

Seasonal abundance of the two maize stem borers *Sesamia calamistis* and *Eldana saccharina* and bionomics of the *Sesamia* egg parasite, *Telenomus busseolae*

By

Konan L. Kouamé

Ingénieur Agronome, Ecole Nationale Supérieure Agronomique
Abidjan, 1984.

M.Sc., Simon Fraser University, 1991.

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in the Department
of
Biological Sciences

© Konan L. Kouamé 1995
SIMON FRASER UNIVERSITY
September, 1995

All rights reserved. This work may not be reproduced in whole or in part, by photocopy or other means, without permission of the author.

APPROVAL

NAME: **Konan L. Kouame**

DEGREE: **DOCTOR OF PHILOSOPHY**

TITLE OF THESIS:

SEASONAL ABUNDANCE OF THE TWO MAIZE STEMBORERS *SESAMIA CALAMISTIS* AND *ELDANA SACCHARINA*, AND BIONOMICS OF THE *SESAMIA* EGG PARASITE *TELENOMUS BUSSEOLAE*

Examining Committee:

Chair: Dr. G. Anderson

Dr. M. Mackauer, Professor, Senior Supervisor,
Department of Biological Sciences, SFU

Dr. F. Schulthess, Research Scientist
International Institute of Tropical Agriculture

Dr. P. Belton, Adjunct Professor
Department of Biological Sciences, SFU

Dr. H. R. MacCarthy, Adjunct Professor
Department of Biological Sciences, SFU

Dr. G. Gries, Assistant Professor
Department of Biological Sciences, SFU
Public Examiner

Dr. R. S. Vernon, Research Scientist
Canada Research Station, Vancouver
External Examiner

Date Approved 19 September 1991

PARTIAL COPYRIGHT LICENSE

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

SEASONAL ABUNDANCE OF THE TWO MAIZE STEM BORERS SESAMIA CALAMISTIS

AND ELDANA SACCHARINA AND BIONOMICS OF THE SESAMIA EGG PARASITE,

TELENOMUS BUSSEOLAE.

Author:

(signature)

Konan L. Kouamé

(name)

26 Sept 1985

(date)

ABSTRACT

The two moths, *Sesamia calamistis* (Lepidoptera: Noctuidae) and *Eldana saccharina* (Lepidoptera: Pyralidae), are common pests of maize in West Africa. Their variations in population numbers, and effects of *S. calamistis* on maize, were investigated from September 1991 to January 1994 at the International Institute of Tropical Agriculture, Cotonou, Bénin. These insects were the predominant stem borers found on maize, but also on wild sorghum and pennisetum grasses, when fresh maize plants were not available. In choice tests in the greenhouse, *S. calamistis* laid more eggs on 40 day-old maize than on older plants, and more on maize than grasses of the same age. These results indicate that grasses are reservoirs for borers and sources of infestation of maize fields. *S. calamistis* attacked maize from four weeks after planting; *E. saccharina* attacked from silking. Numbers of moths caught in light traps were positively correlated with wind speeds and relative humidity, but they were negatively correlated with temperatures. Moth catches were higher around new moon than full moon.

Timing and level of plant infestations by *S. calamistis* reduced growth and yield of maize, with the timing of attack being the most important. Pre-tasseling was the most attractive and susceptible stage of maize plant to *S. calamistis* attack.

The within-plant distribution of immature borers depended on the stages of development of the borers and the plants. On maize, eggs were preferentially laid below the first ear, followed by the part above the ear. About 40 days after planting, most larvae and pupae were found in the ears. Thus dissection of the whole plant is not necessary for sampling; scrutiny of leaf sheaths below the ear can

provide reliable estimates of the numbers of eggs, whereas the ear is the best sampling unit for larvae and pupae. On wild sorghum, the borers were equally distributed between the main stems and the lateral shoots.

The interaction between *S. calamistis* host plants and the egg parasite, *Telenomus busseolae* (Hymenoptera: Scelionidae), and the effects of age, density and exposure time, of the moth egg on parasitization and development of the parasite, were studied. Under glass, when maize plants of four different stages bearing moth eggs were exposed together, wasps parasitized equally the eggs. The results were similar when maize and wild grasses were exposed together. In an arena, *T. busseolae* showed density-dependent parasitism, the percentage of parasitism increasing with higher numbers of moth eggs. *T. busseolae* successfully parasitized, and developed in eggs that were up to 4-day-old, but it preferred those younger than two days. Relatively more wasps emerged from young than old eggs. Developmental time was not affected by the age of host eggs, but varied with rearing temperatures; wasps emerged in 13 - 14 d at 32°C, 14 - 16 d at 28°C, and 18 - 20 d at 26°C.

RÉSUMÉ

Les variations des populations de *Sesamia calamistis* (Lepidoptera: Noctuidae) et de *Eldana saccharina* (Lepidoptera: Pyralidae), deux importants ravageurs du maïs en Afrique de l'Ouest, et les effets de *S. calamistis* sur le maïs, ont été étudiés à l'Institut International d'Agriculture Tropicale à Cotonou, au Bénin, de Septembre 1991 à Janvier 1994. Ces insectes étaient les plus nombreux foreurs de tige trouvés dans le maïs, mais aussi dans deux graminées non cultivées, le sorgho sauvage et le pennisetum, surtout lorsque des plants frais de maïs n'étaient pas disponibles. Dans des essais en serre, *S. calamistis* déposait plus d'oeufs sur les plants de maïs de 40 jours que sur les plants plus âgés, et plus d'oeufs sur le maïs que sur le sorgho et le pennisetum de même âge. Ces résultats indiquent que les graminées sauvages sont des abris et des sources d'infestation des champs de maïs. *S. calamistis* infestait les plants de quatre semaines, alors que *E. saccharina* les infestait à partir de l'épiaison. Le nombre de foreurs adults recoltés dans des pièges lumineux était corrélé positivement à la vitesse du vent et à l'humidité relative, mais négativement à la température. Un plus grand nombre de ces insectes était piégé pendant la nouvelle lune que pendant la pleine lune.

Le stade du maïs au moment de l'infestation et le nombre d'oeufs de *S. calamistis* avaient une influence négative sur le développement de la plante et réduisait sa productivité, mais l'effet lié au stade de développement était le plus important. Les stades avant la floraison étaient les plus critiques pour les attacks de *S. calamistis*.

La répartition des boreurs dans les plants dépendait du type de foreurs et de plantes hôtes. Sur le maïs, *S. calamistis* déposait ses

oeufs de préférence sur la partie de tige en dessous de l'épi, puis sur celle au dessus. A partir de 40 jours après semis, la plupart des larves et des chrysalides se trouvaient dans l'épi. Ceci démontre que la dissection de l'entière plante n'est pas nécessaire pour l'échantillonnage; l'inspection de la partie de plante en dessous de l'épi peut permettre une estimation fiable du nombre d'oeufs, alors que l'épi est la partie à inspecter pour estimer le nombre de larves et de chrysalides. Sur le sorgho sauvage, la distribution était la même entre la tige principale et les branches latérales.

L'interaction entre le parasite des oeufs, *Telenomus busseolae* (Hymenoptera: Scelionidae), et les plantes hôtes de *S. calamistis*, ainsi que les effets de l'âge des oeufs hôtes, de leur densité et leur temps d'exposition, sur le parasitisme et le temps de développement du parasite ont été étudiés. En serre, lorsque des plants de maïs de 4 stades, portant des oeufs de *S. calamistis*, étaient exposés ensemble, la guêpe parasitait le même nombre d'oeufs sur chaque stade. Le résultat était pareil lorsque le maïs, le sorgho et le pennisetum de même âge étaient exposés ensemble. Au laboratoire, le nombre d'oeufs parasités croissait avec le nombre initial d'oeufs hôtes disponibles. *T. busseolae* parasitait et développait dans des oeufs de 0 à 4 jours, mais préférait les oeufs de moins de deux jours, et plus d'adults émergeaient de ces oeufs que des oeufs plus âgés. Le temps de développement des guêpes n'était pas affecté par l'âge des oeufs au moment de la parasitisation, mais variait avec la température d'élevage; les guêpes émergeaient entre 13 et 14 jours à 32°C, entre 14 et 16 jours à 28°C, et entre 18 et 20 à 26°C.

Dédicace

À ma femme, Béatrice

À mes enfants, Didier, Nelly, Benifien

Pour leur compréhension et leur patience.

ACKNOWLEDGEMENTS

I wish to express my deep gratitude to my senior supervisor, Dr. M. Mackauer, for his guidance, patience and support during the course of my study.

I am grateful to Dr. F. Schulthess for accepting me in his laboratory at the International Institute of Tropical Agriculture (I.I.T.A), Cotonou, Bénin. and for providing valuable assistance during my research work.

I am indebted to Dr. H.R. MacCarthy for his patience in editing several drafts of my dissertation and for making helpful suggestions. I thank Dr. P. Belton, for serving on my supervisory committee and for providing advice.

I thank Dr. H.R. Herren, former Director of IITA-Plant Health Management Division (PHMD), for providing an IITA fellowship, and for his advice. I benefited from discussions and interactions with research scientists and research fellows at I.I.T.A Cotonou (Bénin) and Ibadan (Nigeria); I thank them all. I particularly thank Dr. N.A. Bosque-Pérez for her useful comments and suggestions and for kindly providing thousands of borer eggs and pupae for my experiments. My sincere appreciations to S. Gounou, M. Sétamou, A. Chabi-Olaye, and their technicians, for helping me in many ways. I acknowledge the assistance of Mr. J. Quaye, Mr. Akinwumi, and several members of the staff at I.I.T.A-Cotonou.

I thank my laboratory colleagues and friends at S.F.U.: A. Chau, A. Chow, T. Danyk, J.P. Michaud, R. Notin, M. Otto, C. Piller, and R. Sequeira, for the helpful discussions I had with them and for their useful comments.

I express my deep gratitude to Wayne and Tannis Morris, and other members of the Morris Family, for their unfailing support and friendship during my stay in Canada.

I thank the International Institute of Tropical Agriculture and Simon Fraser University for providing financial support.

TABLE OF CONTENTS

ABSTRACT.....	iii
RÉSUMÉ.....	v
DÉDICACE.....	vii
ACKNOWLEDGEMENTS.....	viii
TABLE OF CONTENTS.....	ix
LIST OF TABLES.....	xi
LIST OF FIGURES.....	xiii
I. GENERAL INTRODUCTION.....	1
II. EFFECTS OF <i>SESAMIA CALAMISTIS</i> ON GROWTH AND PRODUCTIVITY OF MAIZE.....	6
2.1 Introduction.....	6
2.2 Materials and Methods.....	8
2.3 Results.....	11
2.4 Discussion.....	20
III. SEASONAL ABUNDANCE OF <i>SESAMIA CALAMISTIS</i> AND <i>ELDANA</i> <i>SACCHARINA</i> IN MAIZE AND INDIGENOUS GRASS PLANTS.....	24
3.1 Introduction.....	24
3.2 Materials and Methods.....	25
3.3 Results.....	29
3.4 Discussion.....	49
IV. WITHIN-PLANT DISTRIBUTION OF <i>SESAMIA CALAMISTIS</i> AND <i>ELDANA SACCHARINA</i> IN MAIZE AND WILD SORGHUM.....	57
4.1 Introduction.....	57
4.2 Materials and Methods.....	59
4.3 Results.....	63
4.4 Discussion.....	75

V.	INFLUENCE OF HOST-PLANT SPECIES AND PHENOLOGY ON OVIPOSITION BEHAVIOUR OF <i>SESAMIA CALAMISTIS</i> AND <i>TELENOMUS BUSSEOLAE</i>	81
	5.1 Introduction.....	81
	5.2 Materials and Methods.....	83
	5.3 Results.....	86
	5.4 Discussion.....	91
VI.	EFFECTS OF HOST EGG DENSITY, EXPOSURE TIME, AND AGE ON PARASITIZATION BY, AND DEVELOPMENT OF, <i>TELENOMUS BUSSEOLAE</i>	96
	6.1 Introduction.....	96
	6.2 Materials and Methods.....	98
	6.3 Results.....	101
	6.4 Discussion.....	114
VII.	GENERAL CONCLUSIONS.....	120
	REFERENCES.....	125

LIST OF TABLES

Table	Page
2.1	Coefficients of correlation between sesamia-days, maize growth, damage symptoms and yield variables, recorded on plants artificially infested with different numbers of <i>S. calamistis</i> eggs from July to September 1992 (trial 1)14
2.2.	Mean numbers of borers, plant growth and yields, in maize plants artificially infested with different numbers of <i>S. calamistis</i> eggs from July to September 1992 (trial 1)15
2.3	Mean numbers of borers, plant growth and yields, in maize plants artificially infested with different numbers of <i>S. calamistis</i> eggs from October to December 1993 (trial 2) (Mean±SE).....17
2.4.	Coefficients of correlation between pest numbers, maize growth, damage symptoms and yield variables recorded at harvesting on plants artificially infested with different numbers of <i>S. calamistis</i> eggs from October to December 1993 (trial 2).....18
2.5.	Effect of time (A) and severity (B) of infestation on growth and yield of maize plants artificially infested at different stages of development with 15 or 30 <i>S. calamistis</i> eggs (Two-factor ANOVA).....19
3.1	Coefficients of correlation between various weather factors and numbers of adult stem borers trapped in maize and grass fields between July 1992 and January 1993 at I.I.T.A Cotonou, Bénin.....48
4.1	Mean numbers ($m \pm SEM$)* and percentages (%) of <i>S. calamistis</i> and <i>E. saccharina</i> collected on different parts of maize plants.....65
4.2	Taylor's power law analysis: regression of Log(variance) on Log(mean) for larvae of <i>S. calamistis</i> and <i>E. saccharina</i> on maize plants and wild sorghum tillers from July to October 1992.....70

5.1	Numbers of egg batches and eggs laid by <i>S. calamistis</i> and parasitized by <i>T. busseolae</i> on 15 maize plants at four phenological stages (Mean±SE).....	87
5.2	Numbers of egg batches and eggs laid by <i>S. calamistis</i> and parasitized by <i>T. busseolae</i> on forty-day-old maize plants and grass tillers (Mean±SE).....	88
5.3	Numbers of egg batches and eggs laid by <i>S. calamistis</i> and parasitized by <i>T. busseolae</i> on post-tasseling maize (70 DAP) and forty-day-old grass tillers (Mean±SE).....	89
6.1	Parasitism by <i>T. busseolae</i> exposed to <i>S. calamistis</i> egg masses of different sizes in vials, with emergence and sex ratio of adult parasites (Mean±SE; n=17 females).....	104
6.2	Parasitism by <i>T. busseolae</i> , and offspring and sex ratio of the parasites emerged from <i>S. calamistis</i> eggs of different ages at the time of parasitization, and reared at 28±2°C, 75±5% RH, and 12:12 D:L photoperiod (Mean±SEM).....	105
6.3	Preference by, and suitability of, <i>T. busseolae</i> among different ages of <i>S. calamistis</i> eggs exposed by pairs in a vial (n= number of females used in each comparison; < 1 = eggs of less than 1 day).....	108
6.4	Preference by <i>T. busseolae</i> among <i>S. calamistis</i> eggs of three age groups exposed simultaneously in a vial, and emergence of adult parasites from parasitized eggs reared at 28±2° C, 75±5% RH, and 12:12 D:L photoperiod (Mean±SEM, n= 17 females).....	110

LIST OF FIGURES

Figure	Page
2.1 Cumulative numbers of immature <i>S. calamistis</i> (a) and <i>E. saccharina</i> (b) collected on plants artificially infested with different numbers of <i>S. calamistis</i> eggs in trial 1: W4-15=plants infested 4 weeks after planting with 15 <i>S. calamistis</i> eggs; W4-30=plants infested 4 weeks after planting with 30 eggs; W6-15=plants infested 6 weeks after planting with 15 eggs; W6-30=plants infested 6 weeks after planting with 30 eggs; W9-15=plants infested 9 weeks after planting with 15 eggs; W9-30=plants infested 9 weeks after planting with 30 eggs.....	12
3.1 Numbers of immature <i>S. calamistis</i> and <i>E. saccharina</i> found on maize (a,b) and grasses (c,d), in trial 91-2, between October 1991 and January 1992 Columns show the numbers of eggs, larvae, and pupae per plant.....	30
3.2 Numbers of immature <i>S. calamistis</i> found on maize (a) and grasses (b), in trial 92-1, between July and October 1992. Columns show the numbers of eggs, larvae, and pupae per plant.....	33
3.3 Numbers of <i>S. calamistis</i> moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-1, between July and October 1992.....	36
3.4 Numbers of immature <i>E. saccharina</i> found on maize (a) and grasses (b), in trial 92-1, between July and October 1992. Columns show the numbers of larvae, and pupae per plant.....	37
3.5 Numbers of <i>E. saccharina</i> moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-1, between July and October 1992.....	38
3.6 Numbers of immature <i>S. calamistis</i> found on maize (a) and grasses (b), in trial 92-2, between October 1992 and January 1993. Columns show the numbers of eggs, larvae, and pupae per plant.....	41
3.7 Numbers of <i>S. calamistis</i> moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-2, between October 1992 and January 1993.....	42

3.8	Numbers of immature <i>E. saccharina</i> found on maize (a) and grasses (b), in trial 92-2, between October 1992 and January 1993. Columns show the numbers of larvae and pupae per plant.....	43
3.9	Numbers of <i>E. saccharina</i> moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-2, between October 1992 and January 1993.....	44
3.10	Percentages of maize plants infested by stem borers in relation to time after planting, during two maize growing seasons.....	46
3.11	Mean numbers of moths caught in light traps in relation to moon phases between July 1992 and January 1993.....	47
4.1	A developed maize plant can be subdivided into four parts: below ear (P1), between ear and tassel (P2), from uppermost leaf to end of tassel (P3), and ear.....	60
4.2	Schematic mapping of a developed wild sorghum tiller showing main stem and lateral shoots.	61
4.3	Numbers of larvae of <i>S. calamistis</i> (a) and <i>E. saccharina</i> (b) collected on various parts of maize plant. Columns show the mean numbers per plant.....	67
4.4	Numbers of larvae and pupae of <i>S. calamistis</i> (a) and <i>E. saccharina</i> (b) collected on various parts of sorghum tillers. Columns show the mean numbers of larvae and pupae per plant...68	
4.5	Spatial distribution of <i>S. calamistis</i> and <i>E. saccharina</i> on maize between July 1992 and January 1993, at IITA-Cotonou, according to Taylor's power law. The log-transformed of observed means of larvae are plotted against the corresponding variance.....	71
4.6	Spatial distribution of <i>S. calamistis</i> and <i>E. saccharina</i> on wild sorghum between July 1992 and January 1993, at IITA-Cotonou, according to Taylor's power law. The log-transformed of observed means of larvae are plotted against the corresponding variance.....	72
4.7	The observed proportion of infested maize plants as a function of field density of <i>S. calamistis</i> (a) and <i>E. saccharina</i> (b).....	73

4.8	Optimal number of samples to be taken to estimate mean densities of <i>S. calamistis</i> and <i>E. saccharina</i> on maize (solid lines) and wild sorghum (broken lines) using enumerative sampling procedures. Two reliability levels are used (D=0.3: thin lines; D=0.2: thick lines).....	74
6.1	Number of <i>S. calamistis</i> eggs parasitized by <i>T. busseolae</i> when exposed for different periods. Data points show the mean numbers of eggs parasitized by 15 females.....	103
6.2	Emergence time of adult <i>T. busseolae</i> developing in <i>S. calamistis</i> eggs parasitized at different stages and reared at 28±1°C, 75±5% RH, and 12:12 D:L photoperiod. Columns show the mean numbers of adults emerged on 14 th , 15 th , and 16 th days after parasitization.....	112
6.3	Emergence time of adult <i>T. busseolae</i> developing in <i>S. calamistis</i> eggs reared at different temperatures, 75±5% RH, and 12:12 D:L photoperiod. Columns show the mean numbers of male and female parasites.....	113

Chapter I

GENERAL INTRODUCTION

The pink stalk borer, *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), and the African sugarcane borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae), are well-known pests of thick-stemmed graminaceous crops in tropical Africa. Their distribution and importance in different ecological regions has been the topic of several investigations. In West Africa, both species are often reported from maize. The larvae of *S. calamistis* feed most often on the young stems, causing the death of the growing points, called dead-hearts. Plant loss due to 'dead hearts' can be up to 50% (Kaufmann, 1983; Bosque-Pérez and Mareck, 1990). The tunneling activity of the larvae causes disruption of sap flow and breakage of stalks. Also, damage by *S. calamistis* to the husks opens an entrance to other pests and fungi. Feeding by *E. saccharina* larvae causes early senescence of leaves, reduced translocation, lodging, and direct damage to the ears (Atkinson, 1980; Kaufmann, 1983; Bosque-Pérez and Mareck, 1990). Reported yield losses due to these stem borers vary greatly between ecological zones, regions and seasons, and can be as high as 100% (Leyenaar and Hunter 1977; Girling 1980; Bosque-Pérez and Mareck, 1991; Gounou *et al.*, 1994). Detailed information on the biology of these pests has been documented (Girling, 1978; Atkinson, 1980; Kaufmann, 1983; Cochereau, 1985).

Female *S. calamistis* lay eggs on maize plants, between the stems and the leaf sheaths. The period of incubation is approximately

five days and, upon hatching, the young larvae bore into the stem. The eggs of *E. saccharina* are laid on a variety of supports including debris on the soil, maize stubbles, and margins of the leaf sheaths. Newly hatched larvae, aggressive and mobile, feed on organic debris for a few days before infesting maize plants and boring into stems. Both borers pupate inside stems and cobs, or between husks. Although *S. calamistis* and *E. saccharina* infest maize, they are also found on native wild grasses and sedges, which are thought to be their natural hosts (Bowden 1976; Atkinson 1980).

Other lepidopterous maize stem and cob borers are also reported, including *Sesamia botanophaga* (Tam and Bowden) (Noctuidae), *Busseola fusca* (Fuller) (Noctuidae), *Chilo partellus* (Swinhoe) (Pyralidae) *Coniesta ignefusalis* (Hampson) (Pyralidae), and the cob borer *Mussidia nigrivenella* Ragonot (Pyralidae). Most of these borers are either occasional pests in different regions or key pests of indigenous crops, such as sorghum and millet. With the exceptions of *C. partellus* and the larger grain borer, *Prostephanus truncatus* (Coleoptera: Bostrichidae), all these pests appear to be native to Africa (Ingram, 1983; Omolo and Seshu Reddy, 1985).

To control *S. calamistis* and *E. saccharina*, insecticides have been used, and sources of resistance have been identified (IITA, 1980; Mihm, 1985; Bosque-Pérez *et al.*, 1989). But chemical and genetic control methods alone proved to be ineffective. An integrated approach that combines several control methods, including biological control, is essential. The prerequisite for successful control is a clear understanding of the biology, ecology and behaviour of pests and their natural enemies, and the interactions between them and the crop.

However, because these pests presumably are native to Africa, classical biological control by the importation of exotic agents would not be a first choice. The role of native natural enemies needs therefore to be evaluated.

In West Africa, *S. calamistis* and *E. saccharina* are hosts of several natural enemy complexes (Mohyuddin and Greathead, 1970; Polaszek and Kimani, 1990; Polaszek, 1992; Polaszek *et al.*, 1993). However, most of the parasites reported seem to be poorly adapted to the cultivated host maize, and are of low or no significance as controls. The parasites appear late in the second season of the year when the damage to the crop is already done. One exception seems to be the parasitoids belonging to the *Telenomus busseolae* complex (Hymenoptera: Scelionidae) which attack the eggs of *S. calamistis*. Work done at IITA-Bénin showed that these parasites have a measurable effect on *S. calamistis* populations in farmers' fields in the Republic of Bénin (Chabi-Olaye, 1992; Sétamou and Schulthess, 1995). However, for reasons yet to be determined, they are not effective in suppressing *S. calamistis* populations.

Maize, *Zea mays* L., was introduced into Africa in the 16th century from its native Mesoamerica, and now is one of the most widely grown cereal crops in Africa. Its genetic diversity and multiple uses account for its cultivation in a wide range of environments. It is a staple for a large proportion of the population (CIMMYT 1991). In West Africa, maize is an important component of the farming systems and in the diet of many people, and the importance of maize as a crop is increasing. The total area planted to maize in Africa is estimated at 21 million ha. Yields range between 800 and 1200 kg/ha, which is far

below the world average of 3700kg/ha. Stem borers are among the causes of this low yield.

The main objectives of my study were:

- 1) to determine the relationship between *S. calamistis* infestation and growth of maize, especially the phenological stage of the plant at the time of infestation;
- 2) to investigate variations in the numbers of *S. calamistis* and *E. saccharina* in relation to growing seasons and distribution of immature stages within the host plants; and
- 3) to study selected aspects of the biology and behaviour of the *T. busseolae* species-complex, the principal *S. calamistis* egg parasite. Because the predominant species in Bénin is *T. busseolae* Gahan, the parasite will be referred to as *T. busseolae*.

This thesis contains seven chapters, with the first and the last serving as a general introduction and a general conclusion respectively. Chapter II examines the relative incidence of timing (ie, stage of the plant) and level (ie, number of eggs per plant) of infestation of *S. calamistis* on maize growth and productivity. In addition, the chapter underlines the pest status of *S. calamistis* and suggests further work on this insect. Chapter III determines the numbers of *S. calamistis* and *E. saccharina* on maize according to the seasons and the stages of development of the host plants. The role of two indigenous, non-cultivated host grasses, wild sorghum, *Sorghum arundinaceum*, and feathery pennisetum, *Pennisetum polystachion*, on stem borer populations is also examined. The question of how immature stages of these borers are distributed in the host-plants is addressed in Chapter IV. This chapter proposes sampling procedures needed for reliable

estimates of borer densities in the field. Chapter V deals with the oviposition behaviour of *S. calamistis* and *T. busseolae* on host-plants of different species and stages. Finally, chapter VI examines the influence, if any, of age and density of host eggs, and rearing temperature, on the parasitization behaviour and developmental rate of *T. busseolae*.

Chapter II

EFFECTS OF *SESAMIA CALAMISTIS* ON GROWTH AND PRODUCTIVITY OF MAIZE

2.1 Introduction

Among several species of stem borers occurring in Africa, the noctuid *S. calamistis* is among the most serious pests of maize (Harris, 1962; Pollet *et al.*, 1978; Kaufmann, 1983; Warui and Kuria, 1983; Bosque-Pérez and Mareck, 1990; Gounou *et al.*, 1994) and rice (Pollet, 1977; Nwanze, 1988). Several workers have shown that the development and distribution of this pest depend on many factors, such as climatic conditions, agronomic practices and host plants (Ingram, 1958; Usua, 1968c; Girling, 1978; Kaufmann, 1983; Sampson and Kumar, 1983; Atachi, 1984; Thomas-Odjo, 1984; Bosque-Pérez and Mareck, 1990; Shanower *et al.*, 1991; Gounou *et al.*, 1994). The eggs of *S. calamistis* are generally laid in leaf sheaths and, upon emergence, the larvae bore into the stem (Kaufmann, 1983) and feed on plant tissues. The holes and tunnels provide access to the plant for pathogens which can cause fungal diseases. The damage caused to maize may be severe, and the yield loss very high. For many stem borers, information is available on the consequence of the infestations to maize plants and yield (Usua, 1968a; Warui and Kuria, 1983; Van Rensburg *et al.*, 1988a,b; Bosque-Pérez and Mareck, 1991). For instance, the relationship between the numbers of plants damaged by the noctuid stem borer, *Busseola fusca* (Fuller), and yield loss, has

been extensively studied (Walker, 1960; 1981; Van Rensburg *et al.* 1988a,b). An investigation by Usua (1968a) and Van Rensburg *et al.* (1988a,b) of the effect of this borer on the vegetative growth of maize showed that the rate of plant growth decreased with increasing numbers of larvae; Walker (1960) found a rectilinear relationship between plant damage and yield loss; the studies of Van Rensburg *et al.* (1988a) also indicate that variations in growth and yield are related to varying levels of infestation. Bosque-Pérez and Mareck (1991) showed that infestations of maize by *E. saccharina* decreased yield by up to 36%, and that grain weight was negatively related to the percentage of stem tunnelled. A negative relationship between plant damage and yield was also observed in plants attacked by the European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae) (Chiang and Hodson, 1950; Guthrie *et al.*, 1975; Lynch, 1980; Lynch *et al.*, 1980; Umeozor *et al.*, 1985). Most of these studies showed that the severity and nature of the damage inflicted on maize by stem borers are variable and may depend on the variety of maize, the planting time, the stage of development at which the host plant is attacked, and the level of infestation. Although their highest field populations appear towards the end of the second planting season (Shanower *et al.*, 1991; Gounou *et al.*, 1994), relatively high numbers of *S. calamistis* are also observed during other months of the year. Therefore, the moths may lay variable numbers of eggs on different growth stages of the plants.

In this chapter, I tested the hypothesis that the number of eggs laid by *S. calamistis*, and the stage of plant development at infestation, influence the subsequent growth and yield of maize. I determined the relative incidence of these two factors on the crop.

Knowledge of the most sensitive stage of the plant is indispensable information for effective protection of the crop against pests.

2.2 Materials and methods

Experimental design

I planted two fields of maize on the experimental farm of the International Institute of Tropical Agriculture (IITA), Bénin, on land previously planted with maize. I planted three seeds of the maize variety 'TZE (95 days)' per hole. On the planting day, I broadcast by hand a compound of NPK15/15/15 fertilizer at a rate of 70 kg/ha; the same fertilizer was again applied at 30kg/ha four weeks after planting. I thinned the maize to one plant per hole three weeks after planting to obtain a density of 50,000 plants/ha (5 plants/m²). Spacing was 25 cm between plants and 80 cm between rows. Plots were weeded by hand-hoeing three times during the course of the experiment, the first time five weeks after planting. The two fields were planted, one in July 1992 (trial 1) and the other in October 1993 (trial 2). I divided each field into plots of 35 m² separated by 2 m-wide strips. The plots were arranged in a randomized block design with four replicates.

In trial 1, I used eight infestation treatments: on three dates (weeks after planting = WAP) and two levels of artificial infestation (15 or 30 eggs), one natural infestation (Control), and one chemical control (Furadan). Artificial infestations of the maize plants were done at four WAP (early growth), six WAP (shortly before tasseling), and nine WAP (ear formation). The eggs were obtained from a laboratory colony. Before the infestations, egg masses were kept on

damp paper in open petri dishes to enhance hatching. After a 3-day-incubation period, the eggs were in the 'black-head' stage and ready to hatch. Egg masses containing damaged or infertile eggs were discarded. The plants were moderately watered once a week before and after infestations. I infested each plant with one egg mass containing either 15 or 30 *S. calamistis* eggs. Single egg masses were placed between the leaf sheath and stem with a camel-hair brush, at about 35 cm above the ground, avoiding direct sunlight. The plants infested with 15 eggs per mass at four WAP are described as W4-15, those infested with 30 eggs per egg mass at four WAP are W4-30, etc. In the control, natural infestation was allowed to occur. In the chemical treatment, the plants were protected against borer infestation by application of the systemic insecticide, carbofuran (Furadan: [2,3-dihydro-2,2-dimethyl-7-benzofuranyl methyl carbamate]). The insecticide was applied three times: at planting, at week four after planting and shortly after ear formation. At planting, 5 mg of the granular product were incorporated in the planting holes; in the second and third applications, the same quantity of granular carbofuran was placed in the whorls and the leaf sheaths.

Because only limited numbers of *S. calamistis* eggs were available for trial 2, only five infestation treatments were considered: at 4 and at 6 WAP with two levels of infestation, and the natural infestation. Borer infestations are usually low during the dry season, and I did not include the carbofuran treatment.

Data collection:

In trial 1, starting one week after infestation, I selected 10 plants per plot every week and cut them off for dissection. During the dissection, leaves of the maize plants were carefully removed and the stems were opened to record the following data: the numbers of eggs, larvae and pupae, and the damage symptoms on the plants (number of holes bored, and the length of tunnels in each stem), and the growth values of the plants (height and diameter at the stem base). When ears were available, I removed the husk leaves to estimate the percentage of damaged grains. Damages to plants or grains were recorded, whether caused by *S. calamistis* or other borers. At harvesting, 20 plants per plot were again sampled and the same information as above was gathered. The cobs from each plant were then separately placed in paper envelopes and dried at 100°C for three days to determine cob and grain dry weights.

In trial 2, the above data were recorded only at 8 WAP and at harvesting.

Data analysis

I used borer numbers on each sampling date from trial 1 to calculate the cumulative borer-days (B-days). A borer-day is defined as the sum of the product of the mean number of borers observed on consecutive sampling dates multiplied by the numbers of days between samplings, that is:

$$B_{i+1} = B_i + (N_i + N_{i+1})/2 * (D_{i+1} - D_i - 1) + N_{i+1}$$

where B_i and B_{i+1} are borer-days on two consecutive sampling dates, and D_i and D_{i+1} , and N_i and N_{i+1} are the mean numbers of borers on these two sampling dates. Borer-days were plotted against the day after planting (DAP). For trial 1, I determined the relationship between the number of borer-days, growth values of, and damage to, the plant using a correlation analysis, including all the data across all sampling dates. In trial 2, a correlation analysis was also used to determine the relationship between the number of borers, damage to the plant, and the yields, using data collected at harvesting. In both trials, I used a One-Way ANOVA to compare the numbers of *S. calamistis*, the values of plant growth and the yield variables between treatments. When significant differences were obtained, I used Fisher's LSD (Least Significant Difference) test (Sokal and Rohlf, 1981) to separate the means.

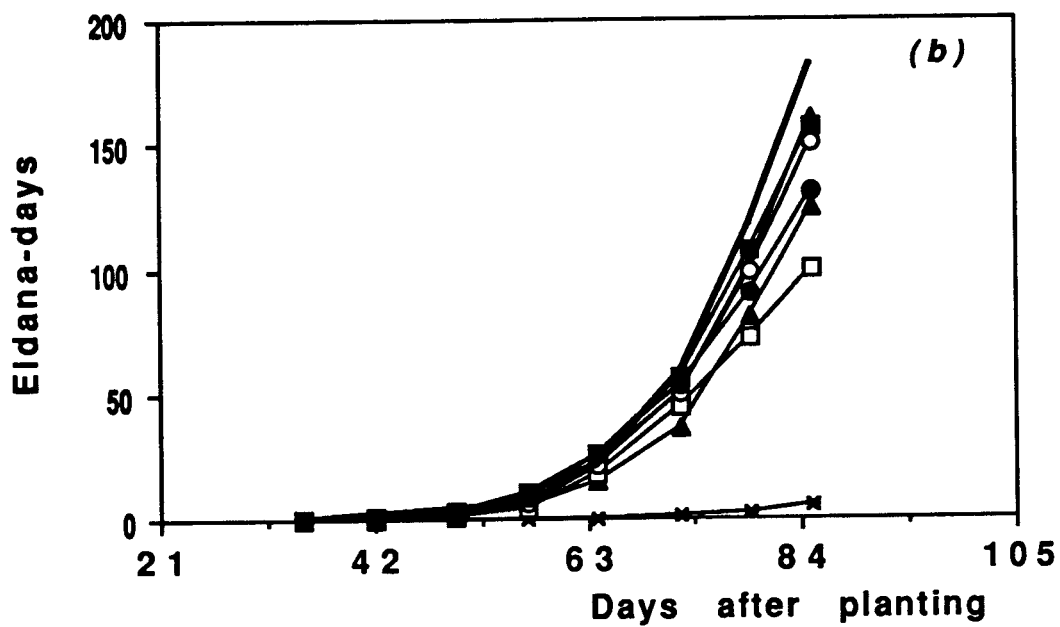
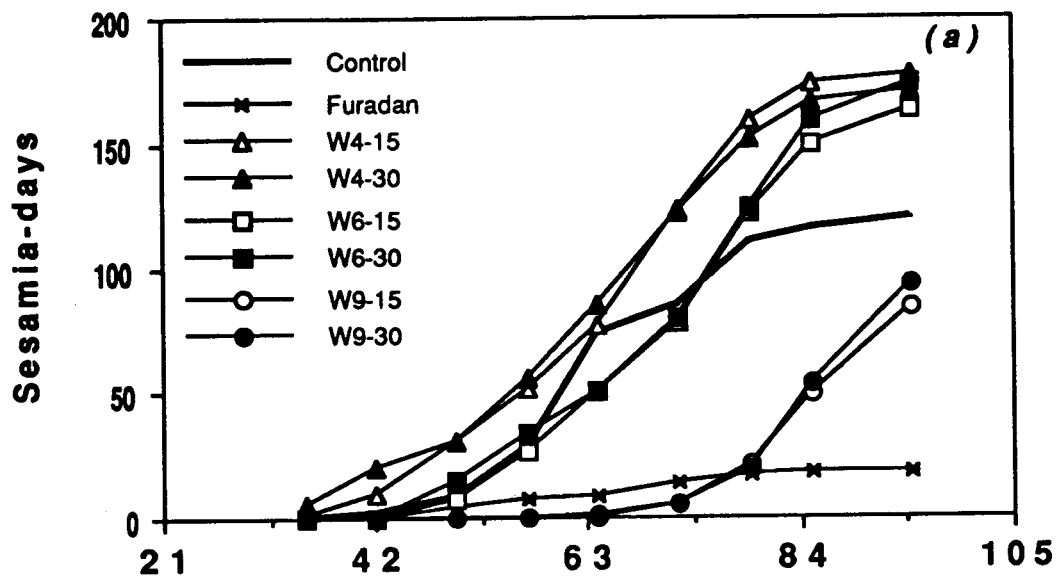
With data from trial 2, I applied a Two-Factor ANOVA to determine the relative effect of time of infestation and number of *S. calamistis* eggs at infestation on plant growth and yields. All percentages were arcsine transformed before analysis.

2.3 Results

Trial 1 (July-September, 1992)

Quelea birds severely damaged cobs during this trial. Figure 2.1 shows the evolution of the cumulative numbers of *S. calamistis* and *E. saccharina* for each treatment. For the plots treated with carbofuran (Furadan), the cumulative numbers of both borers were consistently low throughout the trial, relative to numbers in the other treatments. In the plots artificially infested with *S. calamistis* eggs at 4 and 6

Figure 2.1 Cumulative numbers of immature *S. calamistis* (a) and *E. saccharina* (b) collected on plants artificially infested with different numbers of *S. calamistis* eggs in trial 1: W4-15 =plants infested 4 weeks after planting with 15 *S. calamistis* eggs; W4-30=plants infested 4 weeks after planting with 30 eggs; W6-15=plants infested 6 weeks after planting with 15 eggs; W6-30=plants infested 6 weeks after planting with 30 eggs; W9-15=plants infested 9 weeks after planting with 15 eggs; W9-30=plants infested 9 weeks after planting with 30 eggs.



WAP, Sesamia-days (see data analysis) increased steadily one week from infestation until about 80 DAP, then reached a plateau until after harvesting. Sesamia-days in the naturally infested plots (Control), also increased regularly, but the curve ran below those of the W4-15 and W4-30 plots and the plateau was reached relatively earlier (Figure 2.1a). At harvesting, which was carried out 105 DAP, there were no significant differences between sesamia-days of W4-15, W4-30, W6-15 and W6-30. Except in the plants treated with carbofuran, relatively high numbers of *E. saccharina* were also collected, but this stem borer appeared in the plots only around and after 65 DAP, when the maize plants were fully grown. The numbers of eldana-days increased rapidly to reach values between 100 and 182 borer-days at harvesting. Correlation analysis showed that the cumulative number of *S. calamistis* was highly and positively related to the number of holes and the length of tunnels bored in the stems; sesamia-days were also significantly correlated with the weight of grain but not with the damage and weight of cob (Table 2.1).

Table 2.2 shows the mean numbers of *S. calamistis* and *E. saccharina*, plant growth, damage, and yields collected in each treatment. The mean numbers of *S. calamistis* and *E. saccharina* were significantly lower in the Furadan-treatment than in the other treatments; in addition, the plants grew significantly taller with less damage in this treatment (One-Way ANOVA: $F = 9.480$; $df = 7,2390$; $P=0.0001$). However, no significant difference was found in cob and grain weights between the eight treatments.

Table 2.1 Coefficients of correlation between sesamia-days, maize growth, damage symptoms and yield variables recorded on plants artificially infested with different numbers of *S. calamistis* eggs from July to September 1992 (trial 1).

	1	2	3	4	5	6	7	8
1=sesamia-days								
2=height								
3=diameter								
4=holes #								
5=tunnel length								
6=% cob damage								
7=cob weight								
8=grain weight								
1.	=							
2.	.04	=						
3.	-.18	.34	=					
4.	.62*	-.10	-.03	=				
5.	.68*	.04	-.21	.70*	=			
6.	.29	-.10	-.05	-.03	.15	=		
7.	-.27	.52*	.13	-.39*	-.22	-.07	=	
8.	-.36*	.51*	.20	-.38*	-.11	-.01	.87*	=

Values shown with an asterisk (*) are significant at P<0.05 (critical value, r=0.349, df=30).

Table 2.2 Mean numbers of borers, plant growth, damage*, and yields**, in maize plants artificially infested with different numbers of *S. calamistis* eggs from July to September 1992 (trial 1).

Variables	Treatments							
	Furadan Control	W4-15	W4-30	W6-15	W6-30	W9-15	W9-30	
<i>S. calamistis</i>	0.33a ¹	3.99b	3.29b	3.47b	3.50b	3.74b	3.56b	4.24b
<i>E. saccharina</i>	0.15a	3.96b	3.52b	2.67c	2.40c	3.76b	3.74b	3.14b
Plant height	127.4a	107.7b	118.4c	110.7b	120.9c	126.7ac	119.0c	115.9bc
Tunnel length	0.63a	17.47b	15.48b	18.07b	15.67b	18.63b	19.67b	18.38b
Cob damage	2.00a	9.31b	9.85b	9.56b	9.48b	12.01b	11.78b	10.80b
Hole number	0.19a	5.91b	5.86b	5.29b	7.32b	6.22b	7.31b	6.42b
Cob weight	104.5a	92.90a	89.94a	88.03a	93.33a	93.87a	94.77a	91.54a
Grain weight	82.6a	75.08a	76.63a	84.08a	75.54a	74.12a	75.49a	72.80a

*: Combined damage by all borers. **: For cob and grain weights, data were from the last sampling (harvest) date; for other variables, means were from data over all sampling dates. ¹ : Means within rows sharing the same letter(s) are not significantly different (One-Way ANOVA, $P \leq 0.05$ followed by Fisher's LSD test).

Trial 2 (October-December, 1993)

The mean numbers of borers, plant growth and yields recorded in trial 2 are shown in Table 2.3. The mean numbers of *S. calamistis* collected in treatment C were not significantly different from those in W4-15 and in W6-15, but they were significantly lower than those in W4-30 and W6-30 (One-Way ANOVA: $F = 5.891$, $df = 4,394$, $P = 0.0001$). For *E. saccharina*, which appeared late in the season, as in trial 1, there was no significant difference between the mean numbers in the five treatments. Plant stem diameter, and cob and grain weights were significantly higher in the Control compared with W4-15 and W4-30, but not different from W6-15 and W6-30. The numbers of holes and the length of tunnels bored were not significantly different between the Control, W4-15 and W4-30, but were lower than in W6-30; cob damage did not significantly differ between treatments. When plants infested at the same stage were compared, I collected higher numbers of *S. calamistis* on those infested with 30 than 15 eggs, but the height and stem base diameter of the plants were not significantly different. When plants infested with the same egg load were compared, those infested at 4 WAP were smaller and had lower yields than those infested at 6 WAP. However, the extent of damage did not follow any particular trend; longer tunnels were bored in 6-WAP plants, but cob damage was not significantly greater. Table 2.4 shows the correlation coefficients between the numbers of borers found in each treatment and plant growth and yield. It indicates that the mean number of *S. calamistis* was negatively related to yield. The mean number of *E. saccharina* had a significant positive relationship with plant and cob damage, but not with yield. Two other cob borers, *Cryptophlebia*

Table 2.3 Mean numbers of borers, plant growth, damage* and yields** in maize plants artificially infested with different numbers of *S. calamistis* eggs from October to December 1993 (trial 2) (Mean±SE).

Variables	Treatments				
	Control	W4-15	W4-30	W6-15	W6-30
<i>S. calamistis</i>	0.10±0.05a	0.29±0.11a	0.70±0.14b	0.30±0.08a	0.69±0.14b
<i>E. saccharina</i>	0.66±0.15a	0.68±0.13a	0.65±0.16a	0.61±0.14a	0.50±0.14a
plant height	156.76±2.4a	148.15±2.6b	152.68±2.1ab	155.86±2.4a	159.46±2.6a
diameter	1.60±0.03a	1.51±0.03b	1.49±0.02b	1.61±0.03a	1.55±0.02a
tunnel length	3.53±0.72a	4.75±0.70a	4.86±0.78a	5.06±0.79ac	7.05±0.91bc
cob damage	1.62±0.39a	1.77±0.53a	1.35±0.40a	2.83±1.09a	3.80±0.96a
hole number	0.76±0.16a	1.10±0.16a	1.11±0.18a	1.0±0.17a	1.51±0.20b
cob weight	59.34±1.75a	53.68±1.73b	50.57±1.61b	60.85±1.49a	61.39±1.46a
grain weight	44.93±1.58a	40.04±1.36b	37.95±1.38b	47.04±1.28a	48.60±1.26a

*: combined damage by all borers. **: For cob and grain weights, data were from the last sampling date; means of all other variables were from data over all sampling dates. 1 : Means within rows sharing the same letter(s) are not significantly different (One-Way ANOVA, $P \leq 0.05$ followed by Fisher's LSD test).

Table 2.4 Coefficients of correlation between pest numbers, maize growth, damage symptoms and yield variables recorded at harvesting on plants artificially infested with different numbers of *S. calamistis* eggs from October to December 1993 (trial 2).

	1	2	3	4	5	6	7	8	9	10	11
1 = <i>S. calamistis</i>											
2 = <i>E. saccharina</i>				4 = <i>M. nigrivenella</i>		7 = tunnel length				10 = cob weight	
3 = <i>C. leucotreta</i>				5 = height		8 = holes				11 = grain weight.	
				6 = diameter		9 = % cob damage					
1.	=										
2.	.03	=									
3.	-.06	-.08	=								
4.	-.01	.06	-.03	=							
5.	-.07	.01	.03	-.07	=						
6.	-.09	.06	.05	.02	.35*	=					
7.	.32*	.45*	.02	-.02	.05	.02	=				
8.	.33*	.51*	-.01	-.01	.05	.05	.85*	=			
9.	.34*	.11*	.03	.06	-.03	-.10	.13*	.16*	=		
10.	-.13*	-.02	.00	-.04	.35*	.38*	-.02	-.03	-.10	=	
11.	-.10*	-.04	-.01	-.04	.29*	.32*	-.03	-.02	-.09	.94*	=

Values shown with an asterisk (*) are significant at $P \leq 0.05$ (critical value, $r = 0.098$, $df = 396$).

Table 2.5 Effect of time (A) and severity (B) of infestation on growth and yield of maize plants artificially infested at different stages of development with 15 or 30 *S. calamistis* eggs (Two-factor ANOVA).

Variable	Factor	F-test	DF	P value
plant height	A	8.832	1,316	0.003
	B	2.770	1,316	0.097
plant diameter	A	7.641	1,316	0.006
	B	2.290	1,316	0.135
hole number	A	0.711	1,316	0.400
	B	2.173	1,316	0.141
cob damage	A	4.784	1,316	0.029
	B	0.123	1,316	0.731
cob weight	A	32.571	1,316	0.0001
	B	0.670	1,316	0.415
grain weight	A	44.441	1,316	0.0001
	B	0.044	1,316	0.842

leucotreta and *Mussidia nigrivenella*, were collected; but their relationship with cob and grain weights was not significant. Yield, as measured by cob weight without husk, was related to plant height, diameter and borer damage by the multiple regression equation

$$\text{Cob weight} = 5.71 + 0.16\text{height} + 17.4\text{diam} - 0.07\text{stem damage} \\ - 0.2\text{Arcsine}(\text{Cob damage})$$

(F = 25.270, df = 4,394, P = 0.0001).

A Two-factor ANOVA (Table 2.5) showed that on cob and grain weights and on plant growth, time of infestation had a greater effect than the number of eggs (severity).

2.4 Discussion

Differences in plant size indicated that infestations by *S. calamistis* reduced growth in maize plants. Similar observations have been reported for several maize stem borers (Lynch, 1980; Van Rensburg *et al.*, 1988a,b). Chiang and Hodson (1950) and Lynch (1980) observed that maize infestation by the European corn borer, significantly reduced the growth of the maize plant. Reduction of plant size by *S. calamistis* infestation could be explained mainly by the boring activities of the larvae, which may hinder the normal flow of sap, leading to the disruption of physiological processes. This disturbance often weakens the plant and produces 'dead hearts' and breakage (Chiang and Hodson, 1950).

The results of trial 2 showed that yield, as measured by weight of grain per plant, varied between different treatments. The borers may limit yield by weakening plants and interfering with their physiological processes; they may impede also the normal filling of the

grains, reducing final weight. Yield reductions by stem borer may not only result from a decrease in grain weight (Guthrie *et al.*, 1975; Bosque-Pérez and Mareck, 1991), but could also be a consequence of direct destruction of kernels. Presumably, a certain number of larvae which infested younger plants bored upward to the ears to feed on kernels. Van Rensburg *et al.* (1988a) observed that direct damage to the ears in their earliest development can result in total yield loss. Although larvae of *E. saccharina* were collected, their numbers were not significantly different between treatments.

The significant relationship between grain weight and tunnel length indicated that plant damage by *S. calamistis* could satisfactorily predict the extent of expected yield losses. However, the mean number of *S. calamistis* obtained at harvesting did not seem to be a good indicator of yield loss, although Walker (1981) suggested it as a possible method of assessment. Borer count at harvesting did not necessarily indicate the level of populations in the earlier stages of plant development. Therefore, the cumulative number of *S. calamistis* (Sesamia-days) appeared to be a better predictor of yield loss than mean numbers of the borer.

The reduction of plant growth and the extent of yield loss varied with times and levels of infestation. At a given infestation level, the extent of the reduction of plant growth and yield decreased with the stage at which the plant was infested so that infestations in early developmental stages of the plants yielded lower grain weights than later infestations. Van Rensburg *et al.* (1988b) found that damage to maize plants and yield loss from the noctuid maize stalk borer, *B. fusca*, decreased with later infestations. The time of infestation may

have affected plants, and therefore yields, in several ways. With a developed root system, plants infested in their late stage could compensate for tissue destruction, and sustain and survive heavy plant damage, by using nutrients accumulated in their earlier development, or by retrieving more nutrients from the soil than young plants. In addition, an infestation occurring within four weeks after planting should result in larvae that developed better than those on old plants, because they fed on more tender tissues than late-infesting larvae. Larvae from early infestations may also cause more direct damage to ears since they are fully developed at the beginning of ear formation. Although the data of trial 1 could not be used in yield analysis due to bird damage, it appeared from trial 2 that the time up to five WAP was the most sensitive period of the maize plant to *S. calamistis* attack. This suggested that, to protect the maize plant effectively against infestations by the borer, appropriate control measures should be taken from plant emergence up to about six WAP.

Data from both trials consistently showed that, at a given stage of plant growth, the two infestation levels were not different. Thus, plant growth values and extent of damage were similar at 15 and 30 eggs per plant. Non-significant differences in yield were observed also between the 15 and 30 eggs/plant in trial 2. This result indicated that, although infestation definitely reduced growth and yield of maize, the number of *S. calamistis* at infestation was not important. This finding disagrees with observations of Usua (1968a) on *B. fusca* in maize. With varying populations of the borer, this author found that the rate of plant growth decreases and damage increases as the numbers of borers increase. Other workers have previously noticed a positive relationship

between borer numbers and growth and yield of maize (Van Rensburg, 1988a,b). The difference between previous research and mine may be explained by the fact that I started the infestations with eggs, instead of larvae. With eggs, naturally high egg mortality caused by predation, parasitism, desiccation and infertility may have occurred, reducing the expected difference between numbers of larvae per plant in some of the treatments. The reduced difference in larval numbers between treatments could also be explained by eventual larval migration between plants and density-dependent mortality. This may indicate that the difference of 15 eggs/plant used in these trials was not sufficient to produce significant differences in yield. Furthermore, the results indicate that there is a limit in the numbers of eggs or larvae below which no significant difference will appear between two or more levels of infestation; 15 larvae might cause about the same amount of damage as 30. Usua (1968a) and Van Rensburg (1988a) found a non-linear relationship between the number of larvae of *B. fusca* and the extent of damage and yield of maize.

In conclusion, the comparison of the impact of the two factors showed that both time and level of infestation of maize by *S. calamistis* affected the growth and yield of the crop. However, within the limits of this study, time of infestation had a more pronounced effect than the number of eggs.

Chapter III

SEASONAL ABUNDANCE OF *SESAMIA CALAMISTIS* AND *ELDANA SACCHARINA* IN MAIZE AND INDIGENOUS GRASSES

3.1 Introduction

Examination of the literature indicates that many studies have been devoted to the distribution of maize stem borers in Africa (Ingram, 1958; Harris, 1962; Usua, 1968b; Girling, 1978; Sampson and Kumar, 1983; Atachi, 1984; Thomas-Odjo, 1984; Cochereau, 1982. Van Rensburg *et al.*, 1987b; Bosque-Pérez and Mareck, 1990; Shanower *et al.*, 1991; Gounou *et al.*, 1994). Nevertheless, no consistent distribution pattern is shown regarding ecological zones. For example, *S. calamistis* is reported both as a wet-area species and a dry-zone species, depending on the study. The same contradictory reports exist for *E. saccharina*. The establishment of a borer species in a given area is sometimes associated with its biology and feeding habits (Usua, 1968b; Girling, 1978; Atkinson, 1980). It appears that the occurrence of borers and their population sizes vary according to ecological zones, time of year (Sampson and Kumar, 1983; Shanower *et al.*, 1991; Gounou *et al.*, 1994), the species and physiological stages of the host-plant (Bosque-Pérez and Mareck, 1990; Mitchell *et al.*, 1984). Atkinson (1980) discussed the host-plant range of some stem borers. Apart from maize, *S. calamistis* and *E. saccharina* are also found on a wide variety of sedges and graminaceous plants. It is suspected that these non-cultivated host plants act as reservoirs for infestation of newly

planted maize (Sampson and Kumar, 1986). Several authors have also reported that insect population variations are affected by population intrinsic factors, such as adult activities, and by some extrinsic factors, such as moonlight and weather conditions. Moonlight presumably interferes with the efficiency of light trap catches (Bowden, 1973a; Bowden and Church, 1973; Dent and Pawar, 1988; Jönsson and Anderbrant, 1993), but may also influence insect activities by inducing physiological changes (Bowden, 1973b; Girling 1978; Kiyomitsu *et al.*, 1993). For several stem borer species, weather, particularly rainfall, temperature, relative humidity, and wind, affect the moth's activities (Van Rensburg *et al.*, 1987a; Cox *et al.*, 1981) which often determine the severity of infestations (Dang and Seshu-Reddy, 1983; Johnson, 1983; Witz *et al.*, 1992). Concerning *S. calamistis* and *E. saccharina*, little information is available on the influence of the above factors.

In this chapter, I examine the seasonal variations of populations of two important stem borers in Bénin, *S. calamistis* and *E. saccharina*, on maize and two indigenous non-cultivated wild grasses, and the influence of moonlight and weather conditions on adult flight activities as measured by adult catches in light traps.

3.2 Materials and methods

3.2.1 Experimental design and planting procedures

Planting sites

I planted three fields, with maize, wild sorghum, *Sorghum arundinaceum* and pennisetum, *Pennisetum polystachion*, at the

experimental farm of IITA-Bénin on land previously planted with maize. Each field was approximately 2,500 m² in size. Fields were disc-harrowed to destroy weeds, grasses, and maize from earlier plantings. The fields were close to a collection of native wild grasses and sedges, and were surrounded by open areas covered with various crops including cassava, millet, and cow-pea. Maize was also planted in farmers' fields around the station. The experiments were carried out during three successive maize-growing seasons between October 1991 and January 1993.

Planting procedures

Maize. I planted three grains of the maize variety 'TZE (95 days)' per hole. On the planting day, I broadcast by hand a compound NPK15/15/15 fertilizer at a rate of 70 kg/ha; the same fertilizer was again applied at a rate of 30kg/ha four weeks after planting. I thinned the maize to one plant per hole three weeks after planting to obtain a density of 50,000 plants/ha (5 plants/m²). Spacing was 25 cm between plants and 80 cm between rows. Weeding started five weeks after planting, and was done every three week, by hand-hoeing. Planting and harvesting for the first growing season occurred on 4 October, 1991 and on 22 January, 1992 (91-2 trial); for the second and third growing seasons, planting and harvesting occurred on 6 July and 5 October, 1992 (92-1 trial) and on 24 September, 1992 and 18 January, 1993 (92-2 trial), respectively. Trial 91-2 and trial 92-2 occurred during the dry season, whereas trial 92-1 was in the rainy season.

Grasses. I planted the wild sorghum and pennisetum fields in single blocks, separated from the maize plot by about 10 m. Grass turfs were planted at a density of 5 plants/m². The soil was prepared

as described for maize, and I applied the same NPK fertilizer at planting at the same rates. I planted the grasses two to three weeks before the maize and watered them as needed during the first four weeks after planting to ensure optimal growth. When fully developed, wild sorghum and pennisetum had on average six and 15 tillers/plant (29 and 103 tillers/m²), respectively.

Light traps

I set six light traps in the 92-1 and 92-2 trials, three in the maize field and three in the grass fields, three to four weeks after maize was planted. Each light trap consisted of a kerosene lamp suspended at about 25 cm over a plastic bowl (40 cm in diam) containing soapy water. The bowl was placed 1.3 m above ground. I lighted the lamps every day at 18:30h and turned them off at 06:30h the next morning. The traps were operated for another two to three weeks after harvesting.

3.22 Data collection

Starting three to four weeks after planting, I sampled every week 20 maize plants (30 for the 91-2 trial) and 60 tillers of each grass species. The plants and tillers were selected at random and cut off at soil level. The leaves were carefully removed to search for borer eggs, larvae and pupae; stems were split open to record the number of borer larvae and pupae. When the cobs were available, they also were examined for borers. Insect eggs, larvae, and pupae were determined to species.

For the light traps, I inspected the bowls every day between 07:00h and 08:00h to record the number and sex of *S. calamistis* and *E.*

saccharina. Throughout the trials, lunar phases, temperature, relative humidity, and wind speed were recorded at the experimental farm to investigate the influence of these factors on flight activities of the two stem borer species. Dissections and moth catches continued several weeks after harvesting.

3.23 Analysis of data

I analyzed the data separately for each season and for each borer species. To construct abundance curves, I determined the mean numbers of individuals per sampling date and plotted them against the time (days) after planting. On a given sampling date, I calculated the mean numbers of each developmental stage as well as the total number of borers, and I compared these numbers between host plants by ANOVA. I then summed the numbers of all developmental stages to obtain the total number collected per host plant. Finally, the numbers of *S. calamistis* on maize and those on grass species were pooled to obtain the total numbers of *S. calamistis* collected per season. Comparisons were made between host-plants and between seasons using a Two-Sample t-test.

I made the same calculations and comparisons for *E. saccharina*, and compared the total number of *S. calamistis* with that of *E. saccharina*. Means are shown with their standard errors, unless otherwise indicated.

To evaluate the effects of weather factors on borers' flight activities, I made a correlation analysis between weather factors and the proportion of infested plants, and between weather factors and numbers of moths trapped.

3.3 Results

3.31 Seasonal variations of borer populations

October 1991 - January 1992 trial (91-2)

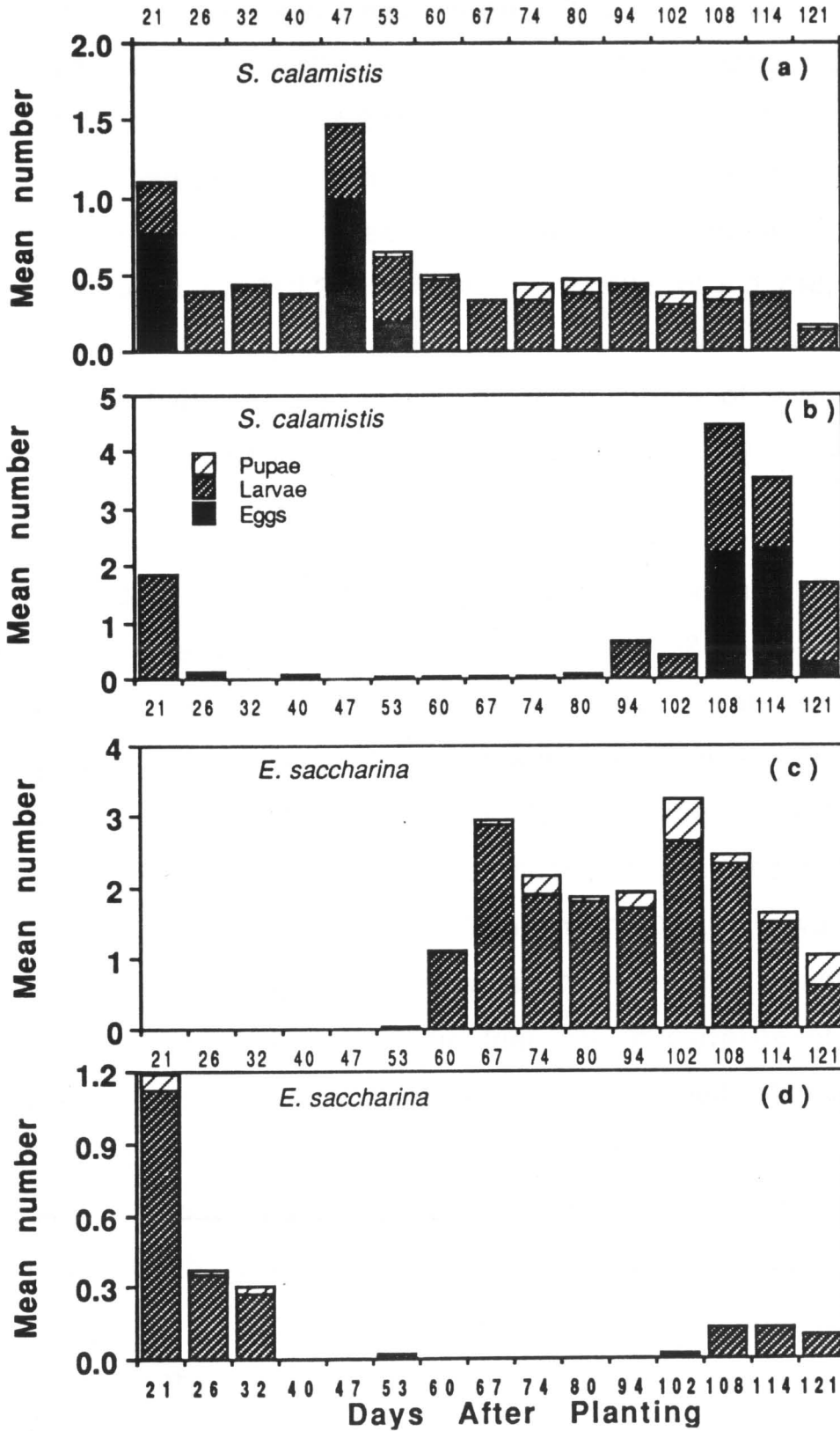
S. calamistis

From plant dissection, I collected on maize three *S. calamistis* egg masses containing 23, 30, and 5 eggs. These egg masses were collected three, seven, and eight weeks after planting, respectively (Figure 3.1a). I found the first larvae 21 days after planting (DAP). Their mean numbers per plant and sampling date were between 0.10 ± 0.06 and 0.47 ± 0.20 , with the exception of the last sample which did not contain any larvae. Pupae were first collected at 53 DAP. Their mean numbers were low, fluctuating between 0 and 0.10 ± 0.06 per plant and sampling date. Larvae and pupae were found, although in very low numbers, in several samples after harvesting.

On grasses, the first *S. calamistis* eggs (1.11 ± 0.71) were found 108 DAP (Figure 3.1b), which corresponds to the harvesting period of maize. About the same mean numbers of eggs were observed on sorghum and pennisetum five weeks after harvesting. As on maize, I collected larvae on the first sampling date (21 DAP); but from that period on, very few larvae (between 0.01 ± 0.01 and 0.04 ± 0.02) were found until about 94 DAP when higher numbers were once more collected. The mean numbers of larvae increased from 0.32 ± 0.28 on day 94 to 1.12 ± 0.27 at harvesting. Extremely low numbers of pupae (0 to 0.02 ± 0.02) were collected on wild sorghum and polystachion.

The relative numbers of borers on each host plant varied with the time of sampling. Before harvesting, the mean numbers of eggs and

Figure 3.1 Numbers of immature *S. calamistis* and *E. saccharina* found on maize (a,c) and grasses (b,d), in trial 91-2, between October 1991 and January 1992. Columns show the numbers of eggs, larvae, and pupae per plant.



larvae collected per week on maize were significantly higher than those collected on grasses (eggs: maize = 0.16 ± 0.11 , grass = 0, ANOVA: $F = 9.301$, $df = 1,1798$, $P = 0.002$; larvae: maize = 0.33 ± 0.06 , grass = 0.10 ± 0.03 , ANOVA: $F = 14.921$; $df = 1,1798$; $P = 0.0001$). During the period from harvesting to the end of sampling, I collected significantly more *S. calamistis* per week on wild grasses than on maize (eggs: maize = 0, grass = 1.0 ± 0.27 , ANOVA: $F = 93.480$; $df = 1,748$; $P = 0.042$; larvae: maize = 0.17 ± 0.04 , grass = 0.82 ± 0.08 , ANOVA: $F = 17.811$; $df = 1,1798$; $P = 0.0001$). Significantly higher numbers of larvae per tiller were collected on sorghum than on pennisetum.

E. saccharina

Only one *E. saccharina* egg batch containing 17 eggs was collected on maize plants during the entire 91-2 trial. Although few eggs were collected, relatively high numbers of larvae were found on both types of host plants. The first larvae on maize were collected eight weeks after planting (53 DAP). Their numbers rapidly increased from week nine and reached a maximum between weeks 10 and 16, with means varying between 2.87 ± 0.55 and 1.50 ± 0.47 larvae per plant. A slight decrease occurred after week 13, but the means remained relatively high until the end of the trial. The occurrence of high larval populations coincided with the post-tasseling period of maize. During the whole sampling period, I collected an average of 0.91 ± 0.10 larvae per plant. Pupae were collected from 67 DAP with 0.07 ± 0.05 pupae/plant to the end of the trial (Figure 3.1c). The average number over the trial period was 0.13 ± 0.02 , ranging from 0.07 ± 0.05 to 0.60 ± 0.18 /plant.

All the *E. saccharina* larvae and pupae observed on grass were collected on wild sorghum. No larvae were found on pennisetum. Relatively high numbers of larvae (0.56 ± 0.10 larvae/plant) were collected at the beginning of sampling and none at 46 DAP (Figure 3.1d). The numbers increased again from 108 DAP (average: 0.07 ± 0.01). Very few pupae were collected.

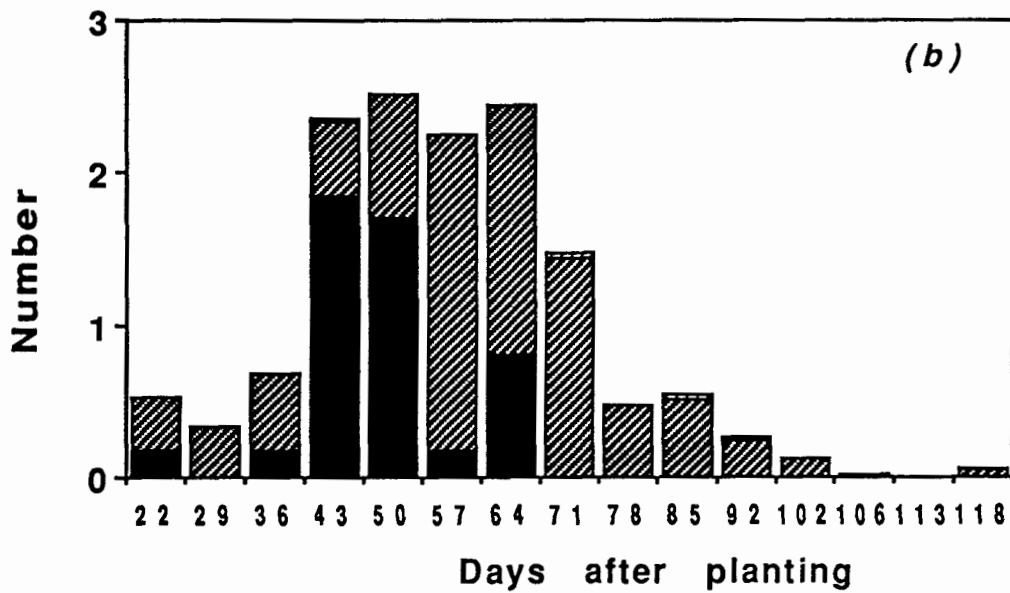
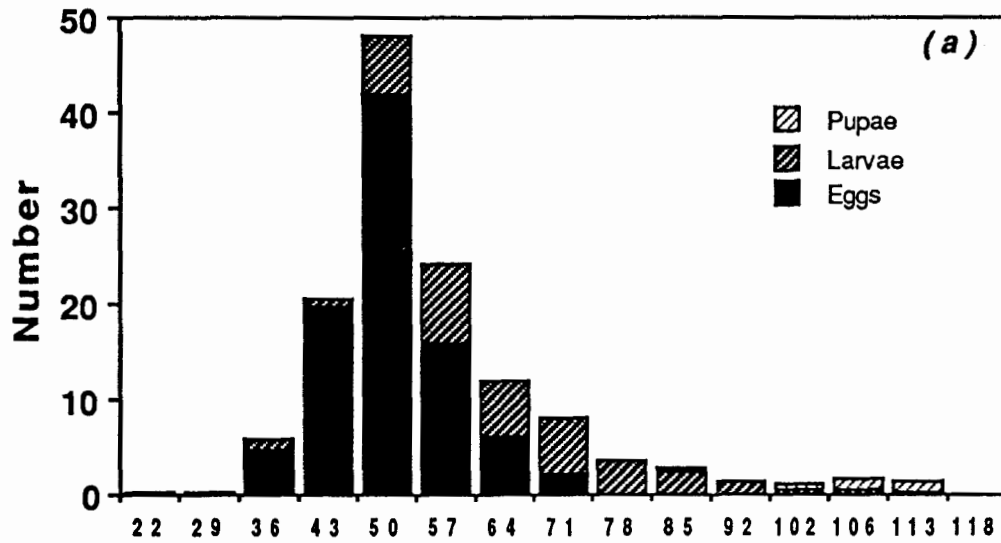
For the 91-2 season, the mean numbers of larvae plus pupae of *S. calamistis* per maize plant (0.35 ± 0.05) were significantly lower than those of *E. saccharina* (1.13 ± 0.14) (t-test, $t = 6.96$, $df = 1,509$; $P = 0.0001$). On grass, however, *S. calamistis* was the most abundant (*S. calamistis*: 0.18 ± 0.03 ; *E. saccharina*: 0.08 ± 0.01) (t-test, $t = 7.94$, $df = 1,2039$, $P = 0.0001$). But when the numbers on maize and grasses were combined, no significant difference was found between the mean number of *S. calamistis* (0.21 ± 0.03) and *E. saccharina* (0.29 ± 0.03) (ANOVA: $F = 3.47$; $df = 1,3898$; $P = 0.063$).

July 1992 - October 1992 trial (92-1)

S. calamistis

Figure 3.2 shows the mean numbers of different developmental stages of *S. calamistis* in maize and grass fields from July to October 1992. On maize, I collected eggs mainly between 36 and 64 DAP. The number of eggs per plant increased rapidly to reach a maximum of 42.0 ± 12.62 around 50 DAP, and decreased to 0 after three weeks (Figure 3.2a). Larvae were collected from the second to the last sample; however, until week five after planting, the average number/plant was low (0.60 ± 0.11); it increased sharply thereafter to a

Figure 3.2 Numbers of immature *S. calamistis* found on maize (a) and grasses (b), in trial 92-1, between July and October 1992. Columns show the numbers of eggs, larvae, and pupae per plant.



maximum of 8.50 ± 2.30 around day 57. There was a gradual decrease until harvesting, and the mean number of 0.33 ± 0.07 was observed a week after harvesting day. Pupae were collected from 85 DAP to the last sampling date. Means fluctuated between 0 and 1.0, with the highest numbers observed at the end of the trial.

Activities of *S. calamistis* adults were principally observed between 45 and 65 DAP (Figure 3.3a). The first adults were trapped 20 DAP. Catches between 20 and 45 DAP were variable with numbers fluctuating between 0 and 5 individuals per night. After 45 DAP, numbers increased sharply with a peak on day 60 with 72 individuals/night. High numbers of moths were trapped until day 64. The numbers of catches dropped and few moths (between 0 and 6) were again trapped per night from 64 DAP until harvesting. Over the sampling period, the mean number of males trapped (4.23 ± 0.77) was significantly higher than the mean number of females (2.87 ± 0.64) (t-test: $t = 3.41$, $df = 1,118$, $P = 0.0001$).

On grass species, the mean numbers of eggs per plant varied between 0 and 1.85 ± 1.21 . They peaked around 43 DAP (Figure 3.2b). Slightly more eggs were collected on wild sorghum (0.64 ± 0.27 , $n=719$ tillers) than on pennisetum (0.17 ± 0.08 , $n=719$ tillers); however, these means did not differ statistically. Although the egg collection period was longer on grasses, the overall mean number of eggs found (0.41 ± 0.14) was significantly lower than on maize. The pattern of variations of the numbers of *S. calamistis* larvae on grass tillers was similar to that on maize. As during the 91-2 trial, the mean number of larvae was significantly lower on grasses than maize. Moths in the grass fields were observed at approximately the same period as in the

maize field. The first individuals were captured at 19 DAP, and higher numbers were caught from day 43. Three peaks of the same amplitude (10, 11, and 10 moths per night) were observed on days 46, 57, and 75, respectively. Between these peaks, the numbers caught fluctuated between 0 and 4 moths/night (Figure 3.3b). Significantly more males (1.34 ± 0.18) than females (0.68 ± 0.12) were captured (t-test: $t = 3.93$; $df = 1,118$; $P = 0.0001$). The overall mean number of *S. calamistis* adults caught in maize (7.20 ± 1.38) was higher than that captured in the grasses (1.97 ± 0.24) (t-test: $t = 4.15$; $df = 1,118$; $P = 0.0001$).

E. saccharina

The numbers of *E. saccharina* in maize and grass fields are shown in Figure 3.4. Larvae were collected weekly on maize from 36 DAP, and their mean numbers steadily increased. The maximum mean number of 6.60 ± 0.89 was observed 78 DAP. A relatively high mean number of 2.83 ± 0.23 was still collected one week after harvest (Figure 3.4a). The overall number of larvae collected during the trial was 2.85 ± 0.23 . Pupae were collected from 92 DAP until harvesting, with an average of 0.23 ± 0.04 . *E. saccharina* adults were first trapped in the maize field at 50 DAP (Figure 3.5a), approximately three weeks after adults of *S. calamistis* were observed in the field. The abundance curve showed three peaks of decreasing importance around 59, 76, and 104 DAP, with 74, 53, and 25 individuals caught per night respectively.

Larvae and pupae were collected on grasses earlier than on maize (Figure 3.4b); however, their mean numbers were significantly lower than on maize (larvae: 0.23 ± 0.02 , pupae: 0.005 ± 0.001). Moths were trapped in grass fields at the same period as in maize. Three peaks

Figure 3.3 Numbers of *S. calamistis* moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-1, between July and October 1992.

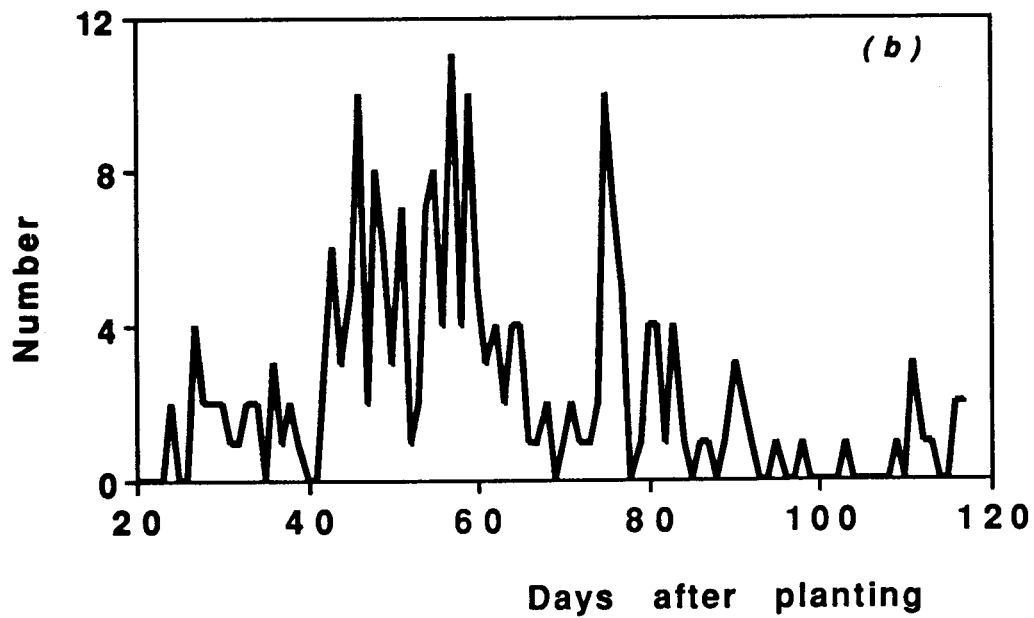
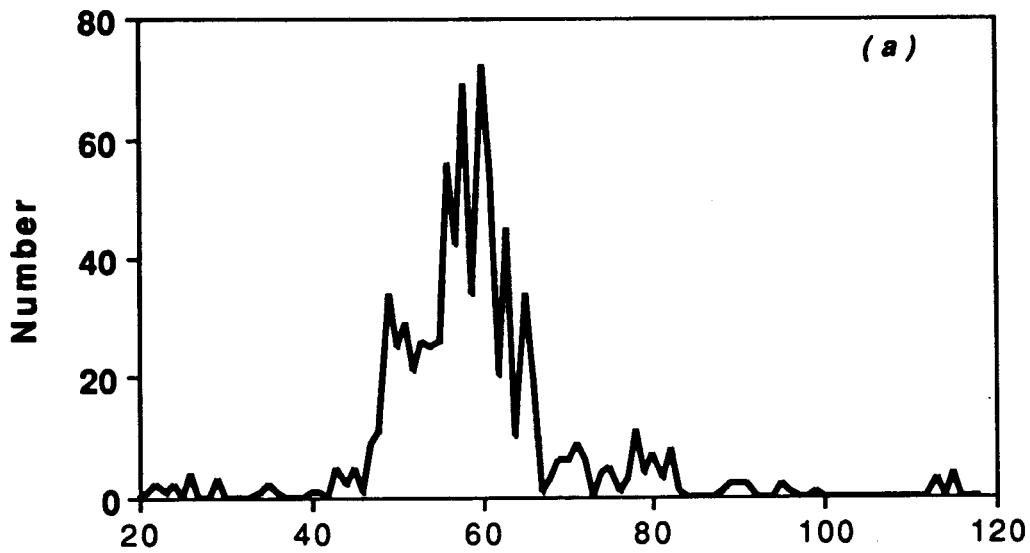


Figure 3.4 Numbers of immature *E. saccharina* found on maize (a) and grasses (b), in trial 92-1, between July and October 1992. Columns show the numbers of larvae, and pupae per plant.

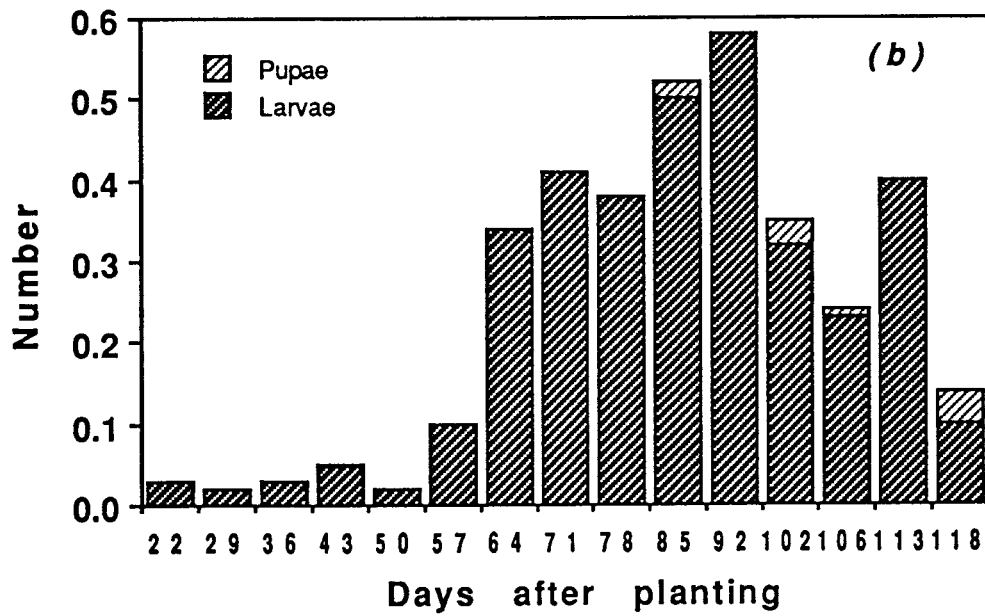
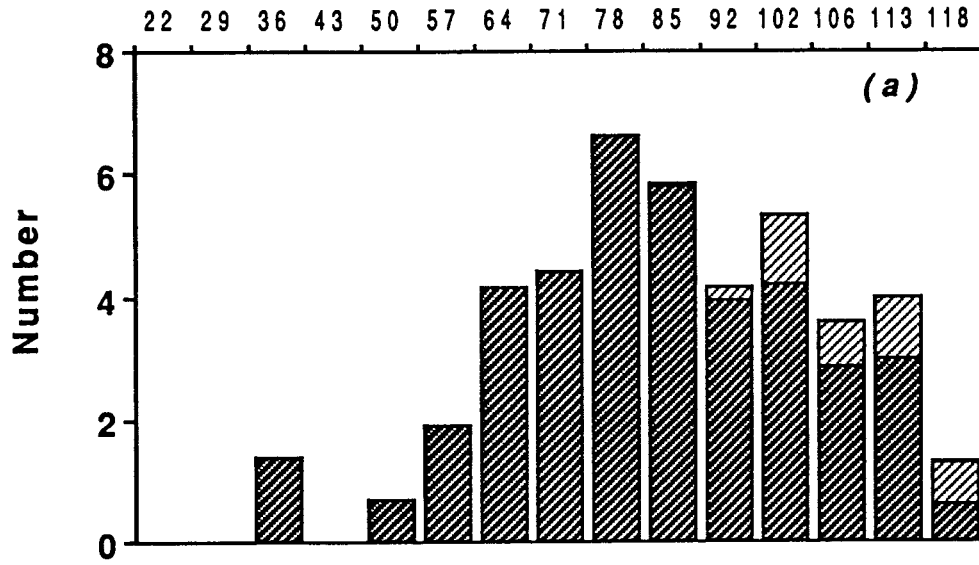
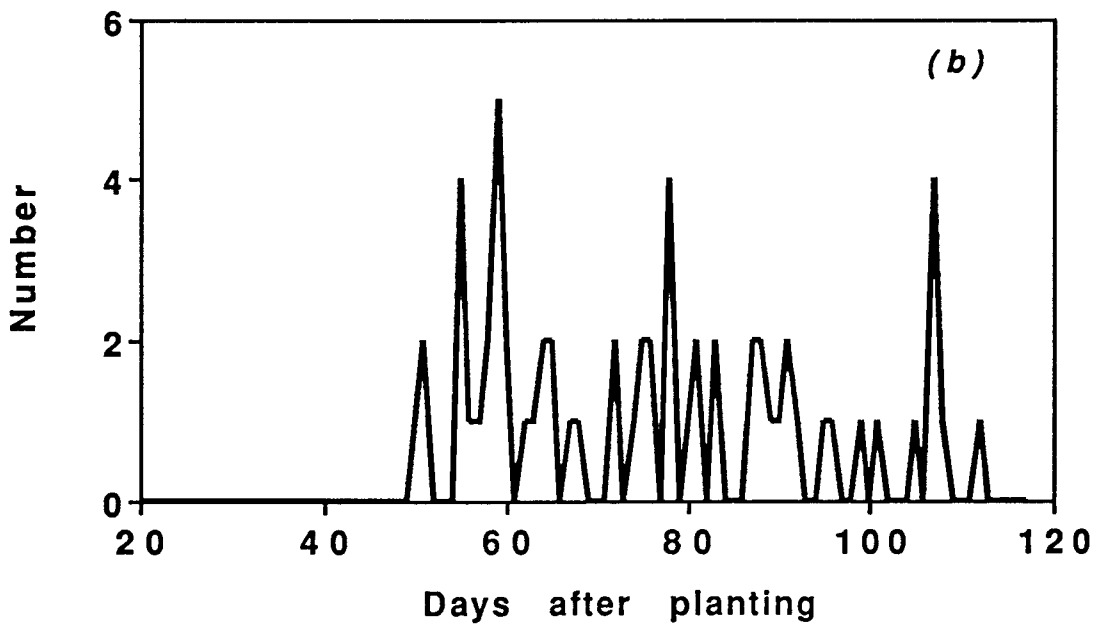
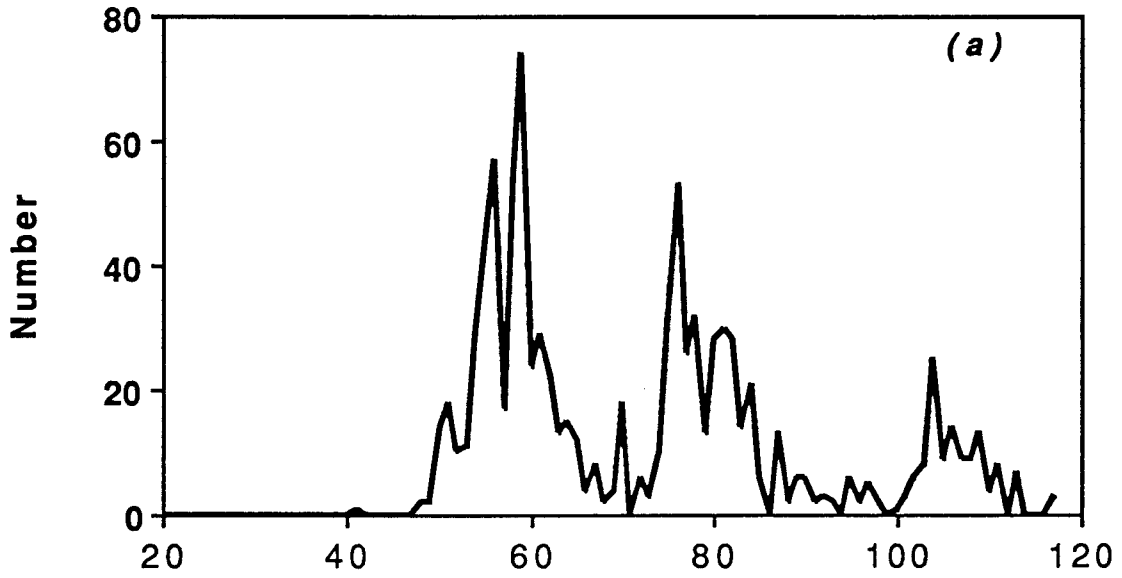


Figure 3.5 Numbers of *E. saccharina* moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-1, between July and October 1992.



appearing at the same periods as in maize, but with lower amplitudes, were also observed (Figure 3.5b).

The mean number of *E. saccharina* adults trapped in grass fields over 111 nights was 0.56 ± 0.09 per night, significantly lower than the number caught in the maize field (8.60 ± 1.31) and also lower than *S. calamistis* adults from grass fields (1.97 ± 0.24). On maize, however, the mean numbers of *S. calamistis* (7.20 ± 1.38) and *E. saccharina* (8.60 ± 1.31) were not significantly different (t-test: $t = 1.28$; $df = 1,110$; $P = 0.204$). Likewise, there was no statistical difference between the total numbers of adult *S. calamistis* (1018) and *E. saccharina* (1017). Nevertheless, the total number of *S. calamistis* (larvae, pupae and adults) was significantly higher than that of *E. saccharina* (ANOVA: $F = 6.591$; $df = 1,3615$; $P = 0.011$).

September 1992 - January 1993 trial (92-2)

S. calamistis

Figure 3.6 shows the numbers of immature *S. calamistis* on maize and grasses during the 92-2 trial. Eggs were collected from 30 to 56 DAP with a maximum mean number of 3.95 ± 2.71 eggs/plant around 49 DAP and larvae were found from 26 DAP until harvesting. The highest numbers of larvae were observed around 70 DAP; their mean number over the sampling period was 0.23 ± 0.04 . Few pupae were collected from 70 DAP to the end of the sampling period (mean: 0.05 ± 0.02). Flight activities of *S. calamistis* were observed from 37 DAP, with the numbers of moths caught per night fluctuating between 0 and 4 until 85 DAP (Figure 3.7a). Higher catches occurred between 85 and 97 DAP with 10 to 11 moths/night, coinciding with the period where high

numbers of pupae were collected. Overall, 142 *S. calamistis* adults were trapped on maize over 135 days, with 78% males.

Eggs were found on grasses only towards the harvesting of maize, from 84 DAP (Figure 3.6). They were collected during three successive weeks and on wild sorghum only. The highest numbers were observed on 92 DAP; the mean number per night over the sampling period was 0.52 ± 0.13 . Very few larvae and pupae were collected from the beginning of the sampling on both grass species. Higher numbers of larvae were found on wild sorghum than on pennisetum. Adults appeared in grass fields from 36 DAP (Figure 3.7b). Their numbers per night varied between 0 and 2. However, two peaks seemed to appear on the abundance curve. The first peak was observed around 40 DAP and the second around 90 DAP with a maximum of 4 and 5 individuals per night. Flight activities were observed until 120 DAP.

E. saccharina

E. saccharina larvae were found on maize plants from 42 DAP to the end of the sampling, with a maximum mean number of 0.95 ± 0.34 collected around 70 DAP (Figure 3.8a). The number of pupae per plant was extremely low. The numbers of larvae and pupae of *E. saccharina* did not significantly differ from those of *S. calamistis* (ANOVA: $F = 0.010$; $df = 1,558$; $P = 0.910$). Very few adults were trapped, compared with the catches in the previous season (Figure 3.9a). Catches started around 50 DAP. The maximum number caught in light traps per night was 4, three-fold lower than the number of *S. calamistis* adults in the maize field.

On grass tillers, *E. saccharina* larvae were collected earlier than in maize (Figure 3.8b). The numbers were high at the beginning of the

Figure 3.6 Numbers of immature *S. calamistis* found on maize (a) and grasses (b), in trial 92-2, between October 1992 and January 1993. Columns show the numbers of eggs, larvae, and pupae per plant.

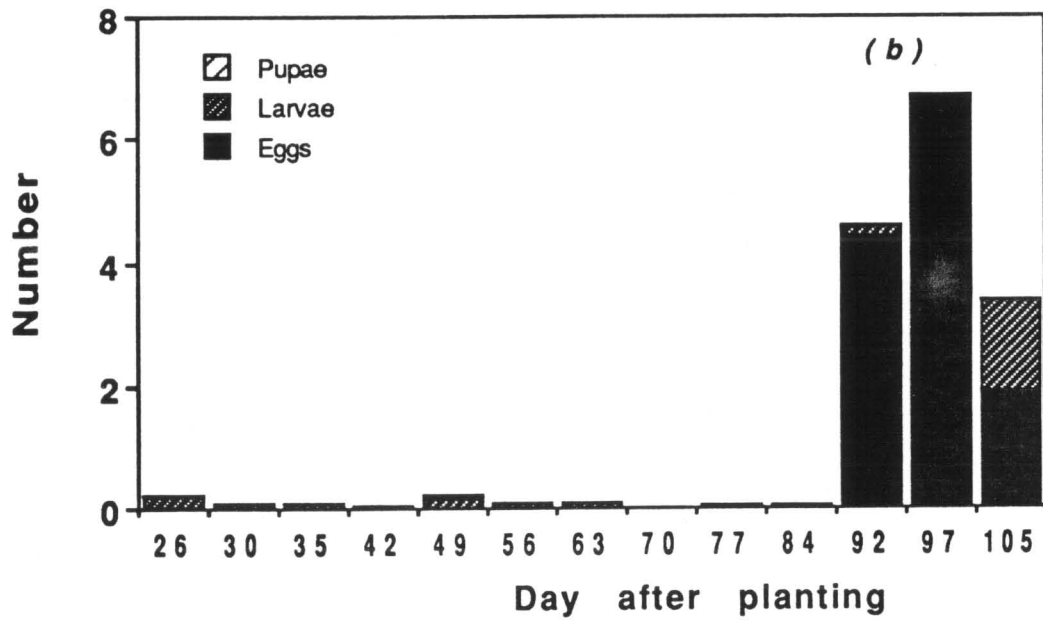
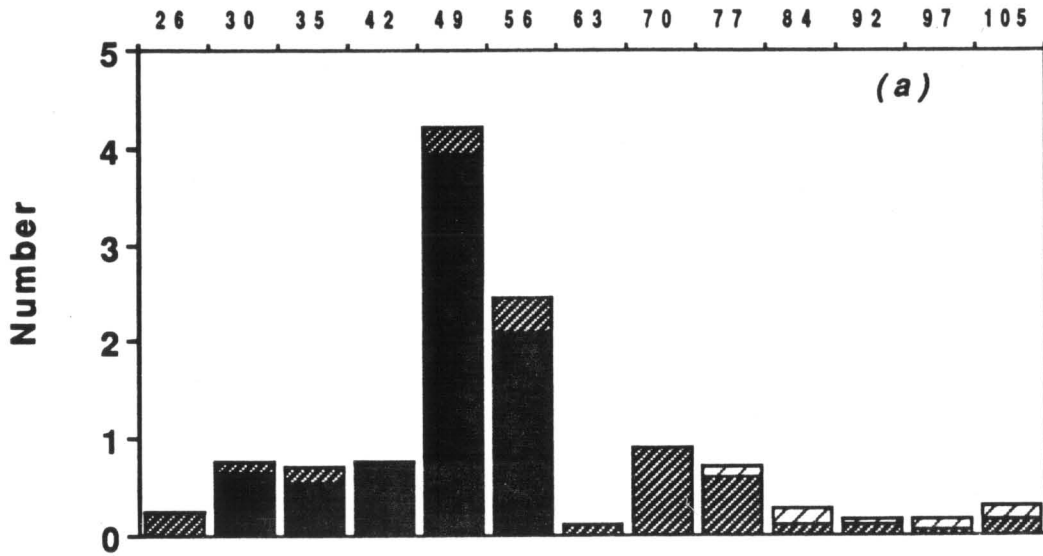


Figure 3.7 Numbers of *S. calamistis* moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-2, between October 1992 and January 1993.

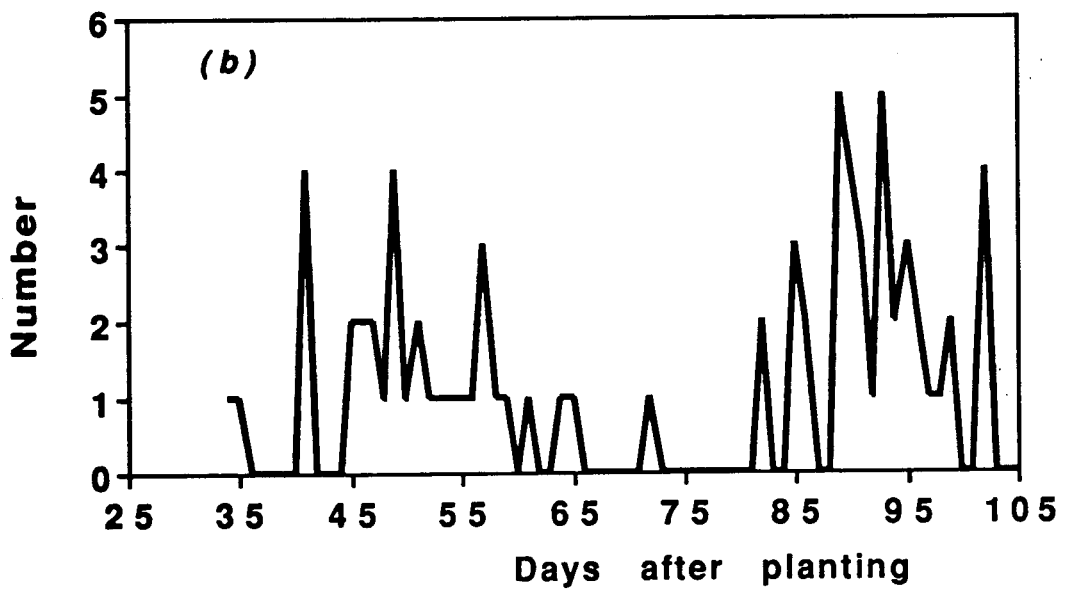
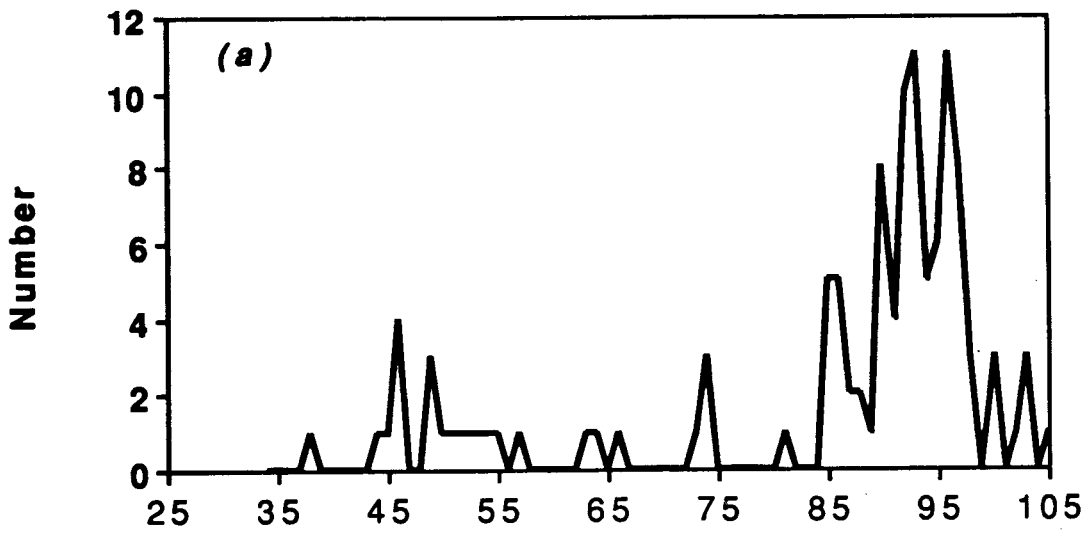


Figure 3.8 Numbers of immature *E. saccharina* found on maize (a) and grasses (b), in trial 92-2, between October 1992 and January 1993. Columns show the numbers of larvae and pupae per plant.

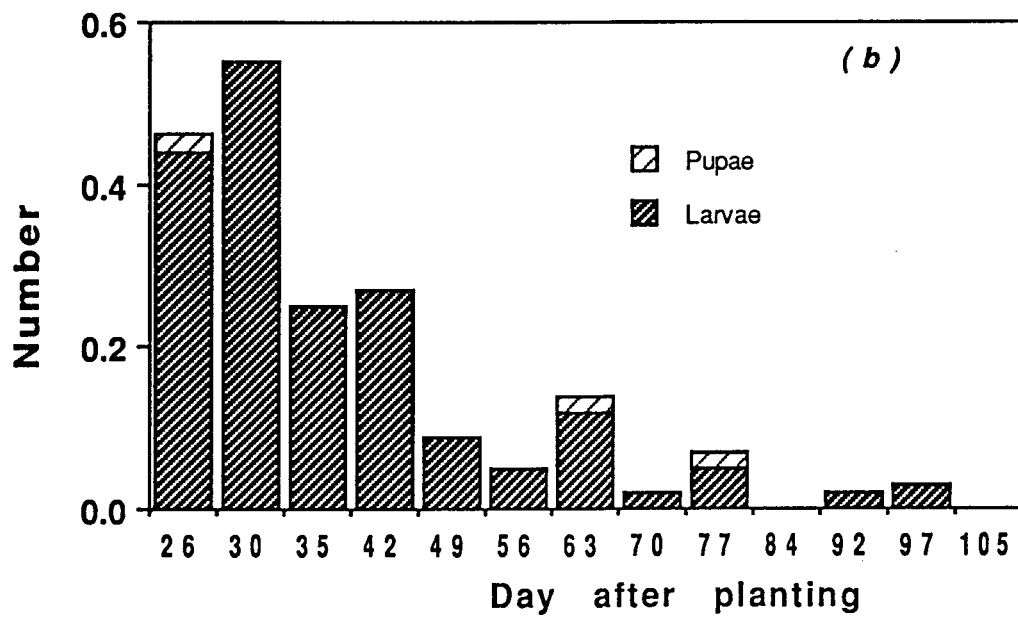
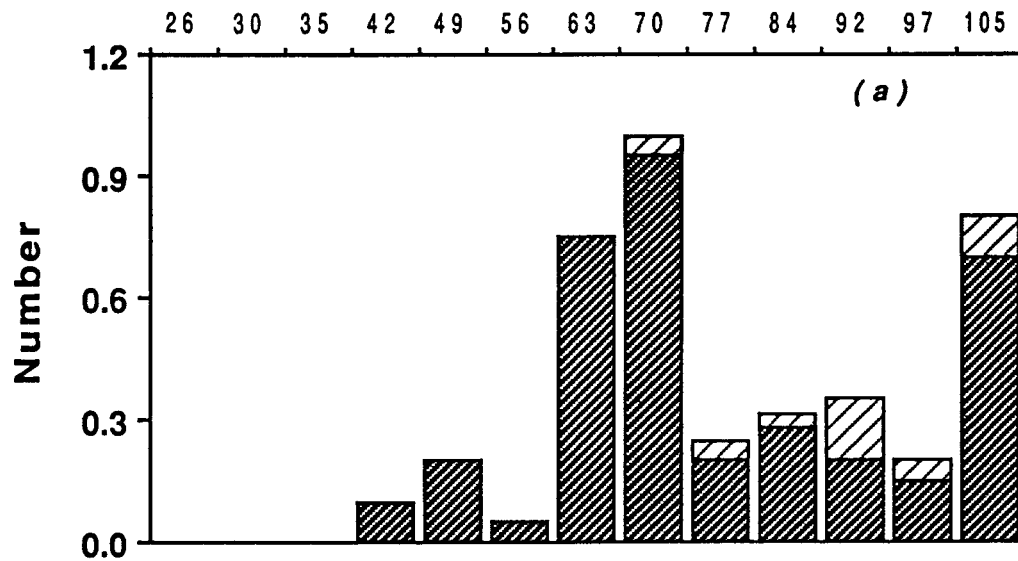
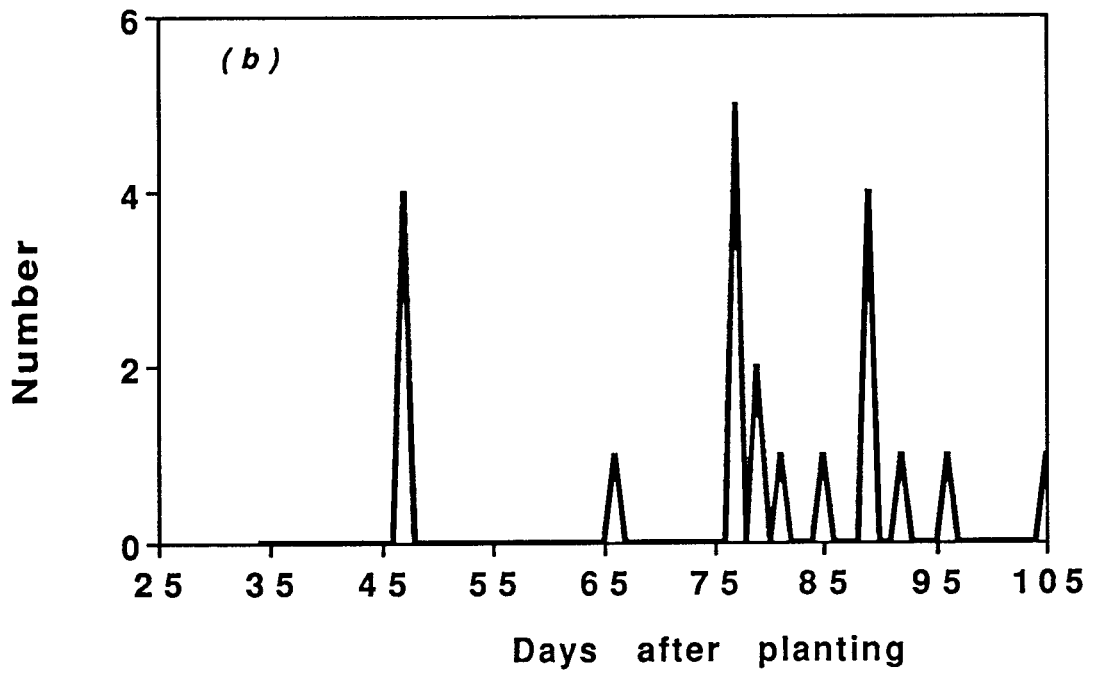
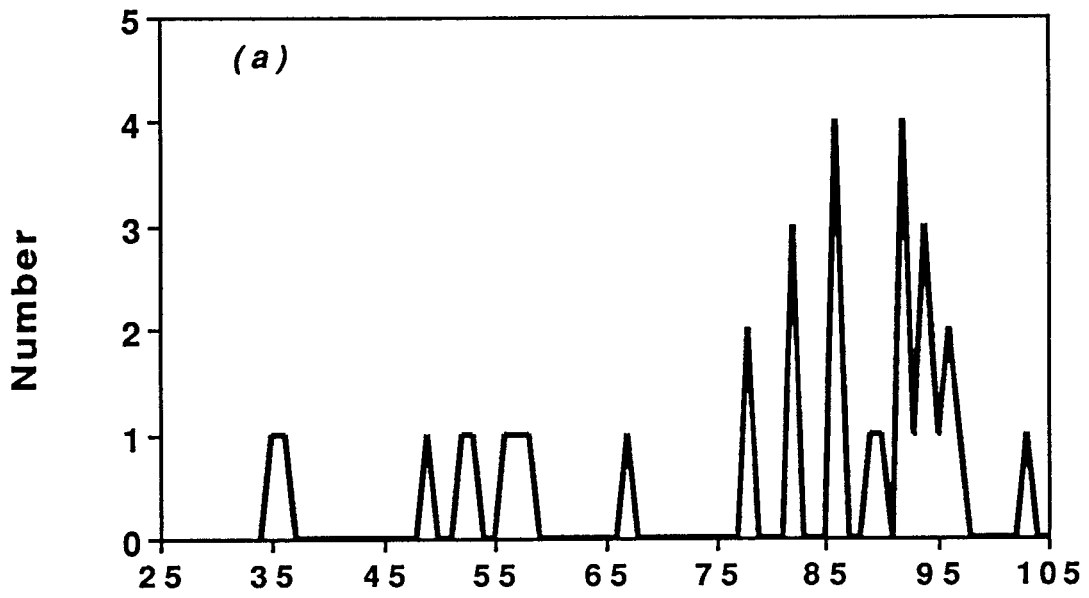


Figure 3.9 Numbers of *E. saccharina* moths caught in light traps per night in maize (a) and grass (b) fields, in trial 92-2, between October 1992 and January 1993.



sampling period and gradually decreased to 0 around 105 DAP. Few pupae were collected. Their highest numbers were observed in the first sample, at the beginning of the season. Catches occurred during few nights from 47 to 105 DAP, with numbers of adults varying between 0 and 5.

3.32 Relationship between lunar phases, weather factors and flight activities

Trap catches in relation to borer infestation on maize

Infestations during the two trials, 92-1 and 92-2, were observed from the beginning of the sampling, ie, 20 DAP. The infestation curves were of sigmoid type and their evolution was similar in the two trials. Infestations increased gradually from about three weeks after planting, and the highest rate of infestation occurred between 50 and 80 DAP, a maximum was reached around 85 DAP. The percentage infestation was highly correlated with the number of immature *S. calamistis* and *E. saccharina* found in stems (Regression: $r^2=0.80$, $F=46.790$, $P=0.0001$), but not with the number of adults trapped. Though infestation curves were similar, the proportion of infested plants was higher in 92-1 than in 92-2. During 92-1, the infestation reached 100% of plants at about 65 DAP, whereas in 92-2 it was only 65% (Figure 3.10).

Relationship between weather conditions and trap catches

The relationship between weather factors recorded between July 1992 and January 1993 and adult catches was investigated by correlation analysis. For the combined data over the two trials, wind

Figure 3.10 Percentages of maize plants infested by stem borers in relation to time after planting, during two maize growing seasons.

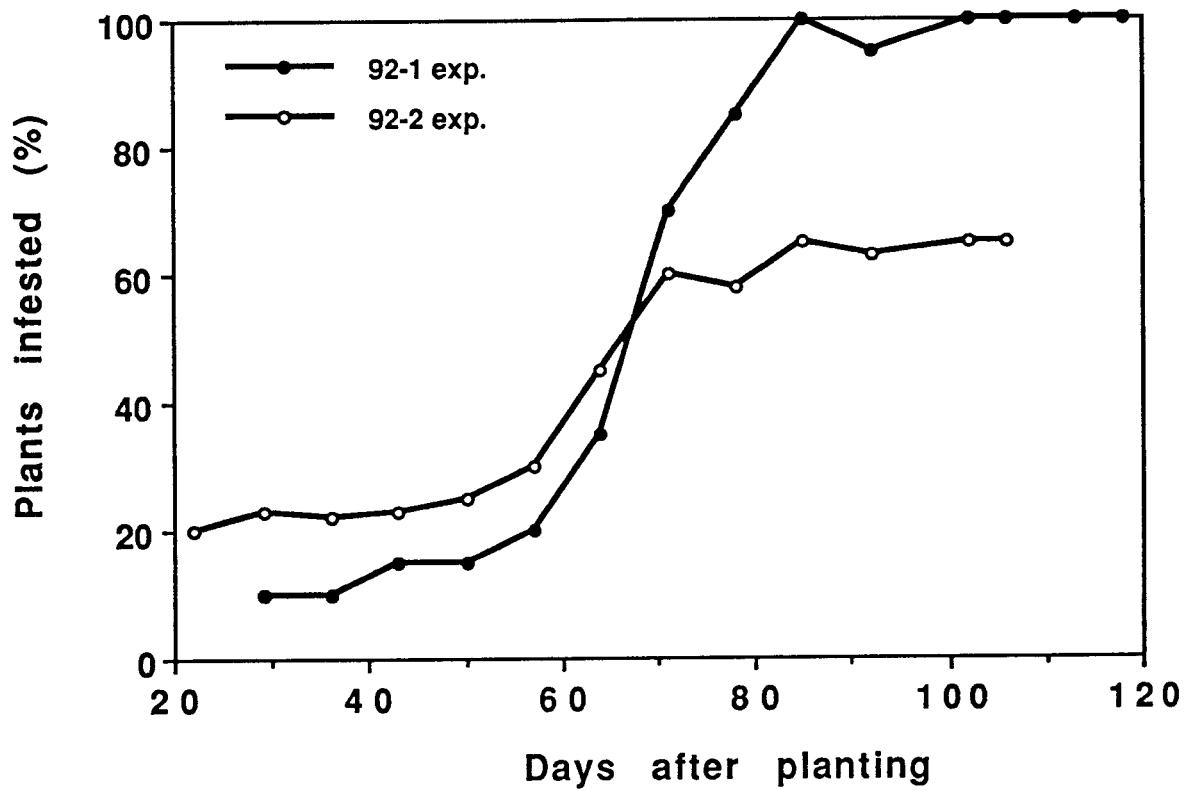


Figure 3.11 Mean numbers of moths caught in light traps in relation to moon phases between July 1992 and January 1993.

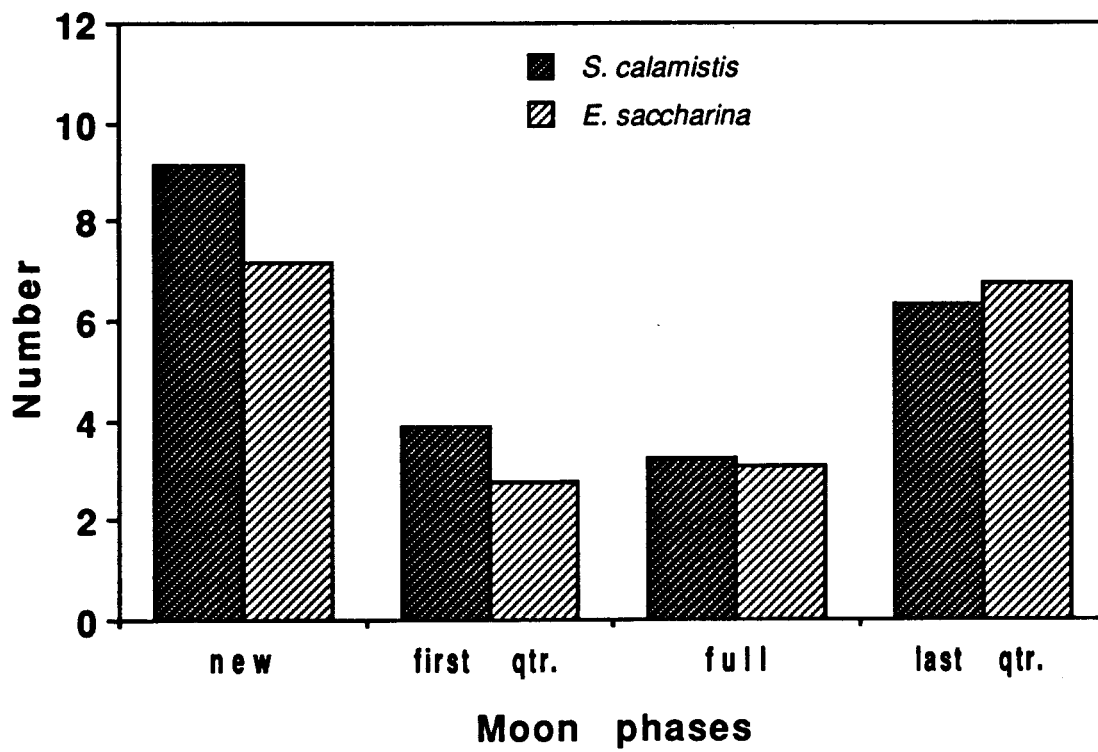


Table 3.1 Coefficients of correlation between various weather factors and numbers of adult stem borers trapped in maize and grass fields between July 1992 and January 1993 at I.I.T.A Cotonou, Bénin.

	1	2	3	4	5	6	7	8	9	10
1 = Wind speed										
2 = Max. temperature					5 = <i>S. calamistis</i> on maize			8 = <i>E. saccharina</i> on grass		
3 = Mean temperature					6 = <i>E. saccharina</i> on maize			9 = Total <i>S. calamistis</i>		
4 = Mean R.H.					7 = <i>S. calamistis</i> on grass			10 = Total <i>E. saccharina</i> .		
1 =										
2.	-.35*	=								
3.	.05	.61*	=							
4.	.36*	-.63*	-.12	=						
5.	.26*	-.28*	-.13*	.13*	=					
6.	.19*	-.24*	-.13*	.19*	.70*	=				
7.	.16*	-.27*	-.19*	.07	.59*	.55*	=			
8.	.01	-.03	-.05	.02	.29*	.50*	.32*	=		
9.	.26*	-.30*	-.14*	.13*	.99*	.72*	.70*	.31*	=	
10.	.18*	-.24	-.13*	.19*	.69*	1.0*	.55*	.56*	-.71*	=

Values shown with an asterisk (*) are significant at $P \leq 0.05$ (critical value, $r=0.122$, $df=237$).

speed and relative humidity were positively correlated with the numbers of adults trapped, in both maize and grass fields (Table 3.1). Generally, wind speed seemed to be favorable to borer flight activities, as shown by the high number of moths trapped. Similar effects were observed regarding relative humidity. Conversely, the number of adults trapped was negatively correlated with temperature. With *E. saccharina* in grass, however, no significant relationship was found between catches and any weather factors.

Relationship between moonlight and adult flight activities

The numbers of moths caught in light traps during the different phases of the moon are shown in Figure 3.11. The data from traps in 92-1 and 92-2 trials were combined. The mean numbers of *S. calamistis* moths trapped during new moon were significantly higher than those collected during full moon (One-Way ANOVA: $F = 2.750$; $df = 3,215$; $P = 0.044$). A significant difference was also observed between the first quarter and full moon. However, no difference was observed between new moon and the last quarter, and between full moon and the first quarter. For *E. saccharina*, ANOVA did not show any significant difference between mean numbers of moths trapped during different moon phases.

3.4 Discussion

The two stem borers, *Sesamia calamistis* and *Eldana saccharina*, were collected in large numbers in maize fields as well as in grass fields during all three trials. Both species occurred together and were the most abundant stem borers. The relative population numbers varied

with the stage of development of maize plants. In addition, some other borers, mostly cob borers, were collected, e.g., *Cryptophlebia leucotreta* (Meryck) (Tortricidae), *Coniesta ignefusalis* (Hampson) (Pyralidae), and *Mussidia nigrivenella* (Ragonot) (Pyralidae). Populations of these cob borers were very low in all trials, however.

These results show that both of the common borer species can develop in the forest-savannah mosaic, as earlier reported by Shanower *et al.* (1991) and Gounou *et al.* (1994). However, they contradicted observations of Atachi (1984) on the distribution of *S. calamistis*. Unlike reports on *E. saccharina* (Girling, 1978; Atkinson, 1980), reports of the ecological distribution of *S. calamistis* have often been contradictory (Kaufmann, 1983; Atachi 1984; Thomas-Odjo, 1984; Bosque-Pérez and Mareck, 1990). The contradiction between present results and earlier observations may be the consequence of important changes in various ecosystems. Atkinson (1980) presumed that the invasion of crops by some stem borers is the result of habitat disturbance. It is possible that habitat disturbance due to large development projects and intensive agriculture in their initial habitats have forced these insects to migrate and adapt to different environments. Examples of changes in species composition are already noticed; *S. botanephaga* (Lepidoptera: Noctuidae) which was the species most often encountered in Bénin and Nigeria several years ago, is now rarely found in these countries, somehow replaced by *S. calamistis*. Similarly, *B. fusca* is now rare in the rain forest of Nigeria, but is now predominant in Cameroun (N'Demah, 1991). This suggests that some geographic and ecological redistributions of borers, and perhaps of other pests, should be considered in any pest management program.

On a per tiller basis, higher numbers of stem borers were collected on maize than on grass species, suggesting that maize was the preferred host. Nevertheless, grasses are host to borers throughout the year; generally, the populations of *S. calamistis* and *E. saccharina* on the two host plants varied in opposite ways. The numbers of borers were higher on grass at the beginning of the trials, and dropped rapidly as the maize grew and the populations on maize started building up. This indicated that wild graminaceous plants act as reservoirs and alternative host-plants. Although they are not as suitable as maize for optimum development (Shanower *et al*, 1993), wild grasses were readily chosen for oviposition when appropriate maize stages were not available. Therefore, they were important sources for maintaining relatively high populations and perpetuating the pests.

The two stem borers attacked the same maize host-plant, but did so at different stages of its growth. *S. calamistis* was the most abundant species when the plants were young, generally around the tasseling period; the numbers of *E. saccharina* were high from silking to the maturity period of maize, when *S. calamistis* populations were declining. The temporal distribution of these stem borers during the developmental stages of maize was consistent with observations of Kaufmann (1983) and Bosque-Pérez and Mareck (1990). This suggested an oviposition preference for particular physiological stages of maize; *S. calamistis* seemed to favor young plants, and *E. saccharina* mature plants. Preference for a particular growth stage of maize may explain the difference in time of appearance of the two stem borers which may be related to the mobility and feeding habits of the larvae (Girling, 1978; Kaufmann, 1983), or could be triggered by some chemical cues

and physical characteristics of the plants (Root and Kareiva, 1984; Myers, 1985).

Adult flight activities were synchronized with the periods of egg collections, and the maximum numbers of larvae lagged about two weeks behind the adults' high activity periods. The sequence of appearance of developmental stages of borers observed in these trials indicated that maize fields were invaded by moths from sources outside the experimental fields, either from farmers' fields or from nearby grasses. However, from how far these adults were flying could not be determined.

Extremely low numbers of pupae were collected, compared with the numbers of eggs and larvae, indicating that a large number of the eggs did not reach the pupal stage. This suggested also that high field mortalities occurred at different levels of the life cycle. Parasitism, predation or diseases, and adverse weather conditions could all contribute to mortality. I observed several species of ants associated with immature stages of borers; their role in field mortality has been reported (Mohyuddin and Greathead, 1970; Girling, 1978). In the present trials, one *S. calamistis* egg parasite, *T. busseolae*, and one pupal parasite, *Pediobus furrus* Gahan (Hymenoptera: Eulophidae), were found. Several species of tachinids emerged from larvae of both stem borers. Although it was not quantified, the part played by these natural enemies in borer mortality may be important. Very high temperatures can desiccate the pests (Sampson and Kumar, 1983), particularly sluggish *S. calamistis* larvae; likewise, it is possible that heavy rains caused larval mortality as they washed away small larvae or inundated

them. Lack of appropriate food or feeding sites on the host plant (Sétamou *et al.*, 1993) could also have caused mortality.

Field observations during all three trials indicated that the numbers of stem borers varied with the seasons. More individuals were found in the rainy period of 1992 than in the two dry seasons of 1991 and 1992. Several reports exist, though few on *S. calamistis*, on seasonal variations of stem borer populations (Dang and Seshu-Reddy, 1983; Sampson and Kumar, 1983; Kfir and Bell, 1993). From these reports, it appears that borer populations are higher during dry than rainy seasons. My observations differed from these conclusions. This difference could be explained by the fact that the 92-1 planting took place in early July compared with April-May, which is the prevailing planting period. In July, borer populations had already built up on maize in earlier plantings. This result showed that, although weather factors may play some role (van Rensburg *et al.*, 1987a), variations in planting date had a considerable influence on population sizes. Thus, when studying borer populations, it is essential to correlate population size with planting time and with plant stages rather than with Julian dates. Such relationships were judiciously used by van Rensburg *et al.* (1987a) for *B. fusca*. My observations showed that *S. calamistis* and *E. saccharina* could breed year-round with several overlapping populations, provided suitable host-plants, notably maize, were available. The peak numbers merely reflected periods when appropriate maize plants were available.

The occurrence of adult populations in the fields, as determined by the size of catches, coincided with that of eggs collected on the host-plants by dissection. This indicated that light traps made from

kerosene lamps could be a relatively efficient tool for estimating seasonal variations of moth populations, although Bowden and Church (1973) advised that catches should be corrected to consider the eventual interference of other light sources. Similar lamps have been successfully used for mass-trapping of rice stem borers (WARDA, 1979) and for studying the populations of a variety of cob and stem borers, including *S. calamistis* and *E. saccharina* (Chiang, 1977; Dang and Seshu-Reddy, 1983). Kerosene lamps used as light traps have the advantage over other traps of being simple, easy to use and manipulate in remote areas. However, like conventional light traps, they are not specific. Therefore, their use requires trained entomologists to identify trap contents. Moreover, light trap catches are influenced by moonlight.

The present study showed clearly that catches of *S. calamistis* and *E. saccharina* moths were affected by the moon's cycle and by weather factors. Higher numbers of moths were caught during new moon than during full moon. Williams (1936) and Bowden (1973a,b; 1982) observed similar variations in several noctuids. The reduced catch at full moon is generally thought to be caused by diminished contrast between background and light emitted by traps, thus reducing the effective radius and attractiveness of the trap light (Williams and Singh, 1951; Bowden and Morris, 1975). But more than simply hampering visual attraction, variations in night darkness may also act as photoperiodic cues for some behavioural and physiological changes (Williams and Singh, 1951; Bowden, 1973a) that increased the moth's activities. Girling (1978) observed that mating and oviposition of *E. saccharina* occurred mainly in the first hours after sunset when light

intensities were low. Kiyomitsu *et al.* (1993) found that take-off behaviour of *Scotinophara coarctata* (Thunberg) (Heteroptera: Pentatomidae) was not simply induced by the full moon illumination, but in combination with insect mating status. It is therefore possible that full moonlight impeded, to some extent, mating, oviposition and, ultimately, the dispersal of moths.

Catch sizes were correlated with wind speed, temperature and relative humidity. Comeau *et al.* (1976) and Pitcairn *et al.* (1990) reached similar conclusions with several other lepidopterous insects. Daily maximum temperature was negatively correlated and showed the highest coefficients compared with other weather factors. Jönsson and Anderbrant (1993) found that air temperature has a positive effect on the flight activity of the European pine sawfly, *Neodiprion sertifer* (Geoffroy) (Hymenoptera: Diprionidae). High daily temperatures may have created unfavorable habitats that forced the moths to move to better environments. As a result, fewer individuals remained in the trial fields and thus fewer moths were caught. Minimum temperature had no influence on moth activity. The reason for this was that the minimum temperature occurred early in the morning, around 05:00h, whereas stem borers are more active in the early hours of the night than during the late hours (Dang and Seshu-Reddy, 1983).

Wind velocity showed a significant positive correlation with catches. The reason for the positive relationship between wind and catches could be that higher wind speed agitated the host plants, disturbing moths at rest which had to fly in search of quieter areas. Nevertheless, it is likely that this relationship is true only within a certain range of wind speeds. Above this range, flight could be

physically prevented (Nakamura, 1976 Pitcairn *et al.*, 1990). Since invading moths flew from adjacent fields, it is also possible that wind velocity increased the diffusion of plant chemical cues that may attract borers to maize.

Relative humidity was also positively related to moth catches, suggesting that it favoured flight activity. Flight activities of *B. fusca* (van Rensburg *et al.*, 1987a) and *M. separatella* (WARDA, 1979) also increase with relative humidity. In contrast to temperature, humidity prolongs moth survival (van Rensburg *et al.*, 1987a). A longer life span may have increased the population density of *S. calamistis* and *E. saccharina*, and therefore have increased the number of moths trapped.

Chapter IV

WITHIN-PLANT DISTRIBUTION OF *SESAMIA CALAMISTIS* AND *ELDANA SACCHARINA* ON MAIZE AND WILD SORGHUM

4.1 Introduction

An important principle of pest management requires that insect pest populations be accurately known in order to intervene effectively at the appropriate time. Thus, correct knowledge of the spatial and temporal distribution of pests on different parts of their host plants is essential. This assumes that all developmental stages of the pests can be efficiently monitored. Maize stem borer females usually lay their eggs in the hidden parts of their host plants (Girling, 1978; Atkinson, 1980; Kaufmann, 1983; Van Rensburg *et al.*, 1987b). The immature stages, i.e. eggs, larvae and pupae, generally live and develop between leaf sheaths and plant stems, inside the stem, or sometimes in the cobs. As a result, their presence is difficult to detect for a reliable estimation of the degree of infestation, except when external damage symptoms such as deadheart, lodging, and frass (Girling, 1978; Bosque-Pérez and Mareck, 1990) are visible. At that point, irreversible damage may have already been caused and it is generally too late to intervene for efficient control. Larval movements inside the host plant can be variable with complex dispersal patterns. Berger (1992) found four phases occurring during the larval dispersal of *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae). Generally, stem borers are highly aggregated at the beginning of their life cycle, but aggregation

becomes less pronounced as the larvae mature (Davis and Pedigo, 1989; Shelton *et al.*, 1986). Therefore, for evaluating pest densities, plants have to be dissected, which demands destructive sampling of whole plants. For species with aggregated between-plant distribution, many plants per field have to be destroyed to estimate pest densities accurately, which may not be economically and ecologically tolerable. There is a need for reliable and fairly simple sampling procedures. Schulthess *et al.* (1991) have described the spatial distribution of five stem borer species on maize, using the combined data from a 5-year sampling period across several ecological zones. However, dispersal is presumably an adaptive behaviour to enhance the survival rate in harsh conditions. Thus, the distribution of immature stages may depend on factors such as environmental and climatic conditions, seasons, and host plant species.

The objectives of this chapter are 1) to determine the abundance and the spatial distribution patterns of the immature stages of *S. calamistis* and *E. saccharina* in two of their common host plants, maize and wild sorghum; and 2) to investigate the possibility of using parts of plants, rather than entire plants, as sampling units. In addition, based on the spatial distribution, an enumerative sampling model will be developed to predict the proportion of infested plants, and to suggest the optimal numbers of sampling units needed for the accurate estimation of borer densities.

4.2 Materials and methods

4.21 Data collection

The experiments were carried out on the experimental farm of I.I.T.A-Cotonou, Bénin, between July 1992 and January 1993. I planted maize and sorghum as described in section 3.2. For sampling, I subdivided the plants into different sampling units. For maize the sampling units were as follows (Figure 4.1): part 1 (P1) was the portion of plant below the ear; part 2 (P2), the section between ear and tassel; and part 3 (P3), from the uppermost leaf to the tassel, and ear. For wild sorghum, I subdivided each tiller into main stem and lateral shoots (Figure 4.2). I also subdivided each tiller into half-lower and half-upper levels. I selected at random 20 maize plants and 60 sorghum tillers every week. Plants and tillers were cut off at soil level and dissected to record the numbers of eggs, larvae, and pupae found in each sampling unit. All damaged plants, even if no insects were found, were considered to be infested.

4.22 Data analysis

Spatial distribution

I calculated the mean numbers and the percentages, summing the total number of eggs, larvae, and pupae recorded in each sampling unit. I used a One-way ANOVA to compare mean numbers and percentages between developmental stages and between plant levels. If the ANOVA showed significant heterogeneity, I applied Fisher's LSD test to separate means. On maize, I compared the numbers between the four sampling units. On wild sorghum, I compared the numbers in the main stems and those in the lateral shoots; I also compared the

Figure 4.1 A developed maize plant can be subdivided into four parts: below ear (P1), between ear and tassel (P2), from uppermost leaf to end of tassel (P3), and ear.

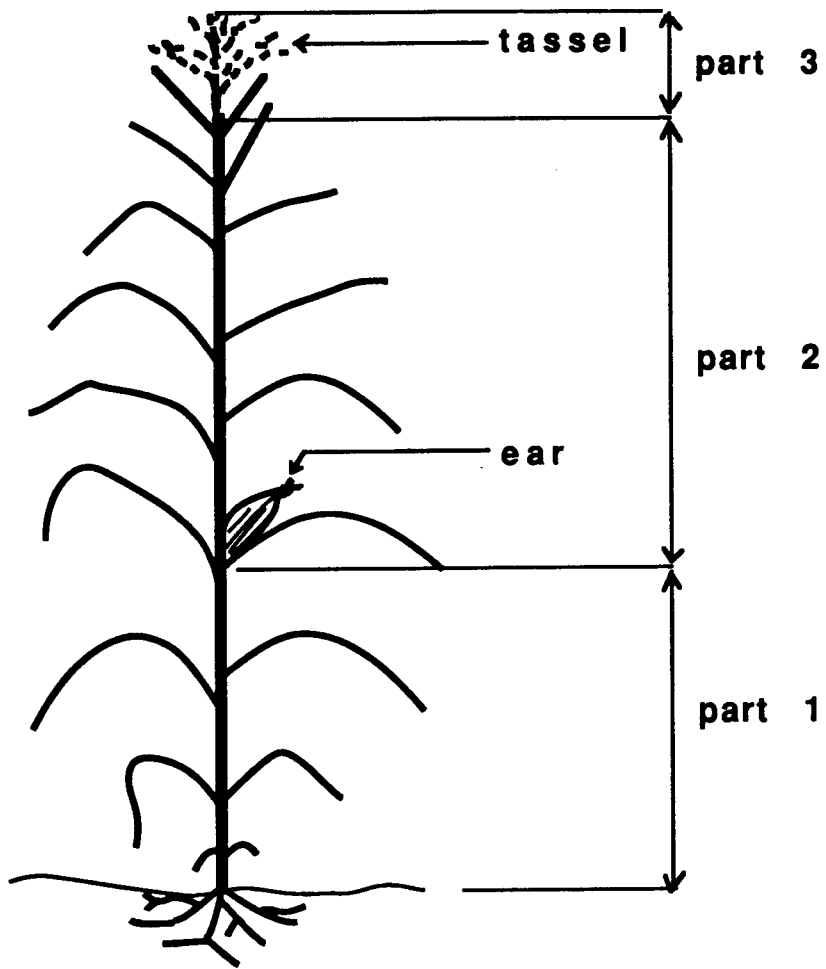
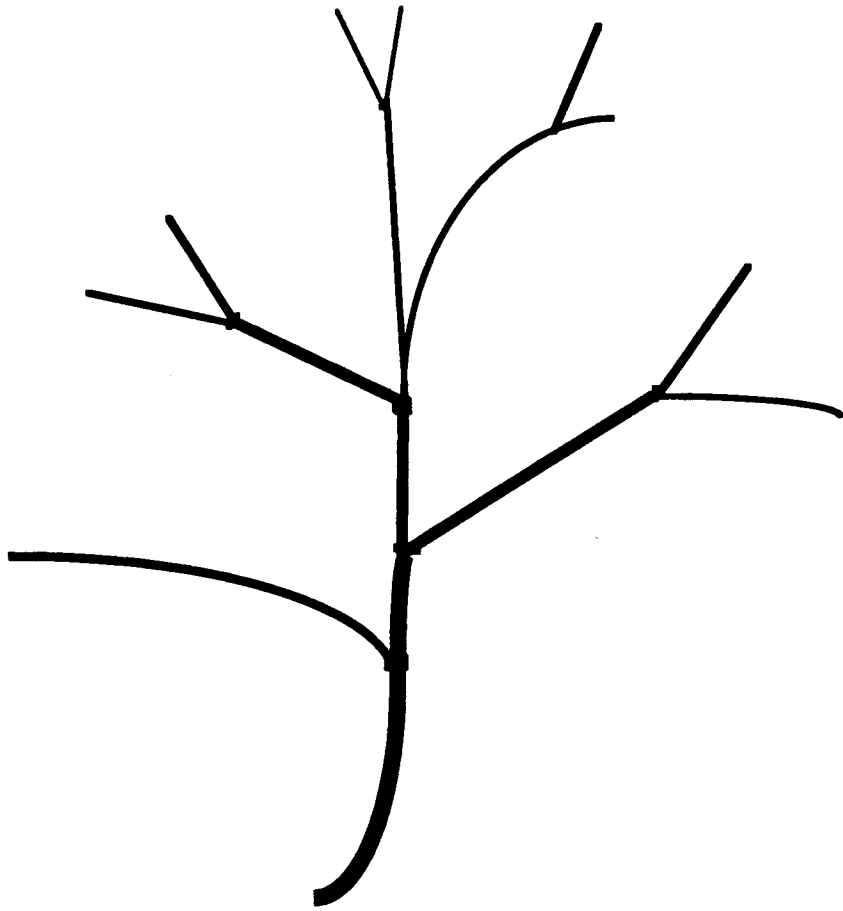


Figure 4.2 Schematic mapping of a developed wild sorghum tiller showing main stem and lateral shoots.



numbers between upper and lower levels of the tiller. All means are shown with their standard errors.

I applied Taylor's power law to investigate the within-plant dispersion of the stem borers. Dispersion is evaluated by the relationship between the variance and the mean density of borer larvae counted in the field. Taylor (1961) described this relationship by the function

$$s^2 = a.m^b$$

where s^2 is the sample variance, m is the sample mean, and the coefficients a and b are fitted values. Taylor's coefficient b is a measure of dispersion of a species: $b > 1$, $b = 1$, and $b < 1$ indicate aggregated, random, and regular distributions, respectively, whereas coefficient a is a sampling factor. The standard method to estimate a and b is to use a linear regression of the natural logarithm of the variance [$\text{Log}(s^2)$] against the natural logarithm of the mean density [$\text{Log}(m)$] (Southwood, 1980). I estimated coefficients a and b from the numbers of larvae collected on maize and wild sorghum, and I compared differences between coefficients using a SNK test. Wilson and Room (1983) used Taylor's power law in a model to describe the relationship between the proportion of infested plants [$P(I)$] and the mean density (m)

$$P(I) = 1 - \text{Exp}[-m \text{Ln}(am^{b-1}) / (am^{b-1} - 1)]$$

where a and b are Taylor's coefficients. Wilson (1982) explained that a and b are necessary to describe dispersion of a species: the more aggregated a species, the smaller the $P(I)$ for a given mean.

Developing sampling plans

Wilson and Room (1983) incorporated Taylor's power law into enumerative and binomial sampling procedures. In the enumerative sampling procedure, the variance s^2 was replaced in Karandinos' (1976) function with $a.m^b$, resulting in the following equation

$$N = (Z_{\alpha/2}/D)^2 a.m^{b-2}$$

in which N is the number of samples to be taken, D is the reliability level expressed as a proportion of the mean and $Z_{\alpha/2}$ is the standard normal deviate (generally fixed at 1.65 for $n > 100$ and a confidence coefficient of 0.9).

4.3 Results

4.31 Within-plant distribution of borers

S. calamistis.

On maize plants, I collected most of the *S. calamistis* eggs (79%) on P1, generally between 20 cm above the ground and the first cob. On P2, I collected 18% and only 3% (47 eggs) of the total number of eggs on P3 (Table 4.1). This proportion of eggs on P3 was found 50 days after planting (DAP). ANOVA showed a significant difference between the mean numbers collected on the three parts ($F = 10.610$; $df = 2,560$; $P = 0.0001$). Except at 50 DAP, when relatively more eggs were collected on P3 than on P2, the order

$$\text{eggs on P1} > \text{eggs on P2} > \text{eggs on P3}$$

was consistently observed on each sampling date. I did not collect any *S. calamistis* eggs in ears.

Larvae had a different distribution pattern in maize plants. The mean numbers of larvae were 1.44 ± 0.25 , 1.76 ± 0.35 and 2.49 ± 0.34 in P1, P2 and ears, respectively. The mean numbers of larvae in P1 and P2 did not significantly differ, but both were significantly lower than those found in the ears. In P3, I collected 11% of the larvae (0.67 ± 0.19), which was significantly lower than in the other parts of the plant. The numbers of pupae collected on maize plants during the experiment were low. The majority of the pupae (84%) were located in the ears.

Figure 4.2 shows the numbers of stem borers collected over time on different parts of maize plants. The relative proportions varied greatly. Up to 43 DAP, most *S. calamistis* larvae were encountered in P1. Between 50 and 60 DAP, P2 had the highest numbers of larvae; at approximately the same period, larvae started appearing in the ears and, from 50 DAP, most of them were in the ears. P3 reached its highest numbers around 50 DAP.

On wild sorghum, the mean number of eggs collected in lateral branches was not statistically different from that in main stems. The mean number of *S. calamistis* larvae collected in the lateral branches was significantly higher than that found in the main stem (Two-Sample t-test, $t = 4.05$; $df = 1,594$; $P = 0.0001$). This was observed on almost all sampling dates (Figure 4.3). However, when numbers of all developmental stages were pooled, no significant difference was found between main stems and lateral shoots, although relatively more individuals were collected on lateral shoots. Likewise, there was no significant difference between mean numbers of eggs and larvae collected at upper and lower levels.

Table 4.1 Mean numbers (m±SEM)* and percentages (%) of *S. calamistis* and *E. saccharina* collected on different parts of maize plants.

		A N O V A					
		P1	P2	P3	Ear	F	P
		(n=199)	(n=180)	(n=184)	(n=164)		
<i>S. calamistis</i>	Eggs m	6.58±1.53a	1.72±0.73b	0.26±0.26b	0b	11.531	0.0001
	%	78.6	18.6	2.8	0		
	Larvae m	1.44±0.25a	1.76±0.35a	0.67±0.19ab	2.49±.34c	6.690	0.039
	%	25.3	27.9	10.8	36.0		
	Pupae m	0.03±0.01a	0.01±0.01a	0a	0.22±0.05b	21.082	0.0001
	%	11.6	4.7	0	83.7		
<i>E. saccharina</i> **							
Larvae m	1.43±0.16a	1.65±0.16a	0.45±0.1b	1.16±15a	12.870	0.0001	
%	33.3	34.7	9.7	22.2			
Pupae m	0.07±0.02a	0.15±0.04a	0.01±0.01a	1.20±.15b	58.160	0.0001	
%	5.4	11.3	0.9	82.4			

* Means within rows sharing the same letter(s) are not significantly different at 0.05 level (ANOVA followed by Fischer's LSD test; df= 3,723). **: *E. saccharina* eggs were not included because only one egg mass was collected.

E. saccharina

In maize, no *E. saccharina* eggs were found. There was no significant difference between the mean numbers of *E. saccharina* larvae collected on P1, P2, and ear, but these numbers were significantly higher than the number in P3 (Table 4.1) (ANOVA: $F = 18.731$; $df = 2,560$; $P = 0.0001$). The same pattern of distribution was observed on all sampling dates and also when larvae and pupae were evaluated separately. Of the total number of *E. saccharina* collected during the trial, larvae accounted for about 95%. The remaining 5% were pupae, found mainly in the ear. The variations in the relative proportions of larvae and pupae in the four sampling units of maize are shown in Figure 4.2b. From the early stage of the plant until about 50 DAP, *E. saccharina* were collected only in P1. The mean numbers in P2 increased rapidly and from 64 DAP, it had the highest population until the end of the test period, whereas the mean numbers on P1 were relatively constant. The numbers in the cob remained lower than in P1 and P2. Few *E. saccharina* were found in P3.

The distribution of *E. saccharina* in wild sorghum did not appear to favor any particular part of the tiller (Figure 4.3b). The numbers of larvae and pupae collected in the main stems and those collected in the lateral shoots were not significantly different. However, the subdivision of sorghum tillers into upper and lower levels showed that significantly more *E. saccharina* were located in the lower than in the upper level (Lower level: 0.32 ± 0.03 ; Upper level: 0.21 ± 0.04) (ANOVA: $F = 5.639$; $df = 1,1066$; $P = 0.018$).

Figure 4.3 Numbers of larvae of *S. calamistis* (a) and *E. saccharina* (b) collected on various parts of maize plant. Columns show the mean numbers per plant.

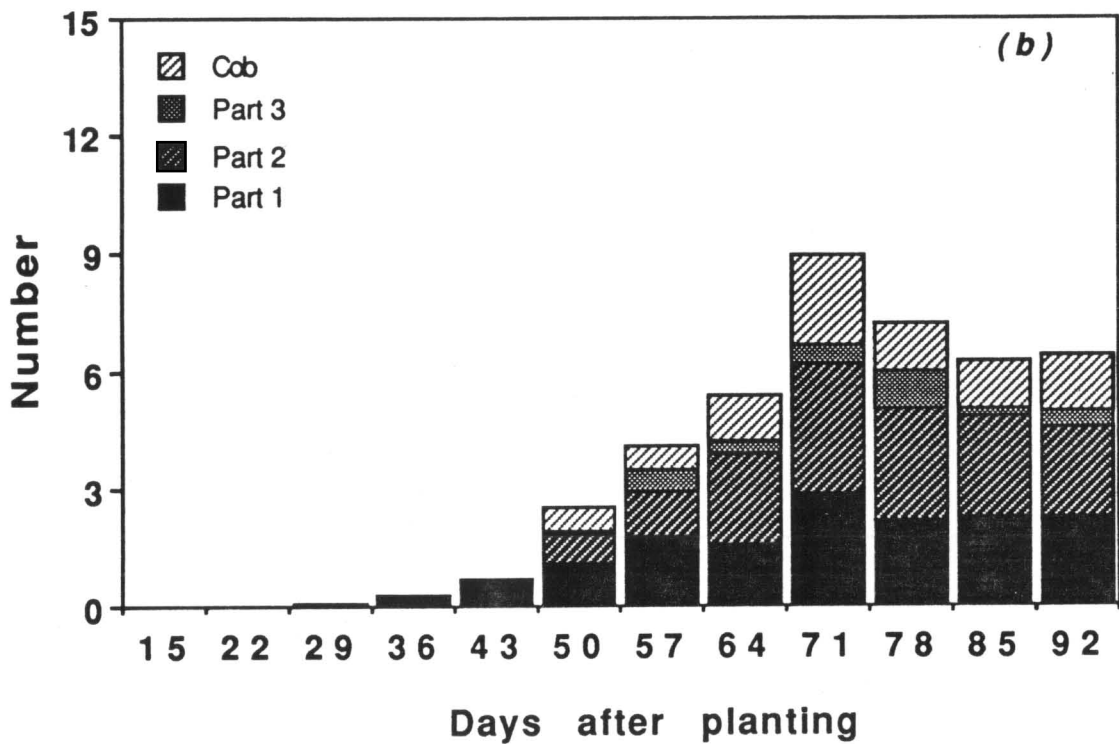
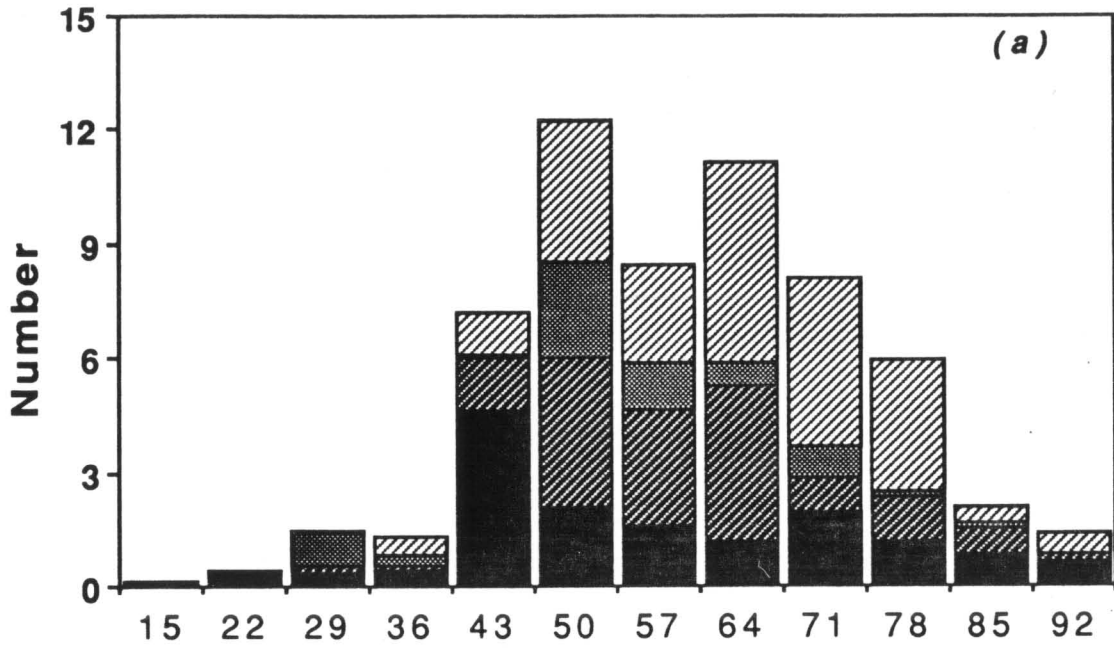
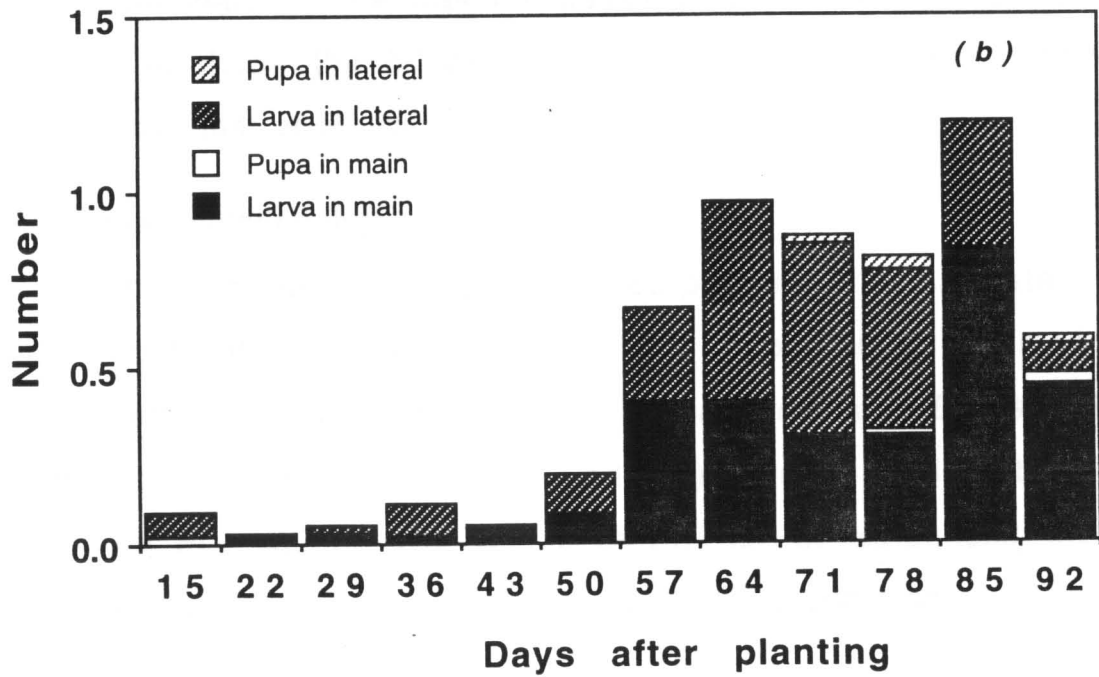
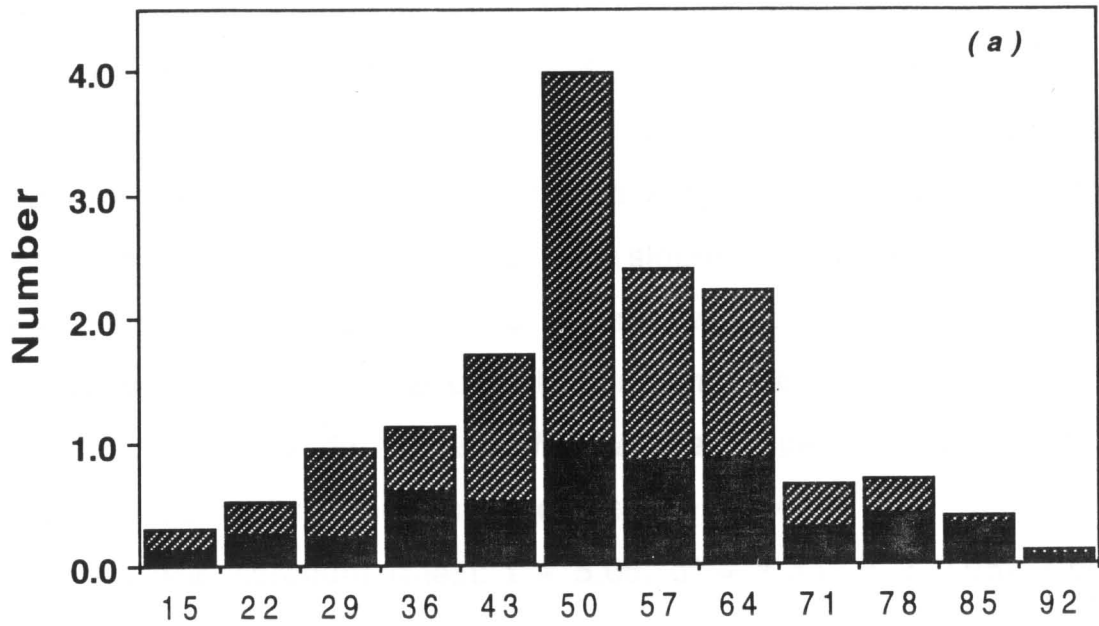


Figure 4.4 Numbers of larvae and pupae of *S. calamistis* (a) and *E. saccharina* (b) collected on various parts of sorghum tillers. Columns show the mean numbers of larvae and pupae per plant.



4.32 Spatial dispersion

The power law satisfactorily described the relationship between the log-transformed and observed means of larvae and the corresponding variance. This relationship was valid for both borer species on both host plants, with r^2 values ≥ 0.90 (Figures 4.5 and 4.6). The results of Taylor's power law analysis for *S. calamistis* and *E. saccharina* on maize plants and wild sorghum tillers are summarized in Table 4.2. On both hosts, Taylor's slopes (coefficient b) were higher than 1.0 for *S. calamistis* and *E. saccharina*. For *S. calamistis*, b on maize was higher than b on wild sorghum (t-test: $t = 5.67$; $df = 1,69$; $P < 0.05$). Similarly, for *E. saccharina* the dispersion coefficient varied with the host plant species, whereas coefficient b was higher on maize than on wild sorghum (t-test: $t = 5.66$; $df = 1,36$; $P < 0.05$). Coefficient b on sorghum was not significantly different from 1.0. For the two borers on maize, there was no statistical difference between b values; but on sorghum, the b coefficient of *S. calamistis* was significantly higher than that of *E. saccharina*.

P(I) mean relationship

The functional relationship (incorporating the estimated values of a and b of Table 4.2) between the proportion of infested maize plants and the density of larvae for *S. calamistis* and *E. saccharina* is shown in Figure 4.7. The modeled P(I) values fitted quite well the observed P(I) values. The values of P(I) for *S. calamistis* increased with the means more slowly than those of *E. saccharina*.

Table 4.2 Taylor's power law analysis: regression of log(variance) on log(mean) for larvae of *S. calamistis* and *E. saccharina* on maize plants and wild sorghum tillers from July to October 1992.

	a	b(±SE)	r ²	n	F	P
<i>S. calamistis</i> on maize	3.975	1.63±0.06c*	0.90	91	772.9	0.0001
" on sorghum	2.270	1.29±0.05d	0.91	70	681.2	0.0001
<i>E. saccharina</i> on maize	6.110	1.64±0.08c	0.91	46	446.3	0.0001
" on sorghum	1.600	1.10±0.04e	0.95	37	668.8	0.0001

* Values of slope (b) with the same letter(s) within columns are not significantly different at 0.05 level (SNK multiple range test).

Figure 4.5 Spatial distribution of *S. calamistis* and *E. saccharina* on maize between July 1992 and January 1993, at IITA-Cotonou, according to Taylor's power law. The log-transformed of observed means of larvae are plotted against the corresponding variance.

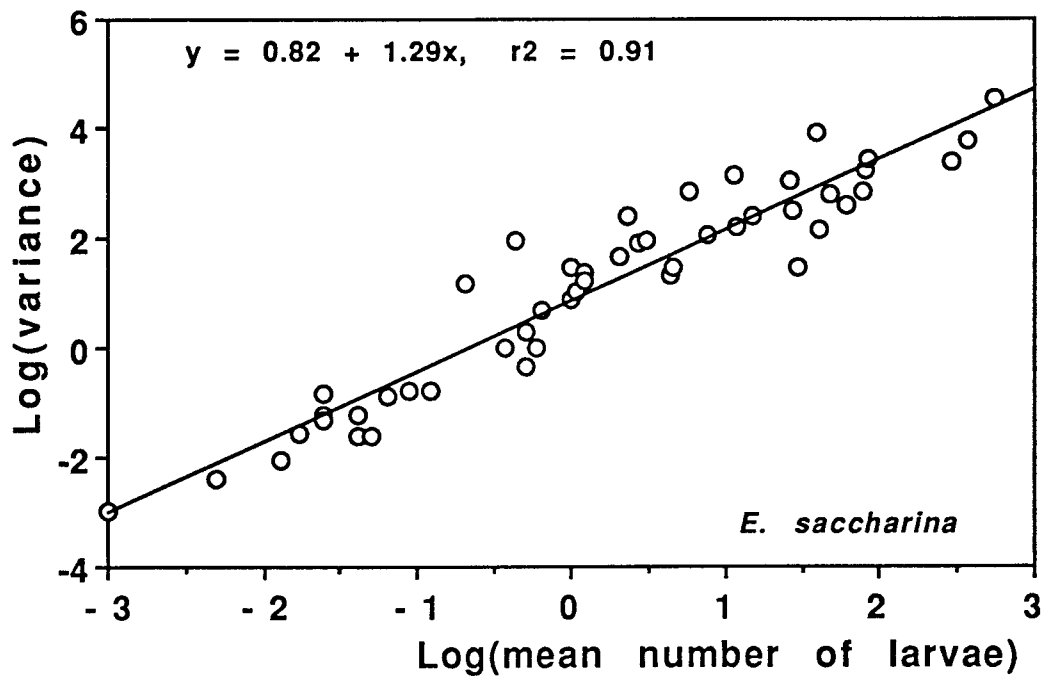
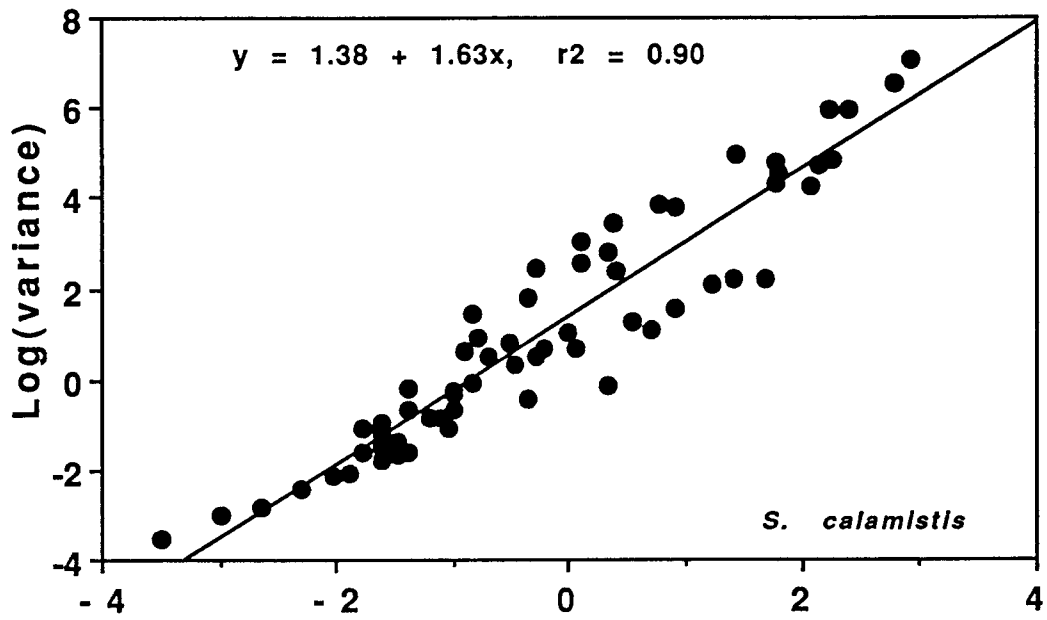


Figure 4.6 Spatial distribution of *S. calamistis* and *E. saccharina* on wild sorghum between July 1992 and January 1993, at IITA-Cotonou, according to Taylor's power law. The log-transformed of observed means of larvae are plotted against the corresponding variance.

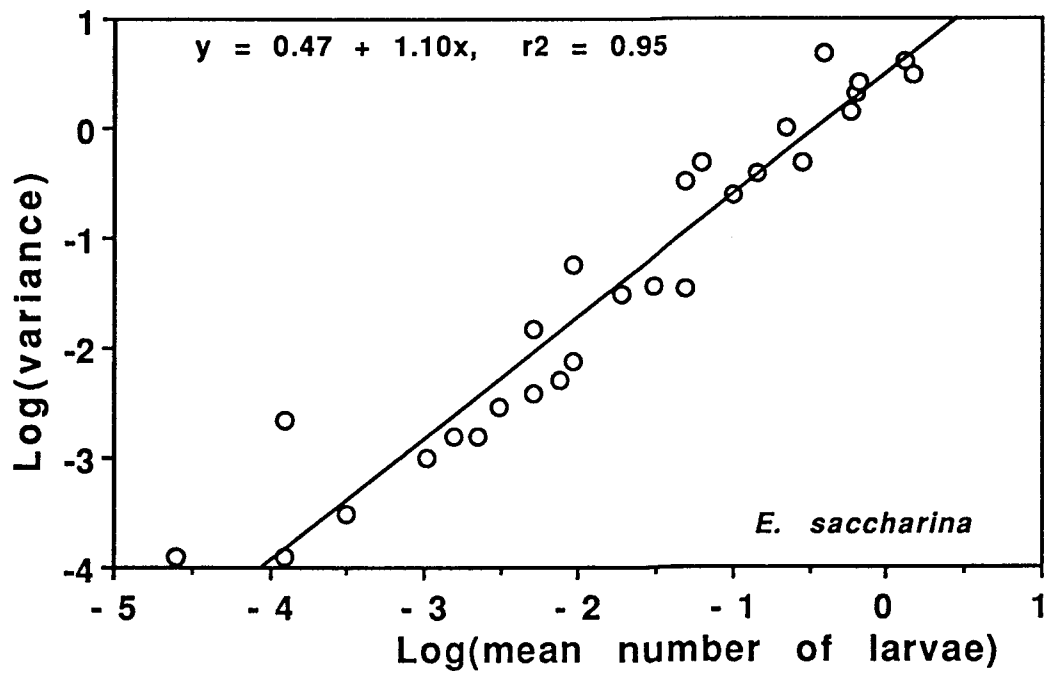
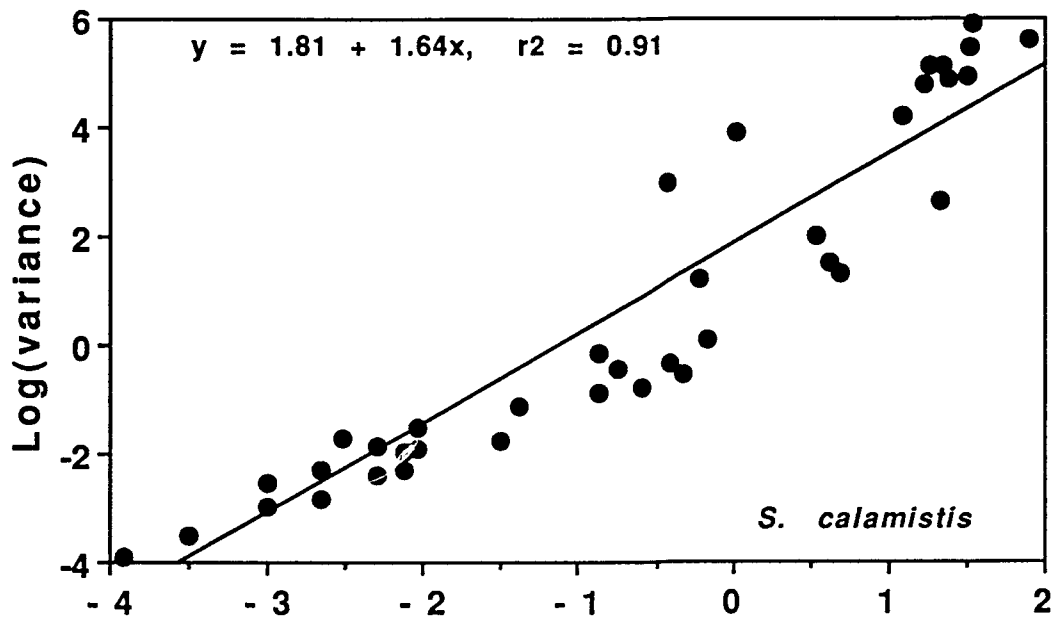


Figure 4.7 The observed proportion of infested maize plants as a function of field density of *S. calamistis* (a) and *E. saccharina* (b).

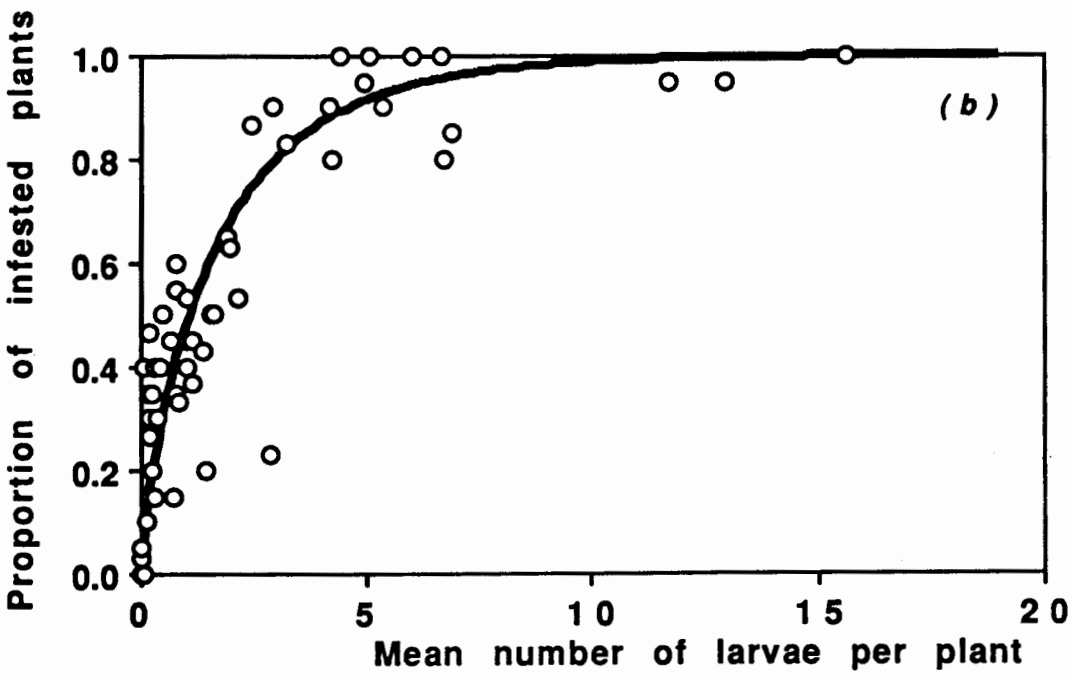
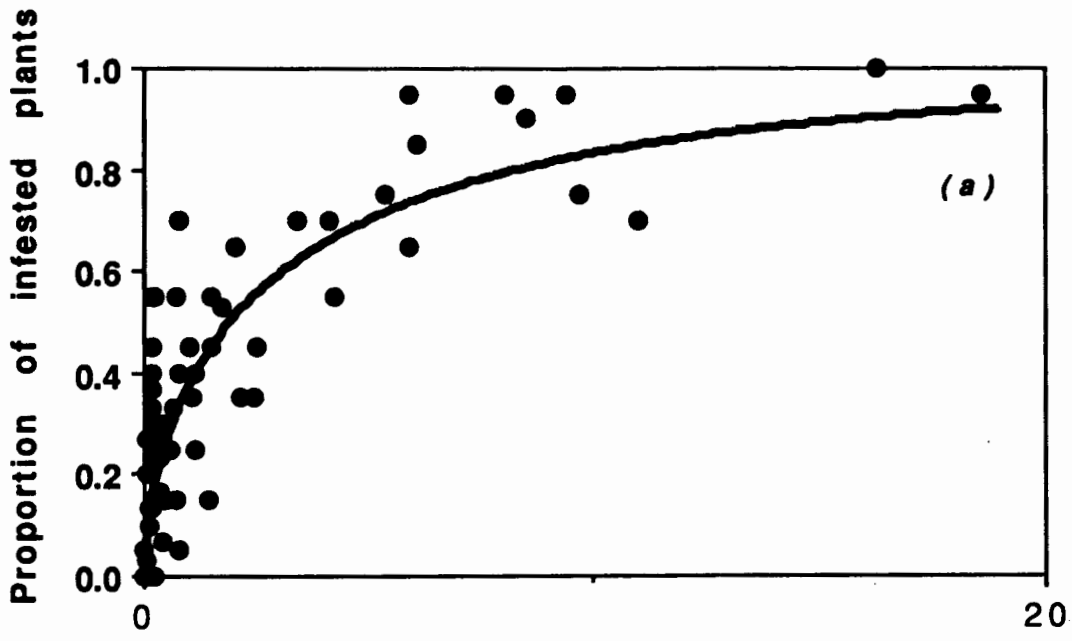
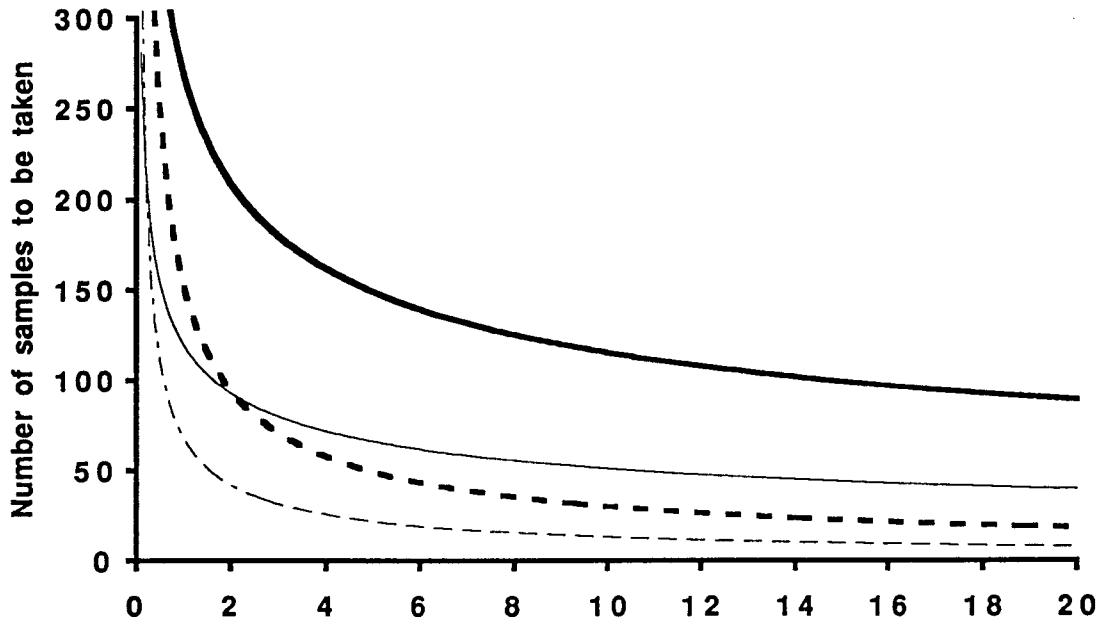
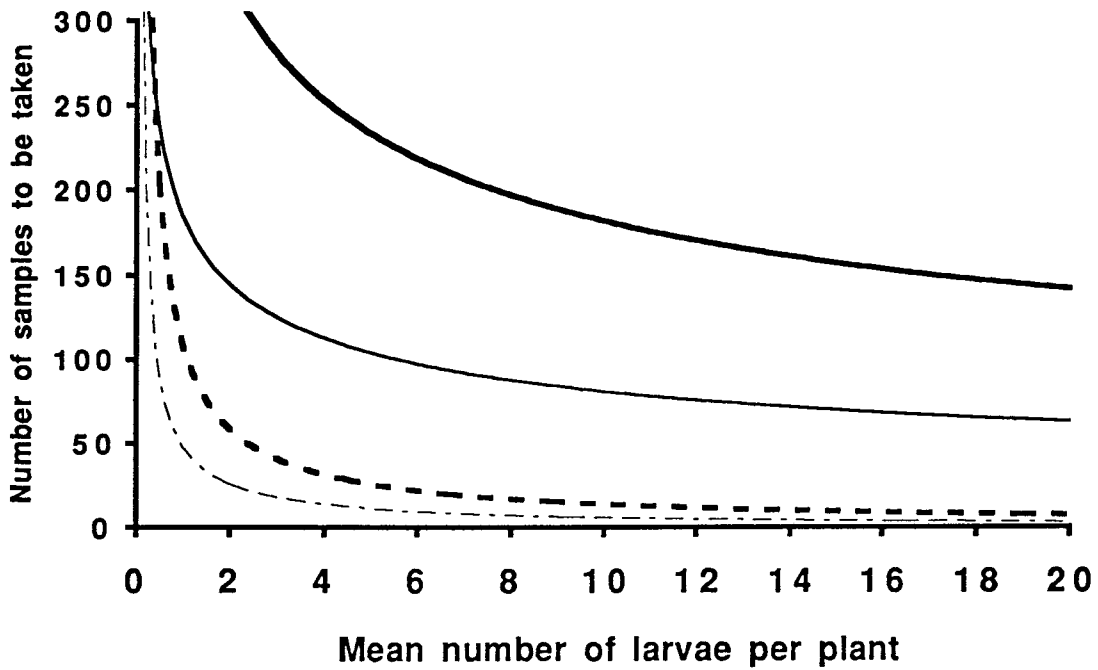


Figure 4.8 Optimal number of samples to be taken to estimate mean densities of *S. calamistis* and *E. saccharina* on maize (solid lines) and wild sorghum (broken lines) using enumerative sampling procedures. Two confidence levels are used (D=0.3: thin lines; D=0.2: thick lines).

S. calamistis



E. saccharina



Mean number of larvae per plant

Sampling plans

Curves predicting the optimal enumerative sampling size for larvae of both stem borers are shown in Figure 4.7. Two confidence levels ($D=0.2$ and $D=0.3$) were considered for different levels of accuracy. At densities of less than 6 larvae/plant, the optimal sample sizes to be taken on maize were always larger than on sorghum, at both confidence levels. At very low larval densities (< 2 larvae/plant), extremely large sample sizes are needed to obtain reliable estimates.

4.4 Discussion

Most *S. calamistis* eggs collected were located on the lower part of maize plants, fewer on parts 2 and 3, and none in the ear. This showed that P1 was the preferred site for oviposition; the ear was the least preferred. The fact that cobs appeared in the field at a later period than did the other parts of the plant could not explain this distribution pattern, since many eggs were collected in P1 as late as 63 DAP, when cobs were already formed (40 DAP). Little published information is available on the within-host distribution of immature stages of *S. calamistis* and *E. saccharina*. In other maize lepidopteran pests, however, the spatial distribution of eggs, larvae, and pupae is well documented. The European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), oviposits preferentially on leaves (Shelton *et al.*, 1986) and more specifically on the leaves below the ear (Sorenson *et al.*, 1993). My results were similar to those of Sorenson *et al.* (1993) and revealed that *S. calamistis* preferred the part below the ear for oviposition. This distribution pattern of eggs could be explained by the structure of the leaf sheaths, which are the most common material

used for oviposition by *S. calamistis* (Kaufmann, 1983). Sheaths located on the upper parts of maize plants and on ear husks are rough and generally hairy. This was possibly a factor for unattractiveness to *S. calamistis* which oviposits mainly on smooth and hairless surfaces (Bosque-Pérez and Dabrowski, 1989). Oviposition preference may also be related to the tightness of the leaf sheaths; sheaths around the stem become loose with age. It is possible that female *S. calamistis* were more successful at inserting their ovipositors through the loose sheaths, and thus laid more eggs in the lower, and older, parts.

Female *S. calamistis* may choose to oviposit in the lower parts of the plant to protect the eggs against severe weather conditions, such as direct sun, which could desiccate the eggs, or heavy rains which could wash them off the plants. It is also possible that some plant cues are responsible for this selective oviposition.

On wild sorghum, no favoured oviposition site was observed either between main and lateral stems or between lower and upper parts of the tiller. The reason for this may be that growth in sorghum is less determined.

The fact that no difference was found between the mean numbers of larvae on P1 and P2 indicated that larvae of *S. calamistis* were more evenly distributed on the maize plant than were eggs. This suggested an active, upward migration of larvae. Upward migration of larvae explained the fact that, although no eggs were found in cobs, high numbers of larvae were collected in cobs as early as 40 DAP; it also explained the differences in larval numbers in different parts of the plant over time. Although no *E. saccharina* eggs were found, the distribution of larvae, and the variations in the mean numbers over

time, indicated that larvae of this species had a similar upward migration. The same larval movements occur with larvae of the pyralid, *C. partellus* (Berger, 1992). The reason for the vertical dispersion of *S. calamistis* and *E. saccharina* can be attributed to a search for food resources and better environments for development. Larvae of both borers hatch from eggs laid generally in batches (Girling, 1978; Atkinson, 1980; Kaufmann, 1983). At emergence, larvae live in high density areas. But as the larvae grow, their nutritional needs increase whereas food becomes limited. With time, the quality of food may deteriorate as the plant matures, and crowding may increase with larval growth. Thus, migration becomes necessary to improve larval survival.

The mean number of larvae found in the cobs was the highest compared with other parts, and more pupae were collected in the cobs than in the stems. These observations suggest that the ear was the most suitable site for larval growth and development, suggesting that in practice ears could be incorporated in or even replace, to some extent, the rather expensive artificial rearing diet (Bosque-Pérez and Dabrowski, 1989).

Active upward movements of larvae occurred also on wild sorghum for the same reasons of food seeking and avoidance of overcrowding. But unlike maize, larvae in sorghum seemed to migrate preferentially to lateral branches where food was more available and fresher than in the main stem.

The pattern of distribution of *S. calamistis* eggs and larvae on the maize plant is important for practical sampling and population prediction. Because the bulk of oviposition occurred on the lower part

of the plant, dissecting the whole plant is not required; examination of the part below the primary ear may be sufficient. More importantly, it appeared that a thorough scrutiny of the leaf sheaths around this part of the plant should give a reliable estimate of the numbers of eggs without plant destruction and dissection. Larvae were naturally more dispersed than eggs and the degree of dispersion increased with time; sampling units must vary consequently. Until approximately 40 DAP, the lower part of the maize plant should give an adequate estimation of *S. calamistis* larval populations. Any sampling after 40 DAP should consider the ear as the main sampling unit. For estimating *E. saccharina* larvae, the same sampling units should be considered, but 10 days to two weeks later.

The results of fitting the data to Taylor's power law indicated that larvae of the two borers were aggregated. However, the extent of aggregation varied with both borer and host plant species. According to Taylor (1961), the degree of aggregation increases with an increase in the magnitude of b , which was larger in *S. calamistis* on maize than on wild sorghum, a finding that confirmed the results from dissection that this borer was more aggregated on maize than on sorghum. Likewise, *E. saccharina* was more aggregated on maize than on sorghum. The difference in aggregation between the two host plants may be explained, irrespective of the random distribution of eggs on sorghum, by an early dispersal of larvae on sorghum. Because sorghum tillers were smaller than maize stems, they contained less food despite the continuous growth of new tillers. In addition, on sorghum the more suitable and acceptable parts are more dispersed than on maize. This study indicated that *S. calamistis* and *E. saccharina* were

equally dispersed on maize. The indices of dispersion found were within the range of those found by Schulthess *et al.* (1991). However, these workers found that *S. calamistis* was more aggregated than *E. saccharina* on maize. The difference between these results and mine may arise from the fact that in their study, Schulthess *et al.* (1991) used data across different ecological zones and over several years and seasons. Since climatic conditions vary between years and ecological zones, it is possible that these variations influenced larval dispersion.

On wild sorghum, I found *E. saccharina* to be less aggregated than *S. calamistis*, presumably because of the high mobility of *E. saccharina* larvae. This borer oviposits on a wide range of materials including plant debris on the soil (Girling, 1978; Atkinson, 1980; Kaufmann, 1983). After hatching, the larvae migrate to adjacent plants. This may partly account for its low aggregation.

Field sampling often shows *S. calamistis* and *E. saccharina* on the same plant, but generally they occupy different parts. Thus, whole plants are recommended as sampling units. The modeled $P(I)$ satisfactorily described the proportions of infested maize plants. This indicated a strong relationship between the proportion of infested plants and the mean number of larvae. Therefore, with this relationship, a non-destructive sampling could be used for estimating the mean numbers of larvae. For the two species studied, Shanower *et al.* (1991) recommended that 40 plants be taken at random to estimate the proportion of infested plants, and Schulthess *et al.* (1991) proposed a binomial procedure. Generally, stem borer larval densities are low in the fields, between 0 and 6 larvae per plant. Using enumerative samplings at these low densities requires that very high numbers of

plants be taken to obtain a reliable estimate. Dissecting great numbers of plants is not economically feasible for field evaluation; it is an exhausting and time-consuming task which demands a high number of field workers. Using parts of the plant, instead of whole plants, could be more cost-effective. In the same way, the relationship P(I)-density could be used. In this case, the proportion of infested plants could be determined using the binomial presence-absence procedure proposed by Schulthess *et al.* (1991).

Chapter V

INFLUENCE OF HOST-PLANT SPECIES AND PHENOLOGY ON OVIPOSITION PATTERNS OF *SESAMIA CALAMISTIS* AND *TELENOMUS BUSSEOLAE*

5.1 Introduction

Choice of oviposition site by phytophagous insects can determine survival and fitness. For several insect species, the resources and protection available on the host plant at the time of oviposition greatly influence the growth, development, and survival of the immature stages (Courtney, 1981; Rausher, 1981; Singer *et al.*, 1988; Bernays and Barbehenn, 1987). The effects of food availability and quality on insect development and survival are well known (Leather *et al.*, 1983; Traynier, 1983; Grüber and Dixon, 1988; Kouamé and Mackauer, 1992; Shanower *et al.*, 1993). For stem borers especially, a suitable host plant is vital since young larvae are often incapable of dispersing rapidly (Berger, 1992; Ampofo and Kidiavai, 1987; Kaufmann, 1983; Girling, 1978) in search of food. In addition, because they live mostly inside a plant stem, their diet consists exclusively of the tissues of a single plant; thus, stem borer larvae are very much affected by changes in host plant physiology (Sétamou *et al.*, 1993). Ovipositional selectivity of female maize stem borers has often been observed indirectly in field studies (Endrody-Younga, 1968; Usua, 1968b; Girling, 1978; Mitchell, *et al.*, 1984; Cochereau, 1985). Bosque-Pérez and Mareck (1990) found that maize infestations by *S. calamistis* occurred when the plants were in an early developmental stage,

whereas other borers such as *E. saccharina* appeared in the field towards the end of the maize growing season. Kaufmann (1983) reported that the population size of *S. calamistis* was regulated by the age of maize and the time of year; he observed that infestations by *S. calamistis* began when the plants were about 30 cm tall, and the peak population of larvae was reached when the plants were 60 cm high. Plant dissection and light trap data reported earlier in Chapter III, showed more *S. calamistis* in younger than older maize plants, and more in maize than in grass. This information suggested that female *S. calamistis* have a preference for laying their eggs on particular types of host plants.

From region-wide surveys of maize fields, it has been reported that *Telenomus busseolae* (Hymenoptera: Scelionidae) is widely distributed in West Africa (Shanower *et al.*, 1991; Gounou *et al.*, 1994). High numbers of parasitized *S. calamistis* eggs have been recorded (Chabi-Olaye, 1992; Sétamou and Schulthess, 1995). These parasites may therefore be potential candidates for the biological control of *S. calamistis* in Africa. In parasitic wasps, host searching and finding ability are often cited as important attributes of successful biological control agents (Messenger, 1976; Huffaker, *et al.*, 1976). Female *S. calamistis* lay their eggs between leaf sheaths and plant stems (Kaufmann, 1983) and on various host plants (Usua, 1968b; Kaufmann, 1983). Considerable information has been accumulated on the searching behaviour of several egg parasites (Altieri *et al.*, 1982; Nordlund *et al.*, 1983, 1987). However, little information is available at present on the searching behaviour of *T. busseolae*, and particularly on its interaction with the host plants of *S. calamistis*.

In this chapter, I test the hypothesis that *S. calamistis* and *T. busseolae* prefer to oviposit on particular physiological stages of maize, and on maize rather than on wild sorghum and feathery pennisetum. The searching behaviour of the parasite is discussed in terms of its relationship with the host plants of *S. calamistis*.

5.2 Materials and methods

5.21 Rearing of *S. calamistis* and *T. busseolae*

S. calamistis was reared according to the method described by Bosque-Pérez and Dabrowsky (1989). A culture of *T. busseolae* was started in the laboratory from individuals that emerged from *S. calamistis* eggs collected during field surveys in Bénin in 1990. At regular intervals, I introduced into the colony adults emerging from parasitized eggs newly collected in the field. To produce parasites, I confined several females in transparent plastic vials with large numbers of *S. calamistis* eggs. After 24 h, I removed the parasites and kept the eggs in vials at room temperature at about $30\pm 2^{\circ}\text{C}$. I observed these eggs every day for parasite emergence and transferred the emerging parasites to similar vials, feeding them with a solution of honey and water lightly streaked across the inside walls of the vials.

5.22 Host plants

In these experiments I used maize, wild sorghum, and pennisetum. The plants were grown in plastic pots of 20 cm in diameter and 30 cm in depth, filled with soil collected in the field. The soil was previously enriched with a 15/15/15 mixed NPK fertilizer at a rate of 100 kg/ha to ensure optimal growth and development of the

plants. For maize, I planted three seeds and thinned to two plants per pot two weeks after emergence. I used turfs for planting the grasses. All plants were watered as needed.

5.23 Experimental procedures

5.231 The effect of maize plant phenology on oviposition

a1. Oviposition preference of *S. calamistis*

I selected potted maize plants at four developmental stages, viz. 20, 40, 50, and 70 days after planting, corresponding to the early, pre-tasseling, tasseling, and post-ear formation stages, respectively, and placed them in a greenhouse on five trays arranged in a circular arena of 4 m in diameter. The greenhouse was kept at $27\pm 2^{\circ}\text{C}$ and $75\pm 5\%$ RH. Each tray carried one plant of each phenological stage. I introduced 70 females and 70 males of two-day-old adult *S. calamistis* in a shallow container placed in the center of the arena. The *S. calamistis* were previously fed with a solution of sugar and kept in a screen cage during 24 h for mating. I inspected the container the next morning to record the number of moths that had moved onto the plants by counting the number remaining in the container. I removed the container from the arena when 50 adult female *S. calamistis* had moved onto the plants, or after a two-day exposure, whichever came first.

a2. Oviposition preference of *T. busseolae*

Two days after the release of *S. calamistis*, I released from a plastic vial 50 to 60 two-day-old mated female of *T. busseolae* into the arena. The vial was kept in the center of the arena for one night. The plants were again left in place for three days to allow the parasites to search for *S. calamistis* eggs; I then cut off all the exposed plants at soil level and dissected them to search for *S.*

calamistis eggs. I recorded the number of egg masses, the number of eggs per mass, and calculated the total and mean numbers of eggs laid on each plant. The first-instar larvae of the borer were also collected and added to the number of eggs laid. The eggs were brought into the laboratory and kept in clear, dry plastic vials. Five days later, I checked these eggs to record the numbers parasitized. The experiment was replicated three times.

5.232 The effect of host-plant species on oviposition of *S. calamistis* and *T. busseolae*

In this set of experiments, I used host plants of the same age, viz. 40-day-old maize plants, wild sorghum, and pennisetum tillers. The three host species were divided equally between five trays, arranged in a circular arena as described above. Each tray included one plant of each host. I released *S. calamistis* and *T. busseolae*, and collected the data as described in section 5.231. For each grass plant, all tillers were dissected.

5.233 The effect of host plant species of different ages on oviposition of *S. calamistis* and *T. busseolae*

Maize plants of post-ear-formation stage, *i.e* 70 DAP or older, and 40- to 50-day-old wild sorghum and pennisetum were used in this experiment. Experimental set-up and data collection were the same as in section 5.231.

5.24 Data analysis

A One-Way ANOVA was used to compare means between host-plant ages and species. A Fisher's LSD multiple comparison was used to separate means. The tested variables were the number of egg batches,

the number of eggs laid by *S. calamistis*, and the percentage of eggs parasitized by *T. busseolae*. All percentages were arcsine-transformed before the analyses. A linear regression was used to determine the relationship between autocorrelated variables. All means are per tiller and shown with their standard errors.

5.3 Results

5.31 Effect of plants on egg laying by *S. calamistis*

Table 5.1 shows the distribution of egg masses and eggs laid by *S. calamistis* and parasitized by *T. busseolae* on maize plants of four phenological stages. Significant differences were found between the mean numbers of eggs laid on different maize stages. The highest mean number was laid on pre-tasseling plants. The next highest mean number was found on 20-day-old plants, but no significant difference was found between these means. Similarly, no significant difference was found between the mean numbers of eggs laid on tasseling and post-tasseling plants; however, the borers laid significantly fewer eggs on these plants than on 20-day-old and pre-tasseling plants. The same trend was observed with the numbers of egg masses laid on the plants according to plant age; the pre-tasseling plants had the highest number per plant, followed by 20-day-old plants. The post-tasseling plants had the lowest number, with only 2.93 ± 0.52 (mean \pm SE) egg masses per plant.

When maize, wild sorghum and pennisetum of the same age were exposed together to *S. calamistis*, the borer laid significantly more eggs on maize than on the other two host plants (Table 5.2). The mean numbers of *S. calamistis* eggs laid on wild sorghum and those laid on

Table 5.1 Numbers of egg batches and eggs laid by *S. calamistis* and parasitized by *T. busseolae* on 15 maize plants at four phenological stages (Mean±SE).

	Phenological stage of maize				A N O V A		
	20 DAP	Pre-tasseling	Tasseling	Post-tasseling	F	P	
Egg batches							
mean no.	4.33±0.50a*	5.93±0.48b	3.73±0.45ac	2.93±0.52c	6.711	0.0006	
total no.	65	89	56	44			
% ¹	25.59	35.04	22.05	17.32			
Eggs laid							
mean no.	208.33±29.91a	295.07±42.79a	132.00±25.53b	128.20±38.29b	5.121	0.003	
total no.	3125	4426	1980	1923			
% ¹	27.28	38.64	7.29	16.79			
Eggs parasitized							
mean no.	150.73±25.30a	221.53±32.99a	82.47±115.64b	97.40±31.17b	5.392	0.003	
total no.	2261	3323	1237	1461			
mean % ²	59.24±3.92a	60.97±2.60a	55.75±3.56a	51.10±7.22a	0.781	0.512	

* Means with the same letter(s) are not significantly different within rows (One-Way ANOVA, $P \leq 0.05$ followed by Fisher LSD test). ¹: percentage of eggs laid on a particular growth stage based on the total number of eggs laid on all stages in the trial. ²: percentage based on the total number of eggs parasitized in all growth stages.

Table 5.2 Numbers of egg batches and eggs laid by *S. calamistis* and parasitized by *T. busseolae* on forty-day-old maize plants and grass tillers (Mean±SE).

	Host plant species		A N O V A			
	Maize (n=15 ¹)	Wild sorghum (n=37)	Pennisetum (n=52)	DF	F	P
Egg batches						
mean no.	1.13±0.24a*	0.24±0.08b	0.12±0.04b	2,101	24.031	0.0001
total no.	17	9	6			
% ²	53.13	28.13	18.75			
Eggs laid						
mean no.	20.33±4.23a	4.31±1.65b	1.87±0.78b	2,101	22.679	0.0001
total no.	305	159	97			
% ²	54.37	28.34	17.29			
Eggs parasitized						
mean no.	13.38±3.78a	2.78±1.35b	0.67±0.47b	2,101	15.701	0.0001
total no.	201	103	35			
mean % ³	52.13±12.27a	59.90±17.71a	40.0±24.49a	2,20	0.281	0.757

* Means with the same letter(s) are not significantly different within rows (One-Way ANOVA, $P \leq 0.05$ followed by Fisher LSD test). ¹: number of tillers. ²: percentage of eggs laid on a particular host plant based on the total number of eggs laid on all three host plants. ³: percentage based on the total number of eggs parasitized in the three host plant species.

Table 5.3 Numbers of egg batches and eggs laid by *S. calamistis* and parasitized by *T. busseolae* on post-tasseling maize (70 DAP) and forty-day-old grass tillers (Mean±SE).

	Host plant species			A N O V A		
	Maize (n=15 ¹)	Wild sorghum (n=37)	Pennisetum (n=52)	DF	F	P
Egg batches						
mean no.	0.56±0.15a*	0.76±0.15a	0.67±0.14a	2,69	0.401	0.672
total no.	10	16	22			
% ²	20.83	33.33	45.83			
Eggs laid						
mean no.	17.44±6.17a	19.57±4.38a	11.06±2.53a	2,69	1.379	0.258
total no.	314	411	365			
% ²	28.81	37.71	33.49			
Eggs parasitized						
mean no.	24.67±7.5a	15.92±3.01a	4.51±1.51b	2,37	7.911	0.001
total no.	222	207	81			
mean % ³	80.39±5.4a	45.09±7.65b	24.3±7.31c	2,34	12.12	0.0001

*: Means with the same letter(s) are not significantly different within rows (One-Way ANOVA, $P \leq 0.05$ followed by Fisher LSD test). 1: n=number of tillers. 2: Percentage of eggs laid on a particular plant based on the total number of eggs laid on the three types of plants. 3: Percentage based on the total number of eggs parasitized in the three host plant species.

pennisetum were not statistically different. Likewise, the number of egg batches collected was higher on maize than on the two grasses.

Between post-ear-formation maize plants and 40-day-old sorghum and pennisetum tillers, the mean numbers of egg batches and eggs deposited by the borer were not significantly different, although the mean numbers on the grasses were only a little higher than the mean number on maize (Table 5.3).

5.32 The effect of host plant on pattern of parasitization

The percentages of *S. calamistis* eggs parasitized by *T. busseolae* on the four maize plant stages did not show any significant differences (One-Way ANOVA: $F = 0.781$; $df = 3,56$; $P = 0.512$) (Table 5.1). When the data collected on all maize stages were considered together, the number of eggs parasitized by *T. busseolae* was positively related to the number of egg batches and the number of eggs laid by *S. calamistis* by the following regression equations

$$y_1 = 45.92x_1 - 56.37 \quad (r^2 = 0.73, df:1,58; t = 12.44, P < 0.001)$$

$$y_2 = 0.75x_2 - 5.89 \quad (r^2 = 0.93, df:1,58; t = 26.90, P < 0.001)$$

where y_1 and y_2 were the numbers of egg batches and eggs parasitized by *T. busseolae*, and x_1 and x_2 were the number of egg batches and the number of eggs laid, respectively.

The mean number of *S. calamistis* eggs parasitized by *T. busseolae* was significantly higher on maize than on sorghum and pennisetum (Table 5.2). This number was again positively related to the number of eggs and the number of egg batches collected. The relationship was described by the regression equations

$$y_3 = 0.82x_3 - 0.35 \quad (r^2 = 0.87, \text{df}:1,102; t = 26.11 \text{ P} = 0.0001)$$

$$y_4 = 17.41x_4 - 0.01 \quad (r^2 = 0.81, \text{df}:1,102; t = 21.06, \text{P} = 0.0001)$$

with y_3 and y_4 being the numbers of egg batches and eggs parasitized and x_3 and x_4 the number of egg batches and the number of eggs laid, respectively. However, when the comparisons were based on the percentage of eggs parasitized by *T. busseolae*, there were no significant differences between the mean numbers on the three host plants.

Between post-tasseling maize and 40-day-old grasses, the mean number of eggs parasitized by *T. busseolae* was significantly higher on maize than on sorghum, which had a higher mean number than pennisetum (Table 5.3). The percentage of eggs parasitized by the wasp was also higher on maize than on the two grass species. Between the two grass species, *T. busseolae* was more successful at parasitizing eggs on sorghum than on pennisetum.

5.4 Discussion

When given a choice between maize and grass plants of the same age, *S. calamistis* laid more eggs on maize than on grasses, whereas females laid more eggs on younger than older maize plants when this was the only host available; but the borers did not show any preference when they were provided with old maize plants and young grass tillers. These egg laying patterns show that female *S. calamistis* do not oviposit at random. They prefer pre-tasseling and young maize plants. Preference of young maize for oviposition explained the higher populations of *S. calamistis*, compared with other borers, in the early

development of maize (Usua, 1968b; Girling, 1978; Kaufmann, 1983; Cochereau, 1985; Bosque-Pérez and Mareck, 1990; Chapter III).

The observed preference of *S. calamistis* for young rather than old maize plants, and for maize rather than grasses, indicates that the borer may be attracted to, and actively selects, maize plants for oviposition. The present experiments did not aim at an investigation of the host plant selection mechanism by *S. calamistis*. Nevertheless, as with some other moth species (Fenemore, 1980; Renwick and Radke, 1988), it is probable that olfactory and visual stimuli were important in the oviposition behaviour of this borer. In the three sets of experiments, the physical properties of the plants and their actual resource contents may have been used by the borer. But *S. calamistis* being a nocturnal insect, it is possible that females responded also to some plant volatiles such as the typical odours emitted by emerging flowers (Candelo and Jacobson, 1979), or chemical constituents in leaves (Renwick and Radke, 1988). The larger stem of the maize plants as compared with grasses may also have affected the choice of the borer, since the probability of an insect encountering a plant could increase with stem diameter (Visser, 1988).

Preference of host plants by *S. calamistis* was probably based on the ability of the plants to ensure better growth and development of the immature stages. Young maize plants were selected over older plants because their tissues can provide enough nutrients for borer development. In addition, young plants presumably had the longer life necessary to allow the immatures to complete their cycle before the plants aged and died.

The ability of the plant to sustain the development of immature borers may likewise have accounted for the choice of the moths to oviposit on maize rather than on the hard grass stems. As maize grew, the quantity of food contained in the stems decreased and its quality declined. At a certain point in plant development, the resources in post-tasseling maize plants may be of equal or even inferior quality to those of young grass plants. *S. calamistis* was shown to have distributed equal numbers of eggs between these two types of hosts to increase the probability of survival of their offspring. Shanower *et al.* (1993) found higher mortalities of immature *S. calamistis* in maize than in wild grasses and concluded that maize plants are more suitable than grass tillers. The high numbers of *S. calamistis* eggs on maize compared with those on grass may have resulted in part from the fact that leaf sheaths on maize are generally looser than those on grasses. Female borers could thus insert their ovipositors readily between the leaf sheaths and stems to lay more eggs on maize than on grass.

My results showed that although wild grass plants are not the most suitable hosts for the development of *S. calamistis* (Shanower *et al.*, 1993), this borer laid some eggs on them when suitable maize plants were not available, confirming that grass plants can help maintain high populations of the borer.

The percentage of *S. calamistis* eggs parasitized by *T. busseolae* was not significantly different between maize plants of different stages; this pattern of parasitization was also observed between maize and grass plants of the same age. This was so, presumably because the parasite had equal opportunity to find and to parasitize the eggs, irrespective of the host plant, which suggested that the host

plant did not influence the parasitization of *S. calamistis* eggs. This result is similar to that reported by Temerak (1981) with a species complex of *Telenomus* wasps in Egypt. In field studies, he found that the numbers of parasitized eggs of *Sesamia cretica* Lederer (Lepidoptera: Noctuidae) did not differ between maize, grain sorghum, and sugar cane, three host plants of the borer. The non-preference of host plant for egg parasitization suggested that plant characteristics were not involved in finding host eggs by these parasites. Thus, either female *T. busseolae* found their host by random search, or used some olfactory cues emitted by adults or eggs of *S. calamistis*. This latter hypothesis is supported by the fact that females of several other lepidopterous insects are known to emit volatiles that attract and induce oviposition by their egg parasites (Noldus and van Lenteren, 1985a,b; Nordlund *et al.*, 1983, 1987). It has also been found that during oviposition, female *Pieris brassicae* (L.) (Lepidoptera: Pieridae) deposit a pheromone on and around the eggs (Nordlund *et al.*, 1983, 1987). I could not explain the increased number of parasitized *S. calamistis* eggs on post-tasseling maize plants, other than on the assumption that eggs on senescing leaf sheaths of maize were more easily reached by *T. busseolae* than eggs on grasses; therefore, the parasite could easily find and parasitize them.

The positive correlation between the number of eggs parasitized by *T. busseolae* and the number of eggs laid by *S. calamistis* suggested that parasitism in this parasite is density dependent. The more host eggs available, the higher the rate of parasitism. This behaviour could be explained by the fact that female *S. calamistis* lay their eggs in batches of several eggs (Kaufmann, 1983). Once female parasites found

and accepted a batch, they tended to parasitize every egg in the batch before leaving in search of another. This parasitization behaviour was observed also by Temerak (1981) in *Telenomus* spp.

Chapter VI

EFFECTS OF HOST EGG DENSITY, EXPOSURE TIME, AND AGE ON PARASITIZATION BY, AND DEVELOPMENT OF, *TELENOMUS BUSSEOLAE*

6.1 Introduction

The scelionid wasp, *Telenomus busseolae*, is a solitary parasite described from eggs of maize stem borers (Bourarach, 1987; Alexandri and Tsitsipis, 1990). During surveys carried out in the past few years, I.I.T.A. workers have found that this parasite was principally collected from eggs of *S. calamistis* and *Busseola fusca* and had a wide distribution in West Africa. The parasite has been reported from Bénin (Shanower *et al.*, 1991; Sétamou and Schulthess, 1995), Côte d'Ivoire and Ghana (Gounou *et al.*, 1994) and Nigeria (Polaszek *et al.*, 1993). Polaszek *et al.* (1993) reported that *T. busseolae* belongs to a complex composed of several species, all of which are parasites of eggs of the genus *Sesamia*. These authors also reported a few records of these parasites emerging from the pyralid stem borer *Coniesta sp.* and *Busseola fusca*. Among the complex described, *T. busseolae* was the most abundant species.

The genus *Telenomus*, which currently includes over 500 species worldwide (Polaszek *et al.*, 1993), is important economically because studies have suggested that several species have the potential for regulating populations of stem borers. Temerak (1981) found that more than 69% of *Sesamia cretica* were parasitized by an unidentified

species of *Telenomus* in Egypt. Chabi-Olaye (1992) reported that up to 84% of *S. calamistis* eggs artificially placed in maize fields were parasitized by *T. busseolae*. Sétamou and Schulthess (1995) observed that 70% of *S. calamistis* eggs collected in maize fields throughout Bénin were parasitized by this species.

Despite the high potential of *Telenomus* spp. for parasitizing the eggs of stem borers, no examples of successful biological control by this genus have been reported from Africa. Elsewhere, limited examples have been documented. The most notable is the use of *T. alsophilae* (Viereck) against *Oxydia tryachiata* (Guenée) (Lepidoptera: Geometridae) in Colombia (Drooz *et al.*, 1977). Caltagirone (1981) reported also the successful use of *Trissolcus basal* (Wollston) against *Nezara viridula* (L.) (Heteroptera: Pentatomidae) in Australia. The lack of success of the telenomines as biological control agents can be attributed to limited knowledge of their taxonomy (Polaszek and Kimani, 1990) and confusion about biological differences between closely related species.

This chapter reports data from experiments I conducted to study the conditions that are necessary for *T. busseolae* to achieve effective parasitization and development. I examined: 1) how the density of eggs, time of exposure and age of *S. calamistis* eggs influence the rate of parasitization; and 2) how host eggs of different ages affect the development and sex ratio of the parasite.

6.2 Materials and methods

6.21 *S. calamistis* eggs, *T. busseolae* and arena

I reared *S. calamistis* and *T. busseolae* in the laboratory as described in section 5.21. Two-day-old *T. busseolae* females used in the present experiments were naive, *i.e.* they had never been exposed to *S. calamistis* eggs prior to the experiments. Upon emergence, females were confined with a group of males for two days so that they could mate. The experiments were done in an arena at room temperature ($30\pm 2^{\circ}\text{C}$). The arena was a clear plastic vial, 5 cm in diameter by 5 cm deep. The eggs exposed to the parasite were held in a controlled environment chamber (Percival, Boone, Iowa 50036), at $28\pm 1^{\circ}\text{C}$, $75\pm 5\%$ RH, and a 12D:12L photoperiod.

6.22 Experimental procedures

6.221 Effect of time of exposure on parasitization

In this experiment, I used *S. calamistis* egg masses containing about 60 to 70 one-day-old eggs. I placed a single egg mass in each vial and introduced one mated female parasite. The eggs were exposed to the parasites for the following periods: 30 min, 1, 2, 4, 6, 12, 18, 21, 24, 27, 30, 33, 42, 48 hours. I kept eggs at $28\pm 1^{\circ}\text{C}$ and inspected them after six days to count those parasitized. For each exposure time, I repeated the experiment 15 times with different females.

6.222 Effect of size of egg mass on parasitization by *T. busseolae*

To investigate the effect of egg mass size on parasitization by *T. busseolae*, I placed in the arena a single one-day-old egg mass of either 10, 20, 30, 40, 60, or more than 70 eggs per mass. I introduced a mated female *T. busseolae*, then left the parasite with the eggs for 6

hours and reared the exposed eggs in the controlled environment chamber. I examined the eggs six days later to record the number parasitized by each female. *S. calamistis* eggs parasitized by *T. busseolae* can be distinguished easily from unparasitized eggs; those parasitized become brown within four to five days. I counted the number of emerged parasites and determined their sex ratio. For each egg density, I repeated the experiment with 17 different naive females.

6.223 Effect of age of egg on parasitization and development

To study the influence of the age of *S. calamistis* eggs on parasitization by *T. busseolae*, I conducted two series of no-choice and choice experiments, a and b. In the a series, I exposed eggs of given ages to a two-day-old female parasite in the arena. In the b series, the parasite was given the choice between eggs of two or three different ages which were exposed together.

a. No-choice experiments

I placed in each arena one *S. calamistis* egg mass containing 20 to 22 eggs of different ages, viz. less than 1, 1, 2, 3, or 4 days old, and introduced into the arena a female *T. busseolae*. After 6h-exposure, I removed the parasite and reared the eggs in the environment chamber. I observed the exposed egg masses six days later to count the eggs parasitized by *T. busseolae* and also recorded the numbers of moth larvae, if any, and the numbers of non-fertile moth eggs, from which no larvae emerged. I considered as 'fertile' moth eggs the total number of parasitized eggs plus those from which larvae emerged. I placed parasitized eggs in the rearing cabinet and observed them daily to record the times of emergence of the adult parasites and their sex

ratio. Parasitized eggs from which wasps failed to emerge were dissected to determine, if feasible, the sex of the non-emerged wasp.

b. Choice experiments

Two sets of tests were made. The first, b1, was a pairwise comparison between two egg masses of different ages, placed in the arena. In the second, b2, three masses of 1-, 2-, and 3-day-old eggs were exposed together, and a female *T. busseolae* was released for 6 h. After the parasite was removed from the arena, each egg mass was transferred to a labelled clear gelatin capsule, and reared in the environment chamber. The numbers of parasitized eggs and the numbers of larvae in each age group were recorded, together with the time of emergence and the sex ratio of *T. busseolae*.

6.224. Effect of temperature on developmental time of *T. busseolae*

I exposed a one-day-old *S. calamistis* egg mass to female *T. busseolae* at room temperature ($30\pm 2^{\circ}\text{C}$) as described above for the a (no-choice) experiments. After 6h, the exposed eggs were divided into two groups; one group was held at $26\pm 1^{\circ}\text{C}$ and the other at $32\pm 1^{\circ}\text{C}$ in different rearing chambers. The emergence times of the parasites were recorded every day. I compared the emergence times with those of adults emerging from one-day-old eggs incubated at $28\pm 1^{\circ}\text{C}$ in the a (no-choice) experiments.

6.225 Data analysis

For each treatment, I pooled the numbers of eggs parasitized by each female wasp across replications. To determine the differences between three or more mean numbers and percentages between

treatments of each experiment, I used a One-Way ANOVA. Fisher's LSD test was used to separate the means that were different. A Two-Sample t-test was used to analyze differences between mean numbers of male and female offspring, and to compare mean numbers in the pairwise age-comparisons. All means are shown with their standard errors.

6.3 Results

6.31 Effect of time of exposure on parasitization

The mean numbers of eggs parasitized by *T. busseolae* varied greatly with times of exposure. Figure 6.1 shows that the mean numbers increased slowly in the first two hours of exposure. During that period, only 13% of females included in experiments lasting 30 min, and 33% in those lasting 2 h, oviposited successfully. The mean number of eggs parasitized per female wasp during 2 h was 1.53 ± 0.9 , but after a 4 hour-exposure, several females had oviposited in at least one egg. As a result, the mean numbers of parasitized eggs quickly increased to 11.07 ± 0.91 . After 4 h, the curve decelerated; from 12 h, there was no clear trend, and the mean numbers varying non-significantly between 12.07 ± 1.08 and 18.07 ± 1.09 . The mean numbers of *S. calamistis* eggs parasitized plotted against length of exposure followed a logarithmic curve of the form

$$y = 2.99 + 9.38\text{LOG}(x)$$

($r^2 = 0.88$) with y being the the number of parasitized eggs and x the period of exposure.

6.32 Effect of size of egg masses on parasitization

The numbers of eggs parasitized by *T. busseolae* were influenced by the size of egg masses. The lowest number of eggs parasitized was in the group of 10 eggs/mass. An increase in egg mass size from 10 to 20 eggs resulted in an increase in the numbers of eggs parasitized from 2.35 ± 0.90 to 11.24 ± 2.30 (Table 6.1). Increases above 20 eggs/mass produced only small increases in the numbers of eggs parasitized, and above 60 eggs/mass no increase was observed. Based on the percentage of eggs exposed to the parasite, an increase in parasitism occurred between 10 and 20 eggs/mass, but decreased with higher numbers.

Egg mass size did not affect adult emergence. The percentages of wasps that emerged from parasitized eggs ranged from 90.18 ± 4.14 to 97.0 ± 1.6 (Table 6.1) and were not significantly different between egg mass sizes (One-Way ANOVA: $F = 0.481$; $df = 5,54$; $P = 0.790$). But the size of each egg mass affected the sex ratio of *T. busseolae*. Male offspring were fewer than female with 10 eggs/mass, increasing with the numbers of eggs, whereas the numbers of females remained relatively constant. At mass sizes of 10, 20 and 30 eggs, significantly more female than male parasites emerged. However, above 40 eggs/mass, no significant differences in the sex ratio were found.

6.33 Effect of egg age on parasitization

No-choice experiments

Female *T. busseolae* parasitized *S. calamistis* eggs in all age groups. But parasitism decreased as the age of the eggs increased (Table 6.2). The mean numbers of eggs parasitized in the less-than-1-day and the 1-day-old eggs were significantly higher than

Figure 6.1 Numbers of *S. calamistis* eggs parasitized by *T. busseolae* when exposed for different periods. Data points show the mean numbers of eggs parasitized by 15 females.

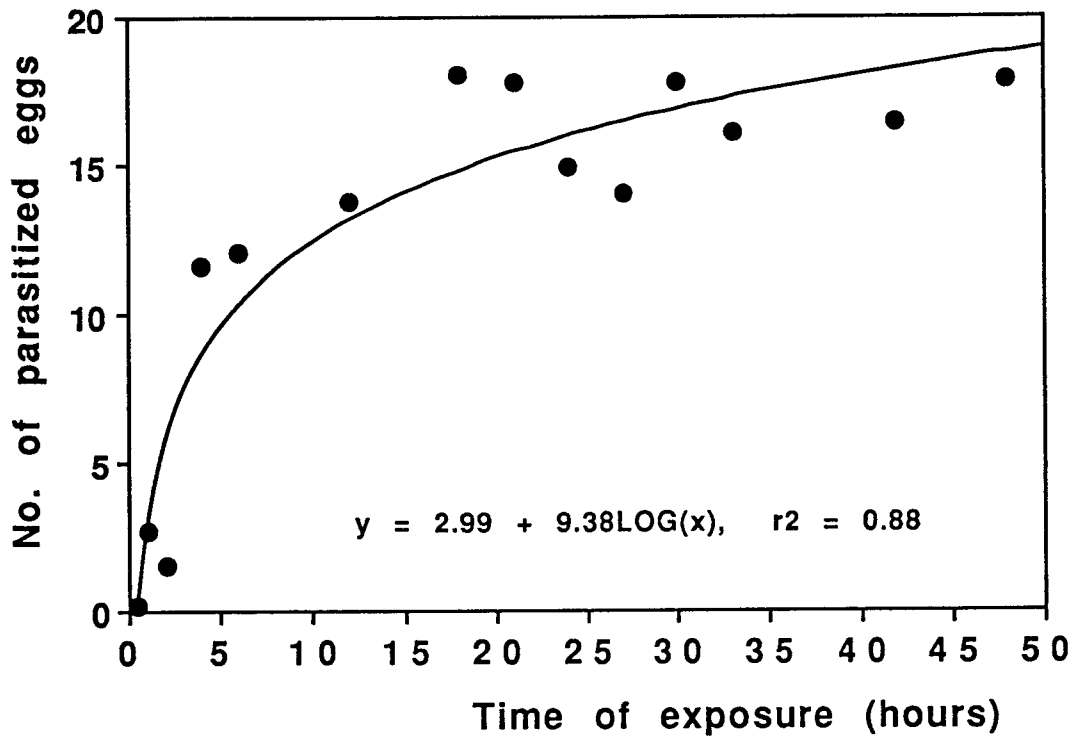


Table 6.1 Parasitism by *T. busseolae* exposed to *S. calamistis* egg masses of different sizes in vials, with emergence and sex ratio of adult parasites (Mean±SE; n=17 females).

Eggs in masses	1 0	2 0	3 0	4 0	6 0	Over 7 0
Parasitized	2.35±0.90	11.24±2.33	12.88±2.92	20.00±3.38	25.18±5.98	18.76±5.93
% ¹	23.32±8.91	54.45±11.32	41.90±9.28	54.71±8.42	41.83±9.92	21.17±6.48
Emerged wasps	2.12±0.79	10.88±2.28	12.71±2.79	21.00±3.25	23.65±5.77	17.47±5.51
% ²	93.93±3.12	93.18±4.44	97.00±1.61	95.63±1.96	93.22±3.73	90.18±4.41
Males	0.53±0.21	2.76±1.15	4.18±1.08	8.0±1.71	8.59±2.53	5.41±2.20
Female	1.59±0.62	8.12±1.97	8.53±2.11	12.88±2.81	15.65±4.58	12.18±4.32
Sex ratio ³	3.00	2.94	2.06	1.61	1.82	2.25

¹: percentages of eggs parasitized based on the number of eggs exposed. ²: percentages of adults emerged based on the number of eggs parasitized. ³: female/male emerged.

Table 6.2 Parasitism by *T. busseolae*, and offspring and sex ratio of the parasites emerged from *S. calamistis* eggs of different ages at the time of parasitization, and reared at 28±2°C, 75±5% RH, and 12:12 D:L photoperiod (Mean±SEM).

Age of eggs (days)	Less than 1 (n*=26)	1 (n*=19)	2 (n*=16)	3 (n*=15)	4 (n*=28)
Parasitized eggs					
No.	14.19±1.65a ⁴	16.11±0.88a	9.00±1.48b	6.93±1.72b	2.61±0.80bc
% ¹	62.96±7.24a	74.95±4.42a	43.82±7.05b	33.26±8.15b	11.96±3.64bc
% ²	68.76±7.81a	80.02±4.60a	48.24±7.66b	37.44±8.84b	14.35±4.33bc
Emerg ed wasps					
No.	13.50±1.60a	14.37±0.77a	8.19±1.37b	5.93±1.47b	1.64±0.50bc
% ³	94.86±1.76a	89.85±1.66a	92.35±2.79a	85.99±3.32a	72.87±7.18b
Males No.	3.54±0.71a	5.16±1.07a	3.50±0.78a	2.4±0.49acd	0.61±0.20bd
Females No.	9.92±1.33a	9.16±1.19a	5.50±1.24b	3.53±1.19bd	0.93±0.36cd
Female/Male	2.80	1.78	1.57	1.40	1.52

*: numbers of repetitions. ¹ based on the number of eggs exposed. ²: based on the number of fertile moth eggs. ³: based on the number of wasps emerged. ⁴ : means with the same letter(s) within rows are not significantly different (One-Way ANOVA, P ≤ 0.05 followed by Fisher's LSD test).

the numbers parasitized in 2-day, 3-day, and 4-day-old eggs. However, no significant differences were found between the mean numbers parasitized in eggs of less than 1-day and 1-day, although higher numbers of eggs were parasitized in eggs of less-than-1-day than in those of 1 day. Similarly, no significant differences were found between 2-day, 3-day, and 4-day-old eggs. In 4-day-old eggs, less than 12% of exposed eggs were parasitized. The same trend was observed when only fertile moth eggs were considered. The percentages of eggs parasitized, whether based on the total numbers of eggs exposed or on the numbers of fertile moth eggs, followed the same pattern: significantly higher parasitism in less-than-1-day and 1-day, than in older eggs. Parasitism by *T. busseolae* was negatively related to the ages of *S. calamistis* eggs and it could be predicted by the regression equation

$$\% \text{ parasitization} = 68.55 - 14.12 \text{ Egg age}$$

($r^2 = 0.73$; $t = 7.74$; $df = 1,102$; $P = 0.0001$). The percentages of adult *T. busseolae* that emerged from parasitized eggs up to 3-days old, were not different between days, but they were significantly higher than the percentages that emerged from 4-day-old eggs. The sex ratio of *T. busseolae* also varied with the age of eggs. From less-than-1-day and 1-day eggs, significantly higher numbers of females than males emerged. The ratio female:male was higher in younger (up to 1-day-old) than in older eggs. This ratio decreased from 2.8 in the young eggs to 1.3 in 4-day-old eggs. Dissection of the parasitized eggs from which parasites failed to emerge, showed that many parasites died as adults;

among these, the majority were females. The highest number of non-emerged parasites was recorded from 4-day-old eggs.

Pairwise comparison

When *S. calamistis* eggs of two ages were exposed together, female *T. busseolae* generally parasitized more young than old eggs. Between newly laid and 1-day-old eggs, slightly more 1-day eggs were parasitized than the new ones, but the mean numbers in the two groups were not significantly different (One-Way ANOVA). Likewise, the mean percentages of adults that emerged from the new and the 1-day-old eggs were not significantly different (Table 6.3). In the other combinations, the patterns of preference were variable. When newly laid eggs were exposed with eggs of any other age, *T. busseolae* parasitized more of the younger eggs. Conversely, when 4-day eggs were exposed together with those of any other age group, significantly fewer 4-day eggs were parasitized, and the percentage of emergence was also lower from the 4-day eggs. In each comparison, significantly more female than male offspring emerged.

Comparison between three age-groups

Table 6.4 shows the mean numbers and percentages of eggs parasitized by *T. busseolae* when 1-day-, 2-day- and 3-day-old *S. calamistis* eggs were exposed simultaneously. Significantly more eggs were parasitized in the 1-day group than in the 3-day group; but the differences between 1-day- and 2-day-old, and between 2-day- and 3-day-old eggs were not significant. The same ranking was observed when the comparisons were based on the numbers of fertile moth eggs: higher numbers of eggs were parasitized in the 1-day- than in the

Table 6.3 Preference by, and suitability of, *T. busseolae* among different ages of *S. calamistis* eggs exposed by pairs in a vial (n= number of females used in each comparison; < 1 = eggs of less than 1 day).

Comparison		<1 & 1-day (n=21)	<1 & 2-days (n=21)	<1 & 3-days (n=21)
Parasitized eggs				
Nb.		10.24±1.70a ⁴	11.90±1.72a	10.57±1.25a
% ¹		58.36±8.35a	52.72±6.22a	50.29±8.15a
% ²		64.69±8.62a	56.60±6.52a	55.12±8.94a
			50.30±7.61a	46.72±9.87a
Emerged wasps				
Nb.		9.33±1.58a	9.81±1.23a	9.52±1.67a
% ³		85.97±3.49a	91.04±2.95a	90.72±4.77a
Males	No.	3.05±0.79a	2.52±0.80a	2.76±1.09a
Females	No.	7.14±1.25a	7.19±1.04a	6.81±1.50a
			3.86±0.77b	2.90±0.78b

Table 6.3 (Continued)

Comparison	<1 & 4-days (n=18)	1-day & 3-days (n=26)	2-days & 4-days (n=32)
Parasitized eggs			
No.	12.11±1.53a	10.23±1.51a	8.59±1.29a
% ¹	58.72±7.31a	46.32±6.73a	40.51±6.01a
% ²	61.27±9.37a	51.68±7.51a	43.05±6.35a
	13.70±4.66b	40.42±6.88a	18.91±4.31b
Emerged wasps			
No.	11a.61±1.44a	9.88±1.52a	8.12±1.23a
% ³	82.70±2.90a	79.73±4.85a	73.62±4.45a
	64.36±9.04a	69.60±5.79a	53.30±6.73b
Males No.	2.83±0.80a	3.04±0.81a	2.72±0.71a
Females No.	7.94±1.28a	5.42±1.18a	5.41±1.01a
	1.39±0.53b	3.88±0.99a	1.22±0.40b

1: Based on the number of eggs exposed. 2: based on the number of fertile moth eggs. 3: based on the number of wasps emerged. 4: means with the same letter(s) within pairs are not significantly different (Paired t-test, $P \leq 0.05$ followed by Fisher's LSD test).

Table 6.4 Preference by *T. busseolae* among *S. calamistis* eggs of three age groups exposed simultaneously in a vial, and emergence of adult parasites from parasitized eggs reared at 28±2° C, 75±5% RH, and 12:12 D:L photoperiod (Mean±SEM, n= 17 females).

Age of the eggs	1-day	2-days	3-days	1-WAY ANOVA	
				F	P
Parasitism based on exposed eggs					
No.	10.82±1.65a*	7.53±1.26a	4.88±1.31ab	4.410	0.017
%	51.66±7.91a	35.51±5.26a	23.00±5.84ab	4.770	0.013
Parasitism based on fertile moth eggs					
%	55.38±8.61a	39.30±6.76a	26.67±7.18ab	3.651	0.034
Emergence					
No.	9.94±1.48a	3.35±0.86b	2.88±0.87b	12.630	0.0001
%	94.08±1.96a	47.59±8.79b	54.05±9.66b	11.821	0.0001
Males No.	3.12±0.96a	1.35±0.64a	1.06±0.49a	2.361	0.105
Females No.	6.82±1.36a	2.00±0.66b	1.82±0.68b	8.840	0.0005

*: Means with the same letter(s) within rows are not significantly different (One-Way ANOVA, $P \leq 0.05$ followed by Fisher's LSD test, $df=2,48$).

3-day-old eggs. The mean numbers and percentages of adults emerging were higher from 1-day- than from 2-day- and 3-day-old eggs. The differences between 2-day- and 3-day-old eggs were not significant. In every age group, the numbers of emergent female wasps were significantly higher than those of males.

6.34 Time of emergence of *T. busseolae*

Effects of egg age

From *S. calamistis* eggs aged up to 4 days, high percentages of adult *T. busseolae* emerged. At $28\pm 1^{\circ}\text{C}$, emergence from newly-laid eggs occurred mostly on days 14, 15, and 16 after parasitization (Figure 6.2), as follows:

day 14---> 34%
" 15---> 53%
" 16---> 13%.

These patterns were similar in the other age groups. Therefore I pooled the data from all groups. When the five age groups were pooled, the emergence was as follows:

day 14 ---> 25%
" 15 ---> 60%
" 16 ---> 15%.

About 61% of adult wasps emerging on day 14 were males, dropping to 27% and 20% on days 15 and 16, respectively.

Effects of different constant rearing temperatures

T. busseolae were incubated in the moth eggs at $26\pm 1^{\circ}\text{C}$, $28\pm 1^{\circ}\text{C}$, and $32\pm 1^{\circ}\text{C}$, and the length of development from oviposition to adult

Figure 6.2 Emergence time of adult *T. busseolae* developing in *S. calamistis* eggs parasitized at different stages and reared at $28\pm 1^{\circ}\text{C}$, $75\pm 5\%$ RH, and 12:12 D:L photoperiod. Columns show the mean numbers of adults emerged on 14th, 15th, and 16th days after parasitization.

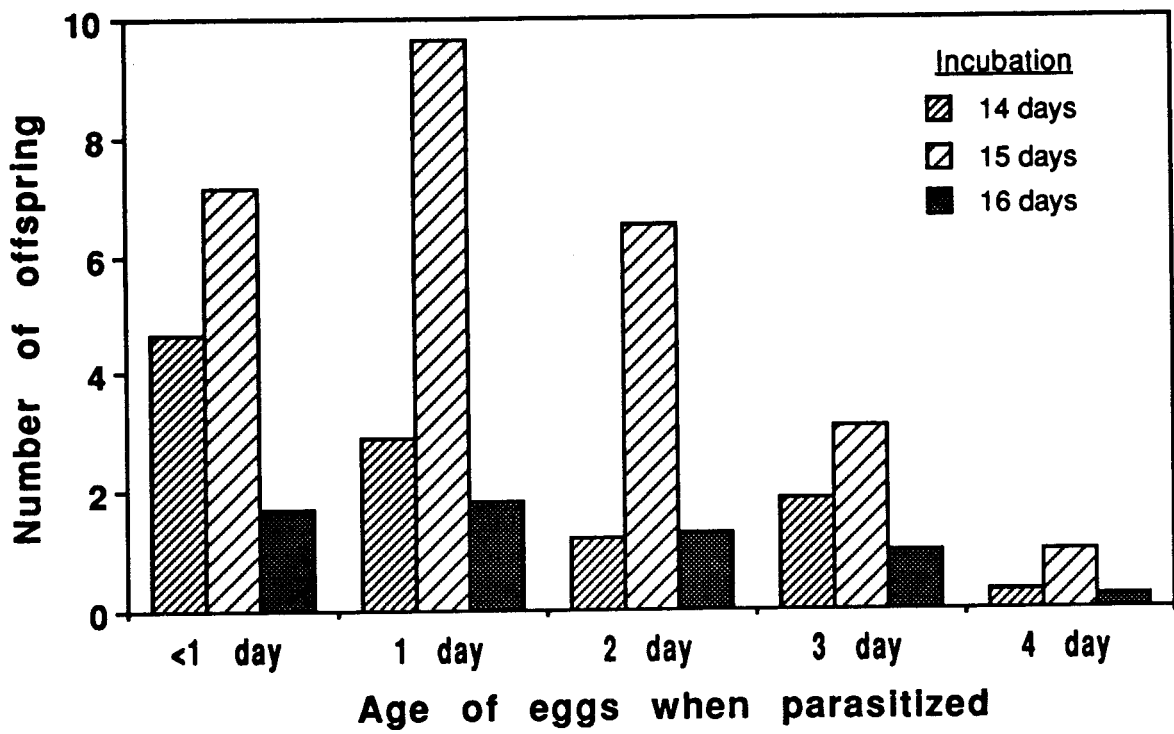
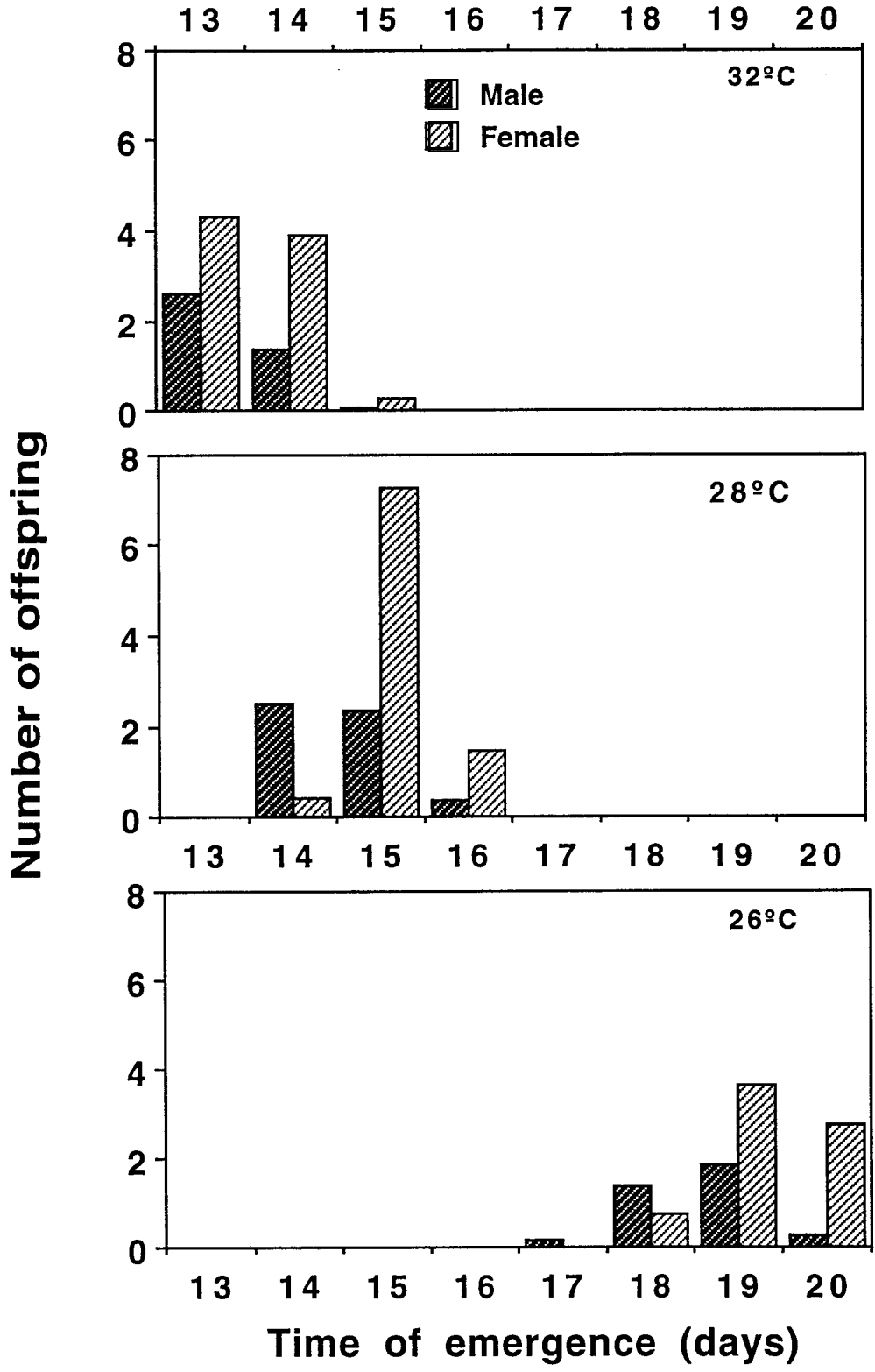


Figure 6.3 Emergence time of adult *T. busseolae* developing in *S. calamistis* eggs reared at different temperatures, 75±5% RH, and 12:12 D:L photoperiod. Columns show the mean numbers of male and female parasites.



emergence, and the percentage of emergence, varied with rearing temperatures (Figure 6.3). At $26\pm 1^{\circ}\text{C}$, adult emergence occurred mostly within four consecutive days, from day 18 to 20. On day 17, only 4 adults (males) emerged from two egg masses. The highest mean number of adults emerged on day 19 with 5.43 ± 0.12 , followed by day 20 with 3.0 ± 0.1 adults. The mean numbers of individuals that emerged between these two days were not significantly different. The percentage of emergence at $26\pm 1^{\circ}\text{C}$ was $71.71\pm 5.24\%$, significantly lower than the percentage at $28\pm 1^{\circ}\text{C}$ and $32\pm 1^{\circ}\text{C}$ (One-Way ANOVA: $F = 6.791$; $df = 2,56$; $P = 0.0023$). The shortest development time was at $32\pm 1^{\circ}\text{C}$, when adults emerged only on days 13 and 14, mostly on day 13 (56.79%). The mean percentage of emergence at $32\pm 1^{\circ}\text{C}$ was 87.35 ± 2.74 , higher but not significantly different from the percentage of emergence at $28\pm 1^{\circ}\text{C}$ (71.71 ± 5.24).

6.4 Discussion

Parasitism of moth eggs was low in the first 2 hours of exposure, but increased rapidly between 2 and 4 hours. The first 2 h were probably needed by the parasite to become accustomed to the environment of the arena before actively searching for eggs. It may also be the time needed by inexperienced females to learn the process of parasitizing moth eggs. After 6 h, few additional eggs were parasitized; it is probable that the parasite spent large amounts of time resting or searching for non-parasitized eggs.

T. busseolae responded to increasing numbers of host eggs by increasing the numbers parasitized in a batch, showing that this parasite has density-dependant parasitization behaviour. Holling

(1959) described three types of functional responses of parasites and predators with regard to the density of their hosts or prey. The type 2 response describes the situation when parasitism increases at a decreasing rate as host numbers increase. The response of *T. busseolae* to *S. calamistis* density was similar to Type 2, common in parasites and predators (Holling, 1961). This pattern of behaviour could be ascribed to the availability of hosts. As the densities of host eggs increased, the time spent by the parasite searching may be shortened, because the numbers of encounters between wasp and moth eggs increased. It follows that more time was spent in parasitizing, rather than in searching for, hosts. Kfir (1983) observed similar density-dependent behaviour in the egg parasite *Trichogramma pretiosum* (Riley). This author observed also that the parasite decreased its rate of search at high host density.

The numbers of eggs parasitized increased up to 20 eggs/mass, then the rate of parasitism decreased, and the numbers of eggs parasitized reached a plateau, which could result from either a limitation of time or of wasp eggs, or both. In separate experiments, I observed that female *T. busseolae* could lay up to 150 eggs in 24 hours (mean: 114 ± 4.12). Therefore, a limitation of parasitism, if any, is probably caused by time of exposure.

Regardless of host density, the percentages of adult parasites that emerged were relatively high and not significantly different between densities. However, increasing the numbers of available host eggs decreased the proportion of female offspring, which may suggest that, when suitable host eggs are scarce, *T. busseolae* lays fertilized, female eggs, prior to male eggs.

T. busseolae parasitized *S. calamistis* eggs in all five age-classes. This ability to parasitize a range of host stages may be useful in mass rearing and particularly in releases. In the field, the parasite may not find all the most desirable eggs, ie, newly laid by the moth, but eggs of different ages will still be available. Although all ages were parasitized, the younger eggs were more attractive than the older ones, and the highest rates of parasitization occurred in eggs less than two days old. Preference for young hosts compared with old ones seems to be common in egg parasites. For example, *T. alsophilae* (Fedde, 1977; Bustillo and Drooz, 1977), *Trichogamma evanescens* Westwood (Lewis and Redlinger, 1969), and *Trichogramma minutum* (Riley) (Marston and Ertle, 1969), attack all ages of available hosts, but young eggs are preferred and most frequently parasitized. In contrast, *T. fariai* Lima does not show any preference for different ages in its hosts, the eggs of *Triatoma phyllosoma pallidipennis* (Stål) (Rabinovich, 1971). High parasitism in young, rather than old eggs may result from hardening of the egg chorion. Hence, wasps may find it hard to insert the ovipositors in older eggs.

The period of incubation of *S. calamistis* eggs is five to six days (Kaufmann, 1983). The embryos of these eggs may start developing about 3 days after they were laid. In these conditions, a large part of the contents of eggs 3 days or older had probably been used for embryo development. It is possible that female *T. busseolae* detected these physical and physiological changes in the embryonated eggs and 'decided' to parasitize mostly those unembryonated. *T. alsophilae* likewise is known to parasitize only unembryonated eggs of *Alsophila pometaria* (Harris) (Fedde, 1977). The acceptance behaviour based on

host age, described in several egg parasites (Lewis and Redlinger, 1969; Pak, 1986), is assumed to be optimal (Waage, 1986) in that it allows females to adjust the number and sex of their offspring in accordance with expected fitness returns.

The fact that immatures developed, and adult wasps emerged, from eggs of all ages, especially from those 4 days-old, indicates that the immatures of the parasite completed their development. This suggests that moth embryos in old eggs are killed at the time of oviposition, at least in some of the eggs. The process by which the moth embryo is eliminated is not known. It has been suspected that the wasp kills the moth embryo by piercing it when ovipositing.

The emergence of wasps was lower from 4-day-old than from younger *S. calamistis* eggs, which again suggests that old eggs were less suitable for parasite development than young eggs. The contents of old eggs had certainly decreased due to the formation of moth embryos, so that there was insufficient food available to sustain the development of the wasp. The duration of development of *T. busseolae* was not affected, at $28\pm 1^{\circ}\text{C}$, by the age of *S. calamistis* eggs at the time of parasitization. The adult wasps emerged between 14 and 16 days. For eggs of all ages, the highest proportion of emergence was on day 15, which suggests that the rate of development was similar in eggs of all ages. This result was similar to those of Jubb and Watson (1971a) with *T. utahensis* Ashmead. The development of this egg parasite did not change when the age of eggs of *Chlorochroa sayi* Stål varied between 1 and 6 days. From these observations, it appeared that the state of moth egg contents did not seriously affect the development of immature parasites. This could be misleading since the

fitness of these offspring was not tested. It will be necessary to investigate the reproductive capability and longevity of the wasps emerging from moth eggs of different ages.

At $28\pm 1^{\circ}\text{C}$, about 15 days were needed for development and adult emergence of *T. busseolae*. At $26\pm 1^{\circ}\text{C}$, up to 20 days were necessary and emergence was spread over a longer period. The fastest emergence occurred at $32\pm 1^{\circ}\text{C}$, with most of the wasps emerging on day 13. This indicates that the rate of development accelerated as the temperature increased. These results were consistent with previous studies on scelionid wasps (Bustillo and Drooz, 1977; Ryan *et al.*, 1981; Ticehurst and Allen, 1973; Jubb and Watson, 1971a,b; Torgersen and Ryan, 1980). Chabi-Olaye (1992) found that the low threshold of temperature for the development of *T. busseolae* was 15°C and the maximum temperature 35°C . My results agree with these observations; furthermore, they showed that the optimum temperature for the development of *T. busseolae* in *S. calamistis* eggs was between 28°C and 32°C . Within the range of temperatures tested here, 32°C proved to be the most suitable, since the adults emerged faster and from a much shorter period than at lower temperatures. This information has a practical application in mass rearing where the emergence of females and males from the same colony must be synchronized to ensure high proportions of mating. In the field however, the high temperatures may desiccate the moth eggs and therefore, be detrimental to the parasite.

Regardless of the age of the moth eggs at parasitization and the rearing temperature, emerging female wasps outnumbered males; but the ratio female:male decreased as the age of the host eggs increased. This showed that female *T. busseolae* laid fertilized eggs, which were

to produce female offspring, in young moth eggs, whereas she laid eggs to produce males in old eggs.

Chapter VII

GENERAL CONCLUSIONS

In tropical Africa, several stem borers cause serious damage to maize and other thick-stemmed cereal crops (Harris, 1962; Usua, 1968b; Leyenaar and Hunter, 1977; Pollet, 1977; Pollet *et al.*, 1978; Warui and Kuria, 1983; Moyal, 1988; Nwanze, 1988; van Rensburg *et al.*, 1988a;b; Bosque-Pérez and Mareck, 1991). Populations vary with the time of year and the stage of development of the host plants (Kaufmann, 1983; Bosque-Pérez and Mareck, 1990; Atkinson, 1980). The extent of damage may depend also on the time of infestation of the host plant and the number of eggs at infestation (Usua, 1968a; Van Rensburg *et al.*, 1987b).

In this study I showed that *S. calamistis* and *E. saccharina* are the predominant borer species in southern Bénin. This finding differs from previous studies which have concluded that *S. calamistis* was a species occurring mostly in forest zones but not in the wet savannah zones (Atachi, 1984; Thomas-Odjo, 1984). This finding indicates that the stem borers have spread and become important pests over larger areas than initially known; this may possibly be due to migrations as a result of disturbance in the borers' primary zones as a result of agricultural development. The finding that relatively high numbers of borers were also collected on wild sorghum and pennisetum grasses, and that *S. calamistis* oviposited in grasses, even when they were given the choice between maize and grass plants, indicates that grasses are important alternative host plants. Therefore, any change

that increases the abundance of grasses will also increase the possibility of the borers to build up high populations; and because grasses are available almost continuously, they act as reservoirs on which the stem borers can maintain themselves in the off-season and re-infest maize fields in the following season. It is thus suggested that maize fields be separated as far as possible from grass fields. One way of achieving this objective would be by the cutting of non-cultivated grasses in and around maize fields.

The two borer species attacked maize at different stages of its growth. *S. calamistis* infested maize when plants were young, whereas *E. saccharina* appeared from silking to harvesting. Either on maize or on grasses, the numbers of borers were affected by planting dates. The populations of the stem borers were higher in the July-September than in the October-January trial. However, other workers reported lower numbers in the first growing season (March-July) than in the second (September-December). My results suggest that several generations of *S. calamistis* and *E. saccharina* can develop in maize fields all year round. The yearly variations of populations depend therefore on the planting patterns of maize. I showed that *S. calamistis* prefers young and pre-tasseling maize plants for oviposition, whereas *E. saccharina* infests the plants from tasseling onwards. If seedings of maize overlap in one area, suitable growth stages of maize plants will be continuously available for oviposition and larval development, increasing the chances of emerging females to encounter suitable host plants and reproduce. It is thus recommended that seeding of the same field or the same area be done at the same time or over a short period.

The time and level of infestation by *S. calamistis* significantly reduced growth of the maize plants and decreased overall yield; but timing of attack had the most pronounced effect. This finding indicates that stem borers are among the main causes of low productivity of maize in West Africa, and points out the need for more effective control measures. The degree of plant growth reduction and yield loss declined with plant age at the time of infestation. Plants infested four weeks after they emerged had lower yields than those infested after six weeks, indicating that young plants are more susceptible to borer attacks than older ones. The time up to five weeks after seeding is the most sensitive period for the maize plant to *S. calamistis* attack. Therefore, the most important period for farmers to protect maize plants against borer infestations is during the period from emergence to about six weeks after emergence.

The distribution of immature borers within their host plants depended on the stage of development of both the borer and the plants. On maize plants, the borers laid most of their eggs on the lowest part, below the ear, followed by the portion immediately above the ear, whereas on wild sorghum, the borers did not show a preference for a particular oviposition site, although lateral shoots had relatively more eggs than main stems. Larvae, as opposed to eggs, were more evenly distributed on all host plants. These patterns of distribution showed that the destruction and dissection of the whole maize plant is not necessary during sampling. It is proposed that the leaf sheaths below the first ear be thoroughly examined to obtain a reliable estimation of the numbers of eggs and young larvae. But, as the larvae become dispersed with time, the sampling unit should vary accordingly. Up to

40 days after planting, the lower part of the maize plant should be used as the main sampling unit for a reliable estimate of the populations of immature stages of *S. calamistis*. After that period, any sampling should consider the ear as the main sampling unit. Sampling of eggs and larvae of *E. saccharina* should be based on the same sampling units, but 10 days to two weeks later. Because larvae seem to develop better in the ear, it is suggested that the ear be used in the rearing diet.

T. busseolae was successfully mass-reared in the laboratory. The wasp parasitized all developmental stages of moth eggs, and had a high rate of emergence around 30°C, which is the mean temperature in the region. This means that the parasite, which is widely distributed in the maize growing area in West Africa, can survive under these conditions long enough to parasitize a large number of host eggs. The efficiency of a parasite is measured in part by its ability to find its host at low densities and to parasitize large numbers of them at high densities (Huffaker and Messenger, 1976). I showed that the rates of parasitism by *T. busseolae* increased with increasing numbers of moth eggs. In addition, *T. busseolae* parasitized more than 54% of moth eggs at densities of ca. 40 eggs per mass. Although this result does not prove the searching efficiency at low densities, it demonstrates that the parasite is efficient at the densities of eggs commonly found in the field.

Judging from the reported percentages of parasitization in the field (Sétamou and Schulthess, 1995) and the success in biological control of the closely related species *T. alsophilae* (Bustillo and Drooz, 1977), it is conceivable that *T. busseolae* has the potential to reduce *S.*

calamistis populations. The reasons why the parasite is not currently effective in controlling field populations of *S. calamistis* is not known and can only be surmised at present. It may be due to a lack of synchronization between the short borer egg-laying period and the peak population of the parasites. For instance, because the bulk of moth eggs is laid on young plants, within approximately three weeks, high populations of the parasite appear in the field when moth eggs have hatched or are in their late stages of development. Furthermore, the numbers of eggs parasitized by *T. busseolae* was not affected by species or stages of the host plants bearing host eggs; it is possible that the parasite spends more time searching on one species or stage than another. Several parasite eggs may be wasted or resorbed during the searching process so that wasps are no longer able to parasitize a large number of moth eggs. Although *T. busseolae* parasitized all moth egg stages, the rate of emergence is reduced in older eggs and more male offspring are produced in older than young eggs. These two factors may reduce the size of populations of the following generations of the parasites. Attempts to manipulate *T. busseolae* by inundative releases especially on young maize plants would therefore be justified. It would allow high populations of parasites to be in the field at the moth's oviposition period. However, to achieve a more successful control of maize stem borer by using the parasite, it seems indispensable to conduct further studies on the searching behaviour of the parasite, and its interaction with the host plant, in order to understand better the system of maize-*S. calamistis* -*T. busseolae* .

REFERENCES

- Alexandri, M.P. and J.A. Tsitsipis. 1990. Influence of the egg parasitoid *Platytenomus busseolae* (Hymenoptera: Scelionidae) on the population of *Sesamia nonagrioides* (Lepidoptera: Noctuidae) in central Greece. *Entomophaga* 35:61-70.
- Altieri, M.A., S. Annamalai, K.P. Katiyar and R.A. Flath. 1982. Effects of plant extracts on the rates of parasitization of *Anagasta kuehniella* (Lepidoptera: Pyralidae) eggs by *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) under greenhouse conditions. *Entomophaga* 27:431-438.
- Ampofo, J.K.O. and E.L. Kidiavai. 1987. *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) larval movement and growth on maize plants in relation to plant age and resistance or susceptibility. *J. appl. Ent.* 103:483-488.
- Atachi, P. 1984. Investigation sur les insectes parasites du maïs en République populaire du Bénin (1975-1982). 47pp.
- Atkinson, P.R. 1980. On the biology, distribution and natural host-plants of *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *J. ent. Soc. Sth. Afr.* 43:171-194.
- Berger, A. 1992. Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. *Bull. ent. Res.* 82:441-448.
- Bernays, E.A. and R. Barbehenn. 1987. Nutritional ecology of grass foliage-chewing insects. pp. 147-175. In Slansky, F. & Rodriguez, J.G. (eds.) *Nutritional ecology of insects, mites, spiders, and related invertebrates*, New York, John Wiley & Sons.
- Bosque-Pérez, N.A. and J.H. Mareck. 1990. Distribution and species composition of lepidopterous maize borers in southern Nigeria. *Bull. ent. Res.* 80:363-368.
- Bosque-Pérez, N.A. and J.H. Mareck. 1991. Effect of the stem borer *Eldana saccharina* (Lepidoptera: Pyralidae) on the yield of maize. *Bull. ent. Res.* 81:243-247.

- Bosque-Pérez, N.A. and Z.T. Dabrowski. 1989. Mass rearing of the maize stem borers *Sesamia calamistis* and *Eldana saccharina* at IITA. In: Toward insect resistant maize for the third world: Proceedings of the International Symposium on Methodologies for Developing Host Resistance to Maize Insects. México, D.F., Centro Internacional de Mejoramiento de Maíz y Trigo. pp. 22-26.
- Bosque-Pérez, N.A., J.H. Mareck, Z.T. Dabrowski, L. Everett, S.K. Kim and Y. Efron. 1989. Screening and breeding maize for resistance to *Sesamia calamistis* and *Eldana saccharina*. In: Toward insect resistant maize for the third world: Proceedings of the International Symposium on Methodologies for Developing Host Resistance to Maize Insects. México, D.F., Centro Internacional de Mejoramiento de Maíz y Trigo. pp. 163-169.
- Bourarach, K. 1987. Inventory of the entomophagous parasites of some noctuidae in Morocco. Ed. INRA, Paris (Les colloques de l'INRA) pp. 55-157.
- Bowden, J. 1973a. The influence of moonlight on catches of insects in light-traps in Africa. Part I. The moon and moonlight *Bull. ent. Res.* **63**:113-128.
- Bowden, J. 1973b. The significance of moonlight in photoperiodic responses of insects. *Bull. ent. Res.* **62**:605-612.
- Bowden, J. 1976. Stem borer ecology and strategy for control. *Ann. appl. Biol.* **84**:107-134.
- Bowden, J. 1982. An analysis of factors affecting catches of insects in light-traps. *Bull. ent. Res.* **72**:535-556.
- Bowden, J. and B.M. Church. 1973. The influence of moonlight on catches of insects in light-traps in Africa. Part II. The effect of moon phase on light-trap catches. *Bull. ent. Res.* **63**:129-142.
- Bowden, J. and M. G. Morris. 1975. The influence of moonlight on catches of insects in light-traps in Africa. III. The effective radius of a mercury-vapour light-trap and the analysis of catches using effective radius. *Bull. ent. Res.* **65**:303-348.
- Bustillo, A.E. and A.T. Drooz. 1977. Cooperative establishment of a Virginia (USA) strain of *Telenomus alsophilae* on *Oxydia trychiata* in Colombia. *J. Econ. Entomol.* **70**:767-770.

- Caltagirone, L.E. 1981. Landmark examples in classical biological control. *Ann. Rev. Entomol.* **26**:213-232.
- Candelo, W.W. and M. Jacobson. 1979. Corn silk volatiles attract many pest species of moths. *J. envir. Sci. Hlth.* **A14**:695-707.
- Chabi-Olaye, A. 1992. Contribution à l'étude de la biologie et de l'écologie de *Telenomus busseolae* (Hymenoptera: Scelionidae), un parasite d'oeuf de *Sesamia calamistis* (Lepidoptera: Noctuidae). Memoire d'Ingénieur agronome. Université Nationale du Bénin. 80pp.
- Chiang, H.C. and A.C. Hodson. 1950. Stalk breakage caused by European corn borer and its effect on harvesting of field corn. *J. Econ. Entomol.* **43**:415-422.
- Chiang, H.G. 1977. Pest management in the Peoples's Republic of China. Monitoring and forecasting insect population in rice, wheat and maize. *Plt. Prot. Bull., F.A.O.* **25**:1-8.
- CIMMYT. 1991. Réalité et tendances - Le maïs dans le monde: potentiel maïsicole de l'Afrique subsaharienne. México, D.F., Centro International de Mejoramiento de Maíz y Trigo. 71pp.
- Cochereau, P. 1982. Observations on the borer *Eldana saccharina* (Lepidoptera: Pyralidae) in maize and sugarcane in Ivory Coast. *Proc. Sth. Afr. Sugar Assoc.*, June, 1982. pp.1-3.
- Cochereau, P. 1985. Ecologie des populations, en Côte d'Ivoire, du foreur africain de la canne à sucre et du maïs *Eldana saccharina* Walker. *Institut des Savanes-ORSTOM*, Côte d'Ivoire.
- Comeau, A., R.T. Cardé and W.L. Roelofs. 1976. Relationship of ambient temperature to diel periodicities of sex attraction in six species of Lepidoptera. *Can. ent.* **108**:415-418.
- Courtney, S.P. 1981. Coevolution of pierid butterflies and their cruciferous foodplants. III. *Anthocharis cardamines* (L.). Survival, development and oviposition on different host plants. *Oecologia* **51**:91-96.
- Cox, P.D., L.A. Crawford, G. Gjestrud, C.H. Bell and C.R. Bowley. 1981. The influence of temperature and humidity on the life cycle of *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae). *Bull. ent. Res.* **71**:171-181.

- Dang Thanh Ho and K.V. Seshu-Reddy. 1983. Monitoring of lepidopterous stem-borer populations by pheromone and light traps. *Insect Sci. Appl.* 4:19-23.
- Davis, P.M and L.P. Pedigo. 1989. Analysis of the spatial patterns and sequential count of plants for stalk borer (Lepidoptera: Noctuidae). *Environ. Entomol.* 18:504-509.
- Dent, D.R. and C.S. Pawar. 1988. The influence of moonlight and weather on catches of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) in light and pheromone traps. *Bull. ent Res.* 78:365-377.
- Drooz, A.T., A.E. Bustillo, G.F. Fedde and V.H. Fedde. 1977. North American egg parasite successfully controls a different host genus in South America. *Science* 197:390-391.
- Endrody-Younga, S. 1968. The stem borer *Sesamia botanephaga* Tams & Bowden (Lepidoptera: Noctuidae) and the maize crop in central Ashanti, Ghana. *Ghana Jnl. Agric. Sci.* 1:103-131.
- Fedde, G.F. 1977. A laboratory study of egg parasitization capabilities of *Telenomus alsophilae*. *Environ. Entomol.* 6:773-776.
- Fenemore, P.G. 1980. Oviposition of potato tuber moth, *Phthorimaea operculella* Zell. (Lepidoptera: Gelechiidae); identification of host-plant factors influencing oviposition response. *NZ J. Zool.* 7:435-439.
- Girling, D.J. 1978. The distribution and biology of *Eldana saccharina* Walker (Lepidoptera: Pyralidae) and its relationship to other borers in Uganda. *Bull. ent. Res.* 68:471-488.
- Girling, D.J. 1980. *Eldana saccharina* as a crop pest in Ghana. *Trop. Pest Management* 26:152-156.
- Gounou, S., F. Schulthess, T. Shanower, W.N.O. Hammond, H. Braima, A.R. Cudjoe, R. Adjakloe, K.K. Antwi and I. Olalaye. 1994. Stem and ear borers of maize in Ghana. Plant Health Management Research Monograph No. 4, *International Institute of Tropical Agriculture*, Ibadan, Nigeria. 23pp.
- Grüber, K. and A.F.G. Dixon, 1988. The effect of nutrient stress on development and reproduction in aphids. *Entomol. exp. appl.* 47:23-30.

- Guthrie, W.D., W.A. Russel, F.L. Neumann, G.L. Reed and R.L. Grindlend. 1975. Yield losses in maize caused by different levels of infestation of second-brood European corn borers. *Iowa State J. of Research*. **50**:239-253.
- Harris, K.M. 1962. Lepidopterous stem borers of cereals in Nigeria. *Bull. ent. Res.* **53**:139-171.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. ent.* **91**:293-320.
- Holling, C.S. 1961. Principles of insect predation. *Ann. Rev. Entomol.* **6**:163-182.
- Huffaker, C.B. and P.S. Messenger. 1976. Theory and practice of biological control. Academic Press, Inc., New York.
- Huffaker, C.B., R.F. Luck and P.S. Messenger. 1976. The ecological basis of biological control, pp. 560-586. In J.S. Packer & D. White (eds.), Proceedings, 15th international congress of entomology. Washington, D.C. *Ent. Soc. Am.*, College Park, Md.
- IITA. 1980. Cereal improvement program: maize. International Institute of Tropical Agriculture, Annual Report for 1979. Ibadan, Nigeria. pp.107-116.
- Ingram, W.R. 1958. The lepidopterous stalk borers associated with graminæ in Uganda. *Bull. ent. Res.* **49**:367-383
- Ingram, W.R. 1983. Biological control of graminaceous stem-borers and legume pod-borers. *Insect Sci. Applic.* **4**:205-209.
- Johnson, D.R. 1983. Relationship between tobacco budworm (Lepidoptera: Noctuidæ) catches when using pheromone traps and egg counts in cotton. *J. Econ. Entomol.* **76**:182-183.
- Jönsson, P. and O. Anderbrant. 1993. Weather factors influencing catch of *Neodiprion sertifer* (Hymenoptera: Diprionidae) in pheromone traps. *Environ. Entomol.* **22**:445-452.
- Jubb, Jr. G.L. and T.F. Watson. 1971a. Development of the egg parasite *Telenomus utahensis* in two pentatomid hosts in relation to temperature and host age. *Ann. Entomol. Soc. Am.* **64**:202-205.

- Jubb, Jr. G.L. and T.F. Watson. 1971b. Parasitization capabilities of the pentatomid egg parasite *Telenomus utahensis* (Hymenoptera: Scelionidae). *Ann. Entomol. Soc. Am.* **64**:452-456.
- Karandinos, M.G. 1976. Optimal sample size and comments on some published formulae. *Bull. Entomol. Soc. Am.* **22**:417-421.
- Kaufmann, T. 1983. Behavioral biology, feeding habits and ecology of three species of maize stem borers: *Eldana saccharina* (Lepidoptera: Pyralidae), *Sesamia calamistis* and *Busseola fusca* (Noctuidae) in Ibadan, Nigeria, West Africa. *J. Georgia Ent. Soc.* **18**:259-272.
- Kfir, R. 1983. Functional response to host density by the egg parasitoid *Trichogramma pretiosum*. *Entomophaga* **28**:345-353.
- Kfir, R. and R.A. Bell. 1993. Intraseasonal changes in populations of the African stem borer *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and its parasitoids in Natal, South Africa. *J. Afr. Zool.* **107**:543-553.
- Kiyomitsu, I., H. Sugyama, N.M.N.b. Nik Salleh and C. Poon Min. 1993. Effects of lunar phase on light trap catches of the Malaysian black rice bug, *Scotinophara coarctata* (Heteroptera: Pentatomidae). *Bull. ent. Res.* **83**:59-66.
- Kouamé, K.L. and M. Mackauer. 1992. Influence of starvation on development and reproduction in apterous virginoparae of the pea aphid, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae). *Can. ent.* **124**:87-95.
- Leather, S.R., S.A. Ward and A.F.G. Dixon. 1983. The effect of nutrient stress on some life story parameters of the black bean aphid, *Aphis fabae* Scop. *Oecologia* **57**:156-157.
- Lewis, W.J. and L.M. Redlinger. 1969. Suitability of eggs of the almond moth, *Cadra cautella*, of various ages of parasitism by *Trichogramma evanescens*. *Ann. Entomol. Soc. Am.* **62**:1482-1484.
- Leyenaar, P. and R.B. Hunter. 1977. Effect of stem borer damage on yield in the coastal savanna zone of Ghana. *Ghana J. Agric. Sci.* **10**:67-70.
- Lynch, R.E. 1980. *Ostrinia nubilalis* : yield losses in relation to hybrid and stage of maize development. *J. Econ. Entomol.* **73**:159-164.

- Lynch, R.E., J.F. Robinson and E.C. Berry. 1980. *Ostrinia nubilalis* : yield losses and damage resulting from a simulated natural infestation. *J. Econ. Entomol.* **73**:141-144.
- Marston, N. and L.R. Ertle. 1969. Host age and parasitism by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *Ann. Entomol. Soc. Am.* **62**:1476-1482.
- Messenger, P.S. 1976. Theory underlying introduction of exotic parasitoids, pp 191-214. In J.F. Anderson & H.K. Kaya (eds.), *Perspectives in forest entomology*. Academic Press Inc., New York.
- Mihm, J.A. 1985. Breeding for host plant resistance to maize stem-borers. *Insect Sci. Applic.* **6**:369-377.
- Mitchell, E.R., V.H. Waddill and T.R. Ashley. 1984. Population dynamics of the fall armyworm (Lepidoptera: Noctuidae) and its larval parasites on whorl stage corn in pheromone-permeated field environments. *Environ. Entomol.* **13**:1618-1623.
- Mohyuddin, A.I. and D.J. Greathead. 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.
- Moyal, P. 1988. Crop losses due to insects in the savannah area of Ivory Coast: a review. *Trop. Pest Management* **34**:455-459.
- Myers, J.H. 1985. Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, *Pieris rapae*. *J. Anim. Ecol.* **54**:193-204.
- N'Demah, R. 1991. Lowland cereals entomology. NCRE Annual Report for 1990. Cameroun.
- Nakamura, K. 1976. The effect of wind velocity on the diffusion of *Spodoptera litura* (F.) sex pheromone. *Appl. Entomol. Zool.* **11**:312-319.
- Noldus, L.P.J.J and J.C. van Lenteren. 1985a. Kairomones for the egg parasite *Trichogramma evanescens* Westwood. I. Effect of volatile substances released by two of its hosts, *Pieris brassicae* L. and *Mamestra brassicae* L. *J. Chem. Ecol.* **11**:781-791.

- Noldus, L.P.J.J and J.C. van Lenteren. 1985b. Kairomones for the egg parasite *Trichogramma evanescens* Westwood. II. Effect of contact chemicals produced by two of its hosts, *Pieris brassicae* L. and *Pieris rapae* L. *J. Chem. Ecol.* **11**:793-800.
- Nordlund, D.A., M.R. Strand, W.J. Lewis and S.B. Vinson. 1987. Role of kairomones from host accessory gland secretion in host recognition by *Telenomus remus* and *Trichogramma pretiosum* with partial characterization. *Entomol. exp. appl.* **44**:37-43.
- Nordlund, D.A., W.J. Lewis and R.C. Gueldner. 1983. Kairomones and their use for management of phytophagous insects. XIV. Response of *Telenomus remus* to abdominal tips of *Spodoptera frugiperda*, (Z)-9-tetradecen-1-ol acetate and (Z)-9-dodecen-1-ol acetate. *J. Chem. Ecol.* **9**:695-701.
- Nwanze, K.F. 1988. Assessment of on-farm losses in millets due to insect pests. *Insect Sci. Applic.* **9**:673-677.
- Omolo B.O. and K.V. Seshu Reddy. 1985. Screening maize genotypes for multiple resistance to stem borers. *Insect Sci. Applic.* **6**:405-408.
- Pak, G.A. 1986. Behavioural variations among strains of *Trichogramma* spp.: a review of the literature on host-age selection. *J. Appl. Entomol.* **101**:55-64.
- Pitcairn, M.J., F.G. Zalom and W.J. Bentley. 1990. Weather factors influencing capture of *Cydia pomonella* (Lepidoptera: Tortricidae) in pheromone traps during overwintering flight in California. *Environ Entomol.* **19**:1253-1258.
- Polaszek, A. 1992. Cereal stem borers and their parasitoids in Africa. *Proc. Exp. Appl. Entomol.* (Netherlands) **3**:70-71.
- Polaszek, A. and S.W. Kimani. 1990. *Telenomus* species (Hymenoptera: Scelionidae) attacking eggs of pyralid pests (Lepidoptera) in Africa: a review and guide of identification. *Bull. ent. Res.* **80**:57-71.
- Polaszek, A., J. A. Ubeku and N.A. Bosque-Pérez 1993. Taxonomy of the *Telenomus busseolae* species-complex (Hymenoptera: Scelionidae) egg parasitoids of cereal stem borers (Lepidoptera: Noctuidae, Pyralidae). *Bull. ent. Res.* **83**:221-226.

- Pollet, A. 1977. Les insectes ravageurs du riz en Côte d'Ivoire. II. La faune rencontrée sur riz irrigué en Côte d'Ivoire centrale (Kotiessou). *Cah. ORSTOM, sér. Biol.*, XII:3-23.
- Pollet, A., N. van Roon and R. Mauritz. 1978. Les ravageurs du maïs en Côte d'Ivoire. Données qualitatives et quantitatives pour la Basse Côte. *Cah. ORSTOM, sér. Biol.*, XIII:71-85.
- Rabinovich, J.E. 1971. Population dynamics of *Telenomus fariai* (Hymenoptera: Scelionidae), a parasite of chagas' disease vectors. III. Preferences for and progeny from different age classes of host eggs. *Ann. Entomol. Soc. Am.* 64:29-32.
- Rausher, M.D. 1981. Host plant selection by *Batte philenor* butterflies: the roles of predation, nutrition and chemistry. *Ecol. Monogr.* 51:1-20.
- Rønwick, J.A.A. and C.D. Radke. 1988. Sensory cues in host selection for oviposition by the cabbage butterfly, *Pieris rapae*. *J. Insect Physiol.* 34:251-257.
- Root, R.B. and P.M. Karieva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* 65:147-165.
- Ryan, R.B., R.W. Mortensen and T.R. Torgersen. 1981. Reproductive biology of *Telenomus californicus* Ashmead, an egg parasite of the Douglas-fir tussock moth: laboratory studies. *Ann. Entomol. Soc. Am.* 74:213-216.
- Sampson, M.A. and R. Kumar. 1983. Population dynamics of the stem-borer complex on sugar-cane in Southern Ghana. *Insect Sci. Appl.* 4:25-32.
- Sampson, M.A. and R. Kumar. 1986. Alternative host plants of sugar cane stemborers in southern Ghana. *Insect Sci. Appl.* 7:539-541.
- Schulthess, F., N.A. Bosquez-Pérez and S. Gounou. 1991. Sampling lepidopterous pests on maize in West Africa. *Bull. ent. Res.* 81:297-301.
- Sétamou, M. and F. Schulthess. 1995. The influence of egg parasitoids belonging to *Telenomus busseolae* (Hymenoptera: Scelionidae) species complex on *Sesamia calamistis* (Lepidoptera: Noctuidae) populations in Southern Bénin. *Bioc. Sci. Tech.* (In press).

- Sétamou, M., F. Schulthess, N.A. Bosque-Pérez and A. Thomas-Odjo. 1993. Effect of nitrogen and silica on the bionomics of *Sesamia calamistis* (Lepidoptera: Noctuidae). *Bull. ent. Res.* **83**:405-411.
- Shanower, T., F. Schulthess and N.A. Bosque-Pérez 1993. The effect of larval diet on the growth and development of *Sesamia calamistis* (Lepidoptera: Noctuidae) and *Eldana saccharina* (Lepidoptera: Pyralidae). *Insect Sci. Applic.* **14**:681-685.
- Shanower, T., F. Schulthess and S. Gounou. 1991. Distribution and abundance of some stem and cob borers in Bénin. *Plant Health Management Research Monograph No. 1. International Institute of Tropical Agriculture*, Ibadan, Nigeria. 18pp.
- Shelton, A.M., J.P. Nyrop, A. Seaman and R.E. Foster. 1986. Distribution of European corn borer (Lepidoptera: Pyralidae) egg masses and larvae on sweet corn in New-York. *Environ. Entomol.* **15**:501-506.
- Singer, M.D., D. Ng and C.D. Thomas. 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* **42**:977-985.
- Sokal, R.R. and F.J. Rohlf. 1981. Biometry, The principles and practices of statistics in biological research, 2nd edition. pp. 232-262. W.H. Freeman & Company, San Francisco.
- Sorenson, C.E., G.G. Kennedy, J.W. Van Duyn and J.R. Bradley, Jr. 1993. Distribution of second generation European corn borer, *Ostrinia nubilalis*, egg masses in field corn and relationship to subsequent tunneling damage. *Entomol. exp. appl.* **68**:15-23
- Southwood, T.R.E. 1980. Ecological methods with particular reference to the study of insect populations, 2nd edition, London, Chapman and Hall.
- Taylor, L.R. 1961. Aggregation, variance and the mean. *Nature*, London **189**:321-357.
- Temerak, S.A. 1981. Qualitative and quantitative survey on the oophagous wasps attacking the pink borer, *Sesamia cretica* Led. (Lepidoptera: Noctuidae) on 3 graminaceous crops in Upper Egypt. *Z. ang. Ent.* **91**: 398-402.

- Thomas-Odjo, A. 1984. Contribution à l'étude de la biologie et de l'écologie de *Sesamia calamistis* en Côte d'Ivoire centrale. *Thèse Doctorat 3^{ème} Cycle*. Université de Paris-Sud, 109pp.
- Ticehurst, M. and D.C. Allen. 1973. Notes on the biology of *Telenomus coelodasidis* (Hymenoptera: Scelionidae) and its relationship to the saddled prominent, *Heterocampa guttivitta* (Lepidoptera: Notodondidae). *Can. ent.* **105**:1133-1143.
- Torgersen, T.R. and R.B. Ryan. 1980. Field biology of *Telenomus californicus* Ashmead, an important egg parasite of Douglas-fir tussock moth: *Ann. Entomol. Soc. Am.* **74**:185-186.
- Traynier, R.M.M. 1983. Influence of plants and adult food on the fecundity of the potato moth, *Phthorimaea operculella* (Zell.) (Lepidoptera: Gelechiidae). *Ent. exp. appl.* **33**:145-154.
- Umeozor, O.C., J.W. Van Duyin, G.G. Kennedy and J.R. Bradley, Jr. 1985. European corn borer (Lepidoptera: Pyralidae) damage to maize in Eastern North Carolina. *J. Econ. Entomol.* **78**:1488-1494.
- Usua, E.J. 1968a. Effect of varying populations of *Busseola fusca* larvae on the growth and yield of maize. *J. Econ. Entomol.* **61**:375-376.
- Usua, E.J. 1968b. The biology and ecology of *Busseola fusca* and *Sesamia* species in South-Western Nigeria. I. Distribution and population studies. *J. Econ. Entomol.* **61**:830-833.
- Usua, E.J. 1968c. Temperature and relative humidity effects on the development of the immature stages of the maize stemborers *Busseola fusca* and *Sesamia calamistis*. *J. Econ. Entomol.* **61**:1090-1093
- Van Rensburg, J.B.J., G.D.J. van Rensburg, J.H. Giliomee and M.C. Walters. 1987a. The influence of rainfall on the seasonal abundance and flight activity of the maize stalk borer, *Busseola fusca* in South Africa. *S. Afr. J. Plant Soil* **4**:183-187.
- Van Rensburg, J.B.J., J.H. Giliomee and M.C. Walters. 1988a. Aspects of the injuriousness of the maize stalk borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *Bull. ent. Res.* **78**:101-110.
- Van Rensburg, J.B.J., M.C. Walters and J.H. Giliomee. 1987b. Ecology of the maize stalkborer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *Bull. ent. Res.* **77**:255-269.

- Van Rensburg, J.B.J., M.C. Walters and J.H. Giliomee. 1988b. Response of maize to levels and times of infestation by *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *J. ent. Sth. Afr.* 51:283-291.
- Visser, J.H. 1988. Host-plant finding by insects: orientation, sensory input and search patterns. *J. Insect Physiol.* 34:259-268.
- Waage, J.K. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation, pp. 63-95. In J. Waage & D. Greathead (eds.), *Insect parasitoids*. Academic Press, London.
- Walker, P. 1981. The relation between infestation by lepidopterous stem borers and yield of maize: methods and results. *EPPO Bulletin* 11:101-106.
- Walker, P.T. 1960. The relation between infestation by the stalk borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) and yield of maize in East Africa. *Ann. appl. Biol.* 48:780-786.
- WARDA. 1979. West African Rice Development Association. Annual Report. Monrovia, Liberia.
- Warui, C.M. and J.N. Kuria. 1983. Population incidence and the control of maize stalk-borers, *Chilo partellus* (Swinh.), *C. Orichalcociliellus* Strand and *Sesamia calamistis* Hmps. in coastal province, Kenya. *Insect Sci. applic.* 4:11-18.
- Williams, C.B. 1936. The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap. *Phil. Trans. R. Soc. (B)*226:357-389.
- Williams, C.B. and B.P. Singh. 1951. Effect of moonlight on insect activity. *Nature, Lond.* 167:853.
- Williams, C.B., B.P. Singh and S. El-Ziady. 1956. An investigation into the possible effects of moonlight on the activity of insects in the field. *Proc. R. ent. Soc. Lond. (A)*31:135-144.
- Wilson, L.T. 1982. Development of an optimal monitoring program in cotton: emphasis on the spider mites and *Heliothis* spp. *Entomophaga* 27:45-50.
- Wilson, L.T. and P.M. Room. 1983. Clumping patterns of fruit and arthropods in cotton, with implications for binomial sampling. *Eviron. Entomol.* 12:50-54.

Witz, J.A., J.D. Lopez, Jr. and M.A. Latheef. 1992. Field density estimates of *Heliiothis virescens* (Lepidoptera: Noctuidae) from catches in sex pheromone-baited traps. *Bull. ent. Res.* **82**:281-286.