensity levels of stem borers in maize and sorghum and the effect on yeild under different intercropping patterns. *Insect Sci. Applic.* 4: 33-37.

Okuda, T. (1988). Effect of artificial wetting and rainfall on the larval diapause of a stem borer, *Busseola fusca* in Western Kenya. *Entomologia Experimentalis et Applicata* 48: 263-267.

Oliver, B.F. and Gifford, J.R. (1975). Weight differences among stalk borer larvae collected from rice line showing resistance in field studies

(Lepidoptera:Pyralidae). *J. econ. Ent.* 68: 134.

Oloo, G.W. (1989). The role of local natural enemies in population dynamics of *Chilo partellus* (Swinh.) (Pyralidae) under subsistence farming systems in Kenya. *Insect Sci. Applic.* 10(2): 243-251.

O'Meara, G.F.; Gettman, A.D.; Evans, L.F. Jr. and Scheel, F.D. (1992). Invasion of cemeteries in Florida by *Aedes albopictus*. *Journal of the American Mosquito Control Association* 8: 1-10.

O'Meara, G.F.; Gettman, A.D.; Evan, L.F. Jr. and Curits, G.A. (1993). The spread of *Aedes albopictus* in Florida. *American Etomologist* 39: 163-172.

Omolo, E.O. (1983). Screening of local and exotic maize lines for stem borer resistance with special reference to *Chilo partellus*. *Insect Sci. Applic.* 4: 105-108.

Omolo, E.O. and Seshu Reddy, K.V. (1985a). Screening maize genotypes for multiple resistance to stem borers. *Insect Sci. Applic.* 6: 405-408.

Omolo, E.O. and Seshu Reddy, K.V. (1985b). Effect of different sorghum-based cropping systems on insect pests in Kenya. In *Proc. of the International Sorghum Entomology Workshop, 15-21 July 1984, Texas A & M University. College Station, TX USA. ICRISAT Patancheru, India.* pp. 395-401.

Overholt, W.A.; K. Ogedah and P.M. Lammers (1994a). Distribution and sampling of *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) in maize and sorghum at the Kenya coast. *Bull. ent Res.* 84: 367-378.

Overholt, W.A.; Ngi-Song, A.J.; Kimani, S.W.; Mbapila, J.; Lammers, P. and Kioko, E. (1994b). Ecological considerations of the introduction of *Cotesia flavipes* Cameron (Hymenoptera:Braconidae) for biological control of *Chilo partellus* (Swinheo) (Lepidoptera:Pyralidae) in Africa. *Biocontrol News and information* 15(2): 19N-24N.

Overholt, W.A.; Ngi-Song, A.J.; Omwega, C.O; Kimani-Njogu, S.W.; Mbapila, J.; Sallam, M.N. and Ofomata, V. (1997). A review of the introduction and establishment of *Cotesia flavipes* Cameron (Hymenoptera:Braconidae) in East Africa for the biological control of cereal stemborers. In *Proceedings of the International Workshop on Tropical Gramineous stem borers, ICIPE, 14-16th May 1996.*

Paine, T.D.; Birch, M.C. and Svihra, P. (1981). Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera:Scolytidae). *Oecologia* 48: 1-6.

Painter, R.H. (1951). *Insect resistance in crop plants*. Macmillan, New York.

Painter, R.H. (1958). Resistance of plants to insects. *Ann. Rev. Entomol.* 3: 267-290.

Panda, N.; Pradhan, B.; Samalo, A.P. and Rao, P.S.P. (1975). Note on the relationship of some biochemical factors with the resistance in rice varieties to yellow rice borer. *Ind. J. Agric. Sci.* 45: 499-501.

Park, T. (1948). Experimental studies of interspecies competition 1. Competition between species of flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecol. Monogr.* 18: 265-308.

Park, T. (1954). Experimental studies of interspicies competition 11. Temperature, humidity, and competition in two species of *Tribolium*. *Physiol. Zool.* 28: 177-238.

Park, T. (1955a). Ecological experimentation with animal populations. *Sci. Monthly* 81: 271-275.

Park, T. (1955b). Experimental competition in beetles with some general implications. In: *The numbers of man and animals*. Oliver and Boyd, Ltd., London, for the Institute of Biology pp. 69-82.

Park, T. (1957). Experimental studies on interspecies competition. 111. Relation of initial species proportion to competitive outcome in populations of *Tribolium*. *Physiol. Zool.* 30: 22-40.

Päts, P. (1991). Activity of *Chilo partellus* (Lepidoptera:Pyralidae): eclosion, mating and oviposition time. *Bull. ent. Res.* 81: 93-96.

Päts, P. (1992). *Reproductive biology of the cereal stem borer Chilo partellus*. Dissertation, Swedish University of Agricultural Science, Uppsala.

Päts, P. and Ekbom, B. (1992). Infestation and dispersal of early instars of *Chilo partellus* (Lepidoptera:Pyralidae) at different densities. *Environ. Entomol.* 2(5): 1110-1113.

Petersen, B. (1947). Die geographische Variation einiger Fennoskandischer Lepidopteren. *Zool. Bidrag Uppsala* 25: 329-531.

Patterson, J.T. (1943). Studies in the genetics of *Drosophila*. III. the Drosophilidae of the Southwest. Univ. of Texas pub, No. 4313.

Peacock, B.E.; Smith, J.P.; Gregory, P.G.; Loyless, T.M.; Mulrennen, J.A. Jr.; Simmonds, P.R.; Padgett, L. Jr. Cook, E.K. and Eddins, T.R. (1988). *Aedes albopictus* in Florida. *Journal of the American Mosquito Control Association* 4: 362-265.

Petersen, B. (1968). Die geographische Variation einiger Fennoskandischer Lepidopteren. *Zool. Bidrag Uppsala* 25: 329 -531.

Pianka, E.R. (1976). Competition and niche theory. In: *Theoretical ecology. Principles and applications* (R.M. May ed.), Philadelphia: Saunders pp. 114-141.

Pimentel, D.; Hunter, M.S.; LaGro, J.A. Efroymson, R.A.; Landers, J.C.; Mervis, F.T.; McCarthy, C.A. and Boyd, A.E. (1989). Benefits and risks of genetic engineering in agriculutre. *Bioscience* 39: 606-614.

Polnik, A. (1960). Effects of some intraspecies processes on competition between two species of flour beetles, *Latheticus oryzae* and *Tribolium confusum*. *Physiol. Zool.* 33(1): 42-57.

Pradhan, S. and Prasad, S.K. (1955). Correlation between the degree of damage due to *Chilo partellus* Swin. and the yield of Jowar grain. *Indian J. Entomol.* 17: 136-137.

Purseglove, J.W. (1972). *Tropical crops- monocotyledons*. London; Longman, p. 607.

Ramachandran, R. (1987). Influence of host-plants on the wing dispersal and the survival of an Australian geometrid caterpillar. *Entomologia Experimentalis et Applicata* 44: 289-294.

Ramadan, M.M.; T.T.Y. Wong; and J.W. Beardsley (1992). Reproductive behaviour of *Biosteres arisanus* (Sonan) (Hymenoptera:Braconidae) an egg-larval parasitoid of the oriental fruit fly. *Biological Control* 2: 28-34.

Reilly, J.J. and W.L. Sterling (1983). Interspecific association between the red imported fire ant (Hymenoptera:Formicidae), aphids, and some predaceous insects in a cotton agroecosystem. *Environ. Entomol.* 12: 541-545.

Renkonen, O (1938). Statisch-okologischeUntersuchungen uber die terrestiche kaferwelt der finnischen bruchmoore. *Ann. Zool. Soc. Bot. Fenn. Vanamo* 6: 1-231.

Ricklefs, R.E. (1973). *Ecology*. Nelson, London.

Rivany, E. (1964). Influence of man on insect ecology in arid zones. *Ann. Rev. Entomol*. 9: 41-62.

Robinson, G.S. (1975). *Macrolepidoptera of Fiji and Rotuma*. E.W. Classey Ltd., Faringdon, Oxon. UK. p. 362.

Robinson, J.F.; Klun, J.A. and Brindley, T.A. (1978). European corn borer: A nonpreference mechanism of leaf feeding resistance and its relationship to 1,4 benzoxazin-3-one concentration in dent corn tissue. *J. econ. Ent*. 71: 461-465.

Rodriguez-del-Bosque, L.A.; J.W. Smith Jr. and H.W. Browning (1990). Seasonality of cornstalk borers (Lepidoptera:Pyralidae) in northeastern Mexico. *Environ. Entomol*. 19: 345-356.

Roome, R.E. (1980). Dispersal of newly hatched *Chilo partellus* (Swinhoe) larvae from sorghum cultivars. *Z. ang. Ent*. 90: 174-180.

Ross, S.E. and Ostle, K.R. (1990). Dispersal and survival of early instars of European corn borer (Lepidoptera:Pyralidae) in field corn. *J. econ. Ent*. 83(3): 831-836.

Sachan, G.C. and Rathore, Y.S. (1983). Studies on the complete protection of sorghum crop against insect pests by chemicals and thuricide at various stages of crop growth. *Pesticides* 17: 15-16.

Sadakathulla, S. and Mani, M. (1978). Influence of intercropping on the incidence of sorghum pest. *Sorghum newsl.* 21: 70.

Sale, P.F. and R. Dybdahl (1978). Determinants of community structure for coral reef fishes in isolated coral heads at loggonal and reef slope sites. *Oecologia* 34: 57-74.

Sampson, M.A. (1982). *The biology of the lepidopterous stemborers on sugarcane (Saccharum officinarum L.) in Ghana.* Ph.D. thesis. University of Ghana, Legos.

Sampson, M.A. and Kumar, R. (1983). Population dynamics of the stem borer complex on sugarcane in southern Ghana. *Insect Sci. Applic.* 4: 25-32.

Sampson, M.A. and Kumar, R. (1985). Borer damage and estimation of loss caused by sugarcane stem borers in Southern Ghana. *Insect Sci. Applic.* 6: 705-710.

Sartees, G. (1966). *Aedes (Stegomyia) albopictus*: a summary of present knowledge with particular reference to competition with *Aedes aegypti*. *World Health Organization: Vector Control* 66: 195.

Sarup, P. Panwar, V.P.S. Marwaha, K.K. and Siddiqui, K.H. (1971). Management of maize pests with particular reference to the stalk borer, *Chilo partellus* (Swinhoe) under resource constraint. *J. Entomol. Res.* 2: 5-14.

SAS Institute (1987). *SAS/STAT guide for personal computers, version 6* ed. SAS Institute, Cary, NC.

Saxena, K.N. (1985). Behavioural basis of plant resistance or susceptibility to insects. *Insect Sci. Applic.* 6: 303-313.

Saxena, K.N. (1990). Mechanisms of resistance/susceptibility of certain sorghum cultivars to the stem borer *Chilo partellus*: role of behaviour and development. *Entomologia Experimentalis et Applicata* 55: 91-99.

Saxena, K.N.; A.M. Nour; F.D.O. Odawa and S.M. Otieno (1992). Components and mechanism of resistance in sorghum to stem borers. *Annual Report of the International Centre of Insect Physiology and Ecology (ICIPE)* pp. 42-45.

Scheltes, P. (1978). *Eclogical and physiological aspects of aestivation-diapause in the larvae of two pyralid stalk borers of maize in Kenya.* Ph.D Thesis Landbouwhogeschool, Wageningen.

Schoener, T.W. (1970). Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408-418.

Schoener, T.W. (1974). Some methods for calculating competition coefficient from resource utilization spectra. *Am. Nat.* 108: 332-340.

Schoener, T.W. (1983). Field experiments on interspecific competition. *Am. Nat.* 122: 240-285.

Schoener, T.W. (1988). Ecological interaction. In *Analytical Biogeography*. ed. A.A. Myers, P.S. Giller. New York: Chapman and Hall pp. 255-97.

Schulthess, F.M.S.; Bosque-Perez, N.A. and Gounou, S. (1991). Sampling Lepidopterous pests on maize in West Africa. *Bull. ent. Res.* 81: 297-301.

Schulthess, F.M.S.; Bosque-Perez, N.A. and Thomas-Odjo, A. (1993). Effect of plant nitrogen and silica on the bionomics of *Sesamia calamistis* (Lepidoptera: Noctuidae). *Bull. ent. Res.* 83: 405-411.

Schuster, M.F. and H.A. Dean (1976). Competitive displacement of *Anagyrus antoninae* (Hymenoptera:Encyrtidae) by its ecological homologue *Neodusmetia sangwani* (Hymenoptera: Encyrtidae). *Entomophaga* 21: 127-130.

Selhime, A.G.; M.H. Muma; W.A. Simanton and C.W. McCoy (1969). Control of the Florida red scale in Florida with the parasite *Aphytis holozanthus*. *J. econ. Ent.* 62: 954-955.

Seshu Reddy, K.V. (1983a). Sorghum stem borers in eastern Africa. *Insect. Sci. Applic.* 4: 33-39.

Seshu Reddy, K.V. (1983b). Studies on the stem borer complex of sorghum in Kenya. *Insect Sci. Applic.* 6: 3-10.

Seshu Reddy, K.V. (1985a). Relative susceptibility and resistance of some sorghum lines to stem borers in western Kenya. *Insect Sci. Applic.* 6: 401-

404.

Seshu Reddy, K.V. (1985b). Sorghum (Serena) yield loss due to *Chilo partellus* infestation. *ICIPE Thirteenth Annu. Rep.* 1985 p. 6.

Seshu Reddy, K.V. (1988). Assessment of on-farm yield losses in sorghum due to insect pests. *Insect Sci. Applic.* 9: 679-685.

Seshu Reddy, K.V. (1989). Sorghum stem borer in eastern Africa. *International workshop on sorghum stemborers .Patancheru, India* 17-20 Nov. 1987 pp. 33-40.

Seshu Reddy, K.V. (1990). Cultural control of *Chilo* spp. in graminaceous crops. *Insect Sci. Applic.* 11(4/5): 703-712.

Seshu Reddy, K.V. (1991). Insect pests of sorghum in Africa. *Insect Sci. Applic.* 12: 563-657.

Seshu Reddy, K.V. and J.C. Davies (1979). Pests of sorghum and Pearl millet and their parasites and predators recorded at ICRISAT centre, India up to August 1979. *Cereal Entomology Department Progress Report 2 ICRISAT Patancheru, A.P., India.* p. 23.

Seshu Reddy, K.V. and Omolo E.O. (1985). Sorghum insect pest situation in Eastern Africa. In *Proc. of the International Sorghum Entomology Workshop, 15-21 july 1984, Texas A & M University. College Station, TX USA. ICRISAT Patancheru, India.* pp. 31-36.

Seshu Reddy, K.V., Walker, P.T. (1990). A review of the yield losses in graminaceous crops caused by *Chilo spp. Insect Sci. Applic.* 11(4/5): 563-569.

Settle, W.H. and L.T. Wilson (1990). Invasion by the variegated leafhopper and biotic interaction: parasitism, competition and apparent competition. *Ecology* 71: 1461-1470.

Shanower, T.; Schulthess, F. and Gounou, S. (1991). Distribution and abundance of some stem and cob borers in Benin. *Plant Health Management Research Monograph No. 1. International Institute of Tropical Agriculture, Ibadan, Nigeria.* p. 18.

Shanower, T.G.; Schulthess, F. and Bosque-Perez, N. (1993a). Development and fecundity of *Sesamia calamistis* Hampson (Lepidoptera:Pyralidae). *Bull. ent. Res.* 83: 237-243.

Shanower, T.G.; Schulthess, F. and Bosque-Perez, N. (1993b). The effect of larval diet on the growth and development of *Sesamia calamistis* Hampson (Lepidopterra:Noctuidae) and *Eldana saccharina* Walker (Lepidoptera:Pyralidae). *Insect Sci. Applic.* 14(5/6): 681-685.

Sharma, H.C. (1985). Strategies for pest control in sorghum in India. *Trop. Pest Manage.* 32: 167-185.

Sharma, V.K. and S.M. Chatterji (1971). Preferential oviposition and antibiosis in different maize germplasm against *Chilo partellus* (Swinhoe) under cage conditions. *Ind. J. Ent.* 33: 299-311.

Sharma, A.N. and Sharma, V.K. (1987). Studies on the economic injury level in maize, *Zea mays* L. to stem borer *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae). *Trop. Pest Manage.* 33: 44-51.

Simberloff, D. (1981). Community effects of introduced species. In *Biotic crises in Ecological and Evolutionary Time* (ed. M.H. Nirecki), Academic Press, New York pp. 53-81.

Singh, G. and Sandhu, G.S. (1978). Oviposition behaviour of maize borer *Chilo partellus* (Swinhoe) in the field. *Ind. J. Ent.* 40(2): 191-196.

Singh, B.U. and B.S. Rana (1984). Influence of varietial resistance on oviposition and larval development of stalk-borer *Chilo partellus* (Swin.) and its relationship to field resistance in sorghum. *Insect Sci. Applic.* 5: 287-296.

Singh, D., Tyagi, B.N., Khosla, R.K. and Avasthy, K.P. (1971). Estimates of the incidence of pests and diseases and consequent field losses in the yield of maize (*Zea mays* L.). *Indian J. Agric. Sci.* 41: 1094-1097.

Singh, U.C.; Misra, U.S; Dhamdhere, S.V. and U.S. Dwivedi (1985). Carry-over of the sorghum stalk borer, *Chilo partellus* (Swinhoe) in off-season in different crops. *J. Ent. Res.* 9(2): 170-173.

Sithole, S.Z. (1989). Sorghum stem borers in southern Africa. *Proceedings of the International Workshop on Sorghum Stem borers, ICRISAT Centre, Patancheru, India*, 17-20 November 1987, pp. 41-47.

Skoroszewski, R.W. and H. Van Hamburg (1987). The release of *Apanteles flavipes* (Cameron) (Hymenoptera:Braconidae) against stalk-borers of maize and grain-sorghum in South Africa. *J. Entomol. Soc. S. Afr.* 50: 249-255.

Smith, R.F. (1970). Pesticides: Their use and limitations in pest management. In *Concepts of Pest Management* (Ed. Rabb, R.C. and Guthrie, F.C.) Raleigh, NC, USA, North Carolina State University.pp. 6-29.

Smith, R.L. (1980). *Ecology and field biology*. Harper and Row. New York. p. 835.

Sogawa, K. (1982). The rice brown planthopper: feeding physiology and host plant interactions. *Ann. Rev. Ent.* 27: 49-73.

Solomon, M.E. (1973). Ecology in relation to the management of insects. In *Insects: Studies on Population Management* (Ed. Geir, P. W.; Clark, L.R.; Anderson, D.J. and Nix, H.A.). Canberra, Australia: Ecological Society of Australia pp. 153-167.

Southwood, T.R.E. (1978). *Ecological methods*. John Wiley and Sons Inc. New York. p. 524.

Southwood, T.R.E. and Way, M.J. (1970). Ecological background to pest management. In *Concepts of Pest Management* (Ed. Rabb, R.L. and Guthrie, F.E.). North Carolina State University Press, Raleigh, North Carolina, pp. 6-29.

Spieth, H. and T.C. Hsu (1950). The influence of light on the mating behavior of seven species of the *Drosophila melanogaster* species group. *Evolution* 4: 316-325.

Starks, K.J. (1969). Some cereal crop insects in East Africa. *E. Afr. Agric. For. Res. Org., Serere Res. Stn., Uganda (Mimeo).*

Starks, K.J. and Dogget, H. (1970). Resistance to a spotted stem borer in sorghum and maize. *J. econ. Ent.* 63: 1790-1795.

Stewart, K.W. and Walton, R.R. (1964). Oviposition and establishment of the southwestern corn borer on corn. *J. econ. Ent.* 57(5): 628-631.

Stiling, P.D. and Strong, D.R. (1983). Weak competition among Spartina stem borers, by means of murder. *Ecology* 64: 770-778.

Stiling, P.D. and Strong, D.R. (1984). Experimental density manipulation of stemboring insects: some evidence for interspecific competition. *Ecology* 65: 1683-1685.

Strauss, S.Y. (1988). The Chrysomelidae: A useful group for investigating herbivore-herbivore interactions. In *Biology of Chrysomelidae*, ed. P.

Jolivet; E. Petitpierre; T.H. Hsiao, Boston: Kluwer Academic pp. 91-105.

Strong, D.R. (1981). The possibility of insect communities without competition: hispine beetles on Heliconia. In *Insect Life History Patterns: Habitat and Geographic Variation,* ed. R.F Denno; H. Dingle. New York: Springer-Verlag pp. 183-94.

Strong, D.R. (1982). Harmonious coexistence of hispine beetles on Heliconia in experimental and natural communities. *Ecology* 63: 1039-1049.

Strong, D.R. (1983). Natural variability and the manifold mechanisms of ecological communities. *Am. Nat.* 122: 636-660.

Strong, D.R.; J.H. Lawton and T.R.E. Southwood (1984). *Insects on plants: community patterns and mechanisms*. Harvard University Press, Cambridge, MA. pp.313.

Sturtevant, A.H. (1929). The genetics of *Drosophila simulans*. *Carnegie Inst. of Wash. Pub.* 399: 1-62.

Swaine, G. (1957). The maize and sorghum stalk borer *Busseola fusca* (Fuller), in peasant agriculture in Tanganyika Territory. *Bull. ent. Res.* 48: 177-722.

Taley, Y.M. and K.R. Thakare (1976). Studies on the carry-over of *Chilo partellus* Swin. through sorghum stubbles. *Sorghum News* 21: 52.

Taley, Y.M. and Thakare, K.R. (1980). Note on the population dynamics in carryover of *Chilo partellus* (Swinhoe). *Ind. J. Agric. Sci.* 58: 635-637.

Tams, W.H.T. (1932). New species of African Heterocera. *Entomologist* 65: 1241-1249.

Tams, W.H.T. and Bowden, J. (1953). A revision of the Africa species of *Sesamia* Guenee and related genera (Lepidoptera:Agrotidae). *Bull. ent. Res.* 43: 645-678.

Taneja, S.L. and Nwanze, K.F. (1989). Assessment of yield loss of sorghum and pearl millet due to stem borer damage. *In Proc. International Workshop on Sorghum Stem Borers*, 17-20 November 1987, ICRISAT Center, India. 95: 1-4.

Tayabi, K. and Azizi, P. (1984). Influence of silica on rice yield and stem borer (*Chilo supermain*) in Rasht/Iran in 1979-1980. *Pesticides* 17: 20-22.

Tokro, P.G. and Saxena, K.N (1991). Some aspects of the feeding responses in the stem borer *Chilo partellus* Swinhoe (Lepidoptera:Pyralidae). *Acta Biologica Hungarica* 42(4): 385-395.

Torto, B.; Hassanali, A.; and Saxena, K.N. (1990). Chemical aspects of *Chilo partellus* feeding on certain sorghum cultivars. *Insect Sci. Applic.* 11(4/5): 649-655.

Torto, B.; Hassanali, A.; Saxena, K.N. and Nokoe, S (1991). Feeding responses of *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) larvae to sorghum plant phenolics and their analogs. *Journal of Chemical Ecology*

17(1): 67-78.

Unnithan, G.C. (1988). Certain factors determining mating, fecundity and egg fertility in the sorghum stem-borer, *Chilo partellus*. *Proceedings 18th International Congress of Entomology, Vancouver, B. C., Canada*, July 3-9 1988, pp. 379.

Unnithan, G.C. and Seshu Reddy, K.V. (1986). Infestation and carryover of sorghum stemborer and the potential role of destruction of crop residue as a cultural control practice. In *Proceedings of the International Conference on Tropical Entomology. 31 Aug-5 Sep 1986 Nairobi, Kenya* pp. 32.

Unnithan, G.C. and Seshu Reddy, K.V. (1989). Incidence, diapause and carryover of the cereal stem borers on Rusinga Island Kenya. *Trop. Pest Manage*. 35(4): 414-419.

Unnithan, G.C. and Paye, S.O. (1991). Mating, longevity, fecundity, and egg fertility of *Chilo partellus* (Lepidoptera:Pyralidae): Effects of delayed or successive matings and their relevance to pheromonal control methods. *Environ. Entomol*. 20(1): 150-155.

Usua, E.J. (1970). Diapause in the maize stemborer. *J. econ. Ent.*. 63: 1605-1610.

Usua, E.J. (1973). Induction of diapause in the maize stemborer, *Busseola fusca*. *Entomologia Experimentalis et Applicata* 16: 322-328.

Usua, E.J. (1974). Observations on the physiology of diapause and non-diapause larvae of *Busseola fusca* (Fuller) (Lepidoptera:Noctuidae). *Bull. ent. Res.* 63: 513-518.

Utida, S. (1953). Interspecific competition between two species of bean weevil. *Ecology* 34(2): 301-307.

van den Berg, J.; J.B.J. van Rensburg and K.L. Pringle (1991). Comparative injuriousness of *Busseola fusca* (Lepidoptera:Noctuidae) and *Chilo partellus* (Lepidoptera:Pyralidae) on grain sorghum. *Bull. ent.. Res.* 82: 137-142.

van den Bosch, R.; P.S. Messenger; A.P. Gutierrez (1982). *An introduction to biological control*. Plenum Press, New York. P. 247.

van Hamburg, H. (1979). The grain-sorghum stalk-borer, *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae) seasonal changes in adult populations in grain sorghum in the Transvaal. *J. ent. Soc. Sth. Afr.* 42: 1-9.

van Hamburg, H. (1980). The grain-sorghum stalk-borer, *Chilo partellus* (Swinhoe) (Lepidoptera:Pyralidae): survival and location of larvae at different infestation levels in plant of different ages. *J. ent. Soc. sth. Afr.* 43: 71-76

van Hamburg, H. and Hassell, M.P. (1984). Density dependence and the augumentative release of egg parasitoids against graminaceous stalk borers. *Ecological Entomology* 9: 101-108.

van Rensburg, N.J. and van Hamburg, H. (1975). Grain sorghum pests: An integrated control approach. *Proc. I Congr. Entomol. Soc. S. Afr.* pp. 151-162.

Verma, A.N. and Singh, S.P. (1989). Cultural control of sorghum stem borers. In *Proc. Int. Workshop on Sorghum Stem Borers, 17-20 November 1987. International Crops Research Institute (ICRISAT) for the Semi-Arid Tropics, Patancheru, A. P. 502324, India.* pp. 81-87.

Walker, P.T. (1960). Insecticide studies on the maize stalkborer *Busseola fusca* (Fuller) in East Africa. *Bull. ent. Res.* 51: 521-531.

Waloff, N. (1968). Studies on the insect fauna on Scotch broom *Sarothamnus scoparius* (L.) Wimmer. *Adv. Ecol. Entomol.* 5: 87-209

Warui, C.M. and Kuria, J.N. (1983). Population incidence and the control of maize stalk borer *Chilo partellus* (Swinhoe), *C. orichalcociliellus* Strand (Pyralidae) and *Sesamia calamistis* Hmps (Noctuidae) in Coast Province, Kenya. *Insect Sci. Applic.* 4: 11-18.

Wheatley, P.E. (1961). The insect pests of agriculture in the Coast Province of Kenya. V- Maize and sorghum. *E. Afr. Agric. For. J.* 27: 105-107.

White, T.C.B. (1978). The relative importance of food shortage in animal ecology. *Oecologia* (Berl.) 336: 71-86.

White, T.C.B. (1984). The availability of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* (Berl.) 33: 71-86.

Wiens, J.A. (1977). On competition and variable environments. *Am. Sci.* 65: 590-597.

Wiklund, C. and Fagerstrom, T. (1977). Why do males emerge before females? *Oecologia* (Berl.) 31: 153-158.

Woodhead, S. and S.L. Taneja (1987). The importance of the behaviour of young larvae in sorghum resistance to *Chilo partellus*. *Entomologia Experimentalis et Applicata* 45: 47-54.

Youdeowei, A. (1989). Major arthropod pests of food and industrial crops of Africa and their economic importance. In Yaninek, J.S. and Herren, H.R. (eds). *Biological control: a sustainable solution to crop pest problems in Africa. Ibadan, Nigeria, IITA*. pp. 31-50.

Youm, O. (1984). *Stemborers attacking Sorghum bicolor L. Moench and Zea mays L. in the Lower Rio Grande Valley*. M. S. thesis, Texas A & M University College Station.

Young, W.R. and G.L. Teetes (1977). Sorghum entomology. *Ann. Rev. Entomol.* 22: 193-218.

Appendix 1. **Quantities of maize consumed (mean±std) by *C. partellus* and *C. orichalcociliellus* on a 4 days interval**

	Food consumed (grams)																
Borer species	Age (days)																
	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68
C. partellus	0.05± 0.04	0.07± 0.04	0.11± 0.05	0.15± 0.06	0.17± 0.07	0.18± 0.10	0.22± 0.13	0.27± 0.15	0.24± 0.13	0.13± 0.08	0.12± 0.07	0.07± 0.01	0.06± 0.01	0.05± 0.01	0.05± 0.01	0.05± 0.00	0.04± 0.00
C. orichalcociliellus	0.03± 0.02	0.05± 0.02	0.08± 0.03	0.11± 0.04	0.12± 0.04	0.13± 0.04	0.13± 0.03	0.12± 0.03	0.12± 0.04	0.11± 0.04	0.11± 0.03	0.10± 0.03	0.10± 0.03	0.09± 0.03	0.08± 0.03	0.08± 0.04	0.09± 0.06
F-value	3.92	3.25	2.26	1.83	3.51	7.15	15.73	20.50	13.50	4.24	6.06	24.08	27.35	37.51	59.13	-	-
Pr > F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.03	0.31	0.30	0.25	0.20	-	-

Appendix 2. **Quantities of sorghum consumed (mean±std) by *C. partellus* and *C. orichalcociliellus* on a 4 days interval**

Borer species	Food consumed (grams) Age (days)																
	4	8	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68
C. partellus	0.05± 0.05	0.04± 0.04	0.05± 0.05	0.07± 0.04	0.08± 0.04	0.09± 0.04	0.10± 0.04	0.09± 0.03	0.10± 0.03	0.09± 0.04	0.08± 0.02	0.07± 0.02	0.07± 0.02	0.06± 0.02	0.05± 0.01	0.05± 0.01	0.05± 0.00
C. orichalco ciliellus	0.04± 0.02	0.04± 0.02	0.05± 0.02	0.05± 0.02	0.06± 0.02	0.06± 0.02	0.07± 0.02	0.07± 0.02	0.07± 0.02	0.07± 0.01	0.07± 0.02	0.07± 0.02	0.06± 0.01	0.05± 0.01	0.05± 0.01	0.05± 0.01	0.05± 0.01
F-value	6.73	8.13	8.68	6.12	4.97	4.89	3.98	3.21	2.61	6.06	1.31	1.56	5.63	7.83	1.97	1.20	25.00
Pr > F	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.04	0.00	0.63	0.46	0.06	0.12	0.71	1.00	0.25

Appendix 3. Quantities of maize and sorghum stems (mean±std) consumed by *C. partellus* and *C. orichalcociliellus*on a daily basis.

Host plant	Food consumed (grams)		F-value (row wise)	Pr > F (row wise)
	C. partellus	*C. orichalcociliellus*		
Maize	0.18±0.10Aa	0.11±0.04Ab	39.82	0.0001
Sorghum	0.08±0.04Ba	0.06±0.03Bb	4.27	0.0426
F-value	42.96	34.69		
Pr > F	0.0001	0.0001		

Appendix 4. Mean number of days (mean±std) taken by *C. partellus* and *C. orichalcociliellus* to complete larval development in maize and sorghum stems.

Host plant	Number of days to pupation		F-value	Pr > F
	C. partellus	*C. orichalcociliellus*		
Maize	26.7±7.70b	29.9±13.10a	4.20	0.0417
Sorghum	38.8±11.12b	49.7±11.19a	13.58	0.0005

Means in the same column with different letters are significantly different P ≤ 0.05

Appendix 5. Quantities of maize and sorghum stems (mean±std) consumed by *C. partellus* and *C. orichalcociliellus* in a larval lifetime.

Host plant	Food consumed (grams)		F-value	Pr > F
	C. partellus	C. orichalcociliellus		
Maize	4.8±3.36Aa	3.2±1.35Ab	20.25	0.0001
Sorghum	3.1±1.53Ba	2.8±1.11Aa	0.36	0.5532
F-vallue	11.83	1.19		
Pr > F	0.0008	0.2775		

Means in the same row with different lower case letters are significantly different P ≤ 0.05

Means in the same column with different upper case letters are significantly different P ≤ 0.05

Appendix 6. Numbers of newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from maize and sorghum plants.

Host plant	Numbers dispersing				G-test (row wise)
	N	*C. partellus*	N	*C. orichalcociliellus*	
Maize	320	89	320	9	87.25*
Sorghum	320	38	320	18	7.94*
G-test (column wise)		26.07*		3.15	

A significant difference (P ≤ 0.05) is indicated by an asterisk

Appendix 7. Distance covered (mean±std) by newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from maize and sorghum plants.

Host plant	Mean distance covered (cm)				F-value	Pr>F
	N	*C. partellus*	N	*C. orichalcociliellus*		
Maize	320	45.8±24.4Aa	320	27.8±14.2Ab	4.75	0.0317
Sorghum	320	36.3±17.3Ba	320	27.4±10.1Ab	4.10	0.0478
F-value (column wise)		4.77		0.01		
Pr>F (column wise)		0.0308		0.9350		

Means in the same column with different upper case letters are significantly different P≤ 0.05

Means in the same row with different lower case letters are significantly different P ≤ 0.05

Appendix 8. Rate of dispersal of newly hatched larvae of *C. partellus* and *C. orichalcociliellus* from maize and sorghum plants.

Host plant	Mean rate of dispersal		F-value	Pr>F
	C. partellus	*C. orichalcociliellus*		
Maize	2.18±1.61Aa	0.68±0.31Ab	7.71	0.0066
sorghum	1.28±0.63Ba	0.88±0.46Ab	5.75	0.0200
F-value (column wise)	11.13	1.39		
Pr>F (column wise)	0.0011	0.2496		

Means in the same row with different upper case letters are significantly different P≤ 0.05

Means in the same column with different lower case letters are significantly different P ≤ 0.05

Appendix 9. Frequency distribution of distances covered by newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from maize plants.

Distance	Numbers dispersing	
	C. partellus	*C. orichalcociliellus*
0	231	311
>0 <20	9	3
>20 <40	33	5
>40 <60	27	1
>60 <80	14	0
>80 <100	4	0
>100	2	0

Appendix 10. Frequency distribution of distances covered by newly hatched larvae of *C. partellus* and *C. orichalcociliellus* dispersing from sorghume plants.

Distance	Numbers dispersing	
	C. partellus	*C. orichalcociliellus*
0	282	302
>0 <20	11	5
>20 <40	13	12
>40 <60	12	1
>60 <80	2	0
>80 <100	0	0
>100	0	0

Appendix 11. Mean time taken by diapausing larvae of *C. partellus* and *C. orichalcociliellus* to terminate diapause

Borer species	N	Pupation	N	Adult
C. partellus	550	9.68±4.45b	443	16.45±4.33b
C. orichalcociliellus	197	14.36±9.86a	160	20.85±10.59a
F-value		76.1		52.63
Pr > F		0.0001		0.0001

Means in the same column with different letters are significantly different P = 0.05

Appendix 12. Mean time taken by male and female diapausing larvae of *C. partellus* to terminate diapaue

Sex	N	Pupation	N	Adult
Male	182	9.43±4.71a	176	16.22±4.47a
Female	292	9.71±4.29a	267	16.60±4.23a

Means in the same column with the same letter are not significantly different P > 0.05

Appendix 13. Mean time taken by male and female diapausing larvae of C. *orichalcociliellus* to. terminate diapause.

Sex	N	Pupation	N	Adult
Male	49	11.47±6.49b	45	19.20±6.84b
Female	122	14.80±10.79a	114	21.54±1.71a

Means in the same column with different letters are significantly different $P \leq 0.05$