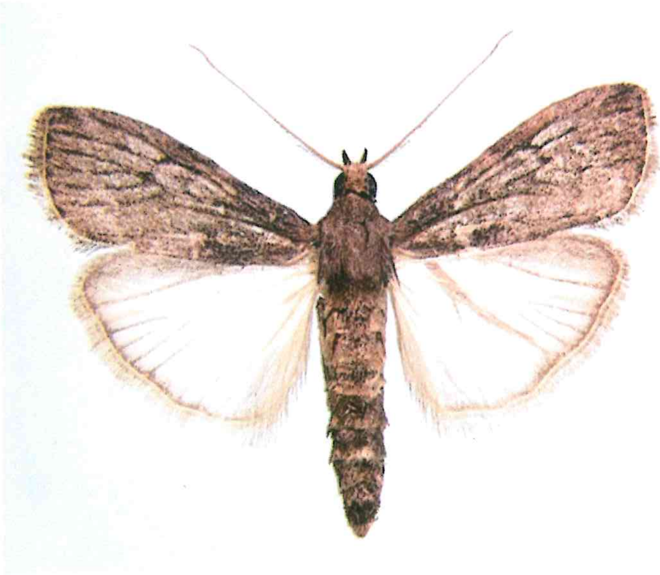
Ecology and management of *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae), a cob borer of maize in West Africa



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Abstract

Ecology and management of *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae), a cob borer of maize in West Africa

Mamoudou Sétamou

Investigations on the ecology of and control options for the maize cob borer, *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae), were conducted in the different agro-ecological zones of the Republic of Benin, West Africa.

Country-wide surveys in maize fields and on-station experiments revealed that the borer is the most abundant and the most damaging pest of pre-harvest maize. The damage of *M. nigrivenella* also continues during the first two months of the storage period. A simple mathematical model, relating *M. nigrivenella* cob infestation levels at harvest and maize yield losses due to the borer was developed. Yield losses caused by *M. nigrivenella* in the field could be determined by calculating the percentage of cobs infested by the borer.

Pre-harvest infestation of maize cobs by *M. nigrivenella* was also associated with *Aspergillus flavus* infection and subsequent aflatoxin contamination in stored maize

The incidence of the borer varied with the agro-ecological zones. The borer is particularly damaging in the Guinea Savannas of central and northern Benin. The evaluation of the host plant range revealed the polyphagous feeding behaviour of *M. nigrivenella*. Moreover, the high abundance of *M. nigrivenella* in the Guinea Savannas was most likely due to the overlapping fruiting periods of host plants in these zones.

Life table studies of *M. nigrivenella* on natural host plant materials demonstrated the preference of the borer for jackbeans, *Canavalia enseiformis* (L.) DC. (Fabaceae). In order to avoid that this new cover crop in West Africa constitutes a potential source of infestation of *M. nigrivenella* for neighbouring maize fields, planting of jackbeans should be timed in such way that its fruiting period precedes that of maize.

Larvae of *M. nigrivenella* showed an aggregated distribution on fruits of most wild and cultivated host plant species, except for *Gardenia* spp. (Rubiaceae). Spatial distribution on a particular host plant species was highly correlated to the respective

fruit sizes. Sample sizes and time expenditures needed to estimate *M. nigrivenella* populations at a precision level of 25% on the various host plants were determined.

The flight activity of *M. nigrivenella* moths was affected both by weather factors and availability of fruits of major host plant species.

Delaying the harvest of maize increased the incidence of the borer. Sun-drying of cobs at harvest for a week, however, reduced further damage in store.

Investigations on the natural enemies revealed only few parasitoid species attacking *M. nigrivenella* and their presence was associated with the different wild host plant species. No natural enemies could be collected from maize and other crops. Parasitoids were found only on wild host plant species with the pupal parasitoid, *Antrocephalus crassipes* Masi (Hymenoptera: Chalcididae) being the most abundant species. Levels of parasitism were rather low. In future, biological control of *M. nigrivenella* should therefore pursue the 'novel-association' or the re-distribution approach of natural enemies, since highly efficient parasitoids of *M. nigrivenella* were found e.g., in Cameroon.

Zusammenfassung

Ökologie und integrierte Bekämpfung des Maiskolbenbohrers *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) in Westafrica

Mamoudou Sétamou

Untersuchungen zur Ökologie und integrierten Bekämpfung des Maiskolbenbohrers *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) wurden in den unterschiedlichen agrar-ökologischen Zonen der Republik Benin (Westafrika) durchgeführt.

Mittels landesweiter Prospektionen in Maisfeldern, sowie Feldversuchen auf der Station des International Institutes of Tropical Agriculture (IITA) in Abomey-Calavi, Benin konnte nachgewiesen werden, daß *M. nigrivenella* ein extrem häufiger und sehr bedeutender Schädling von Feldmais in Benin ist. Des weiteren verursacht *M. nigrivenella* zusätzliche Maisverluste während der ersten zwei Lagermonate. Ein einfaches mathematische Modell, daß den prozentualen Anteil der von *M. nigrivenella* befallenen Kolben zum Zeitpunkt der Ernte und die Maisverluste in Beziehung setzt, wurde entwickelt. So konnten durch *M. nigrivenella* verursachte Ertragsverluste einfach durch den Befall der Kolben durch den Schädling ermittelt werden.

Ein initialer Feldbefall von Maiskolben durch *M. nigrivenella* war darüber hinaus mit einer nachfolgend erhöhten Infektion des Mais durch *Aspergillus flavus* im Lager korreliert, was zu einem stärkeren Kontamination des Lagergutes durch Aflatoxine führte.

Das Auftreten von *M. nigrivenella* variierte in den unterschiedlichen agrar-ökologischen Zonen Benins. Besonders hohe Schäden wurden in den Guinea Savannen von Zentral- und Nordbenin verzeichnet. Untersuchungen zum Wirtspflanzenspektrum von *M. nigrivenella* unterstrichen die polyphage Natur des Schädlings. Die starke Präsenz von *M. nigrivenella* in den Guinea Savannen wurde höchstwahrscheinlich durch die überlappenden Perioden der Fruchtbildung bei mehreren natürlichen Wirtspflanzen hervorgerufen.

In Lebenstafeluntersuchungen mit *M. nigrivenella* auf natürlichen Wirtspflanzen zeigten die Larven eine starke Präferenz für *Canavalia enseiformis* (L.) DC.

(Fabaceae), einem unlängst nach Westafrika importierten Bodenbedecker. Um zu verhindern daß sich *C. enseiformis*-Felder zu einer möglichen Infestationsquelle von *M. nigrivenella* für benachbarte Maisfelder entwickeln, sollte der Aussaattermin des Bodenbedeckers so gewählt werden, daß die Fruchtbildung bei *C. enseiformis* vor der bei Mais einsetzt.

In den meisten Früchten von wilden und kultivierten Wirtspflanzen von *M. nigrivenella*, außer bei *Gardenia* spp. (Rubiaceae), traten die Raupen in aggregierter Form auf. Die Verteilung und das Auftreten der *M. nigrivenella* Larven war eng mit der Fruchtgröße der unterschiedlichen Wirtspflanzen korreliert. Stichprobenumfänge und der zeitliche Aufwand um die Dichte von *M. nigrivenella* Populationen auf den unterschiedlichen Wirtspflanzen mit einem Präzisionsniveau von 25% abschätzen zu können wurden entwickelt.

Die Flugaktivität der adulten Falter von *M. nigrivenella* wurde sowohl von meteorologischen Faktoren als auch von der Präsenz von Früchten wichtiger natürlicher Wirtspflanzen bestimmt.

Ein späte Maisernte erhöhte den Befall durch den Schädling, wohingegen eine zusätzliche Trocknung der Kolben in der Sonne vor der Einlagerung die Nachernteverluste im Lager deutlich reduzierte.

In Untersuchungen zum Spektrum der natürlichen Feinden von *M. nigrivenella* konnten nur wenige Parasitoidenarten identifiziert werden, deren Auftreten des weiteren mit dem von einzelnen natürlichen Wirtspflanzen des Schädlings verbunden waren. Im Maisökosystem sowie in anderen landwirtschaftlichen Kulturen konnten keine natürliche Feinden entdeckt werden. Mehrere Parasitoidenarten wurden hingegen in Assoziation mit wilden Wirtspflanzen von *M. nigrivenella* identifiziert, wobei der Puppenparasitoid *Antrocephalus crassipes* Masi (Hymenoptera: Chalcididae) sich als die häufigste und bedeutendste Parasitoidenart erwies. Nichtsdestotrotz wurden nur geringe Parasitierungsraten ermittelt. In Zukunft sollten sich demnach Aktivitäten im Bereich der biologischen Bekämpfung von *M. nigrivenella* maßgeblich auf den 'neue Assoziationen-' bzw. 'Redistributionsansatz' konzentrieren, da sehr effiziente Parasitoidenarten von *M. nigrivenella* beispielsweise unlängst in Kamerun entdeckt wurden.

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1 Introduction

Maize, *Zea mays* L. (Poacae), is one of the most important food crops grown in Africa. In Benin, maize constitutes the principal staple for the majority of the population (Miracle, 1966; CIMMYT, 1988) and it is grown both as a subsistence and as a commercial crop. Maize is cultivated throughout the country, and in 1994 the area covered by maize represented approximately 40% of the total land cultivated (MDR, 1995). In theory maize has a high yield potential, but yields in Benin are far below the world average. Average yields of 950 kg/ha are common in the country (MDR, 1995). Many factors, such as low soil fertility, inadequate farming practices, environmental stress, pests and diseases are responsible for these yields.

Lepidopterous stem and cob borers are considered to be the major insect pests of maize in Africa. The cob borer, *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) is one of the key borers attacking maize in West Africa (Bosque-Pérez & Mareck, 1990; Shanower *et al.*, 1991, Moyal & Tran, 1991a). Because of its feeding behaviour, i.e., attacking the maize grain, *M. nigrivenella* constitutes a major limiting factor for maize production in West Africa. Typically, more than half of the cobs in the field are infested by the borer (Whitney, 1970; Sétamou, 1996), but reported yield losses vary only between 5 and 15% (Moyal & Tran, 1991b; Sétamou *et al.*, 1999a). *Mussidia nigrivenella* damage, however, also predisposes maize to pre- and post-harvest infestations by beetle pests, *Aspergillus flavus* Lk. Fr. infections and subsequent aflatoxin contamination (Sétamou *et al.*, 1998). Hence, both the quantity and the quality of the maize are affected by *M. nigrivenella*.

The distribution of the genus *Mussidia* is mostly limited to Africa. Of eight known species, five are native to Africa, two to Réunion and Madagascar island in the Indian Ocean, and one to the Himalayan region (Janse, 1941). Although described for the first time in 1888 by Ragonot (Moyal, 1988), *M. nigrivenella* is a poorly known species. Most of the reports on *M. nigrivenella* are based on scattered observations of the borer in stored commodities and mainly cacao. *Mussidia nigrivenella* is widely distributed throughout sub-Saharan Africa (Fig 1.1; CAB, 1996). It has been reported from different parts of the African continent (Janse, 1941; Le Pelley, 1959; Whitney, 1970; Staeubli, 1977; Bordat & Renand, 1987; Moyal, 1988), but the borer is particularly abundant in West Africa where it has been recently recognised as an economically important pest of maize (Whitney, 1970; Atachi, 1985; Bosque-Pérez & Mareck, 1990; Moyal & Tran 1991; Shanower *et al.*, 1991; Silvie, 1993). Incidence of the borer in maize varied between the different agro-ecological zones, with a higher prevalence of *M. nigrivenella* in the Savanna zones of West Africa (Moyal, 1988; Gounou *et al.*, 1994; Sétamou, 1996). The reasons for this variability in *M. nigrivenella* incidence and distribution are poorly understood.

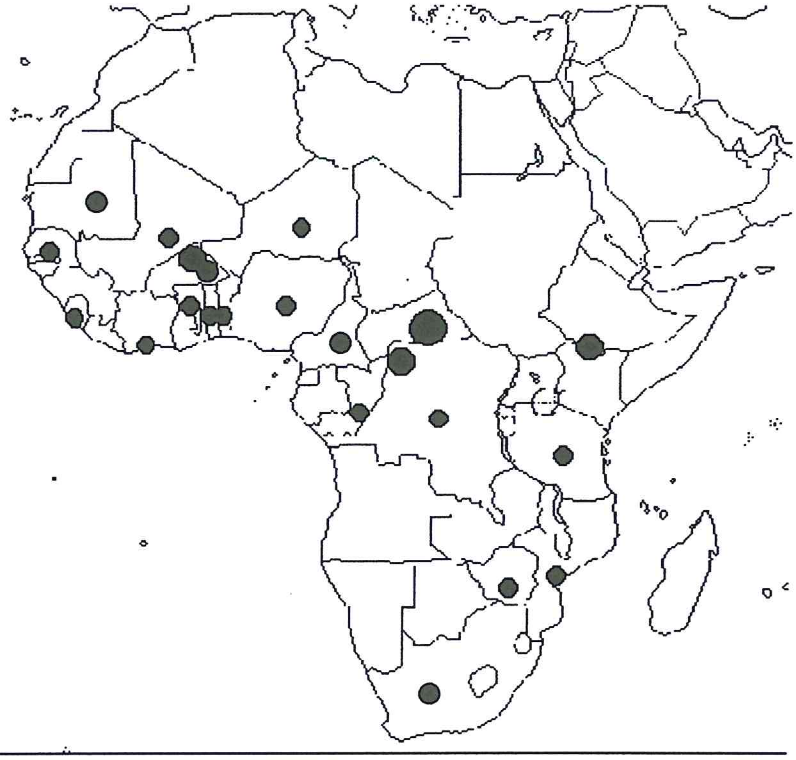

Fig. 1-1 Current distribution of *M. nigrivenella* in Africa (● present).

Mussidia nigrivenella is a highly polyphagous herbivore (Moyal 1988; Silvie, 1993; Sétamou, 1996). In addition to maize, the borer attacks a great variety of plants, including cotton (*Gossypium hirsutum* L.), cocoa (*Theobroma cacao* L.), lima bean (*Phaseolus lunatus* L.), jackbean (*Canavalia enseiformis* (L.) DC.), velvetbeans (*Mucuna pruriens* DC.), the néré-tree (*Parkia biglobosa* (Jacq.) Benth.), and the shea butter-tree (*Butyrospermum parkii* (G. Don) Kotschy) (Moyal, 1988; Silvie, 1993; Sétamou, 1996).

Mature fruiting structures of its various host plants are attacked by the borer, and the feeding of larvae on the reproductive plant parts often result in damage influencing yield directly. On maize, the eggs are laid on the silks and the husk of the cob

(Moyal, 1988; Bosque-Pérez & Mareck, 1990). Soon after emergence, neonate larvae enter the cob and feed cryptically in the grains, often causing extensive damage in maize (Fig. 1.2). Prior to pupation, the last instar larvae leave the grains and pupae are formed in a tough cocoon near the exit holes. The pupae develop in 10-12 days. Adults (Fig 1.2) mate the same day of emergence, and no pre-oviposition period have been observed. Oviposition lasts for 5-7 days. The generation time of the borer is roughly 38 days on maize (Bordat & Renand, 1987; Moyal & Tran, 1991b; Bolaji & Bosque-Pérez, 1998; Sétamou *et al.*, 1999b).

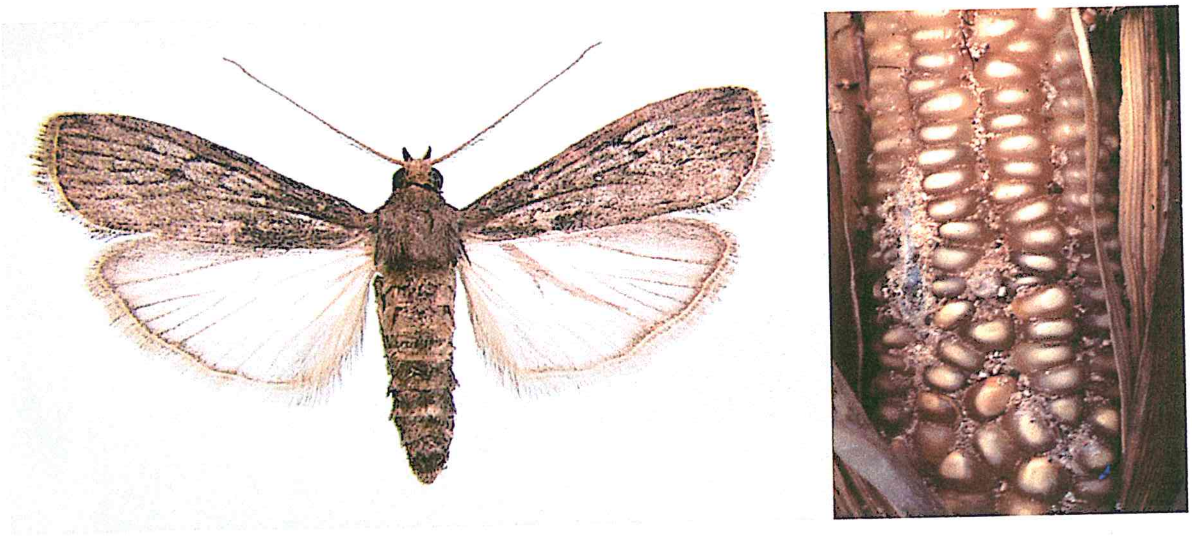

Fig. 1-2 Adult of *M. nigrivenella*, and damage done by its larvae on maize cob.

In order to meet the food requirements of the rising population in West Africa, every effort needs to be made to increase the agricultural productivity. The reduction of losses in quality and quantity of maize grain due to pests such as the cob borer *M. nigrivenella* is of utmost importance.

In the developed countries of the north, pest control largely depends on synthetic insecticides. However, due to the cryptic nature of the larvae, *M. nigrivenella* is particularly difficult to control with insecticides (Moyal, 1988). While contact insecticides do not affect the borer, the use of systemic insecticides with a long persistence in maize entails grave risks of poisoning the consumer. In general, insecticides are most often beyond the economic reach of West African farmers, can cause resistance in pests, have adverse effects on the environment (e.g., destruction of natural enemies of the pests), and can impose serious health hazards to both farmers and consumers (Balk & Koeman, 1984). Finally, synthetic insecticides have to be applied repeatedly and their impact on pest population dynamics is by definition not sustainable.

Host plant resistance, habitat management and biological control, including the use of natural enemies, are methods of pest control that have attracted increasing attention as alternatives to conventional plant protection, relying only on synthetic insecticides. Such an approach could also be implemented against *M. nigrivenella*, though few studies have been conducted up to date on the potential of these various control options against the borer. Despite some reports on the biology, and the pest status of *M. nigrivenella* in various countries in West Africa (Whitney, 1970; Daramola, 1986; Bosque-Pérez & Mareck, 1990, Moyal & Tran, 1991, Shanower *et al.*, 1991; Silvie, 1993, Gounou *et al.*, 1994; Sétamou, 1996), there is a conspicuous lack of sound data on the ecology and natural mortality factors of the borer. Such information is crucial for the development of sustainable management strategies against *M. nigrivenella*.

The overall aim of the present study was therefore to provide additional information concerning the pest status, the biology and ecology of *M. nigrivenella* and on the control options that could be applied to reduce the damage and losses due to the borer.

In the following chapter, Chapter 2, we attempt to assess the importance of the borer in maize. During country-wide surveys we gathered the necessary data on *M. nigrivenella* distribution and incidence in Benin. In addition, in on-station field experiments we sought to determine the damage potential of the borer. Simple and rapid techniques for evaluation of maize yield losses incurred due to the borer were also developed.

Research on qualitative maize losses by *M. nigrivenella* are reported in Chapter 3. The objectives were to describe the interactions between *M. nigrivenella* infestations and fungal infections of maize, especially by the aflatoxin-producing fungus *Aspergillus flavus* Lk. Fr.

Chapter 4 describes the host plant range of *M. nigrivenella* in the different agro-ecological zones of Benin. This information will help to understand why *M. nigrivenella* is more prevalent in the Savannas of West Africa. Studies on the population dynamics on various wild and cultivated host plants were conducted and their potential use as reservoirs or trap plants of the borer is discussed.

In Chapter 5, the biological parameters of *M. nigrivenella* were studied on different host plants, including maize and two important cover crops. These data will improve our understanding of the feeding behaviour of the borer in fields, and also might predict the number of generations that can occur in a cropping season.

The main objectives of chapter 6 were to describe the spatial distribution of *M. nigrivenella* on various host plants, and to design sampling techniques for accurate estimations of the borer populations with a given precision level. The sampling related-costs were also determined.

Long-term data on flight activity of *M. nigrivenella* as affected by host plant availability and weather factors is presented in chapter 7.

In chapter 8, we studied the effect of two farming practices, i.e., varying the harvest date and sun-drying of the maize prior to storage on the infestation and damage levels of *M. nigrivenella* in maize. The objective was to develop practical recommendations for farmers with the aim to minimise losses due to the borer.

Chapter 9 presents an evaluation of different parasitoid species as natural enemies of *M. nigrivenella* and their impact on borer populations on the different host plants. Logistic multiple regression analyses were used to determine the most important factors influencing the level of parasitism of *M. nigrivenella* larvae and pupae.

In the last chapter, i.e., chapter 10, we discuss the implications of our results for the future development of sustainable control strategies against *M. nigrivenella*.

These studies were conducted over four years, from 1994 until 1997, both in farmers' fields and on the station of the International Institute of Tropical Agriculture (IITA) in Abomey-Calavi, Republic of Benin, West Africa.

2 Monitoring and modeling of field infestation and damage by *M. nigrivenella*[1]

2.1 Abstract

In many countries in West Africa, the pyralid cob borer *Mussidia nigrivenella* Ragonot occasionally causes severe damage to pre- and post-harvest maize. Between 1992-95, the distribution of and damage caused by *M. nigrivenella* were studied in Benin using survey data and an on-station field experiment. The borer was distributed across the whole country, and at maturity on average 25% of the cobs sampled in maize fields were infested. Damage levels varied with agro-ecological zones and were highest in the Guinea Savannas. However, borer-related yield losses were comparatively low. Results of the on-station field experiment showed that three insecticide treatments did not provide sufficient control. A model was developed to estimate maize losses caused by *M. nigrivenella*, using the percentage of infested cobs which explained 93% of the variance. Extrapolation of field data indicated a 25% yield loss once a 100% infestation of maize cobs was reached. For surveys in maize fields the model is a valid tool for a rapid assessment of crop losses caused by lepidopteran cob borers.

2.2 Introduction

Lepidoteran stem and cob borers are the most important field pests of maize in West Africa (Bosque-Pérez & Mareck, 1990). The predominant species in Benin are the noctuid *Sesamia calamistis* Hampson, the pyralids *Eldana saccharina* Walker and *Mussidia nigrivenella* Ragonot, and the tortricid *Cryptophlebia leucotreta* (Meyrrick) (Atachi,1987; Shanower *et al.*, 1991). The impact of the stemboring *S. calamistis* and *E. saccharina* in Benin has been extensively studied (Atachi, 1989; Shanower *et al.*, 1991; Schulthess *et al.*, 1991; 1997; Sétamou *et al.*, 1995) but little information exists on yield loss caused by *M. nigrivenella* although it is widely distributed and represents about 70% of the pest populations found in maize cobs (Sétamou *et al.*, 1998). *M. nigrivenella* attacks maize in the field and continues to damage the grain

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during the first 2 months of storage (Sétamou, 1996). The objective of this study was to provide information on the distribution and pest status of *M. nigrivenella* in Benin. For this purpose, survey data were collected in the different agro-ecological zones of Benin and subsequently used for the development of a model to elucidate the relationship between infestation levels of and the yield losses caused by *M. nigrivenella*. In addition, the damage potential of *M. nigrivenella* in artificially infested plots was compared with insecticide treated maize in an on-station field trial.

2.3 *Materials and Methods*

Surveys. Four surveys during the main growing seasons between 1992 and 1995 were conducted in the 4 agro-ecological zones of Benin, i.e., from south to north: the Forest Savanna Mosaic (FSM), the Southern Guinea Savanna (SGS), the Northern Guinea Savanna (NGS), and the Sudan Savanna (SS). For the 1992 and 1993 surveys, maize cobs were sampled in fields at maturity, just before harvest. A total of 28 and 71 fields were sampled in 1992 and 1993, respectively, across the different agro-ecological zones. In 1994 and 1995, a different sampling procedure was used: 20 and 15 fields per agro-ecological zone were surveyed in 1994 and 1995, respectively. The fields were randomly chosen, at a distance of 10-15 km in the FSM, and of 40-50 km in the more expansive 3 northern zones (SGS, NGS, and SS) (Fig. 2.1). For assessment of percent cob damage, pest numbers and species composition in each field, a randomly selected destructive sample of 20 cobs was taken from each field. The fields were divided into 4 quadrants, and 5 cobs were randomly sampled in each.

Model. The grain losses (GL) due to lepidopteran cob borers, were calculated by subtracting the actual grain weight (GW) from the predicted healthy grain weight (GW_h):

$$GL\ (g) = GW_h - GW, \qquad (1)$$

$$\text{with } GW = R_g \times Cw, \qquad (2)$$

$$\text{and } GW_h = R_g\ [Cw\ (1 - D) + Cw\ (R_d \times D)], \qquad (3)$$

Rg is the cob to grain ratio, computed using 500 healthy cobs collected at harvest during the surveys in 1994 (Fig 2.2). Cw is the dehusked cob weight measured in g. D is the percentage of grains damaged by lepidopteran borers per cob. R_d is the ratio between healthy and damaged grains, determined by regressing the weight of 20 damaged on 20 healthy grains; grains were randomly taken from the same cob, for a total of 100 cobs collected during the surveys in 1994 (Fig 2.3).

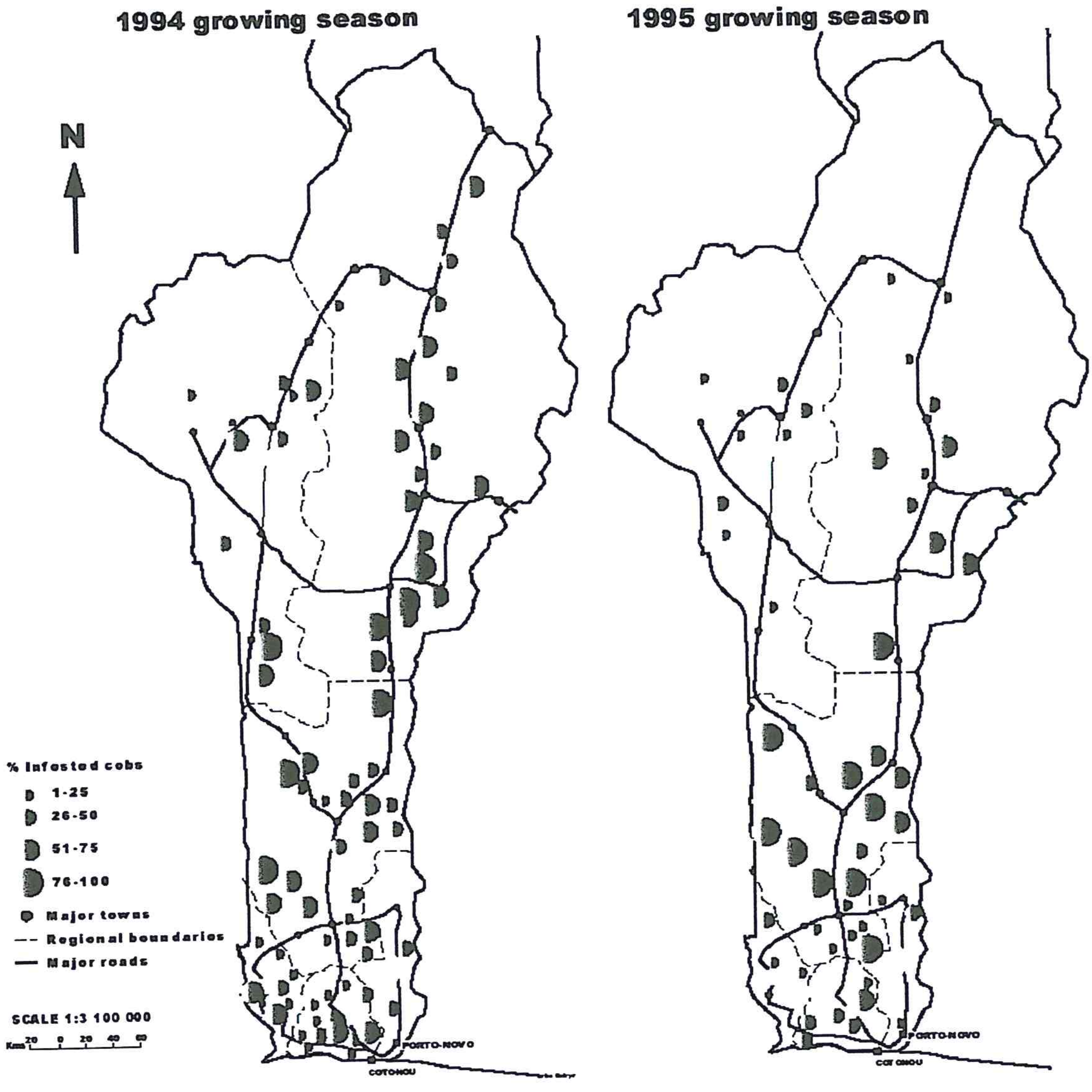

Fig. 2-1 Incidence of *M. nigrivenella* in maize fields before harvest in Benin.

The survey data of 1994 and 1995 were used to develop a regression model, relating the average grain loss per field to the level of cob infestation by *M. nigrivenella* at harvest. The model was developed to predict losses due to *M. nigrivenella* at harvest. The data sets of 1992 and 1993 were used to validate the predictions of field losses by the model. The predicted yield losses were compared to the observed losses, using a t-test with Bonferroni-probability-adjustment (Sokal & Rohlf, 1995).

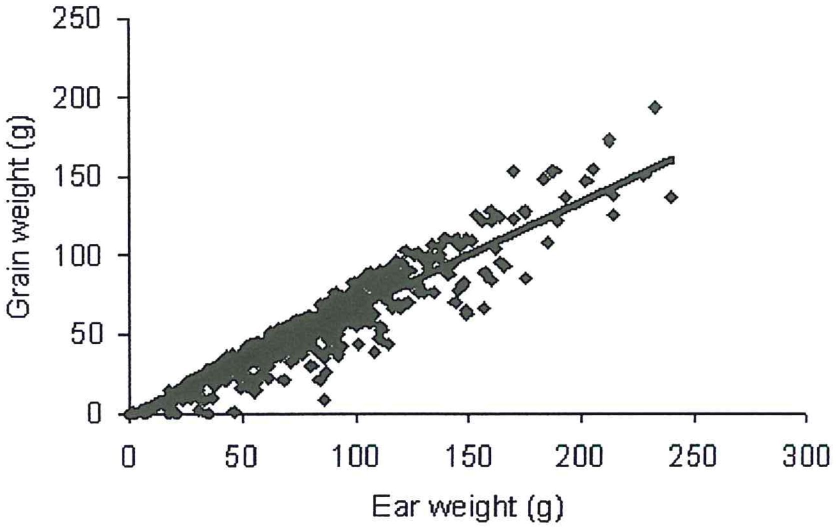

Fig. 2-2 Relationship between healthy cob weight and corresponding grain weight of maize grown in Benin in 1994 ($y = 0.67x$, $R^2 = 0.97$, $N = 500$, $P < 0.001$).

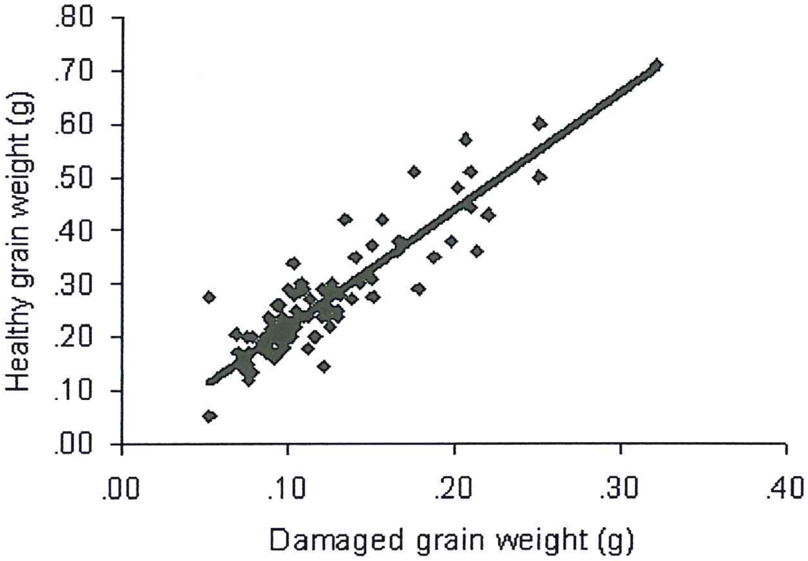

Fig. 2-3 Relationship between healthy grain weight and damaged grain weight collected on the same cob ($y = 2.20x$, $R^2 = 0.80$, $N = 100$, $P < 0.001$).

On-station field experiment. The field trials were conducted at the Benin station of the International Institute of Tropical Agriculture (IITA) in Cotonou, Republic of Benin, during the main growing season of 1994 and 1995. The 90-days maize variety

TZESR (Tropical *Zea* Early Maturity and Streak Resistant) was used. The experiment was laid out as a randomized block design, with 3 and 4 blocks (i.e., replications) in 1994 and 1995, respectively. The distance between blocks was 2 m. The blocks contained 3 plots (for the respective treatments), separated by a distance of 1 m. Each plot consisted of 200 maize plants, sowed at a distance of 80 cm (between rows) by 40 cm (within rows). The treatments consisted of an insecticide treatment control (T0), cobs artificially infested with larvae of *M. nigrivenella* (T1), and naturally infested plants (T2). In the T0 treatment the plants were sprayed with Cymbush (ai cypermethrin) at the rate of 0.15 kg (ai)/ha 5 weeks, 7, and 9 weeks after sowing (WAS). The insecticide was sprayed using an Electrodyn sprayer (Imperial Chemical Industries PLC, England). Two rows were sprayed at the same time, keeping the nozzle 40 cm above the canopy of the crop. At the soft dough stage, i.e., 9 WAS, the T1 plots were artificially infested with *M. nigrivenella* from a stock culture, by placing 5 first instar with a fine camel hair brush on the silks of each cob. At harvest, 10 cobs were randomly selected from the 8 central rows of each plot by avoiding the cobs of the 2 plants at the end of each row.

Data collection. In the surveys and in the field experiments, cobs were dissected immediately after sampling. De-husked cob weight, number of all pests per cob and the percentage of grains damaged per lepidopteran species were recorded. Borer species feeding exclusively on grains, like *M. nigrivenella* and *C. leucotreta*, start their damage from the tip of the cob. *Cryptophlebia leucotreta* larvae penetrate the grains and feed inside without producing any noticeable frass, whereas *M. nigrivenella* larvae produce conspicuous amounts of silky frass, which is easily detected as the larvae bore into the grains (Sétamou, 1996). Stem borers like *S. calamistis* and *E. saccharina* also feed on grains, but the type of damage they produce differs considerably from that of cob borers. *Sesamia calamistis* larva damage goes from the surface to the inner part of the grain. This borer is often hidden by the frass it produces (Shanower *et al.,* 1991). *Eldana saccharina* larva damage starts from the rachis with conspicuous amounts of wet frass on the surface of the grains (Bosque-Pérez & Mareck, 1990). For beetle pests, the numbers were recorded per species but their damage was recorded without any species distinction.

Maize variety was not considered in the analysis. However, farmers in the FSM and partly also in the SGS generally had planted 3-months maize varieties. In the other zones, mainly 4-months varieties were grown.

Statistical Analysis. Analyses were performed with SPSS for Windows (Norusis & SPSS Inc., 1993). The variances of the different parameters measured during the 4 surveys were compared using the F-test (Sokal & Rohlf, 1995). Due to the high variability between years in most of the pest variables measured, the data were analyzed separately for agro-ecological zone effects. Data were subjected to analysis of variance (ANOVA), and in case of significant F-values at $P < 0.05$, the means were compared with the Student Newman Keuls (SNK) test (Zar, 1974).

Correlations were calculated to investigate relationships between cob weight and different *M. nigrivenella* variables. Stepwise multiple regression analyses (Sokal & Rohlf, 1995) were used to evaluate the impact of the different lepidopteran pests on the total grain damage.

In the field experiments, differences in the various data between treatments were tested using a 1-way ANOVA. Means were separated using the SNK sequential mean comparison (Zar, 1974).

To normalize variances for all analyses, the numbers of insects were square root-transformed, after adding a constant factor of 0.5 to all data points and all percentage values, i.e. damage levels and levels of cob infestation, were arcsine-transformed prior to analysis.

2.4 Results

Surveys. In all years, 4 lepidopteran pests, i.e., *M. nigrivenella*, *C. leucotreta*, *S. calamistis*, and *E. saccharina*, and in 1993 only also *Busseola fusca* Füller (Lepidoptera: Noctuidae) were recorded damaging maize (Table 2.1). In addition, 4 beetle pests, i.e., *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae), *Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae), *Carpophilus* spp. (Coleoptera: Nitidulidae) and *Cathartus quadricolis* Guérin (Coleoptera: Silvanidae) were found in field-sampled maize (Table 2.1). In all years, *M. nigrivenella* was the most abundant lepidopteran pest surveyed, and accounting for > 80% of all cob feeding lepidopteran species collected in maize cobs (Table 2.1).

Mussidia nigrivenella numbers per cob were highest in the Guinea savannas (SGS and NGS), and lowest in the FSM. Considerable between-year variation of *M. nigrivenella* density in the cobs was recorded in the SS (Table 2.1). All other lepidopteran pests were only observed in low numbers. In the FSM, *S. calamistis* was the second most important cob feeding species, whereas *E. saccharina* was found only occasionally on cobs and *C. leucotreta* was mainly observed feeding on the silk (Table 2.1).

Mussidia nigrivenella was widely distributed across the country and was collected in > 90% of the fields (Fig. 2.1 and Table 2.2). The highest percentage of infested fields was always found in the NGS, followed by the SGS. In the FSM and SS, percentage of infested fields varied considerably between the years (Table 2.2).

Across zones and years about 25% of the cobs were infested by *M. nigrivenella* (Table 2.2). Within each year, significant differences in the percentage of infested cobs were found between the agro-ecological zones. As for the percentage of infested fields, lowest values of infested cobs were recorded in the FSM and highest in the NGS, and highest between-year variability in the SS (Table 2.2). Grain damage due to *M. nigrivenella* per cob followed the same trend (Table 2.2). Damage caused by *M. nigrivenella* was much higher than that of other lepidopteran cob borers (Table 2.2).

Multiple regression analyses showed that in all years most of the grain damage was caused by lepidopteran pests (Table 2.3). Beetles significantly contributed to grain damage only in 1994, and their total contribution to the explained variance of the model did not exceed 7%. *Mussidia nigrivenella* was the most important pest, significantly related to grain damage in all 4 surveys, followed by *S. calamistis* (Table 2.3). *Busseola fusca* numbers significantly contributed to the model only for the 1993 survey, but as for *S. calamistis*, its densities were considerably lower than that of *M. nigrivenella* (Table 2.3). The higher partial regression coefficients of *S. calamistis* compared to *M. nigrivenella* in the 1993, 1994 and 1995 models (Table 2.3) suggests, that the individual damage caused by the first is more important than that of the latter borer species. However, in all surveys *M. nigrivenella* was the most abundant borer species in all agro-ecological zones. Therefore, the subsequent analyses of the data focused on *M. nigrivenella*.

Table 2-1 Mean number (±SEM) of insect pests found damaging maize cobs in Benin.

Pest species	Survey year and agro-ecological zones[1]															
	1992				1993				1994				1995			
	FSM (5)[2]	SGS (8)	NGS (9)	SS (4)	FSM (9)	SGS (20)	NGS (23)	SS (19)	FSM (20)	SGS (20)	NGS (20)	SS (20)	FSM (15)	SGS (15)	NGS (15)	SS (15)
Lepidoptera																
M. nigrivenella	0.21[3] ±0.11	0.63 ±0.27	1.34 ±0.43	0.55 ±0.19	0.42 ±0.18	2.07 ±1.21	2.23 ±1.27	0.64 ±0.25	0.52 ±0.13	0.94 ±0.17	2.17 ±0.37	0.80 ±0.19	0.40 ±0.15	3.02 ±0.55	1.07 ±0.35	0.04 ±0.02
S. calamistis	0.04 ±0.03	0.05 ±0.05	0.01 ±0.01	0.00	0.12 ±0.06	0.07 ±0.03	0.02 ±0.01	0.00	0.14 ±0.05	0.05 ±0.02	0.01 ±0.01	0.00	0.09 ±0.04	0.06 ±0.02	0.01 ±0.01	0.00
E. saccharina	0.05 ±0.02	0.12 ±0.07	0.00	0.00	0.14 ±0.05	0.38 ±0.27	0.01 ±0.01	0.00	0.04 ±0.02	0.05 ±0.03	0.03 ±0.02	0.00	0.06 ±0.03	0.06 ±0.03	0.04 ±0.02	0.01 ±0.01
C. leucotreta	0.05 ±0.02	0.09 ±0.06	0.06 ±0.02	0.02 ±0.01	0.06 ±0.02	0.07 ±0.03	0.05 ±0.02	0.03 ±0.02	0.13 ±0.05	0.06 ±0.01	0.02 ±0.01	0.02 ±0.01	0.22 ±0.06	0.24 ±0.08	0.10 ±0.04	0.11 ±0.04
B. fusca	0.00	0.00	0.00	0.00	0.14 ±0.06	0.72 ±0.23	0.28 ±0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera																
S. zeamais	nr[4]	nr	nr	nr	nr	nr	nr	nr	3.26 ±1.13	0.49 ±0.18	2.13 ±0.84	0.24 ±0.17	1.18 ±0.49	0.42 ±0.18	0.00	0.76 ±0.71
C. quadricollis	nr	nr	nr	nr	nr	nr	nr	nr	2.62 ±1.08	0.73 ±0.37	0.72 ±0.19	0.03 ±0.02	3.06 ±1.43	0.67 ±0.39	0.29 ±0.19	0.02 ±0.02
Carpophilus spp.	nr	nr	nr	nr	nr	nr	nr	nr	0.29 ±0.18	0.64 ±0.47	0.10 ±0.05	0.01 ±0.01	0.08 ±0.03	0.44 ±0.13	0.02 ±0.01	0.01 ±0.01

[1] FSM = Forest Savanna Mosaic, SGS = Southern Guinea Savanna, NGS = Northern Guinea Savanna, and SS = Sudan Savanna.
[2] Number of fields sampled.
[3] Values are means of 20 cobs sampled per field.
[4] nr = Data not recorded.

Table 2-2 Infestation of *M. nigrivenella* and damage levels of *M. nigrivenella* and other lepidopteran cob borers in field-sampled maize cobs (Benin, from 1992 to 1995).

Ecological zone	Fields infested by *M. nigrivenella* (%)				Infested cobs per field by *M. nigrivenella* (%)[1]				Mean % grain damaged per cob by *M. nigrivenella*[2]				Mean % grain damaged per cob by other cob borers			
	1992	1993	1994	1995	1992	1993	1994	1995	1992	1993	1994	1995	1992	1993	1994	1995
FSM[3]	72.5	67.5	90.0	93.3	9.2^a	17.9^a	35.3^a	21.7^b	2.6^a	1.4^a	4.3^a	1.0^a	0.8	1.2^b	1.3^{ab}	1.0^b
SGS	97.5	88.6	95.0	100	38.0^b	59.3^c	40.8^a	62.0^d	11.0^b	8.4^c	4.6^a	5.7^c	0.7	1.8^b	1.7^b	0.6^b
NGS	100	100	100	93.3	47.8^b	62.0^c	69.3^b	42.7^c	8.1^b	8.9^c	6.9^b	3.3^b	0.7	1.7^b	0.8^a	0.7^b
SS	90.0	58.4	90.0	46.7	45.0^b	32.6^b	39.8^a	6.5^a	2.0^a	5.0^b	2.7^a	0.2^a	0.5	0.2^a	0.5^a	0.1^a
Prob > F					<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	>0.05	<0.05	<0.05	<0.05

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[1] Means followed by the same letter in each column are not significantly different (Student Newmans Keuls test).
[2] Prior to analysis, damage level and percent infested cobs were arcsine-transformed; means of original data are presented in the table.
[3] FSM = Forest Savanna Mosaic, SGS = Southern Guinea Savanna, NGS = Northern Guinea Savanna, and SS = Sudan Savanna.

Table 2-3 Multiple regression analysis of total grain damage on the mean numbers of feeding insects per cob.

		B[1]	SE[2]	t	*P*	Mean[3]
1) Dependent variable‘	Y % total grain damaged[5]		0.13			6.01
Independent variables	Intercept	-12.75	7.20	2.62	<0.05	-
	X1 no. *M. nigrivenella*	14.48	1.83	6.38	<0.01	0.58
	X2 no. *S. calamistis*	16.32	7.22	2.32	<0.05	0.05
Adjusted-R^2 = 0.68, No. of fields = 26						
2) Dependent variable	Y % total grain damaged		0.52			5.99
Independent variables‘	Intercept	-56.92	8.07	7.05	<0.01	-
	X1 no. *M. nigrivenella*	11.19	1.62	6.91	<0.01	1.09
	X2 no. *S. calamistis*	40.46	5.89	6.87	<0.01	0.12
	X3 no. *B. fusca*	40.42	8.88	4.55	<0.01	0.05
Adjusted-R^2 = 0.63, No. fields = 71						
3)Dependent variable	Y % total grain damaged		0.48			6.55
Independent variables	Intercept	-9.67	4.71	2.05	0.04	-
	X1 no. *M. nigrivenella*	7.40	0.95	7.79	<0.01	1.11
	X2 no. *S. calamistis*	15.78	5.83	2.71	<0.01	0.05
	X3 no. *S. zeamais*	1.50	0.55	2.73	<0.01	1.28
	X4 no. *Carpophilus sp.*	1.96	0.95	2.05	<0.05	0.36
Adjusted-R^2 = 0.50, No. fields = 80						
4) Dependent variable	Y % total grain damaged		0.54			3.50
Independent variables	Intercept	-24.47	5.19	4.71	<0.01	-
	X1 no. *M. nigrivenella*	7.85	0.71	11.03	<0.01	1.13
	X2 no. *S. calamistis*	33.86	6.92	4.89	<0.01	0.04
Adjusted-R^2 = 0.70, No. fields = 60						

[1] B-values are partial regression coefficients.
[2] SE = standard error.
[3] Mean values of the different variables represented means of untransformed data.
[4] Regression 1), 2), 3) and 4) represent relationships between pests and grain damage for year 1992, 1993, 1994 and 1995, respectively.
[5] Prior to analysis, percentage values were arcsin-, and number of insects $\sqrt{(x + 0.5)}$-transformed.

As shown by the correlation coefficients level of grain damage had a more pronounced effect on cob weight than the numbers of *M. nigrivenella* per cob in all years ($r = -0.39^*$, $r = -0.27^*$, $r = -0.30^*$ and -0.42^* in 1992, 1993, 1994 and 1995, respectively with $P < 0.01$ versus $r = -0.15^*$, -0.12^* , -0.18^* and -0.32^* for 1992, 1993, 1994 and 1995, respectively, with $P < 0.01$). Therefore, the mean percentage of grain damage per field was used as an indicator of the pest status to calculate yield losses due to *M. nigrivenella*.

Model. In the 4 surveys, calculated average grain losses due to lepidopteran cob borers did not exceed 9% of the total healthy grain weight (Table 2.4). As already shown in Table 2.2, a large proportion of the grain damage was due to *M. nigrivenella*. Thus the percentage of cobs infested by *M. nigrivenella* was used to predict grain losses of maize due to lepidopteran cob borers. Regressing percentage yield losses due to cob borers (y) on the percentage of infested cobs by *M. nigrivenella* (x) resulted in highly significant models for the 1994 and 1995 survey data sets (for 1994 $y = 0.88 + 0.27x$, $r^2 = 0.72$, $F = 198.2$, $P < 0.0001$; for 1995 $y = 0.75 + 0.28x$, $r^2 = 0.82$, $F = 257.9$, $P < 0.0001$). No significant differences between the slopes of the 2 models were found ($F = 0.15$, df = 1, 58, $P = 0.70$). Moreover, in both regression models, the intercept did not differ significantly from 0 (for 1994 $P = 0.32$, for 1995 $P = 0.19$). Thus the data of the 1994 and 1995 surveys were pooled and used to develop a linear regression model without intercept. The percentage of cobs infested by *M. nigrivenella* explained 93% of the variation in yield loss due to lepidopteran cob borers ($y = 0.27x$, $r^2 = 0.93$, $F = 1861.3$, df = 1, 140, $P < 0.0001$) (Fig. 2.4).

The validation of the model, using the 1992 and 1993 data sets, gave a good match between the observed and the predicted yield losses at harvest (Table 2.5). For both years, no significant differences between the observed yield losses and the predicted yield losses by the model were recorded.

Table 2-4 Effect of lepidopteran cob borers on maize losses (data represent means ± SEM).

Year and zone[1]	CW[2] (g)	GW$_h$[3] (g)	GL[4] (g)	% GL[5]
1992				
FMS	60.8 ± 4.3	43.6 ± 3.2	2.4 ± 0.9	5.5 ± 1.8
SGS	87.8 ± 5.0	76.7 ± 3.9	3.3 ± 0.6	4.3 ± 1.5
NGS	102.0 ± 5.9	82.6 ± 4.5	5.0 ± 0.7	6.1 ± 1.7
SS	103.6 ± 5.4	78.9 ± 4.1	2.2 ± 0.5	2.6 ± 0.4
1993				
FMS	76.4 ± 5.1	61.8 ± 7.1	2.1 ± 0.7	3.4 ± 0.7
SGS	172.5 ± 12.3	127.8 ± 9.5	6.8 ±1.3	5.3 ± 1.1
NGS	110.7 ± 10.9	81.8 ± 6.6	7.3 ±1.1	8.9 ± 0.8
SS	110.2 ± 11.2	83.5 ± 4.7	4.1 ± 0.7	4.9 ± 0.5
1994				
FMS	68.5 ± 7.1	54.8 ± 4.6	4.0 ± 0.7	7.3 ± 1.2
SGS	89.1 ± 5.8	79.7 ± 6.0	4.7 ± 0.8	5.9 ± 0.6
NGS	112.7 ± 8.6	80.7 ± 5.7	6.7 ± 0.8	8.3 ± 1.3
SS	117.7 ± 8.4	97.6 ± 6.1	4.1 ± 0.9	4.2 ± 0.8
1995				
FMS	54.2 ± 4.6	48.4 ± 3.8	1.1 ± 0.4	2.3 ± 0.8
SGS	84.8 ± 10.3	68.4 ± 5.2	3.9 ± 0.8	5.7 ± 1.1
NGS	88.5 ± 6.5	60.5 ± 6.1	2.3 ± 0.5	3.8 ± 1.0
SS	91.3 ± 5.5	66.7 ± 4.8	0.6 ± 0.1	0.9 ± 0.1

[1] FSM = Forest Savanna Mosaic, SGS = Southern Guinea Savanna, NGS = Northern Guinea Savanna, and SS = Sudan Savanna.

[2] Cw = observed weight of the dehusked cobs (in g).

[3] Expected healthy grain weight computed according to equation $GW_h = R_g\,[Cw\,(1 - D) + Cw\,(R_d \times D)]$, with GW_h = expected healthy grain weight, Rg = cob to grain ratio, and D = percentage of grains per cob damaged by cob borers.

[4] Grain loss due to total cob borers computed according to equation $GL\ (g) = GW_h - Rg \times Cw$, GL (g) = grain loss due to total cob borers (for more information see text).

[5] Percentage grain loss computed according to equation $[GL\ (g) / GW_h] \times 100$.

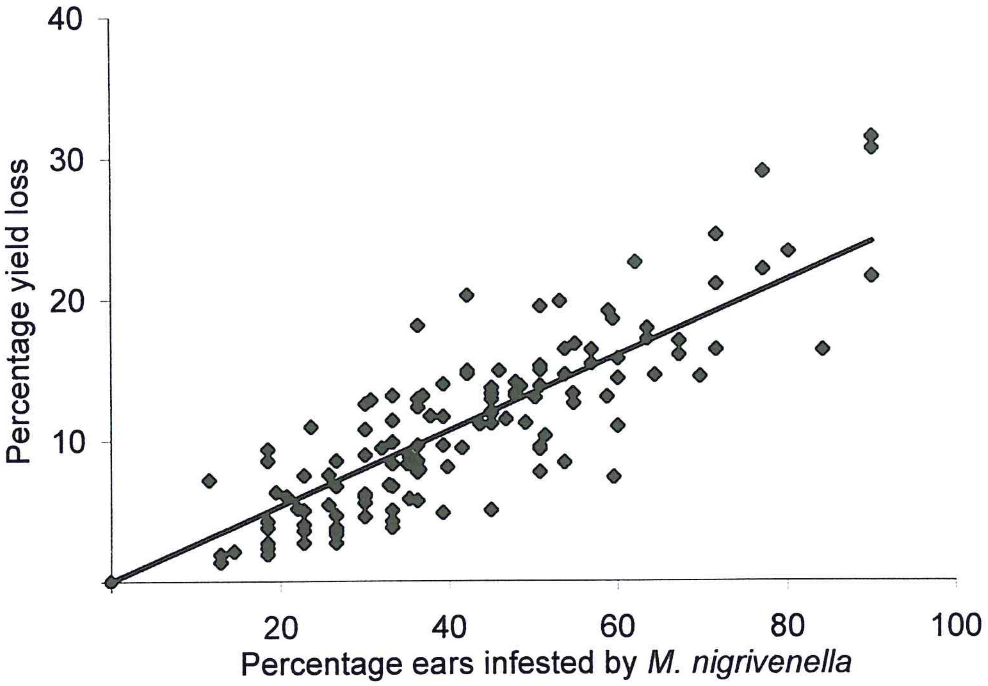

Fig. 2-4 Relationship between percentage yield loss and the percentage of cobs infested by *Mussidia nigrivenella* at harvest in Benin in 1994 and 1995 ($y = 0.27x$, $R^2 = 0.93$, $n = 140$, $P < 0.001$; all percentages arcsine-transformed).

Table 2-5 Observed and predicted grain loss of maize cobs sampled in maize fields.

Year	N	Observed[1] grain loss (%)/cob	Predicted grain loss (%)/cob	t-statistic	Bonferroni adjusted probability	Confidence intervals of difference (P = 0.05)
1992	26	7.6 [3.6, 11.5]	5.9 [3.4, 8.4]	0.97	0.341	-0.9-2.6
1993	71	7.1 [5.2, 8.9]	6.2 [4.9, 7.4]	1.36	0.134	-0.4-2.2

[1] Values in brackets are confidence intervals (*P* = 0.05) of the means.

On-station field experiment. In both years, the percentages of cobs infested by *M. nigrivenella* were significantly higher in the artificial infestation treatment (Table 2.6). In 1994 but not in 1995, no significant differences in percent infested cobs were observed between insecticide treated and naturally infested plots. In 1995, in the T0 and T2 treatments, higher borer infestation levels were recorded compared to the previous year, indicating a year to year variation on *M. nigrivenella* incidence. Artificial infestation did not yield a 100% cob infestation at harvest (Table 2.6), but in 1995 significantly more grains were damaged by *M. nigrivenella* in the T1 (6.5) compared to T0 (2.3) and T2 (3.9) (F = 23.98, df = 2,117, $P < 0.001$). Significantly highest numbers of *M. nigrivenella* per cob were found in the T1 in 1994 but not in 1995 (Table 2.6).

Table 2-6 Effect of artificial and natural infestation of *M. nigrivenella* and an insecticide treatment on infestation levels, population densities and cob weight of maize during 2 field experiments in Benin.

Treatment[1]	Cobs infested (%)[2]		No. of *M. nigrivenella* per cob[2]		Cob weight (g)[2]	
	1994	**1995**	**1994**	**1995**	**1994**	**1995**
T0	31.6a	50.0a	1.0a	1.3ab	97.7b	123.4b
T1	91.7b	87.7c	1.3b	1.4b	78.6a	105.1a
T2	43.3a	62.5b	1.0a	1.1a	92.3b	116.3ab

[1] T0 = insecticide treatment, T1 = artificially infested cobs, T2 = naturally infested cobs.
[2] Means in each column followed by the different letters are significantly different ($p<0.05$; Student Newmans Keuls test).

In both years, the cob weight in the T1 treatment was significantly reduced compared to the insecticide treated control (Table 2.6). Comparing natural and artificial infestation, only in 1994 a significantly reduced cob weight was recorded in the T1 treatment. An artificial infestation of the maize cobs with larvae of *M. nigrivenella* larvae reduced the cob weight of the T1 treatment compared to the insecticide treated control (T0) by an average value of 19.1 g in 1994, and 18.3 g in 1995, respectively. This represents 19.5% for 1994, and 14.8% for 1995, respectively, of the average cob weight in the insecticide treated control plot. In 1995, cobs were in general heavier than in 1994.

2.5 Discussion

Mussidia nigrivenella was the most abundant lepidopteran maize cob borer species throughout all agro-ecological zones of Benin. *M. nigrivenella* has also been reported as a maize pest in forest zones in Nigeria (Bosque-Pérez & Mareck, 1990), Ghana (Gounou *et al.,* 1994) and Côte d'Ivoire (Moyal & Tran, 1991a). The present survey results show a strong effect of agro-ecological zones on the occurrence of *M. nigrivenella* in Benin. The borer was particularly abundant in the Guinea Savannas (SGS and NGS) with only one cropping season. By contrast, lepidopterous stemborers such as *S. calamistis* and *E. saccharina* are generally only of economic importance in areas with 2 cropping seasons, i.e. the FSM and SGS (Gounou *et al.,* 1994, Bosque-Pérez & Mareck 1990, Schulthess *et al.,* 1997) and only during the second cropping season. The high density of *M. nigrivenella* in the Guinea savannas was most likely due to the diversity and abundance of natural host plants of the borer in these zones (Sétamou, 1996). For instance, emerging *M. nigrivenella* populations from pods of the natural host plant *Parkia biglobosa* (Jacq.) Benth. (Mimosaceae) constitute an important source of infestation for nearby maize fields (M.Sétamou, unpublished results).

Cob damage caused by individual *M. nigrivenella* larva was comparatively lower compared to that caused by *S. calamistis*. *Sesamia calamistis* attacks the plant at an early stage and feeds mainly inside the stem; however, older and therefore bigger larvae may bore from the stem into the cob (Bosque-Pérez & Mareck, 1990; Gounou *et al.,* 1994). By contrast, *M. nigrivenella* oviposits on the husks or silk of maize cobs in the milk stage and later (Moyal & Tran, 1991a). Moreover, the larval period of *S. calamistis* lasts for about 30 days (Shanower *et al.,* 1993), and is considerably longer than that of *M. nigrivenella* (Bolaji & Bosque-Pérez, 1998).

The 3 other borer species recorded during the surveys, *B. fusca*, *E. saccharina* and *C. leucotreta*, were only of minor importance. *Busseola fusca* and *E. saccharina* are both stem borers and feed only occasionally on cobs. Moreover, we observed that larvae of *C. leucotreta* feed only on the silk and the upper part of the cobs.

Beetles were of little importance in the present study. Coleopteran pests are usually of minor importance in pre-harvest maize, and grain losses start to increase after 4-5 months of storage (Borgemeister *et al.,* 1998).

In the field experiment, both natural and artificial infestation yielded moderate grain losses, which were mostly below 20%. The low damage potential of *M. nigrivenella* is probably due to the short period in which the borers feed on maize grain. The larval period of *M. nigrivenella* varies from 14 to 18 days (Bordat & Renand, 1987; Moyal & Tran, 1991b; Sétamou, 1996; Bolaji & Bosque-Pérez, 1998). However, the short larval period allows for several generations on the same cob, thereby increasing grain losses. In addition, *M. nigrivenella* damage renders the grain susceptible to *Aspergillus flavus* infection resulting in subsequent high levels of aflatoxin contamination of field and stored maize (Sétamou *et al.*, 1998; Borgemeister *et al.*, 1998).

The regression model could predict well pre-harvest losses of maize due to *M. nigrivenella* and gave good results for cob infestation levels between 0 and 90%. Our 4 years field survey data showed, that the percentage of cobs attacked by *M. nigrivenella* rarely exceeded 60%, corroborating earlier field reports from Benin (Shanower *et al.*, 1991), Nigeria (Bosque-Pérez & Mareck, 1990), Togo (Silvie, 1993), Ghana (Gounou *et al.*, 1994) and Côte d'Ivoire (Moyal & Tran, 1991a). Therefore, our model can be used in future surveys for a rapid assessment of *M. nigrivenella* incidence and damage potential in maize fields.

Using our field derived model for a prediction of post-harvest losses resulted in a significant underestimation of grain losses after 2 months of storage. Therefore this model is of limited use for prediction of maize losses in stores. The main disadvantage of the model for predicting post-harvest losses is, that the model is only based on incidence data, and does not consider the time *M. nigrivenella* larvae feed on maize. In ongoing studies, we are trying to incorporate a time variable in the model, reflecting the duration of storage.

3 Effect of *M. nigrivenella* damage on *Aspergillus flavus* and aflatoxin contamination in maize[2]

3.1 *Abstract*

Maize infection by *Aspergillus flavus* Link and subsequent aflatoxin contamination as affected by insect damage to maize cobs before harvest was studied with surveys in farmers' fields and in a field trial in the Republic of Benin, West Africa. The most important pest species was the lepidopteran cob borer *Mussidia nigrivenella* Ragonot. Percentage of grain infected by *A. flavus* and of samples contaminated with aflatoxin, as well as the mean aflatoxin content of samples, increased with increasing borer damage. Cobs with <2% insect damage had an average of 11.7 and 43.6 ppb of aflatoxin in 1994 and 1995, respectively. Cobs in the highest damage class (i.e., > 10% damage) had an average aflatoxin of 514.6 and 388.2 ppb in 1994 and 1995, respectively. In 1994 only, coleopteran species such as *Sitophilus zeamais* Motschulsky and *Carpophilus* sp. significantly increased levels of aflatoxin in grain samples. In a field trial using *M. nigrivenella* infestation and *A. flavus* inoculation treatments, the presence of the insect feeding resulted in increased kernel infection and aflatoxin contamination. Artificial infestation with *M. nigrivenella* larvae increased aflatoxin content of maize by an average of 45 ppb, whereas inoculation with *A. flavus* spores increased the toxin level by 517 ppb. The significant interaction between infestation and inoculation indicated that higher levels of aflatoxin B1 were found when the fungus was associated with borers than with the fungus alone. *M. nigrivenella* was the major field pest connected with *A. flavus* infection and subsequent aflatoxin production in preharvest maize in Benin.

3.2 *Introduction*

Various fungi can infect maize, *Zea mays* L., before the grain is harvested (Anderson *et al.,* 1975; Fennel *et al.,* 1975; Marasas *et al.,* 1979). The most common species is

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[2] Published as M. Sétamou, K. F. Cardwell, F. Schulthess and K. Hell (1998). Effect of insect damage to maize ears, with special reference to *Mussidia nigrivenella* (Lepidoptera: Pyralidae), on *Aspergillus flavus* (Deuteromycetes: Monoliales) infection and aflatoxin production in maize before harvest in the Republic of Benin. *Journal of Economic Entomology* 91: 433-438.

the aflatoxin-producing *Aspergillus flavus* Link. Infection of maize by *A. flavus* and contamination by aflatoxin before harvest are well documented (Hesseltine *et al.*, 1976; Lillehoj *et al.*, 1977). Aflatoxins, toxic metabolites of the fungi *A. flavus* and *A. parasiticus*, are potent carcinogens which pose serious health hazards to humans and domesticated animals (Diener *et al.*,1987). Aflatoxin concentration allowed in foods and feeds is regulated in many developed countries and in some products, including maize, aflatoxin levels must be kept below 20 ppb (Stoloff *et al.*,1991).

Although fungal infection may also occur on undamaged kernels, physically damaged grains accumulate more aflatoxin than non-damaged grains (Diener *et al.*,1987). Insect damage to husks and grain enhance infection and level of aflatoxin contamination in preharvest maize (Fennel *et al.*,1975). Widstrom (1979) postulated that the involvement of insects in the fungal infection process and the subsequent production of aflatoxins is an important contributor to aflatoxin contamination of agricultural products. Although many studies have been carried out on the interaction between insects and the aflatoxin-producing fungus, *A. flavus*, no attempt has been made in tropical Africa to relate damage caused by maize pests to *A. flavus* infection and aflatoxin contamination.

In the Republic of Benin, West Africa, the most important cob pest of maize in the field is *Mussidia nigrivenella* Ragonot (Sétamou *et al.*,1995). *Mussidia nigrivenella* attacks maize in the field and continues to damage the grain the first two months of storage. *Aspergillus flavus* infection can result in high aflatoxin contamination of maize before harvest in Benin (unpublished data). The objective of the current work was to elucidate the role of insect damage in the contamination of maize before harvest by *A. flavus* and aflatoxin.

3.3 Materials and Methods

Two country-wide surveys were conducted in 1994 and 1995, in the four different agro-ecological zones in the Republic of Benin: the Forest Savanna Mosaic with two growing seasons (April-July and September-November); southern Guinea savanna with the same seasonal pattern as the Forest Savanna Mosaic but lower precipitation; northern Guinea savanna with one growing season (April to September); and the Sudan savanna with also one growing season from late May to

September but dryer than the Sudan savanna. In Forest Savanna Mosaic and southern Guinea savanna, fields were monitored during the major season in July, and in northern Guinea savanna and Sudan savanna in October-November. In each zone, 20 fields in 1994 and 15 in 1995 were sampled, and within each field 20 cobs were chosen. The fields were divided into four quadrants and within each quadrant five cobs were chosen randomly.

The on-station trial was conducted to study the interaction between *M. nigrivenella* and *A. flavus.* The trial was planted in 1994 during the second week of May, at the Benin Station of the International Institute of Tropical Agriculture (IITA), Calavi, situated in the Forest Savanna Mosaic zone. A 90-days maize variety, 'TZESR', an improved IITA streak resistant variety, was used. A factorial experiment was designed to study the main effects of both artificial infestation by *M. nigrivenella* and artificial inoculation with spores *of A. flavus*, and their interaction on aflatoxin levels. Treatments were whole plots, which consisted of 10 rows (8 m each). Treatments were arranged in a randomised block design with three replications. The planting distance was 80 cm between rows and 40 cm within rows. Treatments consisted of control (T0) plots treated with an insecticide to prevent cob damage; artificial infestation with *M. nigrivenella* (T1); artificial inoculation with *A. flavus* spores (T2); and both artificial infestation and inoculation (T3 = T1 × T2). In T0, cypermetrin (Cymbush 3 E [emulsifiable]) was sprayed at the rate of 0.15 kg [AI] /ha, fortnightly between five and nine weeks after planting. The insecticide was sprayed using an Electrodyn (Imperial Chemical Industries PLC, England) sprayer held such that the Bozzle was down wind and slightly behind the user. The Bozzle was positioned between the two crop rows next to the user. Whilst spraying, the user walked at a normal speed (1 m/s). Two rows were sprayed at a time, keeping the nozzle 40 cm above the top of the crop. Both infestations and inoculations were conducted the same day at nine weeks after planting. The T1 and T3 plots were artificially infested by placing five first-instar *M. nigrivenella* onto the silks of the cobs using a camel's-hair brush. In the T2 and T3 plots, cobs were inoculated through the silk channel using a syringe. The tip opening of the needle was inserted into the silk channel to inject 1 ml of an *A. flavus* suspension (1×10^6 spores ml^{-1}). In the T3 treatment, the infestation with *M. nigrivenella* was done immediately after the inoculation. At harvest, 20 cobs were sampled randomly from the eight central rows, avoiding the 2 plants at each end of the row. For both the survey and field trials, the cobs were dissected immediately after harvest. The percentage of grains damaged and the number of insects feeding on cobs were recorded per lepidopteran species, and for coleopteran species only the number of insects found was considered because their damage level at this period was <1% of the total kernels. The lepidopteran species infeodated to cobs such as *M. nigrivenella* and *Cryptophlebia leucotreta* Meyrick start their damage from the tip of the cob. *Cryptophlebia leucotreta* larvae penetrate the kernels and feed inside without noticeable frass; whereas, *M. nigrivenella* larvae produce a lot of silky frass on the kernels which is easily detected because they bore into the kernels. The stem borers *Sesamia calamistis* Hampson and *Eldana saccharina* Walker also feed on kernels but their type of damage differs significantly from that of the cob borers. *Sesamia calamistis* eggs are laid on the inner surface of the husks and newly emerged larvae penetrate the cobs and start feeding on the surface of the kernels. These larvae are often hidden by the frass they produce. *Eldana saccharina* larvae collected on cobs generally emigrate from the stem to the cob. Hence, damage caused by this borer goes from the rachis to the kernels with abundant wet frass rejected on the surface of the kernels.

The cobs were then put in paper bags and brought to the laboratory for further analysis.

The cobs were oven dried for three days at 45°C and then shelled. Five kernels per cob were selected randomly, surface-disinfected for 1 min in 3.5% NaOCl, rinsed twice in sterile distilled water, and plated on sterile filter paper (10 cm in diameter) (Whatman No. 1). Plates were incubated at 25° C for five days. All cultures that developed from the kernels were identified directly on the plates. Percentage of kernel infection per fungal species was based on the total number of kernels plated per field or treatment. The remaining kernels from each field or treatment were mixed and ground in a Romer Mill (Romer Laboratories, Union, Missouri) and assayed for aflatoxin by the method of Thomas *et al.* (1975).

Total aflatoxins (B1, B2) as x = ppb of sample and number of insects were transformed to log (x + 1), and all percentages were arcsine-transformed before analyses. Analyses were performed with SPSS (Norusis & SPSS, 1993). A correlation analysis was done to establish relationships between survey variables. For each year, data were analysed separately. Analysis of variance (Zar, 1974) was conducted to study the effect of treatments in the on-station experiment.

3.4 Results

Four lepidopteran species, *M. nigrivenella*, *C. leucotreta*, *S. calamistis* and *E. saccharina* Walker, and three coleopteran species, *Sitophilus zeamais* Motschulsky, *Carpophilus* spp. F. and *Cathartus quadricollis* Guerin were found on the maize just before harvest. For both years, percentage of fields and of cobs within field infested by the various pests is presented in Table 3.1.

Sesamia calamistis was commonly encountered in maize fields but only on a few cobs thus grain damage by *S. calamistis* was low. For *C. leucotreta*, both percentage of fields and plants infested were relatively high but because the larvae are small, damage by this insect was minor. The sugar cane borer, *E. saccharina* Walker, was encountered in ≈8% of the fields and average grain damage was 0.3% during both years. The predominant lepidopteran species was *M. nigrivenella*, which was found in most fields and infested 45 and 42% of the cobs in 1994 and 1995, respectively. Across both years, the number of *M. nigrivenella* accounted for 80% of the total Lepidoptera found. Mean grain damage caused by this cob borer was 4.7% in 1994 and 3.6% in 1995, accounting for 67-75% of the total insect damage in the 2 years.

Coleopteran species were also routinely found in maize fields, with *Carpophilus* spp. the most frequently encountered and *C. quadricollis* the least common species. For all species, cob infestation was low and average grain damage by coleopteran pests invading maize before harvest was between 0 and 0.8%.

Aspergillus flavus was found in a high percentage of the fields with a kernel infection level of ≈20% in each year. Of the fields infected by *A. flavus*, 48.6 and 52.8% were contaminated by aflatoxins in 1994 and 1995, respectively. Only aflatoxins B1 and B2 were detected in the samples and of these, B1 was at the highest concentration. The mean concentrations of positive samples were 141.5 ppb in 1994 and 145.9 ppb in 1995.

Table 3-1 Insect infestation, mean *A. flavus* infection and mean aflatoxin levels (ppb) in preharvest maize in 1994 and 1995 in Benin across four agro-ecological zones.

Variable	Lepidoptera				Coleoptera			*A. flavus*	
	Mn	*Sc*	*Es*	*Cl*	*Sz*	*Ca*	*Cq*	Infection	Aflatoxin
				1994					
%fields infested[a]	97.5	61.3	7.5	82.5	27.5	40.0	13.8	85.0	41.3
%cobs infested[b]	45.0	5.8	0.6	18.0	10.0	9.2	2.0	74.0	-
Mean[c]	4.7	1.1	0.2	0.8	0.8	0.2	0.0	20.6	59.4
				1995					
%fields infested	70.0	35.0	7.0	93.3	35.0	37.0	21.7	60.0	31.7
%cobs infested	42.0	3.8	0.5	34.0	7.6	9.5	5.8	56.0	-
Mean	3.6	0.4	<0.1	0.5	0.2	0.3	<0.1	19.5	46.2

[a] Percentage of fields infested by each insect species, infected by *A. flavus* and contaminated by aflatoxin.
[b] Percentage of cobs infested by each insect species and infected by *A. flavus*.
[c] Mean percentage of kernels damaged by insect, percentage kernel infected by *A. flavus* and aflatoxin detected in samples
Mn = *M. nigrivenella*, Sc = *S. calamistis*, Es = *E. saccharina*, Cl = *C. leucotreta*, Sz = *S. zeamais*, Ca = *Carpophilus* sp., Cq = *C. quadricollis*.

Correlation coefficients between insect pest infestation variables with the percentage of kernels infected by *A. flavus* are shown in Table 3.2. For both years, *M. nigrivenella* damage was significantly correlated with *A. flavus* infection and aflatoxin contamination. Likewise, percentage cobs infested per field by the borer and the mean number of larvae recovered per cob were significantly correlated with grain infection level and aflatoxin concentration of maize. *Sesamia calamistis* was correlated with *A. flavus* infection but was not significantly associated with aflatoxin production, whereas cob damage caused by *E. saccharina* was significantly correlated with grain infection only in 1994. Mean number of *C. leucotreta* was negatively correlated with *A. flavus* infection and aflatoxin levels in maize. The number of coleopteran species generally was not significantly related to grain infection ($P > 0.05$) but their damage level was significantly and positively correlated ($P < 0.05$) with the level of aflatoxin B2 content of samples during both surveys, and with aflatoxin B1 levels only in 1994 (Table 3.2). *Cathartus quadricollis* had no impact on *A. flavus* infection nor aflatoxin contamination (r=0.09, n=80 in 1994 and r=0.11, n=60 in 1995).

The classification of fields according to *M. nigrivenella* damage levels and the corresponding toxin levels recovered from grains are shown in Table 3.3. During both years, *A. flavus* infection and aflatoxin accumulation tended to increase with insect damage to cobs. Few infected kernels and little aflatoxin were recovered from cobs that were lightly damaged by insects. Contaminated cobs that had between 2 and 4% grain damage had an average aflatoxin B1 content of 54 ppb; >50 % of the samples in this damage class contained no aflatoxin, however. In 1994 and 1995, plants with average borer damage >10% had average aflatoxin B1 levels of 514.6 and 388.2 ppb, respectively.

Table 3-2 Correlations between *A. flavus* infection, aflatoxin contamination, and various insect damage levels in preharvest maize in Benin.

	1994			1995		
Variable	*A. flavus*[a]	B1[b]	B2	*A. flavus*	B1	B2
M. nigrivenella						
% cobs infested	0.30**	0.43**	0.27*	0.28*	0.27*	0.14
% grains damaged	0.35**	0.36**	0.12	0.42**	0.54**	0.25*
No. borer/cob	0.24*	0.36**	0.15	0.15	0.30*	0.13
S. calamistis						
%cobs infested	0.02	0.09	0.11	0.26*	0.14	0.09
% grains damaged	0.12	0.14	0.19	0.26*	0.19	0.10
No. borer/cob	0.27*	0.20	0.12	0.25*	0.14	0.07
E. saccharina						
% cobs infested	-0.02	-0.05	0.03	-	-	-
% grains damaged	0.22*	0.06	0.11	-	-	-
No. borer/cob	-0.04	-0.11	-0.04	-	-	-
C. leucotreta						
% cobs infested	0.03	-0.04	0.00	0.06	0.09	0.01
% grains damaged	-0.07	-0.07	-0.06	0.11	0.04	0.12
No. borer/cob	-0.28*	-0.16	-0.28*	-0.14	-0.26*	-0.19
S. zeamais						
% cobs infested	0.05	0.17	0.22*	0.04	0.18	0.23
Carpophilus sp.						
% cobs infested	0.19	0.22*	-0.08	0.11	0.10	0.07
Coleopteran spp.						
% grains damaged	0.17	0.27*	0.32*	0.14	0.16	0.37*

(-) Correlation not calculated because pest densities were too low; r values marked with * and ** have *P* values <0.05 and <0.01, respectively.

[a] Percentage of grains damaged by all insect species and % kernels infected by *A. flavus* were arcsine-transformed before analysis.

[b] Aflatoxin (B1 and B2) were log(x + 1)-transformed before analysis.

Table 3-3 ***Aspergillus flavus*** **infection and aflatoxin B1 production as a function of percentage cob damage due to insects on maize before harvest in Benin, 1994 and 1995.**

		Mean%		Aflatoxin (ppb)^{a}	
Cob damage class	No. of fields	Grain damage	*A. flavus* infection	Mean	%fields
		1994			
0-2	22	1.1	17.8	43.6	27.3
2-4	19	3.0	20.7	54.3	47.4
4-10	30	5.9	22.8	74.9	43.3
>10	9	12.6	50.9	514.6	66.7
		1995			
0-2	31	0.4	8.2	11.7	17.0
2-4	13	2.7	19.3	54.4	46.0
4-10	12	7.0	15.8	48.3	50.0
>10	4	14.3	29.8	388.2	50.0

[a] Average ppb of aflatoxin in contaminated samples.

In the on-station experiment (Table 3.4), plots artificially infested with *M. nigrivenella* had a significantly higher percentage of grain damage than control plots. Likewise, artificial inoculation with fungal spores significantly increased percentage of grain infected at harvest, and both infestation and inoculation significantly increased aflatoxin B1 concentrations by an average value of 45 and 517 ppb, respectively. The interaction infestation × inoculation was significant for the level of aflatoxin B1, thus more aflatoxin B1 is accumulated in maize in the presence of *M. nigrivenella*. In the mixed treatment (T3), inoculation had no effect on cob damage, indicating that *A. flavus* has no effect on survival of *M. nigrivenella* larvae. The effect of infestation on *A. flavus* infection was not significant but, on a per cob basis, a positive relationship was found between percentage of grain damaged by *M. nigrivenella* and percentage of grains infected by *A. flavus* (r = 0.40*, n=120) in the T0 and T1 treatments.

Table 3-4 Means of *M. nigrivenella* damage (%), *A. flavus* infection (%) and aflatoxin concentrations (ppb) of treatments in the 1994 on-station experiment followed by *F* values of the factorial effect.

Treatments	*M. nigrivenella* damage (%)	*A. flavus* infection (%)	Aflatoxin B1 (ppb)
T0	2.1	28.0	5.0
T1	8.5	37.3	52.8
T2	4.2	76.5	525.0
T3	8.7	88.3	566.7
Factorial Effect			
F-values			
Insect infestation	25.5**	2.8ns	11.6**
A. flavus inoculation	1.7ns	78.4**	91.5**
Interaction	1.2ns	0.03ns	10.3*

To = control; T1 = infested with *M. nigrivenella*; T2 = inoculated with *A. flavus*; T3 = infested with *M. nigrivenella* and inoculated with *A. flavus*; *, significant at $P<0.05$; **, significant at $P<0.01$; ns, non-significant.

3.5 Discussion

These results show that insects help *A. flavus* invade maize before harvest and are correlated with the subsequent contamination of grain by B aflatoxins. However, the importance of insects in aflatoxin contamination may vary according to their mode of action on the cobs. For example, Widstrom *et al.* (1975) showed that the European corn borer, *Ostrinia nubilalis* (Hübner), was more effective than the fall armyworm, *Spodoptera frugiperda* J. E. Smith, in producing conditions that are conducive to high levels of aflatoxin production in grain. In the current study, increase in *A. flavus* infection and aflatoxin levels of samples was mainly due to *M. nigrivenella*. As early as 1914, this borer was mentioned as one of the chief pests attacking grain maize in Southern Nigeria (Lamborn, 1914). The borer usually damages maize from the tip of the kernels (Moyal, 1988), where natural infection of *A. flavus* occurs, and thus could easily promote the spread of the fungus. It frequently eats a channel through a whole line of seeds (Moyal & Tran, 1991a), and thus breaks the testa of grains which constitutes the natural barrier to *A. flavus* growth. Also, because of their numbers, *M. nigrivenella* larvae tend to be highly destructive, and thus favour establishment and spread of *A. flavus* in grain.

Other cob-feeding lepidopteran species were less strongly associated with *A. flavus* infection or aflatoxin levels. This may have been because of the generally low pest infestations encountered in the surveys. In the rainforest and forest/savanna transition as well as in the mid-altitudes of most other western African countries, high numbers of the pyralid *E. saccharina* and the noctuid *Busseola fusca* Fuller, and to a lesser extent *S. calamistis*, are commonly found feeding in the cob (Bosque-Pérez & Mareck, 1991; Gounou *et al.*,1994; Cardwell *et al.*, 1997) often destroying it in the milk stage of cob development. *Eldana saccharina* often feeds on the debris on the soil before penetrating into the stem and later into the cob. Thus, it is likely that *E. saccharina* can be an important vector of the fungus when there is a high pest density. *Cryptophlebia leucotreta* generally feeds only on the silk and on the tip grains, which may explain why it was not associated with fungal infection.

The positive correlation of both *S. zeamais* and *Carpophilus sp.* damage and *A. flavus* infection and aflatoxin levels, despite low associated feeding damage, suggests that these insect pests may also act as vectors of the fungus. Beti *et al.* (1995) reported that the maize weevil enhances growth of *A. flavus* by increasing the area susceptible to fungal growth. *Sitophilus zeamais* was reported to significantly contribute to increased *A. flavus* infection on corn cobs by transporting spores and damaging corn kernels (McMillan *et al.*,1980). Infestation by both beetles species (*S. zeamais* and *Carpophilus* sp.) is associated with *M. nigrivenella* damage on maize cobs (Sétamou, 1996). Before pupating, this borer produces an exit hole through which storage beetles enter the cob. McMillan (1987) also observed that nitidulid beetles such as *Carpophilus* spp. are attracted to damaged cobs, including those caused by cob worms and the European corn borer. They are also found feeding preferentially on mouldy cobs (Wicklow, 1989). Hence, these beetles may infest previously damaged or *A. flavus* infected cobs on which they will disperse fungal spores. In our field trial, artificial infestation with *M. nigrivenella* larvae had no effect on fungal infection. This was likely because of generally low cob damage as well as of relatively high natural infestation by *M. nigrivenella* (i.e., ≈50% of total borer population). The survey suggested that the relationship between damage and fungal infection is non-linear, and cob damage must be considerable (i.e., >10%) to have an effect on infection rates. Field observations show that high damage is mostly associated with older large larvae, which produce exit holes (F. Schulthess, pers.

communication). Also, the inoculum introduced was sufficient to ensure establishment of the fungus on >75% of the grain. Thus, any further effect of the borer may not have contributed significantly to grain infection. Percentage of *A. flavus* infection between insecticide-protected and artificially infested plots was not significantly different, indicating that the borer was not the source of grain infection but only dispersed spores already present on the grains.

The fungus did not affect the damage level by *M. nigrivenella*, indicating that the fungus has no biocidal action. In a laboratory study, Sétamou (1996) showed that diet containing spores of *A. flavus* did not adversely affect growth and development of *M. nigrivenella.* The effect of the fungus and its metabolites on insect biology varies depending on the insect species (McMillan *et al.,*1980a). Although some insects are sensitive to the presence of *A. flavus* in their diets, others are resistant. Dowd (1992) reported that resistant insects feeding on *A. flavus*-contaminated substrates without an adverse effect can vector the fungus. This shows the importance of the relatively unknown cob borer *M. nigrivenella* in the invasion of cobs by *A. flavus*. The negative relationship between *C. leucotreta* variables and *A. flavus* and the toxin levels suggests that the borer may be susceptible to *A. flavus.*

The current study suggests that one of the most important factors determining the levels of aflatoxin found in pre-harvest maize in Benin is the extent of damage caused by *M. nigrivenella*. The rapid increase of aflatoxin B1 noticed at grain damage level >10% suggests an exponential effect of borer damage on aflatoxin accumulation. Wicklow (1991) & Widstrom (1979) reported that maize is particularly vulnerable to *A. flavus* infection when pressure from cob-infesting insects is high. Likewise, McMillan *et al.* (1987) showed that maize cobs inoculated with *A. flavus* only sustained significantly lower aflatoxin amounts than cobs from plots inoculated with *A. flavus* and supplemented with insects. One method to reduce aflatoxin contamination could be the prevention of insect damage. Because of the cryptic behaviour of *M. nigrivenella*, insecticides are not recommended (Moyal 1988; Sétamou *et al.,*1995). Thus, discarding heavily damaged cobs (>10% of the grains) at harvest should reduce the aflatoxin in samples.

4 Host plants and population dynamics of *M. nigrivenella*[3]

4.1 Abstract

The maize cob borer, *Mussidia nigrivenella* Ragonot, is a polyphagous insect pest that feeds on various cultivated and wild plants. Surveys in 4 agro-ecological zones of Benin, conducted between 1993 and 1997, revealed about 20 plant species from 11 plant families hosting the borer, but only 13 host plants enable the borer to develop to the pupal stage. Whereas a maize crop usually supports one generation per season, several generations of *M. nigrivenella* were recorded on *Parkia biglobosa* and *Gardenia* spp. Agro-ecological variation in the availability of wild host plants was noticed. The high abundance of wild hosts in the Guinea Savannas reflects the diversity of the natural flora in these zones. This abundance of *M. nigrivenella* host plants, coupled with their overlapping fruiting periods may be the main reason for the high pest densities on maize, although only 1 maize crop per year is grown in the Northern Guinea savanna. In a field experiment, the highest infestation levels and densities of *M. nigrivenella* occurred on *Canavalia enseiformis* and *Mucuna pruriens*, 2 popular cover crops in West Africa. Maize and cotton were about equally suitable hosts. Thus, fruiting periods of *C. enseiformis* and *M. pruriens* should not precede that of maize, to avoid emerging *M. nigrivenella* populations to shift from the cover crops to maize.

4.2 Introduction

In west africa, *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) has been frequently reported as a pest of maize [*Zea mays* L. (Poaceae)] (Moyal, 1988; Atachi, 1987; Bosque-Pérez & Mareck, 1990; Moyal & Tran, 1991a; Shanower *et al.,* 1991; Gounou *et al.,* 1994) and cotton [*Gossypium hirsutum* L. (Malvaceae)] (Staeubli, 1977; Silvie, 1990). So far, *Mussidia nigrivenella* was reported as a maize pest from western African countries only. Although more than half of the cobs in the field are usually infested by the borer (Whitney,1970; Sétamou, 1996), reported yield losses varied from 5-15% only (Moyal & Tran, 1991; Sétamou *et al.,* 1999a).

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[3] To be published as M. Sétamou, F. Schulthess, S. Gounou, H-M. Poehling, and C. Borgemeister. Host plants and population dynamics of the ear borer *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) in Benin. Submitted to *Environmental Entomology*.

Mussidia nigrivenella damage, however, predisposes maize to pre- and post-harvest infestations by storage beetles, *Aspergillus flavus* Lk.:Fr. infections and subsequent aflatoxin contamination (Sétamou *et al.*, 1998). In addition, damaged cobs are not selected by farmers as seed source (Moyal & Tran, 1991a).

Mussidia nigrivenella infestation and damage vary greatly with agro-ecological zone (Sétamou, 1996). Contrary to stem borers which are more damaging in the Forest and the derived Forest zones in West Africa (Bosque-Pérez & Mareck, 1990; Gounou *et al.*, 1994), *M. nigrivenella* is more damaging in the Guinea Savannas (Moyal & Tran, 1991; Sétamou, 1996). Sétamou (1996) suggested that the variation in borer population densities are due to host plant availability and suitability. *Mussidia nigrivenella* is known to be polyphagous. In addition to maize and cotton, it has been found on stored Cocoa, *Phaseolus* beans and on pods and fruits of a few wild tree species (see overview by Moyal, 1988). It is clear, however, that existing lists of host plants of the borer are less than exhaustive. Moreover, the role of these various alternate host plants for the colonization of maize fields by *M. nigrivenella* is largely unknown. The objectives of the present study were to catalogue the host plant complex of *M. nigrivenella* and to establish its role in population dynamics of the pest across several agro-ecological zones in Benin.

4.3 Materials and Methods

Host plant range. A preliminary 10 days survey on pod and fruit-bearing herbaceous plants and shrubs, sampled in a random manner, was carried out in Benin between August and October 1991. The only new hosts discovered were velvetbean *Mucuna pruriens* DC. (Fabaceae) and jackbean *Canavalia enseiformis* (L.) DC. (Fabaceae) (F.S. and S.G., unpublished data), 2 cover crops, introduced to Africa during the last decade. Additional surveys conducted from July 1993 to December 1995 at 3 months-intervals, concentrated mainly on tree and shrub species which were sampled in a random manner. Plant species with fruiting structures suspected to harbour *M. nigrivenella*, including known host plants (Moyal, 1988), were sampled. Whenever possible, a sample of 20 fruits per tree/shrub species was taken. From January 1996 to December 1997 the various host plants were surveyed at monthly intervals to study the occurrence of *M. nigrivenella* in the 4 agro-ecological zones of Benin, namely, from south to north, the Forest Savanna Mosaic (FSM), the Southern

Guinea Savanna (SGS), the Northern Guinea Savanna (NGS), and the Sudan Savanna (SS) (Fig. 4.1), with highest rainfall of 1400 mm in FSM and lowest of 900 mm in SS. In FSM, the vegetation is poor and mainly anthropogenic, whereas a great diversity of wild plants are found in the other zones. These plants are however more abundant in the Guinea Savannas (SGS and NGS) than in the SS. All collected fruits were first visually examined for eggs or 1st instar larvae of *M. nigrivenella*, and then dissected for borer collection. Because the immature stages are difficult to identify, eggs, larvae and/or pupae collected on the different hosts were brought to the laboratory. The eggs were incubated at 26 ± 2 °C and 65 ± 5% RH, on moistened tissue paper until larval emergence. The emerged larvae as well as the collected larvae were reared on *C. enseiformis* pods, following the protocol developed by Sétamou *et al.* (1999b). Species were identified at the insect museum of the International Institute of Tropical Agriculture (IITA), Calavi, Republic of Benin, using the key of Moyal (1988). The presence of an egg or larva on a plant does not necessarily indicate suitability of the host for completion of life cycle of an insect (Wiklund, 1974). Thus, only plants on which all immature stages and especially pupae were collected were considered as host plants of *M. nigrivenella*.

Abundance studies on wild host plants. Seasonal abundance of *M. nigrivenella* was monitored on 5 major wild host plant species. The same survey sites were visited at monthly intervals for 2 years, i.e., from January 1996 to December 1997 (Fig. 4.1). A survey site consisted of an area of 2 km long along the survey route and 500 m in width. The number of trees of *Adansonia digitata* L. (Bombacaceae) *Gardenia sokotensis* Hutch (Rubiaceae), *Gardenia ternifolia* Schum & Thonn (Rubiaceae), *Parkia biglobosa* (Jacq.) Benth. (Mimosaceae), and *Ximenia americanum* L (Olacaceae) sampled during each survey is presented in Table 4.1. The selection of these host plants was based on the relative abundance of borer populations on these plants recorded during the previous surveys on host plant range. The surveys were carried out during the 1st week of each month. From plants bearing large fruits (diameter > 5 cm), i.e., *A. digitata* and *X. americanum*, and small fruits (diameter < 5 cm), i.e. *G. sokotensis*, *G. ternifolia*, and *P. biglobosa*, 10 and 20 fruits, respectively, were collected per tree. The fruits were dissected and all life stages of *M. nigrivenella* were recorded. Fruit infestation level was established based on the number of fruits with borers and did not include fruits with only signs of previous attack.

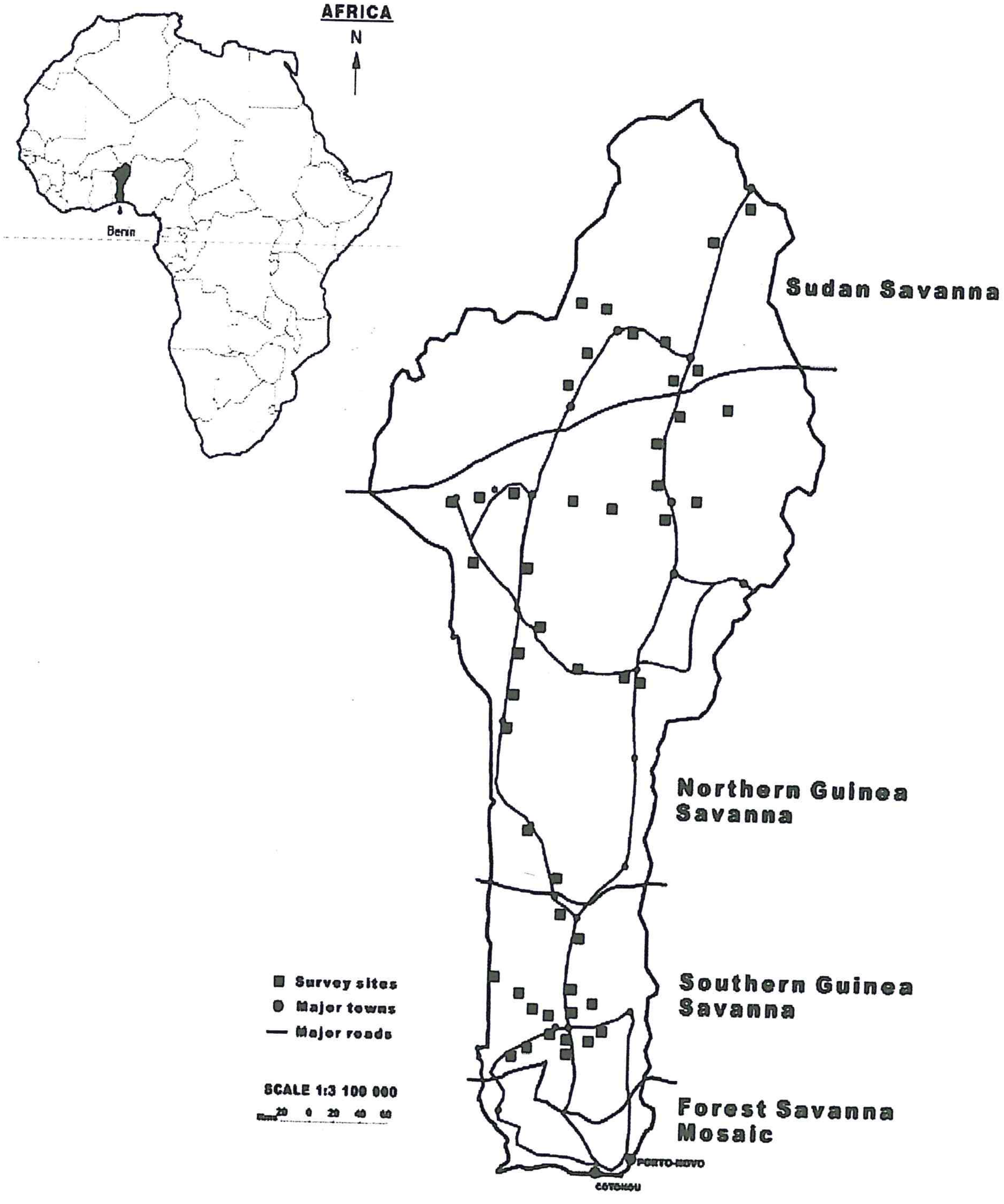


Fig. 4-1 Agro-ecological zones, and survey sites of *Mussidia nigrivenella* host plants in Benin.

Table 4-1 Number of trees/shrubs sampled per survey for *M. nigrivenella* population dynamics studies on selected host plants betwwen 1996 and 1997

Agro-ecological zone[a]	FSM	SGS	NGS	SS	Total
Host plant species					
Adansonia digitata	-	12	10	10	32
Gardenia sokotensis	-	7	12	10	29
Gardenia ternifolia	-	15	15	10	40
Parkia biglobosa	-	26	28	21	75
Ximenia americana	-	5	11	13	29

[a] FSM= Forest savanna mosaic, SGS= Southern Guinea savanna, NGS= Northern guinea savanna, SS= Sudan savanna.

The phenology of the different plant species varied greatly with agro-ecological zone. Due to varying sampling procedures, larval densities among plant species could not be statistically compared.

Abundance studies on crops. *Mussidia nigrivenella* infestations were followed on suitable host crops, i.e., maize, cotton, jackbean, and velvetbean from June to October 1995 in field experiments conducted at the IITA station. Maize is the major staple food in Benin (Miracle, 1966; CIMMYT, 1990) and cotton is the most important cash crop. Jack- and velvetbeans are green manure crops introduced to Africa in the last decade. Their role in improving soil fertility and controlling weeds is well documented (Vissoh *et al.,* 1998; Carsky *et al.,* 1998), and farmers in Benin are increasingly using these 2 cover crops (Vissoh *et al.,* 1998).

The experimental design consisted of a randomized block with 3 replications containing 4 plots each of 25 m × 25 m. The distance between blocks was 4 m, and that between plots within a block 2 m. Each host plant was planted on early May 1995 at a density of 31,250 and 25,000 plant stands/ha for maize and cotton, respectively, and a density of 16,500 plants/ha for both jack- and velvetbeans. Maize and cotton crops received NPK (15-15-15) fertilizer at a rate of 200 kg/ha, 2 weeks after sowing (WAS).

For each crop, sampling started as soon as 50 % of fruits were formed. The borer populations were monitored at weekly intervals until harvest. A systematic sampling procedure was used. Each plot was divided into 4 sectors and 5 fruits were collected at random per sector. The percentage of fruits infested with all stages of

M. nigrivenella in the sample and the mean number of borers per fruit were calculated for each host plant on each sampling date.

The effect of host plant on *M. nigrivenella* infestation levels was evaluated using the closed testing procedures (Hochberg & Tamhane, 1987). The percentage of fruits infested for each host plant species were ranked within sampling date. The Chi-square test was then applied on the total sum of ranks of each host plant, to evaluate independence of *M. nigrivenella* infestations according to host plant using the PROC FREQ procedure (SAS Institute, 1992). For assessment of the effect of host plant on the total densities of *M. nigrivenella*, the borer-days (defined as the sum of mean numbers of borers/plant observed on consecutive sampling dates multiplied by the days between samples, over the total sampling period days) was calculated. This measure was preferred to the borer numbers because both borer densities, and duration of infestation are reflected (Yaninek *et al.,* 1990; Schulthess *et al.,* 1991b). A t-test with Bonferroni probability adjustment was used to compare the log-transformed *M. nigrivenella*-days between the different host plants using the LSMEANS procedure (SAS Institute 1990).

4.4 Results

Host range and population dynamics on wild host plants. *Mussidia nigrivenella* was collected from 20 species of host plants in 11 families (Table 4.2). About 70% of the host plants recorded were non-cultivated species and major new alternative hosts were identified. On > 65% of the host species, almost all immature stages of *M. nigrivenella* were found (Table 4.3). Only eggs were collected from *Piliostigma thonningii* (Schumach) Milne-Redh. (Caesalpiniaceae), and *Sesbania exaltata* (Rafin) (Fabaceae) (Table 4.3). Only eggs and young instar larvae, but no older larvae and/or pupae were found on fruits of 5 other plants, i.e., *Detarium microcarpum* Gill. & Perr. (Caesalpiniacae), *Sterculia cordifolia* (Cav.) R. Br. (Sterculiaceae), *Psophocarpus tetragonolobus* (L.) DC (Leguminoseae), *Tephrosia candida* (Leguminoseae) and *Vigna unguiculata* (L.) Walpers (Leguminoseae) (Table 4.3). Thus these plants are unlikely to be major host plants of *M. nigrivenella*.

The presence and abundance of host plants varied greatly with agro-ecological zone. In the FSM, only cultivated host plants, i.e., maize, *Phaseolus lunatus* L.

(Leguminoseae), *C. enseiformis* and *M. pruriens* were found supporting borer populations (Table 4.2). The highest diversity of host plants was encountered in the Guinea Savannas, with highest frequencies in the NGS. Further north, in the SS, both diversity and frequency of host plants declined but they were still considerably higher than in the FSM (Table 4.2).

Table 4-2 Host plants of *Mussidia nigrivenella* recorded in the different agro-ecological zones[a] of Benin from 1993 to 1997.

Scientific name	Common name	Ecological zone			
		FSM	SGS	NGS	SS
Bombacaceae					
Adansonia digitata L.	baobab	-[b]	++	++	++
Caesalpiniaceae					
Detarium microcarpum Gill & Perr.	tallow tree	-	++	++	++
Piliostigma thonningii (Schumach) Milne-Redh		-	++	++	++
Leguminoseae					
Canavalia enseiformis (L.) DC.	jack bean	++	+	+	+
Mucuna pruriens DC.	velvet bean	++	++	+	+
Psophocarpus tetragonolobus (L.) DC.	winged bean	+	++	++	+
Sesbania exaltata (Rafin)		+	++	++	+
Tephrosia candida		+	++	++	+
Vigna unguiculata (L.) Walpers	cowpea	++	++	++	++
Phaseolus lunatus L.	lima bean	+	+	+	++
Tamarindus indica (L.)	tamarind	-	+	++	++
Malvaceae					
Gossypium hirsutum L.	cotton	-	+	++	++
Mimosaceae					
Parkia biglobosa (Jacq.) Benth.	nitta nut, nere	-	++	++	+
Musaceae					
Musa spp.	banana	+	+	+	-
Olacaceae					
Ximenia americana L.	wild olive	-	+	++	++
Poaceae					
Zea mays L.	maize	++	++	++	++
Rubiaceae					
Gardenia sokotensis		-	+	++	++
Gardenia temifolia Schum & Thonn.	common gardenia	-	++	++	++
Sapotaceae					
Butyrospermum parkii (G. Don) Kotschy	shea butter	-	+	++	+
Sterculiaceae					
Sterculia cordifolia (Cav.) R. Br.	mopopaja tree	-	+	++	++

[a] FSM= Forest savanna mosaic, SGS= Southern Guinea savanna, NGS= Northern guinea savanna, SS= Sudan savanna.

[b] - = host plant absent, + = host plant present, ++ = host plant abundant.

Table 4-3 Occurrence of *Mussidia nigrivenella* Ragonot on collected host plants in Benin (1996 and 1997).

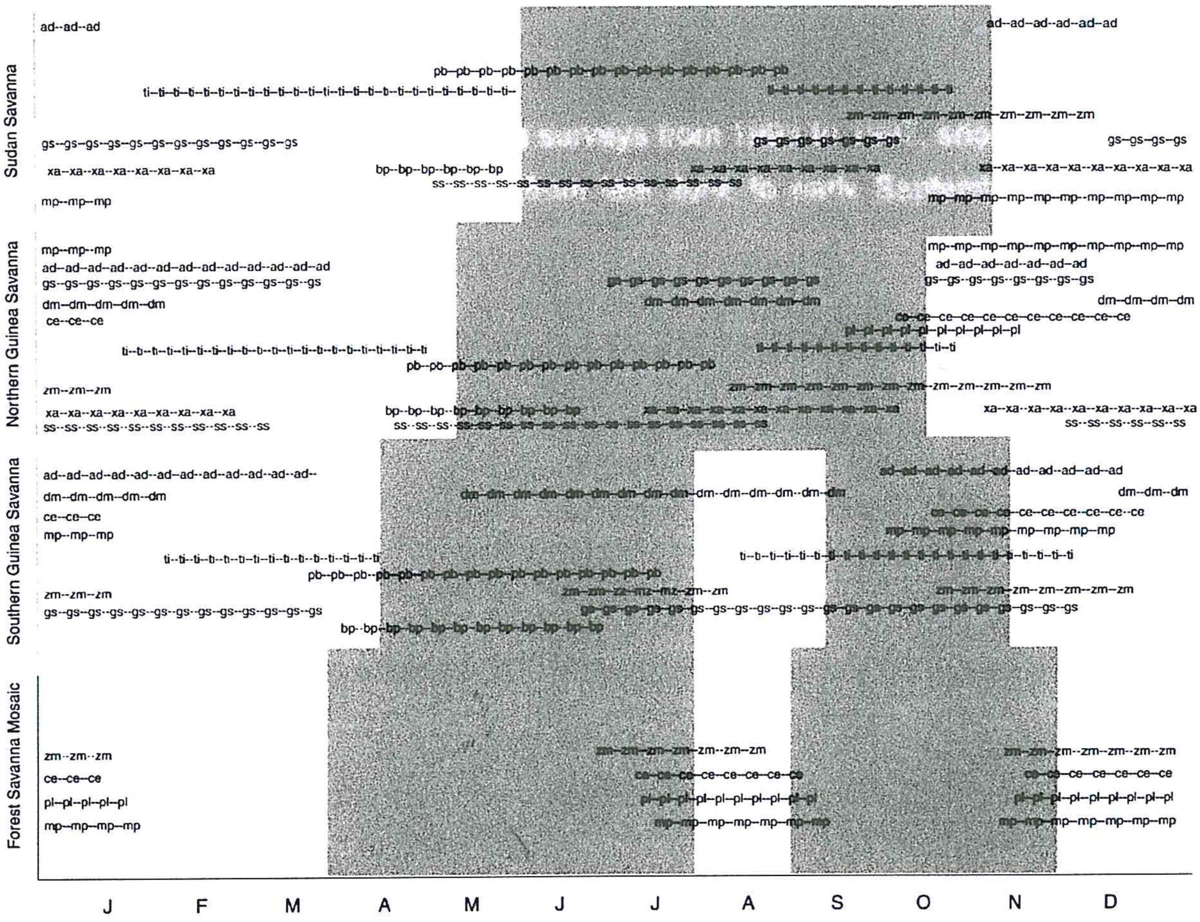
Host plant	Year	Months												Ratio
		J	F	M	A	M	J	J	A	S	O	N	D	E:L:P[e]
A. digitata[a]	1996	29	36	38	21	22	–	–	–	0	12	20	33	14:133:64
	1997	34	28	31	34	–	–	–	0	0	6	17	20	23:95:52
D. microcarpum	1996	13	7	21	0	–	–	–	–	–	–	0	0	32:9:0
P. thonningii	1996	–[d]	–	–	–	–	–	0	27	40	9	–	–	76:0:0
C. enseiformis[b]	1996	134	–	–	–	–	–	–	0	84	78	243	186	112:404:209
	1997	178	–	–	–	–	–	–	7	65	91	189	231	78:426:257
M. pruriens[b]	1996	47	0	–	–	–	–	–	–	–	0	138	86	7:178:86
	1997	28	–	–	–	–	–	–	–	–	12	43	35	40:37:41
P. tetragonolobus	1996	–	–	–	–	–	–	0	4	13	8	7	–	19:13:0
	1997	–	–	–	–	–	–	0	0	0	0	0	–	0:0:0
S. exaltata	1996	–	–	–	–	–	–	–	11	5	0	–	–	16:0:0
	1997	–	–	–	–	–	–	–	0	17	0	–	–	17:0:0
T. candida	1997	–	–	–	–	–	–	0	24	0	–	–	–	17:7:0
V. unguiculata	1996	–	–	–	–	–	–	13	25	–	9	29	0	26:50:0
P. lunatus	1996	–	–	–	–	–	–	–	–	0	0	0	0	0:0:0
	1997	–	–	–	–	–	–	–	–	7	34	22	9	0:23:49
T. indica	1996	14	19	32	30	–	–	–	0	27	14	0	0	15:114:7
	1997	23	17	24	18	3	–	–	0	8	19	0	2	9:97:8
G. hirsutum[b]	1996	0	–	–	–	–	–	–	–	–	8	16	0	24:0:0
P. biglobosa	1996	–	–	19	56	86	104	182	224	26	–	–	–	55:335:307
	1997	–	–	9	64	78	128	200	210	42	–	–	–	124:385:222
Musa spp.[c]	1996	0	0	0	0	–	–	–	–	–	17	0	0	0:7:10
X. americana[a]	1996	49	52	46	14	14	–	–	127	82	21	0	5	96:171:143
	1997	36	107	69	58	23	–	–	201	65	10	6	31	103:214:289
Z. mays[b]	1996	37	–	–	–	–	–	14	29	16	39	45	63	16:135:92
	1997	42	–	–	–	–	–	0	18	27	43	56	59	13:130:102
Gardenia spp.	1996	24	16	30	6	8	6	0	8	19	12	14	20	14:86:63
	1997	20	21	28	28	13	18	4	24	22	17	23	27	6:153:86
B. parkii	1996	–	–	0	7	0	4	–	2	–	–	–	–	0:11:2
S. cordifolia	1996	3	–	–	0	0	0	0	5	0	0	0	0	5:3:0

The data are total numbers of *M. nigrivenella* collected on 20 fruits per host plant; [a] Total *M. nigrivenella* collected on 10 fruits; [b] Total *M. nigrivenella* collected on 20 cobs and pods, respectively, sampled in fields at the IITA station in Abomey-Calavi (FSM); [c] Data based on samples taken on a tree located in the FSM; [d] – = no fruiting bodies available at this time; [e] Ratio Eggs: Larvae: Pupae.

The relative importance of each host in supporting *M. nigrivenella* populations varied according to seasons (Table 4.3). Observations on the fruiting periods of these host plants (Fig. 4.2) based on the 5 years surveys from 1993 to 1997, showed that in the FSM, suitable hosts were available from late June to early September, during the reproductive phase of the 1st maize crop, and again from November until January, at and after maturity of both the second season maize crop and the cover crops. No suitable fruiting structures for the development of the borer were available between February and June. By contrast, in the Guinea Savannas suitable food sources were present throughout the year, but from August to October many host plants bearing fruits did not support larval development. In these zones, maize and *Gardenia* spp. were the main food sources of the borer during this period. In the SS, no food plant was available during the second part of the dry season, i.e., between January and April. Only *Tamarindus indica* L. (Mimosaceae) bore fruits (Fig. 4.2), but this host plant was relatively scarce. Both the proportion of tamarind trees infested and the percentage of fruits infested were < 10% at any sampling occasion. Moreover, *T. indica* fruits supported only low *M. nigrivenella* larval populations (a maximum of 2--3 larvae per infested fruit) and very few pupae were collected on it (Table 4.3). Thus *T. indica* is unlikely to be a major host plant for *M. nigrivenella*.

Although several host plants were collected hosting the borer during the surveys, 5 species of wild host plants appeared to be important in harboring populations of *M. nigrivenella*. High percentage of fruits infested by *M. nigrivenella* and high mean borer densities were recorded on *P. biglobosa*, *A. digitata*, *X. americana*, *G. sokotensis* and *G ternifolia* (Table 4.3). These 5 host plants were mainly present in SGS, NGS, and SS (Table 4.2). However, strong seasonal fluctuations of *M. nigrivenella* populations could be observed (Table 4.3, Fig. 4.3). Because of the similarities in the phenology of *G. sokotensis* and *G. ternifolia*, the data collected on these 2 plant species were pooled under *Gardenia* spp.

Across the 3 northern agro-ecological zones, borer population densities and infestation levels were comparable and followed the same seasonal pattern in each host plant. Thus the data for each of the 4 host plants was pooled across the 3 agro-ecological zones. Additionally, a similar year-year variation in borer numbers and percentage fruit infestation was observed in all 4 host plants (Table 4.3, Fig. 4.3a-d).



Legend: ad = *Adansonia digitata*, bp = *Butyrospermum parkii*, ce = *Canavalia enseiformis*, dm = *Detarium microcarpum*, gs = *Gardenia* spp., mp = *Mucuna pruriens*, pb = *Parkia biglibosa*, pl = *Phaseolus lunatus*, ss = *Sterculia setigera*, ti = *Tamarindus indica*, xa = *Ximenia americanum*, zm = *Zea mays*.
The rainy season in the various zones appeared shaded.

Fig. 4-2 Fruiting periods of the different host plants of *Mussidia nigrivenella* in the different agro-ecological zones of Benin.

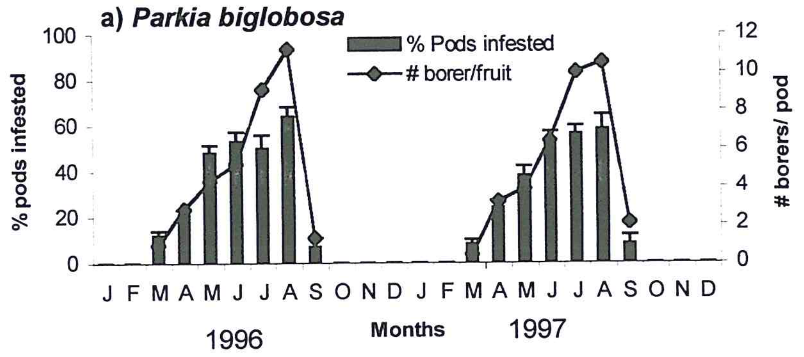
On *P. biglobosa*, *M. nigrivenella* was found from March to early September (Fig. 4.3a), corresponding with the fruiting period of the tree (Fig. 4.2) and the main rainy seasons in the respective agro-ecological zones. Borer populations gradually increased from end March to reach a maximum between July and August, and decreased thereafter. Likewise, the percentage of pods infested per tree increased from 10--20% in March to a maximum of 50--60% in August. Between June and September all *P. biglobosa* trees sampled in all zones were infested. Across the sampling period, percentage of infested trees ranged from 55% to 100%. On average 82% of the trees and 40% of the fruits were infested by the borer. Up to 10 borers were found per pod (Fig. 4.3a).

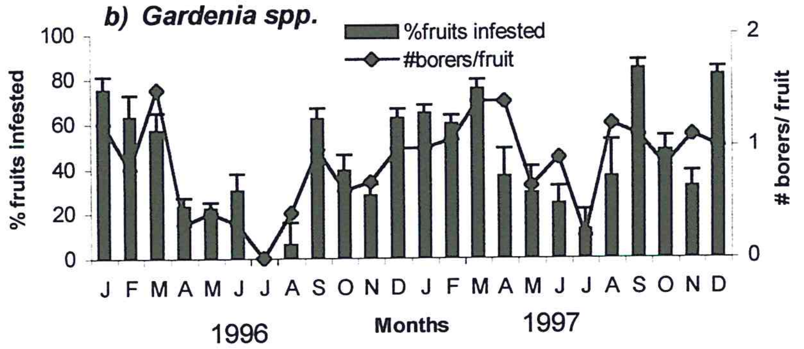
Gardenia spp. fruits were available throughout the year (Table 4.3, Fig. 4.2). However, both the percentage of fruit infested and the densities of *M. nigrivenella* per fruit varied considerably with season. During both years, fruit infestation ranged from 10-80%. Highest population densities were recorded in March, during the dry season, and lowest in July, during the rainy season in all of the agro-ecological zones where the plant was found (Fig. 4.2 & 4.3b). Thereafter, pest densities started to increase, reaching a maximum in March of the following year. Infested *Gardenia* spp. fruits harbored substantially lower numbers of borers than fruits of *P. biglobosa* (Fig. 4.3b), probably because of their smaller size. The percentage of infested *Gardenia* spp. trees varied from 20-76%, with the minimum infestation level occurring in July.

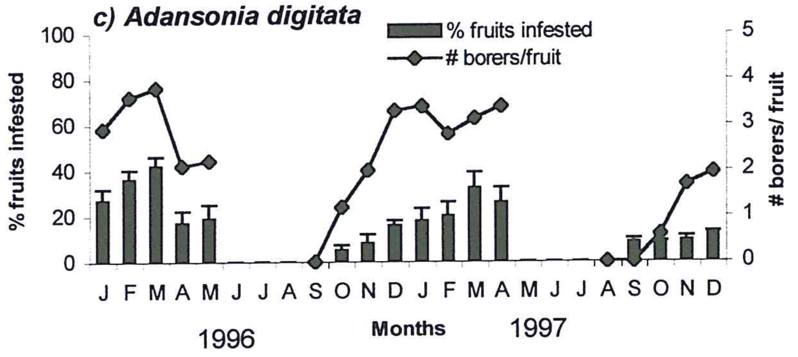
Fruits of *X. americana* and *A. digitata* were mainly found during the dry season (Fig. 4.2) but occasionally fruits of *X. americana* were also collected during the rainy season. In total, > 70% of the *A. digitata* trees were infested, but the level of fruit infestation never exceeded 40% (Fig. 4.3c). Highest borer densities were observed in February and March. The large baobab fruits hosted considerably high numbers of *M. nigrivenella* (Fig. 4.3c). Intact fruits of *X. americana* were rarely observed. Since most of the *X. americana* trees were found in nature reserves, most likely the fruits had been partially consumed by monkeys and baboons. On intact fruits percentage fruit infestation varied from 10--80%, with two peaks in both years, one in February and one in August and minima in June/July (Fig. 4.3d). Among the four wild host plant studied in greater detail, *X. americana* had the highest number of *M. nigrivenella* per infested fruit (Fig. 4.3d). Infestation in *X. americana* followed a similar pattern as in *Gardenia* spp. The proportion of infested *X. americana* trees ranged from 10-30%.

Population dynamics on selected crops. On each crop, *M. nigrivenella* densities per fruit as well as the percentage of fruits infested gradually increased over time (Fig. 4.4a & b). In general, two generations of *M. nigrivenella* were observed on the different host plants (Fig. 4.4a).

On maize, cob infestations occurred from soft dough stage until harvest. The percentage of cobs infested increased within the first three weeks and then leveled off at 10% for three weeks. Thereafter it rapidly increased to a maximum of 32%. The three other host plants set fruits ≈ 90 days after planting and *M. nigrivenella* infestation started on 15 days-old fruits onwards.


a) *Parkia biglobosa*


b) *Gardenia spp.*


c) *Adansonia digitata*

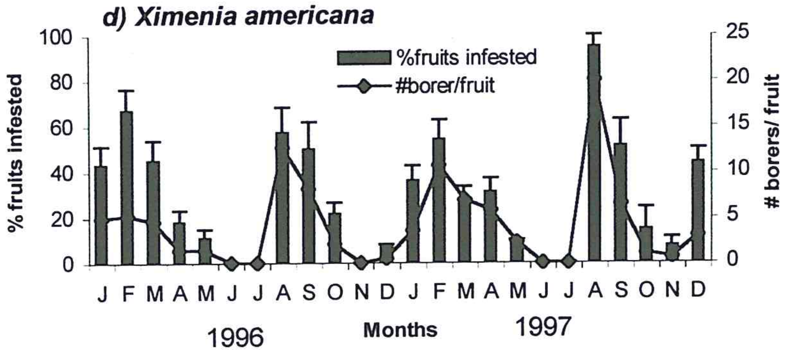

d) *Ximenia americana*

Fig. 4-3 ***Mussidia nigrivenella*** **infestation and mean numbers per fruit on 4 selected wild host plants.**

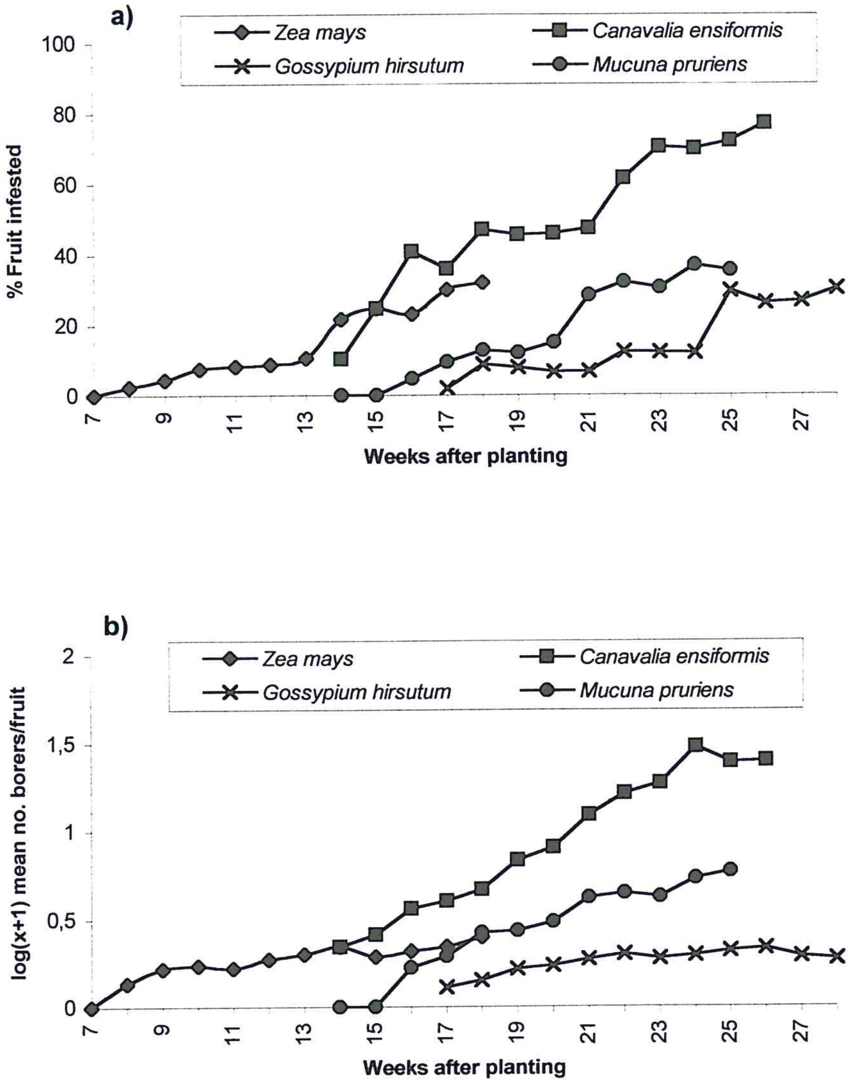


Fig. 4-4 *Mussidia nigrivenella* infestation and mean numbers per fruit on 4 cultivated host plants.

On cotton and the velvetbean, moderate infestation levels were observed with maxima at 30 and 35 % on cotton and velvetbean, respectively. By contrast, on jackbean pods infestation levels were considerably higher and ranged between 10--77%.

There were significant differences between the sum of fruit infestation ranks (Table 4.4) of the different host plants ($\chi^2 = 65.33$, df = 6, $P < 0.001$). *Mucuna pruriens* pods infestation was significantly higher than that of maize and cotton ($\chi^2 = 13.0$, df = 4, $P < 0.05$) but there were no significant differences among the sum of the infestation ranks of maize and cotton when tested alone (χ^2 = 5.6, df = 3, P > 0.05). *Canavalia enseiformis* had significantly higher pods infested compared to *M. pruriens* (χ^2 = 24.0, df = 3, P < 0.001). Hence, the closed testing procedure showed that *M. nigrivenella* infestation was significantly highest on *C. enseiformis,* with highest levels at all sampling occasions (Table 4.4).

Table 4-4 Sum of weekly ranks of *Mussidia nigrivenella* infestation levels observed on four crops in Benin (1995).

Crop	Sum of infestation rank			
	1	2	3	4
Zea mays L.	0	0	5	7
Gossypium hirsutum L.	0	4	5	3
Mucuna pruriens DC.	0	8	2	2
Canavalia enseiformis (L.) DC.	12	0	0	0

The variation in the mean number of borers recorded per fruit followed a similar pattern as fruit infestation (Fig. 4.4b). *Mussidia nigrivenella* densities increased gradually with time on all host plants. On maize and cotton, maximum borer densities were low, with a mean of 1.5 and 1.1 borers per fruit, respectively. On velvetbeans, *M. nigrivenella* densities were moderate but higher than on maize and cotton. *Canavalia enseiformis* hosted the highest borer densities per pod. The mean number of *M. nigrivenella* recorded per pod on *C. enseiformis* varied from 1.2 to 28.9 when most of the fruits were infested. Significant differences were observed when comparing borer-days on different host plants. Borer-days on maize (65.8) and cotton (64.6) were comparable and significantly lower than those observed on velvetbeans (165.5) and jackbeans (765.8) (F = 1704.3, df = 3, 8, P < 0.0001). Significant relationships were obtained between the number of borers per fruit and the percentage of fruits infested recorded per sampling date for each of the host plants (Table 4.5). The slopes of the regressions were significantly different between host plants (*t*-test with Bonferroni probability adjustment, Table 4.5), with *M. pruriens* and *C. enseiformis* having the highest increase in borer densities per unit increase in the pod infestation.

Table 4-5 Relationship between *M. nigrivenella* infestation and number of borers in different crops.

Crop	Intercept ± SE	Slope ± SE	Adjusted-R^2
Zea mays L.	-5.13 ± 1.74	3.01 ± 0.24 c[1]	0.94
Gossypium hirsutum L.	-1.79 ± 3.47	2.57 ± 0.38 c	0.81
Mucuna pruriens DC.	-6.09 ± 2.06	3.72 ± 0.28 b	0.94
Canavalia enseiformis (L.) DC.	15.75 ± 3.47	4.88 ± 0.44 a	0.91

Relationship is $\arcsin\sqrt{y} = a + bx$, where y = percentage fruit infested and x = no. of borers per fruit

[1] Slopes followed by the same letter are not significantly different at $P < 0.05$

4.5 Discussion

During this study, several new host plants for *M. nigrivenella*, including *Gardenia* spp., *M. pruriens*, *X. americana*, *A. digitata* were identified. All the wild trees/shrubs found hosting the borer are native to the West African region, and only the cultivated host plants are of exotic origin. Some of these native perennial host trees such as *P. biglobosa*, *Butyrospermum parkii* (G. Don) Kotschy (Sapotaceae), *T. indica*, and *A. digitata* are of economic and ecological importance in West Africa and are protected species. The leguminous 'néré' tree *P. biglobosa* is a nitrogen fixing species which improves soil fertility (Kessler, 1992). Its fruits are eaten, the inner yellow flour is mixed with water and used as a drink and in some villages to replace sugar (M. Sétamou, unpublished data). The néré kernels are fermented to make local mustard, used as a condiment throughout West Africa (Kessler, 1992). *Tamarindus indica* trees produce a very sour fruit, rich in vitamin C which is thought to be a good cure for colds (Grieve and Leyel 1978). The branches of the tree are gathered, boiled and used as a medicine for fevers, rheumatism, and fatigue (Grieve & Leyel, 1978). The baobab tree *A. digitata* figures in African mythology and is greatly revered. Often, local inhabitants make sacrifices under this tree. Shoots of the tree are eaten in a smoked fish sauce and the white material around the seed is eaten (von Maydell, 1990). The fruits of *B. parkii* are used to make soap and shea butter, the latter being the most important oil used in the Guinea Savannas (Kessler, 1992). These benefits accrue mostly to women who pick, process and sell the by-products of these trees.

Although *P. biglobosa* and *C. enseiformis* have been previously reported hosting *M. nigrivenella* (Moyal, 1988), their importance in the population dynamics of the borer was never studied. Eggs and young instar larvae of *M. nigrivenella* were also collected on fruits of several other plants, which because of the absence of older larvae and pupae appear to be non-host plants. However, they may act as trap plants and thus contribute to a reduction of pest pressure on crops. Our observations reflect the polyphagous nature of *M. nigrivenella*. Other lepidopterous species such as females of *Polygonia c-album* L. and *Cynthia cardui* (L.) (both Lepidoptera: Nymphalidae) also discriminate little between hosts for oviposition (Janz & Nylin, 1997) though the larvae feed only on specific host plants. However, host plant selection in *M. nigrivenella* is at present not clearly understood. Because of their comparatively small size, *Gardenia* spp. fruits hosted relatively low numbers of *M. nigrivenella*. Though the year-round presence of *Gardenia* spp. fruits, coupled with the high percentage of fruits infested, emphasizes the importance of this shrub as a major reservoir of *M. nigrivenella* in Benin. Moreover, *Gardenia* spp. are commonly found in the natural vegetation of Benin, thus permitting high numbers of larvae to develop on a large area. *Ximenia americana* and *A. digitata* bore fruits mainly during the dry season when most of the cultivated host plants were absent. Therefore, these wild hosts might play an important role in regulation of the borer populations. The leguminous species (cultivated and wild) hosted high *M. nigrivenella* densities (Fig. 4.3 & 4.4) and were by far the most frequently infested host plants compared with host plants of other plant families. *Parkia biglobosa,* a perennial leguminous tree, was rarely found non-infested by the borer and the long fruits harboured substantial numbers of *M. nigrivenella*.

Apart of maize, which is widely grown throughout the country, availability and abundance of wild host plants and the two cover crops varied with agro-ecological zones. In the FSM, no host plants were found between February and June. This gap in suitable hosts may seriously affect *M. nigrivenella* populations, which may explain the low infestation levels and densities of the borer found on 1st season maize in the FSM, which matures between June and July (Sétamou, 1996). Most host species were collected in the Guinea Savannas. This diversity of the host plant complex in these zones, coupled with the overlapping fruiting periods may permit a succession of generations throughout the year (see also Fig. 4.2 & 4.3). Hence, *M. nigrivenella* populations in the Guinea Savannas may be maintained at high levels before the maize matures. For instance, maize becomes available as host plant just after the fruiting period of *P. biglobosa* (see Fig. 4.2). Thus borer populations emerging from *P. biglobosa* fruits could shift to maize cobs. This would explain the high borer infestation and damage levels on maize reported from the Guinea Savannas in several West African countries (Moyal & Tran, 1991; Gounou *et al.*, 1994; Sétamou *et al.*, 1999a).

The results of the on-station experiment showed, that *C. enseiformis* is an excellent host for *M. nigrivenella*. Higher fruit infestation and borer densities on this host plant could be the result of either higher larval survival in *C. enseiformis* pods, or greater level of oviposition by the adult females compared with other host plant species. In the laboratory, Sétamou *et al.* (1999b) observed higher survival of *M. nigrivenella* larvae when reared on pods of *C. enseiformis* and *M. pruriens* pods compared with maize cobs. With the actual practice of allowing the cover crops to mature and senesce in the fields, *M. nigrivenella* populations could greatly increase on these plants, thereby endangering the following maize crop. Hence, the on-going large-scale adoption of these crops by farmers in Benin (Vissoh *et al.*, 1998) could change the pest status of *M. nigrivenella* in neighbouring maize fields. Harvested seeds of jack- and velvetbeans can be used as fodder and for human consumption (Udedibie, 1990). However, if properly managed, i.e., the fruiting period of the different crops coincide or pod setting of the cover crops starts after cob formation of maize, these cover crops could reduce *M. nigrivenella* load in maize fields by acting as trap crops.

Most of the previous studies on *M. nigrivenella* were restricted to cultivated crops (Moyal, 1988; Silvie, 1993), which are only temporarily available as host plants. Results presented here show that research on wild host plants in the natural habitat of pest insects is of paramount importance for a comprehensive understanding of the biology and ecology of pests.

5 Bionomics of *M. nigrivenella* (Lepidoptera: Pyralidae) on three host plants[4]

5.1 Abstract

Life table studies of *Mussidia nigrivenella* Ragonot, showed that host plant species had a significant effect on larval survival and developmental time. The maximum percentage of larvae surviving was recorded on jackbean, *Canavalia enseiformis* (36%) and lowest on maize (18%). Mean developmental time for larvae was longest on maize (19.8 days) and shortest on jackbean (17.2 days). Oviposition rate was highest for females resulting from larvae fed on jackbean (mean = 176), followed by velvetbean, *Mucuna pruriens* (mean = 143), and lowest for females where larvae had fed on maize (mean = 127). Longevity of ovipositing females was higher on jackbean (5.4 days) than of those from any other host plants. According to the growth index and life table statistics, jackbean was the most suitable host plant, followed by velvetbean and maize the least suitable. Thus, jackbean should be recommended for use in mass rearing programmes of *M. nigrivenella*, e.g., as a host for parasitoids in future biological control programmes. Because of the high suitability of jack- and velvetbeans for *M. nigrivenella,* planting of these cover crops should be timed in such a manner that the emergence of female moths from mature pods does not coincide with maize plants in a suitable developmental stage for oviposition and development of young *M. nigrivenella* larvae.

5.2 Introduction

The maize cob borer, *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae), is a commonly occurring pest which occasionally causes serious crop damage on maize (Moyal & Tran, 1991b; Bosque-Pérez & Mareck, 1990; Gounou *et al.*, 1994; Sétamou *et al.*, 1998) and cotton (Silvie, 1993) in West Africa. Population densities of *M. nigrivenella* vary according to the different agro-ecological zones in Benin (Sétamou, 1996). Large populations occur in the Guinea Savannas of Benin (Sétamou, 1996), Ghana (Gounou *et al.*, 1994), and Côte d'Ivoire (Moyal, 1988). In addition to maize, Sétamou (1996) identified 16 plant species in Benin on which

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[4] Published as M. Sétamou, F. Schulthess, N. A. Bosque-Pérez; H-M. Poehling, and C. Borgemeister (1999) Bionomics of *Mussidia nigrivenella* (Lepidoptera: Pyralidae) on three host plants. *Bulletin of Entomological Research* (In press).

different life stages of the borer were found. According to Sétamou (1996), the high population densities of *M. nigrivenella* in the Guinea Savannas of Benin are due to the abundance and diversity of various host plants. These comprise several economically important tree species, such as *Parkia biglobosa* (Jacq.) Benth (Mimosaceae) and shea butter, *Butyrospermum parkii* (G. Don) Kotschy (Sapotaceae) and two new cover crops, velvetbean, *Mucuna pruriens* DC. (Fabaceae), and jackbean, *Canavalia enseiformis* (L.) DC. (Fabaceae), introduced to Africa in the last decade. Because of their high nitrogen content, jack- and velvetbeans are used to improve and maintain soil fertility and to reduce soil erosion (Vissoh *et al.*, 1998). In addition, their role in controlling weeds, especially *Imperata cylindrica* (Linnaeus) Raeuschel (Poaceae) is well documented (Vissoh *et al.*, 1998). The grains of these cover crops can also be used as animal fodder and for human consumption (Udedibie, 1990). However, due to the toxicity of the mature seeds of both jack- and velvetbeans, the seeds have to be processed prior to consumption (Udedibie, 1990). Because of the great interest of West African farmers in these new cover crops, it is expected that jack- and velvetbeans will become key components in the farming systems.

Insect development is a key factor in understanding insect ecology. The development of *M. nigrivenella* on maize in the field has been intensively studied (Moyal & Tran, 1991a; Bosque-Pérez & Mareck, 1990; Silvie, 1993; Sétamou, 1996). However, little is known about the borer's performance on other host plant species. Some authors have investigated the biology of *M. nigrivenella* in the laboratory, using meridic diets (Bordat & Renand, 1987; Moyal & Tran, 1991b; Bolaji & Bosque-Pérez, 1998). Insects reared on artificial diets may have different feeding preferences to those feeding on natural host plants (Guthrie *et al.*, 1974). Hence, a better understanding of the biology, ecology and behaviour of a species may be gained by rearing insects on natural host plants.

The objective of this study was to determine host plant suitability of maize and jack- and velvetbeans for *M. nigrivenella*. Studying the performance of *M. nigrivenella* on jack- and velvetbeans could help to predict the risk these cover crops represent as a source of infestation for the borer in maize crops, and also to suggest appropriate management strategies.

5.3 Materials and methods

Plant Material Maize (*Zea mays* L. [Poaceae]) was chosen as a host plant to understand the performance of *M. nigrivenella* on maize cobs in the field. The two other host plant species used in this study were jack- and velvetbeans. All plants were grown at the Benin station of the International Institute of Tropical Agriculture (IITA) in Abomey-Calavi, as mono-crops in blocks of one hectare each. The crops were planted twice at a planting density of 80 cm by 40 cm for maize, and 80 cm by 80 cm for velvet-and jackbeans. The first crops of jack- and velvetbeans were planted in late April 1994. Maize (cv. TZSR [Tropical Zea Streak Resistant; an improved 4-month IITA variety]) was first planted 45 days later, to ensure a synchronisation of the maturity of cobs and pods of each host plant species, since *M. nigrivenella* larvae feed only on mature cobs and fruits (Sétamou, 1996). NPK fertiliser (15-15-15) was applied to the maize crop at a rate of 200 kg/ha three weeks after planting. Cobs and pods with seeds at the dough stage, i.e., completely formed, were used to start the feeding experiment. *Mussidia nigrivenella* oviposits only on maize during this stage (Whitney, 1970; Moyal & Tran, 1991a).

Test larvae Larvae of *M. nigrivenella* used in each experiment originated from an IITA stock culture, maintained for two generations on maize cobs. Newly-oviposited eggs were collected and transferred to incubation chambers consisting of clear plastic containers (20 cm long, 12 cm diameter, 10 cm high), containing moistened tissue paper at the base. The eggs were placed on the tissue paper and incubated at 26 ± 2°C under 12:12 (L:D) photoperiod for approximately five days. On the sixth day, newly emerged larvae (c. one day-old) were transferred onto pieces of diet.

Rearing procedures Maize cobs with husks and pods of jack- and velvetbeans were harvested and cut into 10 cm long pieces. Cut pieces were disinfected in bleach solution (5%) for 30 minutes, and rinsed twice with distilled water. Each piece was infested with 25 first instar larvae of *M. nigrivenella*, and the pieces were grouped (four for maize and eight for jack- and velvetbeans) in plastic rearing containers (14 cm in height and 11 cm in diameter). In each experiment, 25 rearing containers were used for maize and ten containers for each of the other two host plants. Five experiments were conducted between 1994 and 1997, with a total initial population of 12,500 larvae on maize, and 10,000 larvae each for jack- and velvetbeans. The containers were covered with plastic mesh and kept under controlled conditions at 26

± 2°C, 65 ± 5% relative humidity (rh), and a photoperiod of 12:12 (D:L). After 10 days, the diet was renewed for all treatments. As the larvae increased in size, only ten (or fewer) larvae were kept on each plant piece. Subsequently, during larval development, for maize and velvetbean the diet had to be renewed between two and three, and three times, respectively. For jackbean, no further diet renewal was needed before pupation. When pupation started, the containers were examined daily and cocoons were collected. Cocoons were kept individually in gelatine capsules for two days, after which the pupae were removed using a pair of scissors. The pupae were sexed and kept in petri dishes until adult emergence. Two pairs of newly emerged adults were selected from each rearing container for the adult longevity and fecundity study. A total of 250 pairs for maize and 100 pairs for jack- and velvetbeans, respectively were used throughout the study. Adults were allowed to mate and oviposit in boxes (clear plastic cylinders, 10 cm in height and 10 cm in diameter) and were supplied with a piece of cotton wool soaked into sugar-water placed in a small cup, as food source for the adults. Tissue paper with a rough surface was attached to the inside of the box as an oviposition substrate for females. The viability of eggs laid by females which had emerged from the three tested host plants, was studied in each of the five experiments, by incubating 100 randomly selected eggs per host plant treatment.

Data collected The percentage of survival of larvae ten and 16 days after infestation, the percentage of pupae formed, and the duration of the larval and pupal stages were recorded. All pupae were sexed, and the sex-ratio was determined for each host plant. The longevity of adults and the fecundity of adult females were recorded. Developmental time for each life stage (L) was computed after L = nixi/ni, where ni is the number of individuals and xi the time required to complete the developmental stage. The viability of eggs, calculated as the proportion of larvae hatching from the incubated eggs, was recorded. Life table statistics were calculated to estimate the growth rates of *M. nigrivenella* on the three host plants (Southwood, 1978). Net reproductive rate (R0), the growth rate (the intrinsic rate of natural increase r), the finite capacity of increase λ, defined as the number of times a population multiplies itself per unit time, the generation time and the doubling time of *M. nigrivenella* were calculated using a jacknife programme (Hulting *et al.,* 1990).

Statistical analysis Percent survival, developmental times, weight of pupae, female fecundity and life table parameters were subjected to analysis of variance for the effects of larval host plants. Means were separated using the sequential Student Newman Keuls (SNK) test when significant *F*-values were obtained ($P < 0.05$) (Zar, 1974). The sex ratio was compared with an assumed 1:1 ratio using the Wilcoxon $\chi 2$ test of conformity (Sokal & Rohlf, 1995). All percentages were arcsin$\sqrt{x}$-transformed before analysis, and the results presented as back-transformed data.

5.4 Results

The time of conduct of the five independent experiments had no significant effect on any of the variables ($P > 0.05$). Therefore, for each treatment the data were pooled across experiments.

The survival of *M. nigrivenella* larvae was significantly affected by the different host plants, resulting in significant differences in the percentage of pupae formed (Table 5.1). Highest survival was found on jackbean and lowest on maize. The effect of host plants on larval mortality was already apparent ten days after infestation (Fig. 5.1). The larval developmental period was also significantly influenced by host plant, and was shortest on jackbean and longest on maize (Table 5.1). Similarly, female pupae were heaviest on jackbean. However, no significant effects of host plant were observed for male pupal weight, duration of pupal development and the proportion of emerged adults (Table 5.1). The percentage of adults emerging from pupae did not vary with sex ($t = 0.62$, df = 13, $P > 0.05$) and the observed male : female sex ratios on the three host plants (for maize 1: 1.03; for velvetbean 1: 1.02; for jackbean 1 : 1.08) did not differ significantly from a 1:1 ratio (Wilcoxon $\chi 2 = 0.79$, for maize, $\chi 2 = 0.94$ for velvetbean, and $\chi 2 = 1.04$ for jackbean, df = 1, $P > 0.05$ for all three host plants).

Jackbeans yielded a significantly higher proportion of egg-laying females and those females laid significantly more eggs than females emerging from larvae reared on the two other host plants (Table 5.2). In addition, the oviposition period of females emerging from larvae fed on jackbean was significantly longer than those reared on maize and velvetbean (Table 5.2). Adult longevity of males and females was not affected by the host plant species. Oviposition commenced on the day of adult emergence without any pre-oviposition period (Fig. 5.2).

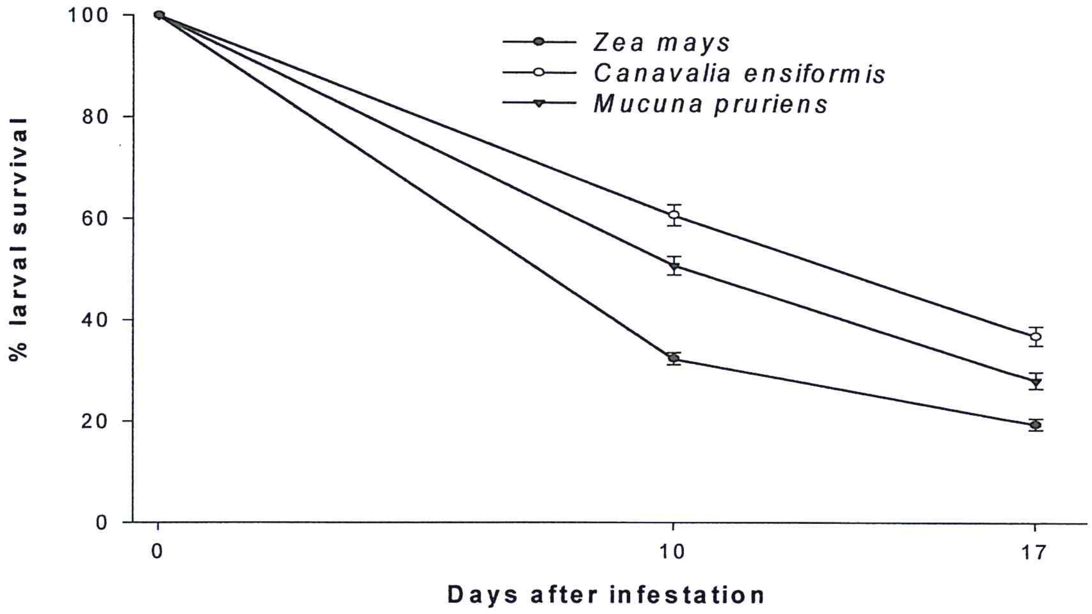

Fig. 5-1 Effect of host plants on mean larval survival of *Mussidia nigrivenella*. N = 125 for maize, and 50 for *C. enseiformis* and *M. pruriens*, respectively; error bars are standard errors of the mean.

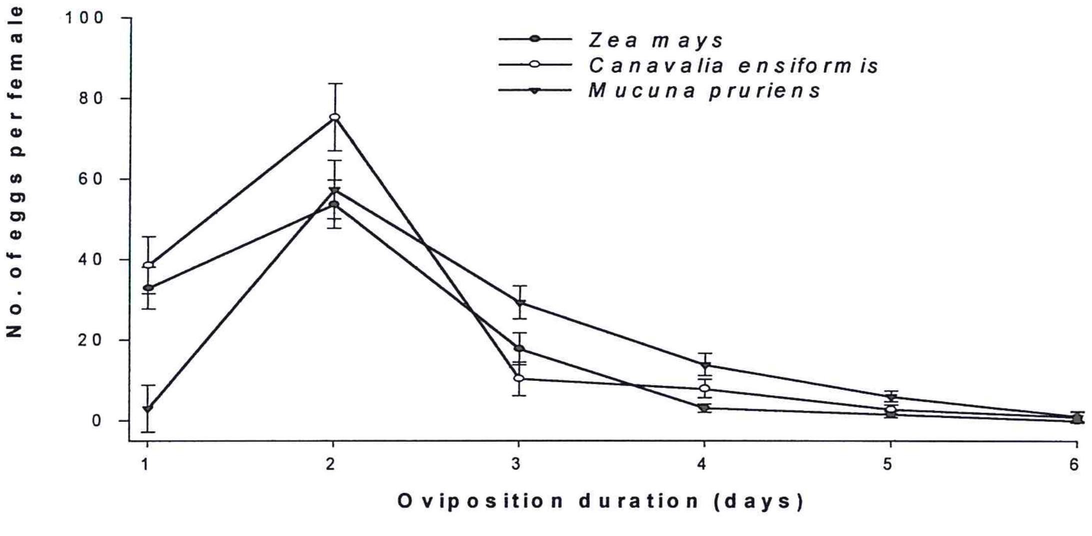

Fig. 5-2 Effect of host plants on mean female fecundity in *Mussidia nigrivenella*. N = 215, 93 and 85 for maize, *C. enseiformis* and *M. pruriens*, respectively; error bars are standard errors of the mean.

Table 5-1 Effect of host plants on mean (± SE) survival, growth and developmental time of *Mussidia nigrivenella*.

Host plant	Larval period (days)	Pupae formed (%)	Pupal weight (mg)		Pupal period (days)		Adult emergence (%)
			males	females	males	females	
Zea mays	19.7 ± 0.05 c[1]	18.4 ± 0.6 a	87 ± 7	102 ± 6 a	10.5 ± 0.03	10.4 ± 0.03	93.4 ± 2.1
	(2304)[2]	(125)	(1148)	(1156)	(1068)	(1080)	(125)
Canavalia enseiformis	17.9 ± 0.03 a	36.2 ± 1.8 c	89 ± 5	113 ± 3 b	10.5 ± 0.02	10.4 ± 0.02	92.2 ± 2.7
	(3618)	(50)	(1715)	(1903)	(1580)	(1758)	(50)
Mucuna pruriens	19.2 ± 0.06 b	28.2 ± 1.4 b	90 ± 5	100 ± 3 a	10.4 ± 0.09	10.4 ± 0.03	94.1 ± 3.1
	(2820)	(50)	(1416)	(1404)	(1330)	(1362)	(50)
F-value	476.00	71.65	0.15	1.19	1.67	0.44	1.23
MSE	5.57	84.97	-	697.83	-	-	-
df total	8741	224	4278	4462	3977	4199	224
P-value	< 0.001	< 0.001	ns	< 0.05	ns	ns	ns

[1] Values in the same column, followed by the same letter, are not significantly different ($P < 0.05$; Student Newman Keuls test)

[2] Values in parentheses are number of observations for each treatment

Table 5-2 Effect of host plants on mean (± SE) adult longevity, fecundity, and egg viability of *Mussidia nigrivenella*.

Host plant	% Adult females laying eggs	No. eggs per female	% eggs fertile	Oviposition period (days)	Adult longevity (days)	
					males	females
Z. mays	86.1 ± 3.4 a[1] (250)[2]	126 ± 16 a (215)	29.4 ± 1.0 (500)	4.7 ± 0.2 a (215)	6.9 ± 1.2 (250)	7.8 ± 1.6 (250)
C. enseiformis	93.2 ± 3.1 b (100)	172 ± 13 b (93)	32.4 ± 1.5 (500)	5.4 ± 0.2 b (93)	7.3 ± 1.2 (100)	8.2 ± 1.1 (100)
M. pruriens	84.7 ± 3.7 a (100)	123 ± 11 a (85)	32.8 ± 1.6 (500)	4.9 ± 0.2 a (85)	7.2 ± 1.4 (100)	8.5 ± 1.4 (100)
F-value	3.81	5.03	2.64	3.27	1.98	2.04
MSE	246.7	674.4	-	1.31	-	-
df total	449	392	1499	392	449	449
P-value	< 0.05	< 0.01	ns	< 0.05	ns	ns

[1] Values in the same column, followed by the same letter, are not significantly different ($P < 0.05$; Student Newman Keuls test)

[2] Values in parentheses are number of observations for each treatment

For all three host plants, the peak of egg laying was observed on the second day of the oviposition period and declined thereafter. Although some females were observed to lay eggs for about ten to 12 days, in all treatments oviposition lasted for an average of five to six days. Females laid more than 90% of their eggs during the first three days of the oviposition period. There were no significant differences in the post-ovipositional period between the three host plants (4.1, 4.2 and 3.8 days on maize, velvet- and jackbeans, respectively). The viability of eggs was not influenced by the parental host plants.

More than 95% of adult mortality of *M. nigrivenella* occurred during the first eight days of adult life span, with peak mortalities on the fifth day for adults emerging from larvae reared on maize and velvetbean, and on the sixth day for jackbean, respectively (Fig. 5.3).

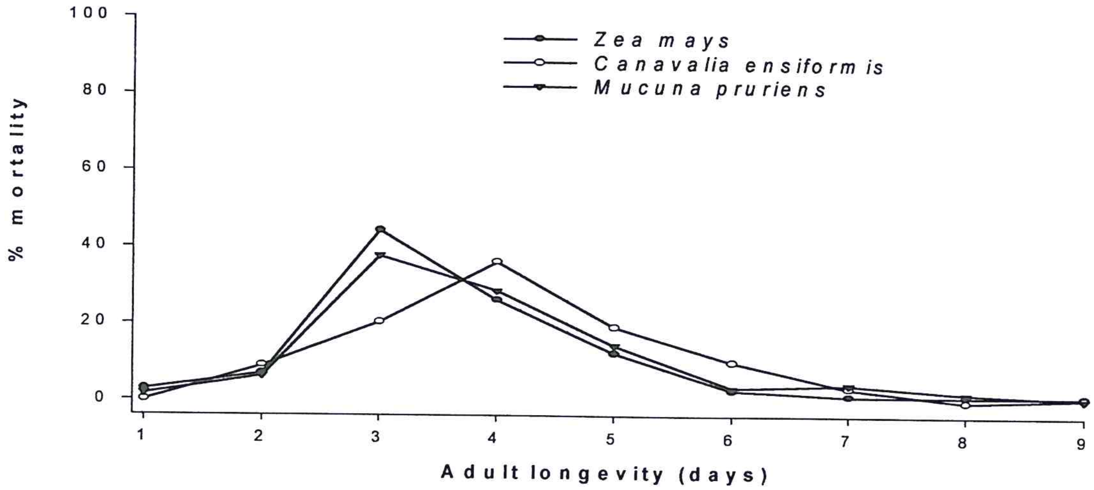

Fig. 5-3 Effect of host plants on mortality pattern of adult *Mussidia nigrivenella*. N = 500 for maize and 200 for *C. enseiformis* and *M. pruriens*, respectively.

The net reproductive rate, the intrinsic rate of increase, the finite rate of increase, the generation time and the doubling time varied significantly with host plants (Table 5.3). The net reproductive rate was highest for females emerging from larvae fed on jackbean (F= 10.84, df = 2, 12, $P < 0.01$, Table 5.3). Generation time was shortest for larvae fed on jackbean (F = 133.48, df = 2, 12, $P < 0.01$), with approximately 35.5 days from egg stage to adult mortality (Table 5.3). The generation time on maize and velvetbean was similar (between 37 and 38 days). The host plant species had a significant effect on the intrinsic rate of increase and the doubling time (Table 5.3). Moths emerging from larvae reared on jackbean produced the highest number of individuals/female/day, followed by those fed on velvetbean. The lowest daily progeny production per female was recorded for moths emerging from larvae reared on maize (Table 5.3). The finite rate of increase was significantly higher on jackbean compared to maize. Doubling time for moths emerging from larvae fed on jackbean was 30% and 19% shorter than on maize and on velvetbean, respectively. The growth index on jackbean was about twice as high as on maize and substantially higher than that on velvetbean. The total progeny was significantly higher on jackbean compared to the two other host plants (Table 5.3).

Table 5-3 Effect of host plants on life table parameters (± SE) and growth index of *Mussidia nigrivenella*.

Host plant	R_0[1]	r	λ	T	DT	Total progeny	GI[2]
Z. mays	10.1	0.071	1.07	37.5	9.8	20.3	0.56
	± 0.4 a[3]	± 0.001a	± 0.002 a	± 0.2 c	± 0.2 c	± 0.8 a	
C. enseiformis	23.8	0.104	1.11	35.5	6.8	47.3	1.17
	± 3.2 b	± 0.005 b	± 0.006 b	± 0.4 a	± 0.3 a	± 6.3 b	
M. pruriens	14.9	0.084	1.09	36.9	8.4	29.7	0.88
	± 1.8a	± 0.004 a	± 0.006 a	± 0.1b	± 0.4 b	± 3.6 a	
F-value	10.84	19.30	11.83	133.48	20.64	10.50	
MSE	22.49	0.0001	0.0001	0.040	0.54	89.65	
df total	14	14	14	14	14	14	
P-value	0.002	< 0.001	0.001	< 0.001	< 0.001	0.002	

[1] R_0 = Net reproductive rate, r = intrinsic rate of increase, λ = finite rate of increase, T = generation time in days, DT = doubling time in days calculated using the jacknife programme described by Hulting *et al.*, (1990).

[2] GI = growth index, computed as the ratio between the percentage of adults emerged and the duration of the immature period (larval and pupal) (Ramasubramanian & Babu, 1989).

[3] Means followed by the same letter, in the same column are not significantly different ($P < 0.05$, Student Newman Keuls sequential test).

5.5 Discussion

Survivorship of larvae of *M. nigrivenella* on maize was consistent with Slobodkin's type IV survival curve (Southwood, 1978), indicating that population decrease mainly occurred during the early instars. The most likely explanation is that the extent and thickness of the maize husk covering adversely affected the establishment of first instar larvae on the cob. Characteristics of husk cover of maize have been reported to have a substantial effect on infestation levels of the maize weevil *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) (Kossou *et al.*,, 1993) and the larger grain borer *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) (Meikle *et al.*, 1998). Moyal and Tran (1991a) observed 90% mortality of the first two instars of *M. nigrivenella* in maize in the field. Once the larvae have successfully established in the cobs, *M. nigrivenella* seems to be protected by the husks from any adverse effect, and as a consequence they suffer only low levels of mortality in later instars. Also, maize grains are nutritious and have a high water content which can reduce the mortality of larvae after their establishment on maize cobs (N. A. Bosque-Pérez, unpublished data). Moyal and Tran (1991a) observed less than 10% mortality of larvae for late instars on meridic diets in the laboratory. Thus, establishment of larvae in the cobs may be one of the most important factors determining the number of larvae found per cob in maize fields. The survival curve for *M. nigrivenella* on jack- and velvetbeans was similar to a Slobodkin's type III survival curve of constant mortality over time (Southwood, 1978). In maize, only the grains were used as a food source by *M. nigrivenella* larvae, whereas on jackbean, larvae were found feeding on every part of the pods and on velvetbean, even on the valves. Thus on jack- and velvetbeans, early instars did not starve before penetration into the pods and as a result, had lower mortality rates than on maize. However, moderately high mortality of larvae was observed on jack- and velvetbeans, possibly due to the handling of the insects during the experimentation.

The observed differences in survivorship of larvae on the three tested host plants in this study may explain the varying infestation levels of *M. nigrivenella* observed in the field at the IITA-Benin station, where considerably more *M. nigrivenella* borers occur on jack- and velvetbeans than on maize cobs (M. Sétamou, unpublished data). Our mortality levels were much higher than the 5% and 24% mortalities recorded by Bordat and Renand (1987) and Bolaji and Bosque-Pérez (1998) respectively, using artificial diets. Artificial diets, however, tend to have higher vitamin and amino acid contents resulting in lower mortality and higher fecundity (Vanderzant, 1974).

The prolonged larval period of *M. nigrivenella* on maize may have been due to the quality of the diet. Numerous studies have shown that diet quality has an important impact on insect developmental time. Bolaji and Bosque-Pérez (1998) observed a reduction in developmental time of *M. nigrivenella* when larvae were reared on a jackbean-based diet compared to maize-based diets. In most cases, the duration of larval period of insects is inversely related to the nitrogen level of the food source (Al-Zubaidi & Capinera, 1983). Duration of the larval period in *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) was shorter when the larvae were reared on maize stems supplied with additional nitrogen (Sétamou *et al.*, 1993). Both jack- and velvetbeans are leguminous crops and therefore contain high levels of protein (Duke, 1981). Moreover, in this study female pupae originating from larvae reared on jackbean were the heaviest, probably as a result of better food quality for the larvae.

The total developmental time of *M. nigrivenella* recorded in the present study and the mean adult life span were comparable to those reported by Bolaji and Bosque-Pérez (1998), though these authors conducted their studies using a meridic diet. The mean number of eggs laid per female was higher on jackbean compared to maize and velvetbean. Differences in the fecundity of *M. nigrivenella* according to the diet used, were also reported by Bolaji and Bosque-Pérez (1998). These authors observed that diets containing flour from leguminous seeds yielded females that laid significantly more eggs than females originating from larvae fed on maize-flour based diets only. A larval diet rich in protein content often results in increased fecundity of many Lepidoptera, e.g., in *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) (Sankeperumal *et al.*, 1989). Applying nitrogenous fertiliser to maize plants increased the number of eggs laid by *S. calamistis* (Sétamou *et al.*, 1993). Egg viability in this study (29-33%) was lower than that observed by Bolaji and Bosque-Pérez (1998) (72-90%), but comparable to that reported by Moyal and Tran (1991a) (25-30%). Adding proteins to the larval diet of *Apomyelois ceratoniae* Zeller (Lepidoptera: Pyralidae) improved fecundity and egg fertility by 30% (Al-izzi *et al.*, 1988). The diet used by Bolaji and Bosque-Pérez (1998) for rearing *M. nigrivenella* contained vitamins and was therefore most likely a better food source than the host plant materials used in the present study.

The effect of host plants on *M. nigrivenella* are best observed by comparing life table statistics. The growth index (Ramasubramanian & Babu, 1989) for maize was lower than that observed for jack- and velvetbeans, whereas the generation time was longest on maize. On jackbean the number of times *M. nigrivenella* population will multiply per generation was more than double of that observed on maize. Thus, maize cobs were nutritionally inferior to the pods of jack- and velvetbeans.

Overall, jackbean proved to be the most suitable host plant for *M. nigrivenella*. Hence, for mass rearing of *M. nigrivenella*, e.g., as host for parasitoids in a biological control programme, jackbean would be an ideal candidate. Moreover, jackbean offers the advantage of only one diet replacement during the larval development.

The present work is part of a larger study on the role of various host plants in the population dynamics of *M. nigrivenella* in West Africa. The higher suitability of jack- and velvetbeans compared to maize might have direct effects on the population dynamics of *M. nigrivenella*, especially considering the high adoption rate of these cover crops by West African farmers. Velvet- and jackbeans can host large populations of *M. nigrivenella* and thereby constitute a viable infestation source for maize. In Benin, generally, *M. nigrivenella* densities in maize fields do not exceed two to three borers per cob (Shanower *et al.*, 1991; Sétamou, 1996). However, in a field experiment conducted at the IITA station in Benin, *M. nigrivenella* densities in a maize field close to fields of velvet- and jackbeans were as high as four to five borers per maize cob at harvest (M. Sétamou, unpublished data). Hence, farming practices should be managed in such a way, that the fruiting periods of jack- and velvetbeans do not precede that of maize, thereby avoiding *M. nigrivenella* populations shifting from cover crops to maize. However, in areas with two maize growing seasons per year (i.e., southern Benin), harvesting the pods of jack- and velvetbeans at maturity could greatly reduce the risk of *M. nigrivenella* infestations in maize.

6 Spatial distribution of and sampling plans for *M. nigrivenella*[5]

6.1 *Abstract*

Spatial distribution of *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) was studied in maize fields and on four major wild host plants in the Republic of Benin, West Africa. Maize cobs were sampled at harvest in 1994 and 1995, and fruits of the wild host plants were collected monthly from January 1996 to December 1997 during the fruiting periods of the respective host species. The spatial distribution was analysed using Southwood's coefficient of dispersion (s^2/m), Iwao's patchiness regression and Taylor's power law (TPL). Iwao's patchiness regression was inappropriate for our data as shown by the non-homogeneity of variance, whereas TPL fitted the data well. Based on Southwood's index of dispersion and TPL, *M. nigrivenella* was aggregated on maize cobs and fruits of three wild hosts, i.e., *Adansonia digitata* L. (Bombacaceae), *Parkia biglobosa* (Jacq.) Benth. (Mimosaceae) and *Ximenia americana* L. (Olacaceae). On *Gardenia sokotensis* Hutch (Rubiaceae), however, the distribution was either regular or random according to the season. Density and aggregation of *M. nigrivenella* were strongly and positively related with the fruit size of the host plants. The optimal number of minor sampling units needed to estimate *M. nigrivenella* densities on the respective host plants in Benin, varied from four fruits on *G. sokotensis* to 10 pods on *P. biglobosa*. These values were used to calculate the time expenditure needed to sample maize fields or wild host plant trees in order to achieve a pre-defined precision level of 25%.

6.2 *Introduction*

The cob borer *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) is one of the most important pest of maize in West Africa, particularly in the Guinea Savannas (Moyal & Tran, 1991b,;Silvie, 1993; Sétamou *et al.,* 1999a). In addition to maize, *M. nigrivenella* attacks several wild host plants, some of which are of economic importance to small-scale farmers in West Africa (Sétamou 1996). Females lay eggs

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on the fruits of wild host plants and the hatching first instars bore into the fruits. Before pupating, last instars bore exit holes into the pericarp or husks (Sétamou, 1996). Contrary to maize on which only one generation of the borer generally occurs, several generations of *M. nigrivenella* were recorded on different wild host plant species in Benin (Sétamou *et al.*, 1999c). The abundance of *M. nigrivenella* on wild host plants, coupled with the overlapping fruiting periods of these plants are important factors determining the borer densities on maize (Sétamou *et al.*, 1999b).

Knowledge of the spatial distribution of insects is important in understanding the biology and ecology of a species as affected by abiotic and biotic factors. Also, information on the spatial distribution of an insect are often the basis for the development of sampling protocols (Bins & Nyrop, 1992). Sampling plans, which allow the estimation of pest densities with a given accuracy level and at minimal costs, are the first step for developing of efficient control options (Wearing, 1988). Several studies have been conducted on the dispersion of lepidopteran stem and cob borers in Africa (Phiri, 1995; Kouamé, 1995; Schulthess *et al.*, 1991; Ndemah, 1999), and sampling plans for *M. nigrivenella* on maize have been developed (Schulthess *et al.*, 1991; Ndemah, 1999). However, little is known about the spatial distribution of *M. nigrivenella* on wild host plants. The dispersion of insect populations is usually species specific (Taylor, 1984), but may vary with densities and between habitats (Anderson *et al.*, 1982).

The objectives of our study were (i) to compare the spatial distribution indices of *M. nigrivenella* on maize, *Zea mays* L. (Poaceae), and on four wild host plants commonly found in West Africa, i.e., *Gardenia sokotensis* Hutch (Rubiaceae), *Parkia biglobosa* (Jacq.) Benth. (Mimosaceae), *Adansonia digitata* L. (Bombacaceae) and *Ximenia americana* L. (Olacaceae) (Sétamou *et al.*, 1999c), and (ii) to determine the number of samples needed to precisely assess population densities of the borer on these host plants.

6.3 Materials and methods

Data collection Several country-wide surveys on maize and four wild host plants were conducted in Benin between 1994 and 1997. For maize, sampling was carried out at maturity during the main cropping seasons of 1994 and 1995, respectively. Maize fields were visited between July and October, depending on the time of maturity of the crop in the different agro-ecological zones (Sétamou *et al.,* 1999a). Borers were sampled in 80 and 60 maize fields in 1994 and 1995, respectively. On each sampling occasion, fields were divided into four sectors and five cobs were randomly collected per sector, giving a total of 20 sampled cobs per field. The fields surveyed varied with regard to maize cultivars and size, but only fields with a size between 0.75-1 ha were considered.

Because of their importance for the population dynamics of *M. nigrivenella* in Benin, the following four wild host plant species were selected: *G. sokotensis.*, *P. biglobosa*, *A. digitata* and *X. americana* (Sétamou *et al.,* 1999c). *Gardenia sokotensis* is a shrub found in the savanna zones of tropical Africa which does not exceed 3 m in height and has small cylindrical fruits (von Maydell, 1990). *Parkia biglobosa* is an important multipurpose leguminous tree from the savanna zone of West Africa. It has been reported to increase soil fertility and crop yields beneath its crown. The plant can reach 20 m in height and has long pods up to 25 cm (von Maydell, 1990). In the Guinea Savannas of Benin densities of 50-100 *P. biglobosa* trees per ha have been reported (Agbahungba & Depommier, 1989). *Adansonia digitata*, the baobab tree, is a deciduous tree reaching 25 m in height with fruits of globose to ovoid or oblong-cylindrical form (von Maydell, 1990). *Ximenia americana* is a shrub or tree which does not exceed 8 m in height and is mainly found in natural reserves of Benin.

Between January 1996 and December 1997, samples were taken once a month during the fruiting periods of the respective wild host plants. The number of host plant trees sampled per month were 13 for *A. digitata*, 29 for *G. sokotensis*, 25 for *P. biglobosa* and 12 for *X. americana*, respectively. Since *M. nigrivenella* borers are found mainly on mature fruits (Sétamou 1996), only fruits at maturity were collected. Fruits were randomly hand-picked from *G. sokotensis* shrubs. From *P. biglobosa*, *A. digitata* and *X. americana* fruits were sampled using a harvest pole of ≈ 6 m length with a knife attached to the top of the pole. However, due to the height of the trees, fruits were only collected from the accessible parts of the trees, i.e., up to 8 m above the ground. For plants bearing big fruits (diameter > 5 cm), i.e., *A. digitata* and *X. americana*, 10 fruits were sampled per tree. For plants with smaller fruits (diameter < 5 cm), i.e., *G. sokotensis* and *P. biglobosa*, 20 fruits were collected per plant, except for *G. sokotensis* between June and August 1996 and 1997, when only 18 fruits per plant were sampled. For all collected fruits and cobs the length and the diameter in the middle of the fruits and cobs, respectively, were measured.

All samples were dissected and the number of *M. nigrivenella* larvae and pupae was counted per cob or fruit. This data was then used to calculate the average number of *M. nigrivenella* per sampling unit (m), and the variance (s^2). In addition, the proportion of infested cobs/fruits (P_1) and the proportion of non-infested cobs/fruits ($P_0 = 1\text{-}P_1$) were estimated for each sampling date and host plant species.

Dispersion analysis To determine the spatial distribution of *M. nigrivenella* on the different host plants, Southwood's coefficient of dispersion D (= s^2/m) (Southwood, 1978), was calculated for each sampling date. D is distributed as a χ^2 variable with n-1 degrees of freedom (Elliot, 1977). Therefore a χ^2-test for goodness-of-fit was run to test for conformity with a random distribution using the index of dispersion (Southwood, 1978). The calculated index ($I_D = s^2(n\text{-}1)/m$) was compared to the expected χ^2 for n-1, where n is the number of samples (cobs/fruits) taken to calculate the mean and the variance. A value of $D = 1$ implies random distribution, whereas a value < 1 indicates a regular and a value > 1 implies an aggregated distribution (Elliot, 1977).

Southwood's dispersion index is considered to be descriptive for the spatial distribution pattern of a given insect (Kuno, 1991). For a quantitative analysis of the distribution of *M. nigrivenella* in maize cobs and the fruits of the four wild host plant species in terms of some ecological meaningful parameters (Kuno, 1991), two models expressing both variance-mean relationships, Iwao's (1968) patchiness regression and Taylor's power law (TPL) (Taylor, 1961), were examined for their suitability.

The expression of Iwao's patchiness regression is as follows:

$$M = \alpha + \beta m$$

where M is the mean crowding index defined by Lloyd (1967) as $M = m + ((s^2/m) - 1)$. The intercept α is the index of basic contagion. At very low densities, an individual *M. nigrivenella* is expected to live together with α other individuals in the same fruit (Taylor, 1984). Hence, α +1 indicates the size of the colony that constitutes the basic unit of distribution. The density-contagiousness coefficient β describes the distribution of individuals in their habitat (Iwao, 1968), with $0 < \beta < 1$, $\beta = 1$, and $\beta > 1$ describing individuals distributed in an uniform, random, and aggregated way, respectively (Iwao, 1968).

Taylor's power law (TPL) relates variance to mean density through:

$$s^2 = am^b$$

where *a* is a sampling factor and *b* is an index of aggregation. Based on TPL, Shen (1990) developed a criterion system for identifying the type of spatial pattern of different insect populations. Thereby the distribution pattern is determined by the 2 parameters *a* and *b*, and by the mean density *m* (Table 6.1). Values of the coefficients *a* and *b* are estimated by regressing the logarithms of the sample variance ($ln\ s^2$) on the logarithms of the sample mean densities ($ln\ m$) for all pairs of means and variances obtained from all sampling dates and sampling units.

Table 6-1 The criterion system used for determining the spatial distribution pattern (SDP) of insect populations based on Taylor's power law (Shen, 1990).

Insect mean in sample $\bar{m}$*	Sampling factor a	Aggregation index b	SDP
= 1	= 1	any real number	random
	> 1	any real number	aggregated
	< 1	any real number	uniform
≠ 1	= 1	= 1	random
		> 1	aggregated
		< 1	uniform
	≠ 1	$= 1 - \frac{\ln(a)}{\ln(m)}$	random
		$> 1 - \frac{\ln(a)}{\ln(m)}$	aggregated
		$< 1 - \frac{\ln(a)}{\ln(m)}$	uniform

* $\bar{m}$ = global mean number of *M. nigrivenella* calculated over all major sample units,
a and *b* are sampling factor and index of aggregation, respectively, obtained from Taylor's power law.

The fit of each data set to the linear regression model was evaluated by the respective R^2 values. The slopes of the regressions were compared to 1 with a *t*-test (t = (slope -1)/SEM of slope, with N-2 degrees of freedom and a probability level of $P = 0.05$) (Sokal & Rohlf, 1995). In addition, analysis of covariance was used to test for homogeneity of the regression coefficients (Sokal & Rohlf, 1995).

The mean volume of cylinder-like fruits of *P. biglobosa*, *G. sokotensis* and *A. digitata* and cobs of *Z. mays* were calculated based on length and diameter of the fruits and cobs, respectively. For the round fruits of *X. americana*, the mean volume was calculated based on the diameter of the fruits. The mean volume of the different fruits and maize cobs was related to TPL aggregation index, using simple correlation analysis (Sokal & Rohlf, 1995).

Mean-incidence relationship The relationship between the proportion of infested sample units (P_1) and mean density (m) was established using the general formula of Wilson and Room (1983):

$$P_1 = 1 - e^{-m\ln\left(\frac{am^{b-1}}{am^{b-1}-1}\right)}$$

where a and b are TPL coefficients.

Estimation of sample size. Since *M. nigrivenella* lives cryptically within its host and generally no external damage is visible on infested maize cobs or fruits of wild host plants (Moyal, 1988; Sétamou 1996), only destructive sampling techniques allow a precise estimation of borer densities. The number of major units, in our study maize fields and wild host plant trees, respectively, as well as the number of minor sampling units, i.e., maize cobs and fruits to be sampled, were determined using the method of optimum sample allocation in two-level samplings (Southwood, 1978; Greenwood, 1996). The two levels were characterised as follows:

M = number of major units available for sampling (may be effectively infinite),

M_s = number of major units actually sampled,

U = number of minor units available within each major unit which is assumed to be the same for all major units,

u = number of minor units actually sampled in each major unit (assumed to be the same for each major unit).

The optimum number of minor sample units to be taken per major sample unit is estimated using Greenwood's (1996) formula:

$$u_{opt} = \sqrt{\frac{\dfrac{c_m}{c_u}}{\left(\dfrac{s_M{}^2}{s_u{}^2} - \dfrac{1}{U}\right)}}$$

where $S_M{}^2$ is the variance of the global mean number of *M. nigrivenella* ($\overline{\overline{N}}$) calculated over all major sample units. $S_u{}^2$ is the mean of all major unit variances. C_m is the basic cost per major sample unit, i.e., the duration of time to locate a maize field or a wild host plant tree, and C_u is the additional cost for each minor unit sampled, i.e., the time spent to sample and dissect each minor unit. During the surveys, it took ≈ 0.5 h to locate a maize field or a wild host plant tree, and between 90 s to 3 min to sample and dissect a maize cob or a fruit.

To achieve a defined percentage relative precision (Q), the general formula for predicting the number of major units needed is calculated after Greenwood (1996):

$$m_p = \frac{s_M{}^2 + s_u{}^2\left(\dfrac{1}{u} - \dfrac{1}{U}\right)}{\dfrac{s_M{}^2}{M} + \left(\dfrac{\overline{\overline{N}}}{200} \times Q\right)^2}$$

The level of relative precision Q is defined as the proportion of the mean ($Q = CI/2n$, where CI is the confidence interval). Since the number of major units tends to be infinite in our sampling area, the ratio $S_m{}^2/M$ will approximate to zero; therefore the number of major units to be sampled is:

$$m_p = \frac{s_M{}^2 + s_u{}^2\left(\dfrac{1}{u} - \dfrac{1}{U}\right)}{\left(\dfrac{\overline{\overline{N}}}{200} \times Q\right)^2}$$

The required sample size for the different host plants was determined for a relative precision level (Q) of 25%, which allows detection of doubling or halving of sample means (Southwood 1978).

In most survey work however, cost limitation is one of the major constraints. According to Greenwood (1996), the optimum allocation of sampling effort to achieve the most precise estimate of pest population densities given a cost limit *C* is:

$$m_c = \frac{C}{C_M + C_u \times u_{opt}}$$

From this equation we derived the value of *C* as:

$$C = m_c \times \left(C_M + C_u \times u_{opt}\right)$$

In order to achieve a relative precision level of 25% required for field studies, m_c is replaced by m_p and then the time expenditures for each host plant is calculated using the formula:

$$C = m_p \times \left(C_M + C_u \times u_{opt}\right)$$

6.4 *Results and Discussion*

Dispersion analysis The mean number of *M. nigrivenella* collected per maize cob and wild host plant fruit throughout the observation period ranged from 1.1 on *G. sokotensis* to 6.7 on *X. americana* (Table 6.2), and was significantly > 1 on all wild host plant species but not for maize (Table 6.2). The mean number of borers was highest on *X. americana* followed by *A. digitata*, whereas the mean numbers of *M. nigrivenella* in maize cobs and fruits of *G. sokotensis* and *P. biglobosa* were comparable. The varying mean borer densities were most likely influenced by differences in fruit sizes between the host plants, with fruits of *A. digitata* and *X. americana* being considerably bigger than fruits of *G. sokotensis* and *P. biglobosa* or maize cobs.

Table 6-2 Mean number (± SE) of *M. nigrivenella* in maize cobs and wild host plant fruits and total number of major sample units, Republic of Benin.

Host plant	Year	Mean (± SE)	*t*-value	*P*-value	n
Z. mays	1994	1.15 ± 0.13	1.09	0.28	80
	1995	1.13 ± 0.22	0.59	0.55	60
	both years	1.14 ± 0.18	1.19	0.24	140
A. digitata	1996	2.07 ± 0.36	2.97	0.005	104
	1997	2.04 ± 0.39	3.71	0.001	102
	both years	2.26 ± 0.26	4.75	<0.001	206
G. sokotensis	1996	1.13 ± 0.05	2.50	0.0.13	348
	1997	1.02 ± 0.06	2.34	0.04	348
	both years	1.08 ± 0.04	2.41	0.02	796
P. biglobosa	1996	1.33 ± 0.10	3.21	0.002	175
	1997	1.06 ± 0.09	3.62	0.001	175
	both years	1.18 ± 0.07	3.62	0.001	350
X. americana	1996	6.95 ± 2.46	2.42	0.034	144
	1997	6.58 ± 1.88	2.97	0.01	144
	both years	6.73 ± 1.47	3.90	0.001	288

Among-cobs dispersion coefficient (D) for *M. nigrivenella* on maize ranged from 2.95 in 1994 to 3.07 in 1995 with I_D (56.05 in 1994 and 58.33 in 1995) lying outside the limits (taken as 0.95 and 0.05) of χ^2 for 19 DF. This suggests a highly aggregated distribution of *M. nigrivenella* on maize . There was no significant difference between the indices for the 2 years (t = 0.254, P = 0.800, DF = 135), thus the data were pooled and a common D of 3.106 was obtained. The monthly index of dispersion on the various wild host plants calculated in both years are presented in Figure 6.1. Very similar trends were observed in the 1996 and 1997. For all wild host plants, except for *G. sokotensis*, the value of D was > 1 (I_D lies outside the 0.95 and 0.05 limits of χ^2) at all sampling occasions, indicating high aggregation of *M. nigrivenella* on these plants. However, we observed a seasonal fluctuation of the D values (Fig. 6.1). On *P. biglobosa*, the D values clearly indicated a decrease in aggregation towards the end of the fruiting period in September, when almost all *P. biglobosa* trees and fruits sampled were infested (Sétamou *et al.,* 1999c). Aggregation on *A. digitata* and *X. americana* changed with time but the values of D remained high throughout the year. A similar aggregation pattern was observed on *G. sokotensis*, though the borers were either regularly or randomly distributed (Fig. 6.1). In most of the cases, *M. nigrivenella* was randomly distributed on *G. sokotensis* fruits ($D = 1$). The data indicated only 3 periods, i.e., March, June and November, of regular distribution ($D < 1$) of *M. nigrivenella* on *G. sokotensis* fruits. In March, fruits of *G. sokotensis* are abundant in the system. Moreover, Sétamou *et al.* (1999c) reported on average > 60% fruit infestation and ≈ 80% of the *G. sokotensis* sampled trees infested by *M. nigrivenella* in March, which might explain the regular distribution of the borer in March in our study. In June-July, very few *G. sokotensis* trees bore fruits, but almost all the trees bearing fruits sampled were infested by *M. nigrivenella* at low densities. New *G. sokotensis* fruits setting was observed in November, which corresponds with the harvest of maize in central and northern Benin. Sétamou *et al.* (1999c) recorded highest *M. nigrivenella* densities in November on *G. sokotensis* fruits, thus most likely during this period females emerging from maize cobs oviposit on fruits of *G. sokotensis*.

Because of the low number of observations in some monthly samples, no attempt was made to calculate the different regressions parameters on a monthly basis. Using the patchiness regression, the explained variance for the different host plants were low and varied between 0.36 for *P. biglobosa* in 1996 to 0.72 for *X. americana* in 1997. Iwao's regression coefficients are estimated with least-squares regression (Tonhasca *et al.*, 1994; Naranjo & Flint, 1995). However, the reliability of the resulting parameters depends on the fulfillment of the statistical assumptions of the least-squares regression (Sokal & Rohlf, 1995). The distribution of residuals of most patchiness regressions indicated strong heteroscedasticity and presence of significant outlier data (Fig. 6.2). Therefore, the assumption of constant variance for the dependent variable was not fulfilled, indicating inflated standard errors for the predicted parameters and low-efficiency for the *t*-tests (Tonhasca *et al.*, 1996). This suggests that the coefficients derived from the Iwao's regression analysis were not suitable for describing the spatial pattern of *M. nigrivenella*.

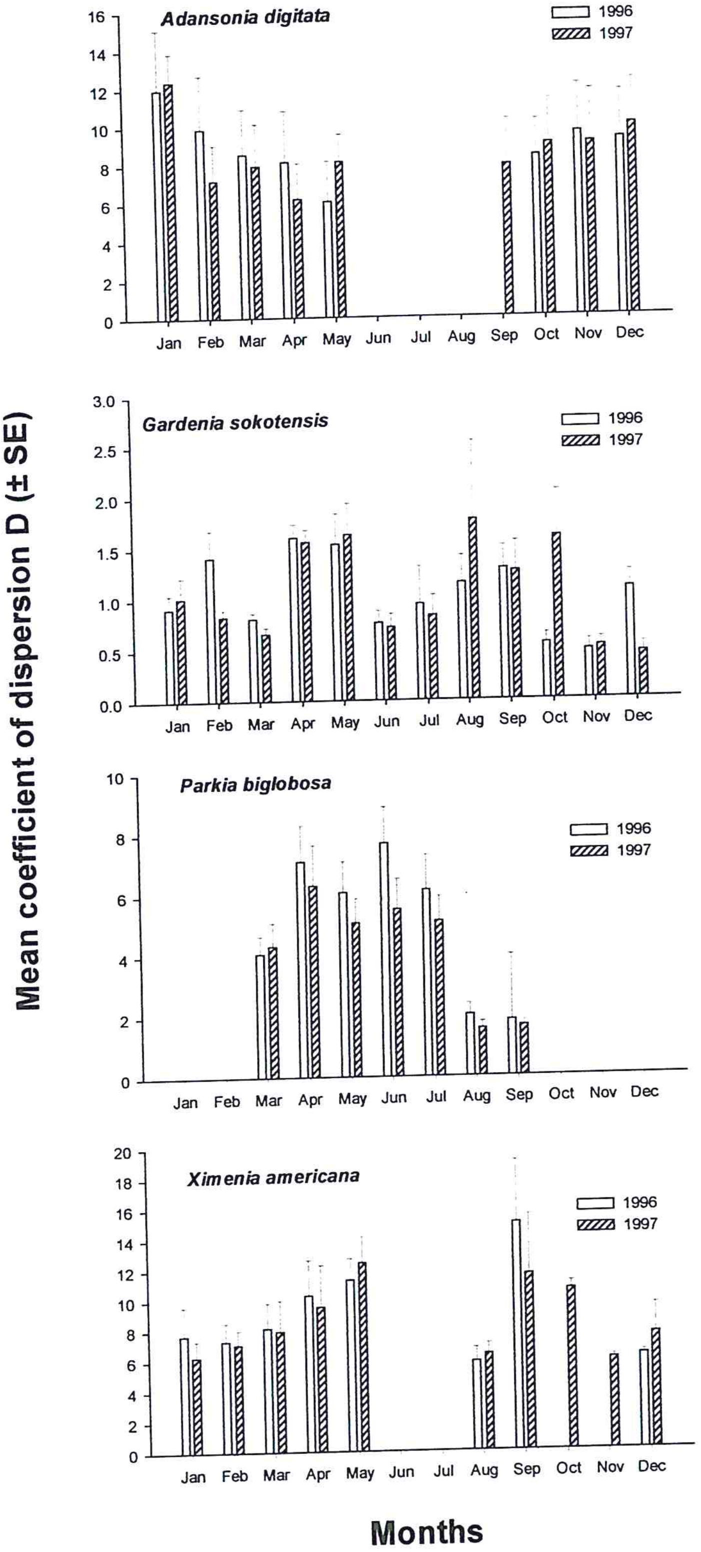

Fig. 6-1 Southwood's dispersion index (± SE) of *Mussidia nigrivenella* on 4 wild host plant species between January 1996 and December 1997, Republic of Benin, West Africa.

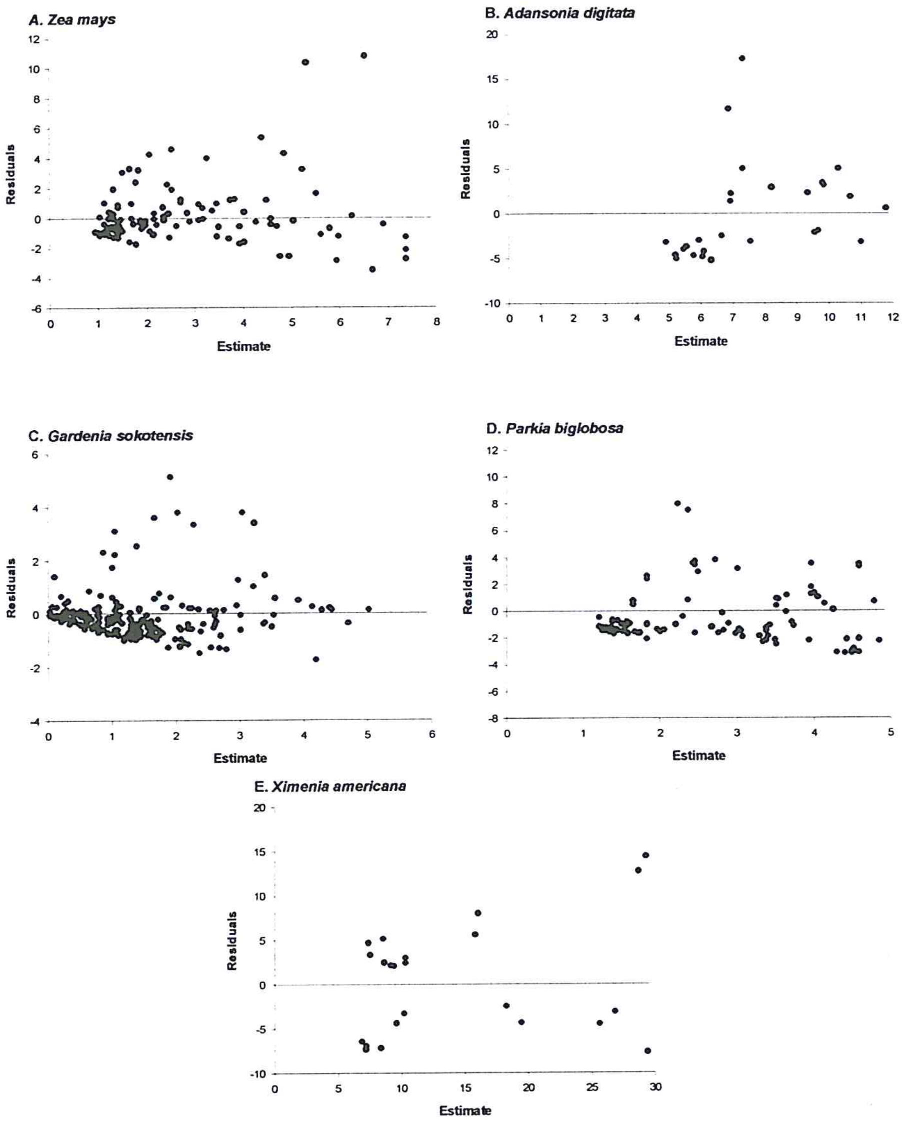

Fig. 6-2 (a-e) Relationship of residuals of Iwao's patchiness regression and mean number estimates of *Mussidia nigrivenella* on maize and 4 wild host plant species in the Republic of Benin, West Africa.

By contrast, Taylor's power law was appropriate and provided an adequate description of variance-mean relationships for all host plants tested (Table 6.3). In all cases the TPL models were linear. The data quality was also good according to Downing's (1986) criterion: R^2 values > 0.80 and se_b/b < 0.20 for all host plant species except for *G. sokotensis*, with an explained variance of 65.1% and 56.0% in 1996 and 1997, respectively. However, the very low se_b/b values (< 0.20) for this host plant showed that the regression is also acceptable. In summary, TPL was a good descriptor for the variance-mean relationship in *M. nigrivenella* on all studied host plants.

For maize, the survey year had no significant effect on the b coefficients of TPL (F = 1.36, P = 0.247). Therefore, the data of the 2-year surveys was pooled and a common regression was computed (Table 6.3). The estimates of the parameters were: $a = 2.68$ ($a > 1$) and $b = 1.360$ ($b > 1$), with a mean borer density per cob of $m = 1.14$ ($m \neq 1$, Table 6.2). According to Shen's (1990) criterion system for TPL (Table 6.1), the spatial pattern of *M. nigrivenella* on maize at maturity was aggregated. These results corroborate earlier findings of Schulthess *et al.* (1991a) in Benin and in Cameroon (Ndemah, 1999), who also reported an aggregated distribution of *M. nigrivenella* on maize cobs. However, our b value is lower than that reported by R. Ndemah. The polyphagous behavior and the abundance of host plants of *M. nigrivenella* in Benin (Sétamou *et al.*, 1999c), may affect the oviposition behavior of the females. In contrast, in the forest and transition zones of Cameroon, alternative host plants of *M. nigrivenella* are rare and maize is the major food plant for the borer (Ndemah, 1999).

On all wild host plants, the b values were significantly > 1 and comparable for the 2 years (Table 6.3). Since the mean densities of *M. nigrivenella* per wild host plant fruit were > 1 (Table 6.2) and also the values of the factor $a \neq 1$, $1 - ln(a)/ln(m)$ was calculated and compared to the index of aggregation for each host plant following Shen's criterion system for TPL (Shen, 1990). Based on these comparisons, the distribution of *M. nigrivenella* was aggregated on *A. digitata*, *P. biglobosa* and *X. americana*, but was uniformly distributed on *G. sokotensis*.

Table 6-3 Taylor Power Law statistics (± SE) for *M. nigrivenella* counts in maize cobs and wild host plant fruits, Republic of Benin.

Host plant	Year	ln (a)	*b*	R^2	*t*-value		*P*-value	*n*
					Intercept	slope	(slope = 1)	
Z. mays	1994	0.973 ± 0.060	1.335 ± 0.049	0.90	16.30***	27.47***	< 0.0001	79
	1995	1.009 ± 0.085	1.392 ± 0.056	0.93	11.82***	24.64***	< 0.0001	46
	both years	0.986 ± 0.049	1.360 ± 0.037	0.91	20.25***	37.16***	< 0.0001	125
A. digitata	1996	1.571 ± 0.125	1.713 ± 0.115	0.86	12.56***	14.84***	< 0.0001	38
	1997	1.522 ± 0.093	1.640 ± 0.083	0.91	16.35***	19.86***	< 0.0001	40
	both years	1.543 ± 0.077	1.673 ± 0.070	0.88	20.04***	24.02***	< 0.0001	78
G. sokotensis	1996	-0.121 ± 0.048	1.448 ± 0.074	0.65	2.54*	19.68***	< 0.001	210
	1997	-0.265 ± 0.062	1.280 ± 0.093	0.56	4.26***	13.79***	0.003	152
	both years	-0.176 ± 0.038	1.384 ± 0.058	0.61	4.64***	22.94**	< 0.0001	362
P. biglobosa	1996	0.988 ± 0.072	1.322 ± 0.062	0.81	13.77***	21.25***	< 0.0001	107
	1997	1.105 ± 0.072	1.389 ± 0.051	0.81	15.38***	27.08***	< 0.0001	126
	both years	1.044 ± 0.050	1.357 ± 0.039	0.84	20.70***	34.77***	< 0.0001	233
X. americana	1996	1.109 ± 0.501	1.484 ± 0.256	0.81	2.21ns	5.80***	< 0.01	29
	1997	1.496 ± 0.318	1.290 ± 0.173	0.80	4.71***	7.49***	< 0.01	36
	both years	1.321 ± 0.266	1.382 ± 0.141	0.80	4.96***	9.78***	0.012	65

ns = no significant difference, * = significant at $P < 0.05$, ** = significant at $P < 0.01$, *** = significant at $P < 0.001$

Aggregated distribution of *M. nigrivenella* on most of the host plants studied here is probably a result of a combination of several factors, i.e., the oviposition behavior of the adult female, suitability of the food source, the size of the host fruits/cob. *Mussidia nigrivenella* females oviposit in a clumped manner preferentially on rough surfaces, like crevasses on fruits or husks (Moyal 1988). Moreover, the size of the maize cobs and the fruits of the different wild host except *G. sokotensis* may reduce cannibalism and allow several larvae to develop within a single fruit/cob. Therefore, newly hatched first instar larvae may not disperse but directly penetrate into the host resulting in relatively high borer infestations (Table 6.2). On the comparatively small fruits of *G. sokotensis*, however, the size of the fruits may limit the number of feeding borers due to high competition of borers for feeding site. A maximum of 5 (more commonly 1) borers was recorded in *G. sokotensis* fruits. The mean volume of the fruits, i.e., 1,474 cm^3 for *A. digitata*, 22 cm^3 for *G. sokotensis*, 31 cm^3 for *P. biglobosa*, 230 cm^3 for *X. americana*, and 509 cm^3 for maize cobs, were positively correlated with the TPL aggregation index ($r = 0.932$, $P < 0.05$). Thus, the size of the fruits and cobs, respectively, had a significant effect on the distribution pattern of *M. nigrivenella*. The bigger the fruit/cob size the more clumped is the distribution of *M. nigrivenella* on this host plant. The suitability of fruits of wild host plants for *M. nigrivenella* has not been studied yet. However, several borers were usually found feeding in the various wild host plant fruits. On maize however, despite a high mortality of early instars (up to 90%), many borers are found feeding on the cobs (Moyal 1988, Sétamou *et al.*, 1999b).

Mean-incidence analysis Wilson and Room's model gave a good fit between the mean *M. nigrivenella* density and the proportion of infested sample units for all host plants tested (Fig. 6.3). According to Wilson (1982), the more clumped a species is distributed, the smaller is the proportion of infested sample units for a given mean density. Consequently, the P_1-m relationship indicates highest aggregation of *M. nigrivenella* on *A. digitata* and lowest on fruits of *G. sokotensis* (Fig. 6.4). The *b* value of *A. digitata* was also significantly greater ($P < 0.05$) than those of the other host plants, whereas the *b* values of host plants other than *A. digitata* did not differ significantly ($P > 0.05$). *Adansonia digitata* has the largest fruits, whereas *G. sokotensis* fruits are the smallest. As most leguminous trees, *P. biglobosa* has long (15-25 cm) pods which can host considerably more borers compared to fruits of

G. sokotensis. Maize and *X. americana* have fruits of intermediate size. The aggregation pattern of *M. nigrivenella* on *Z. mays* and *P. biglobosa* were very similar, and was less clumped than on *X. americana* (Fig. 6.4).

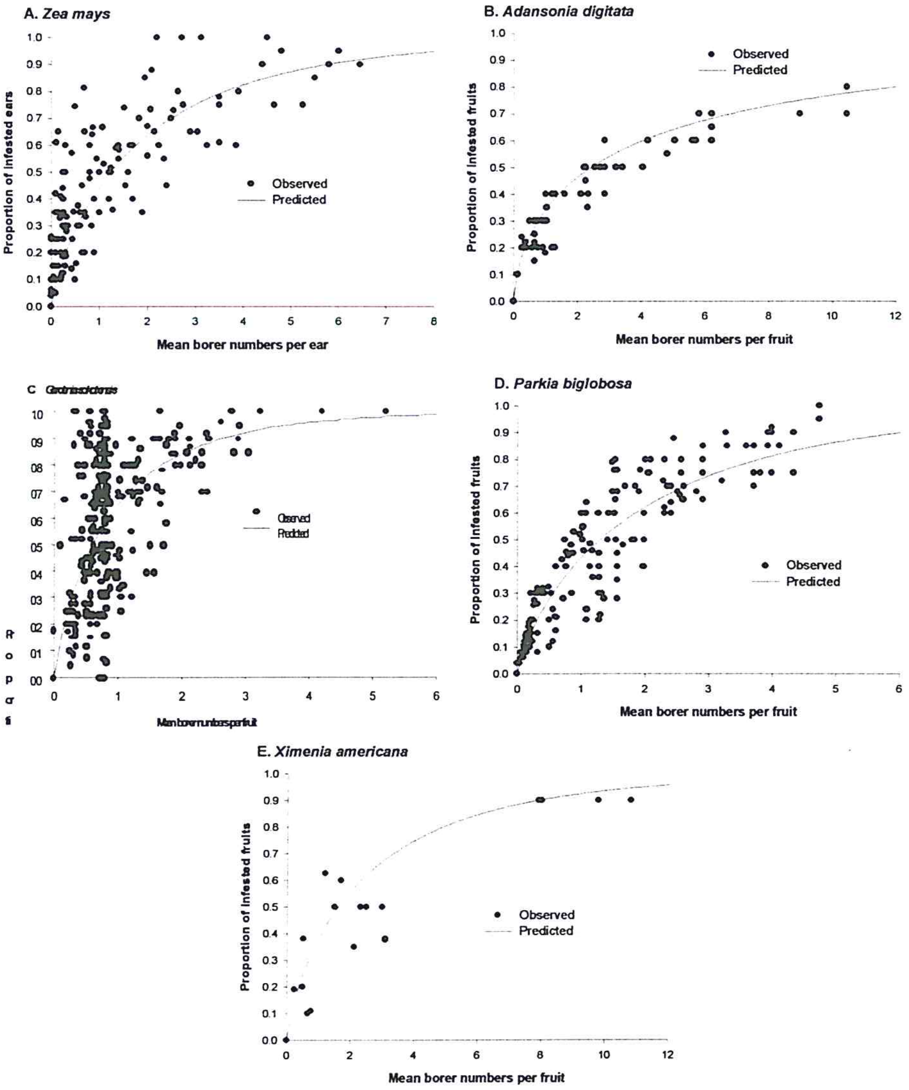

Fig. 6-3 (a-e) Relationship between the proportion of infested maize cobs and fruits of 4 wild host plant species and the mean numbers of *Mussidia nigrivenella* per cob/fruit (Wilson and Room 1983); A. *Zea mays*, B. *Adansonia digitata*, C. *G. sokotensis*, D. *Parkia biglobosa*, and E. *Ximenia americana*.

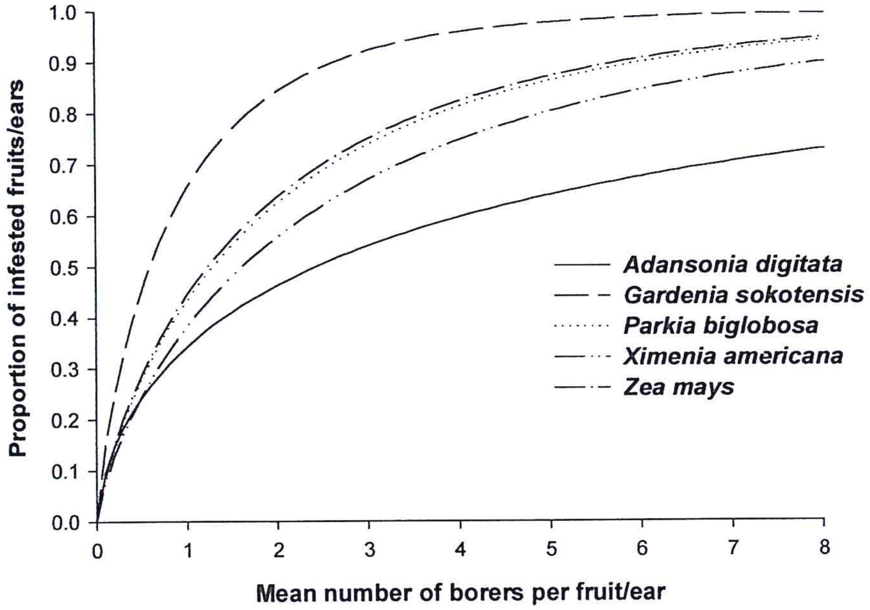

Fig. 6-4 Comparison of the relationship between the proportion of infested maize cobs/fruits of wild host plant and the mean numbers of *M. nigrivenella* per cob/fruit on 5 different host plant species, using Wilson and Room's model (Wilson & Room 1983).

Sample size estimation The optimum number of fruits/cobs per major sampling unit required for the different host plants is presented in Table 6.4. The number of fruits needed for a precise estimation of *M. nigrivenella* population statistics varied from four fruits on *X. americana* to 10 fruits on *P. biglobosa*, which is by far below the number of samples collected during our surveys. Therefore, estimates of mean *M. nigrivenella* densities and related variation per major sampling unit (trees or fields) were adequate. However, the number of trees or maize fields to be sampled at a precision level of *Q* = 25%, needed for field studies, varied from 34 trees of *G. sokotensis* to 104 trees of *A. digitata*. In case of maize, 121 fields must be sampled to achieve a precision level of 25%. These sample size values are consistent with the distribution pattern of *M. nigrivenella* on the respective host plants. For *A. digitata*, with a highly aggregated distribution pattern of *M. nigrivenella*, a considerably higher sample of trees is required than for *G. sokotensis*, where the borers are distributed in more regular way. In general, the low values of minor units needed may be due to the low variability within each major unit whereas the relatively high number of major units to be sampled may reflect high between major units variability. Sétamou (1996) reported higher between maize-fields variability of *M. nigrivenella* infestations than within field variability.

Table 6-4 Number of samples and time budget required to estimate with a precision level of Q = 25% mean numbers of *M. nigrivenella* in maize cobs and wild host plant fruits, Republic of Benin.

Host plant	U*	u	S^2_M	S^2_u	C_u	u_{opt}	m_p	C
Z. mays	25,000	20	2.21	5.13	90 s	7	121	81.7
A. digitata	200	10	5.80	26.07	3 min	7	104	88.4
G. sokotensis	100	20	0.54	1.60	90 s	8	34	23.8
P. biglobosa	1,000	20	1.25	5.74	90 s	10	70	52.5
X. americana	50	10	64.90	71.39	3 min	4	100	70.0

U = total number of minor units (i.e., maize cobs and wild host plant fruits) available on average within each major unit (i.e., maize field or wild host plant tree),
u = number of minor units sampled,
S^2_M = variance of global mean number of *M. nigrivenella* calculated over all major sample units,
S^2_u = mean of all major unit variances,
C_u = time (cost) spent to sample and dissect each minor unit (maize cob or host plant fruit),
u_{opt} = optimal number of minor units to be sampled,
m_p = number of major units required to achieve a certain percentage relative precision,
C = calculated time budget (in h) needed for assessing *M. nigrivenella* densities per host plant with a precision level of 25%.

The time budget needed for estimating *M. nigrivenella* population densities with a relative precision level of 25% on the five host plants studied is given in Table 6.4. The more *M. nigrivenella* is aggregated on the respective host plants, the more time is required for a precise estimation of borer densities. Thus, due to the higher between major unit (i.e., maize fields and/or wild host plant trees) variability, in future surveys on *M. nigrivenella* population dynamics more fields and wild host plant trees, except for *G. sokotensis*, have to be sampled, but less cobs/fruits need to be collected per major unit.

Our results show that mean population densities of *M. nigrivenella* on various host plants can be estimated from the proportion of wild host plant fruits or maize cobs infested, despite the aggregated spatial pattern of borers on most of the studied host plants. In ongoing studies we investigate the potential of biological control of *M. nigrivenella*. However, future releases of indigenous or exotic natural enemies of the borer will necessitate precise data collection on *M. nigrivenella* densities on cultivated and wild host plants before and after the intervention. Our sampling plan is easy to use, and can be applied for quick estimates of pest densities on a region-wide basis, and thus could become a useful tool for future impact assessment studies of natural enemies of *M. nigrivenella*.

7 Flight activity of *M. nigrivenella* in Benin as affected by weather factors and host plants[6]

7.1 Abstract

Studies were conducted in three agro-ecological zones of Benin on the effects of meteorological factors and presence of fruiting structures of wild and cultivated host plants on light trap catches of *Mussidia nigrivenella* Ragonot. In the Forest Savanna Mosaic and the Northern Guinea Savanna, high flight activity was observed during the rainy seasons, with peak trap catches during October, which corresponds with maturity of maize. No clear trends could be observed in the Southern Guinea Savanna. In all zones, lowest flight activity was recorded at the end of the dry season. Multiple regression analysis revealed a strong impact of weather factors and host plant availability on light trap catches of *M. nigrivenella*. Trap numbers increased with average maximum temperature, and decreased with wind speed, total evaporation, and maximum relative humidity. Significantly more moths were trapped in the Guinea Savannas than in the Forest Savanna Mosaic, possibly as a result of lower host plant diversity and abundance in the latter zone.

7.2 *Introduction*

The polyphagous pyralid *Mussidia nigrivenella* Ragonot is a pest on maize cobs and cotton bolls in West Africa (Whitney, 1970; Atachi, 1987; Moyal & Tran, 1991; Gounou *et al.*, 1994; Silvie, 1993; Sétamou *et al.*, 1998). In Benin, *M. nigrivenella* abundance and damage to maize vary between the different agro-ecological zones (Moyal & Tran, 1991; Gounou *et al.*, 1994; Sétamou *et al.*, 1998). The diversity and availability of host plants have been suggested as major factors affecting *M. nigrivenella* densities in West Africa (Sétamou, 1996). Similarly, Shih and Chu (1995) showed that pheromone traps located in the vicinity of some host plants of *Spodoptera litura* (F.) (Lepidoptera: Noctuidae) trapped significantly more adults than those near non-host plants. However, according to Leps *et al.* (1998) the positive correlation between availability of food plants and moth catches in light-traps is

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restricted to monophagous species and no significant effect was observed for polyphagous lepidopteran species.

In addition, for many lepidopteran species light trap catches have been shown to be strongly affected by climatic factors such as temperature, wind and rainfall (Douthwaite, 1978; Bowden, 1982; Tucker, 1983; Taylor, 1986; Dent & Pawar, 1988).

The flight activity of *M. nigrivenella* has never been studied. Here we describe the annual flight cycle of *M. nigrivenella* in three agro-ecological zones of Benin, and examine the potential effects of weather factors and availability of host plants on adult light trap catches.

7.3 Materials and Methods

One walk-in light trap was set up in each of the three agro-ecological zones under study: The Forest Savanna Mosaic (FSM), with a bimodal rainfall distribution allowing for two growing seasons (April to July and September to November) with average rainfall between 1,300 and 1,500 mm and maximum temperature from 25 to 35°C; Southern Guinea Savanna (SGS), with the same seasonal pattern but with lower rainfall, averaging 1,200 to 1,300 mm and higher temperature maxima, ranging from 26 to 38°C; Northern Guinea Savanna (NGS), characterised by unimodal rainfall distribution and one growing season (April to September), with average rainfall of 1,000 to 1,100 mm and temperature maxima from 28 to 40°C. Traps were located in cultivated areas at the International Institute of Tropical Agriculture (IITA) station in Abomey Calavi in FSM, and at the Institut des Recherches Agronomiques du Bénin (INRAB) research stations in Bohicon, SGS, and in Parakou, NGS, respectively. Adults of *M. nigrivenella* were monitored during four consecutive years, i.e., from June 1994 to November 1997 giving a total of 42 sampling months.

The walk-in light trap consisted of an upper funnel-shaped trapping device with a lamp above it, a low collection chamber consisting of a metal structure (1 m × 1 m × 2 m), wrapped around with a metal mesh. The lamp equipped with a 160 w bulb was placed at a height of ca. 2.5 m and was connected to a power source. The traps were run every night from dusk to dawn. Every morning, insects were collected in vials using an aspirator, were anaesthetised with CO_2 and the trap was cleaned. Adults of *M. nigrivenella* were identified and then counted.

The daily weather data i.e., total rainfall (mm), mean wind speed (km/h) and major wind direction, air temperature (minimum, mean and maximum in °C), mean relative humidity (minimum, mean and maximum in %), total evaporation (mm), and solar radiation were obtained from the weather stations of the respective research stations, in all cases located less than 1 km from the light traps. Monthly total rainfall and evaporation, as well as average temperature, wind speed and relative humidity were calculated.

The fruiting periods of the various cultivated and wild host plants of *M. nigrivenella* found in the vicinity of each trapping site (Table 7.1), were recorded monthly on a presence/absence basis (Sétamou *et al.*, 1999c; cf. Chapter 4.4).

Table 7-1 Host plants present in the vicinity of light traps set up in different agro-ecological zones of Benin.

Agro-ecological zone	Host plant species
Forest Savanna Mosaic	*Zea mays* L.
	Canavalia enseiformis (L.) DC.
	Mucuna pruriens DC.
Southern Guinea Savanna	*Zea mays* L.
	Canavalia enseiformis (L.) DC.
	Parkia biglobosa (Jacq.) Benth.
	Adansonia digitata L.
Northern Guinea Savanna	*Zea mays* L.
	Parkia biglobosa (Jacq.) Benth.
	Adansonia digitata L.
	Gardenia spp.

For analysis purposes, *M. nigrivenella* trap catches are presented as monthly totals while temperature and humidity are presented as monthly means, and rainfall and evaporation are summarised as a cumulative value for each months. Analysis of variance was used to compare the monthly numbers of adults trapped between the agro-ecological zones. Mean monthly catches were separated using Tukey test (Sokal & Rohlf, 1995).

Trap catches of *M. nigrivenella* were further analysed using multiple regression analysis with number of moths caught as the dependent variable, the weather variables as independent variables, and wind direction and host plant fruit availability as dummy variables. Interaction terms (among and between climatic variables and host plant species) were calculated as the product of the variables and included in the regression analysis. Analyses were carried out with PROC GLM of SAS (1992), and models were simplified in a stepwise fashion retaining only significant variables. The significance level for inclusion of a variable was set at 10%. Analyses were carried out separately for the FSM and the Guinea Savannas, thereby to know the most influential variables for the different agro-ecological zones.

For all analyses, the trap data were normalised by log(x+1) transformation.

7.4 Results

The seasonal trends of *M. nigrivenella* adult flight activity and some weather data are shown in Fig. 7.1-7.3. Flight activity was mainly observed during the rainy seasons. Within each agro-ecological zone, the pattern of trap catches was similar for each year but was less distinct for the SGS. In the FMS, trap catches increased steeply from the beginning of the rainy season and reached peaks between October – December. Thereafter, they declined gradually to close to zero in February-March. In the SGS, *M. nigrivenella* adults were trapped all year round, with high flight activity recorded between August and December. In the NGS, trap catches in all years sharply increased from April to June, and then gradually reached a maximum in October-November, corresponding with end of the second rainy season. Thereafter *M. nigrivenella* numbers declined steeply and to zero between January-March.

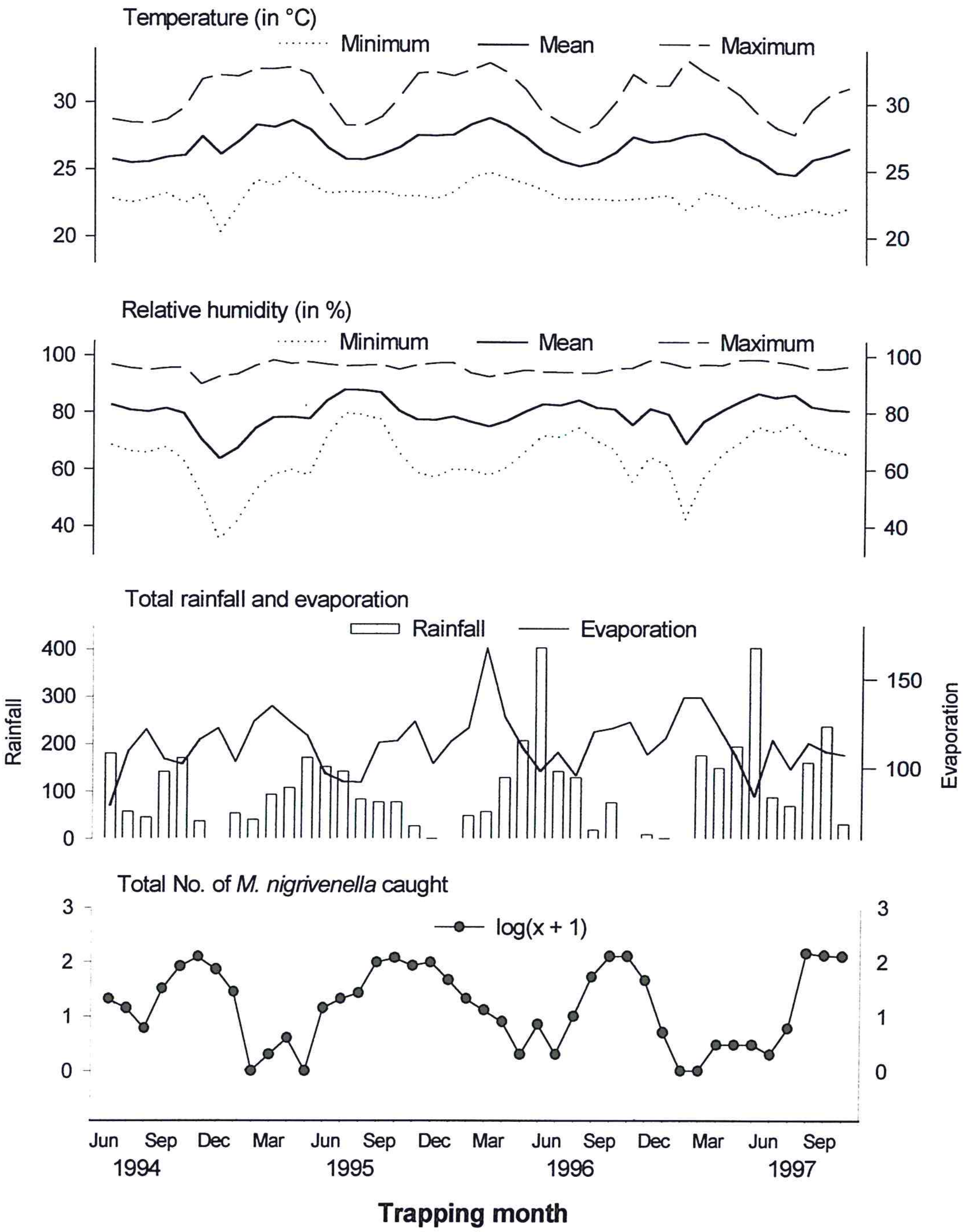

Fig. 7-1 Fluctuations of *M. nigrivenella* trap catches in light trap and corresponding weather data in the Forest Savanna Mosaic, from June 1994 to November 1997.

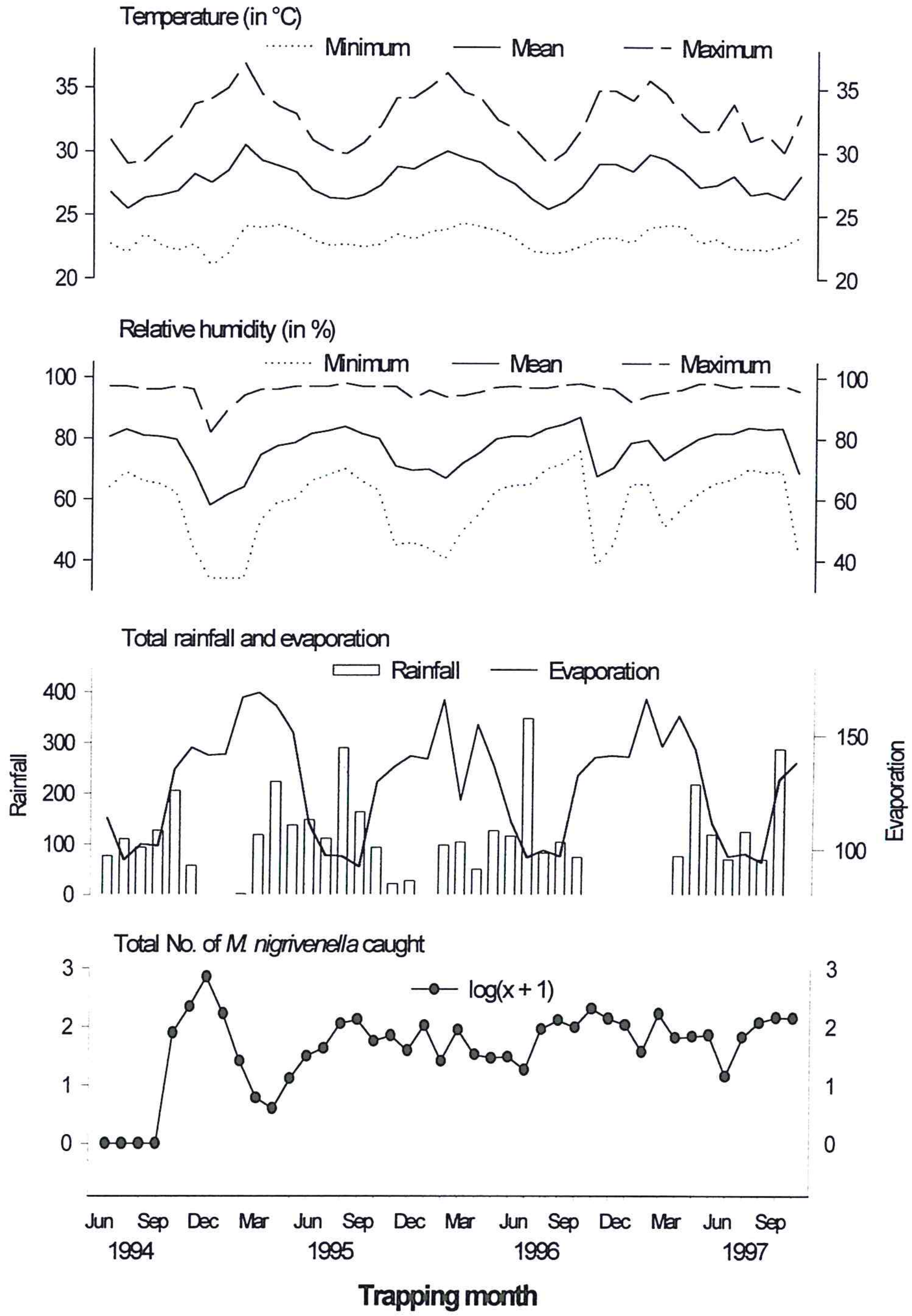

Fig. 7-2 Mean monthly trap catches of *M. nigrivenella* in light trap and corresponding weather data in the Southern Guinea Savanna, from June 1994 to November 1997.

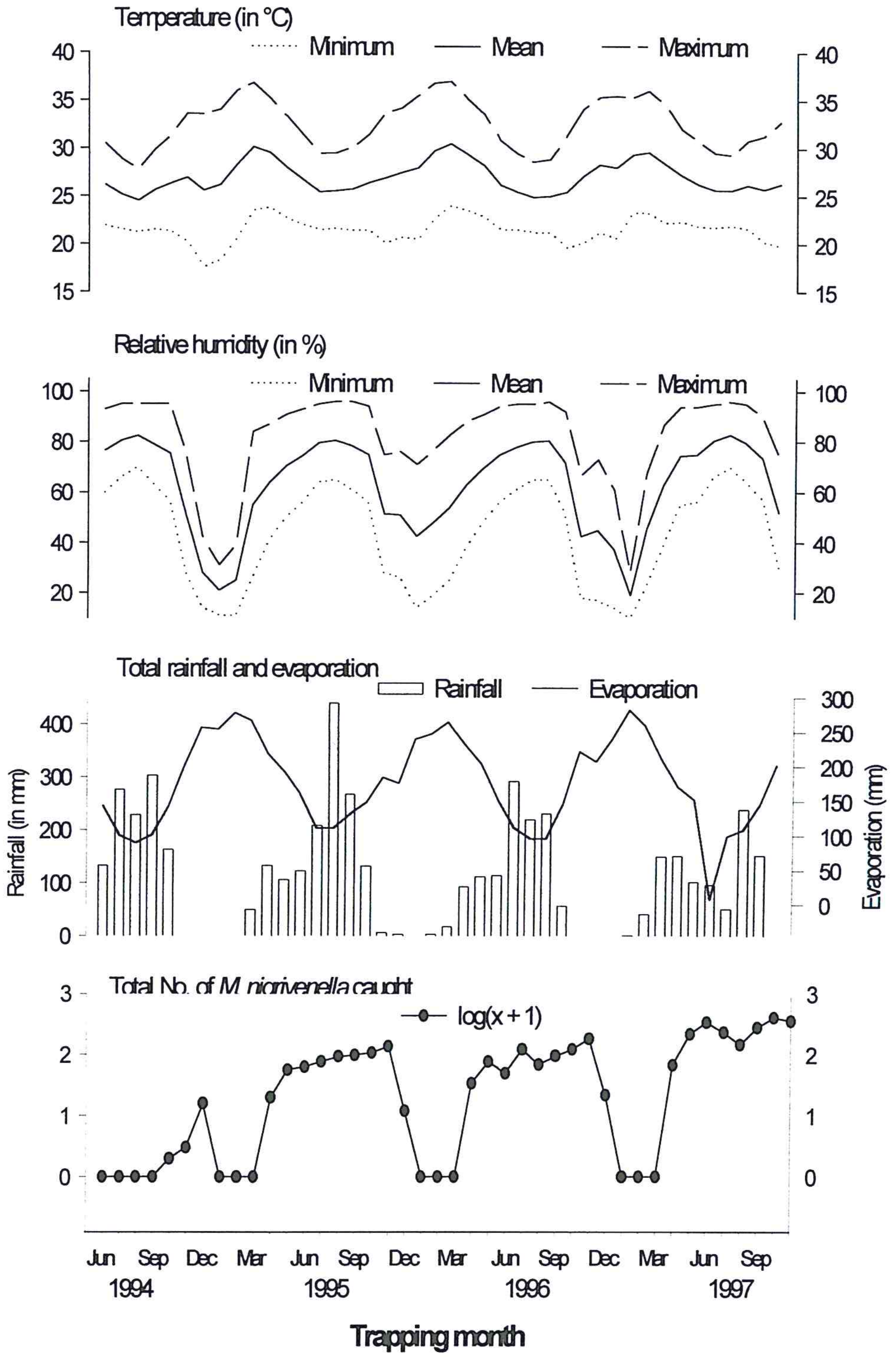

Fig. 7-3 Mean monthly trap catches of *M. nigrivenella* in light trap and corresponding weather data in the Northern Guinea Savanna, from June 1994 to November 1997.

Mean monthly numbers of *M. nigrivenella* caught at the different sites are shown in Fig. 7.4. Significantly more *M. nigrivenella* were trapped in the NGS and SGS (*P* = 0.015 and 0.045, respectively) than the FSM. No significant differences in trap catches were found between the two locations in the NGS and SGS (*P* > 0.05) (Fig. 7.4).

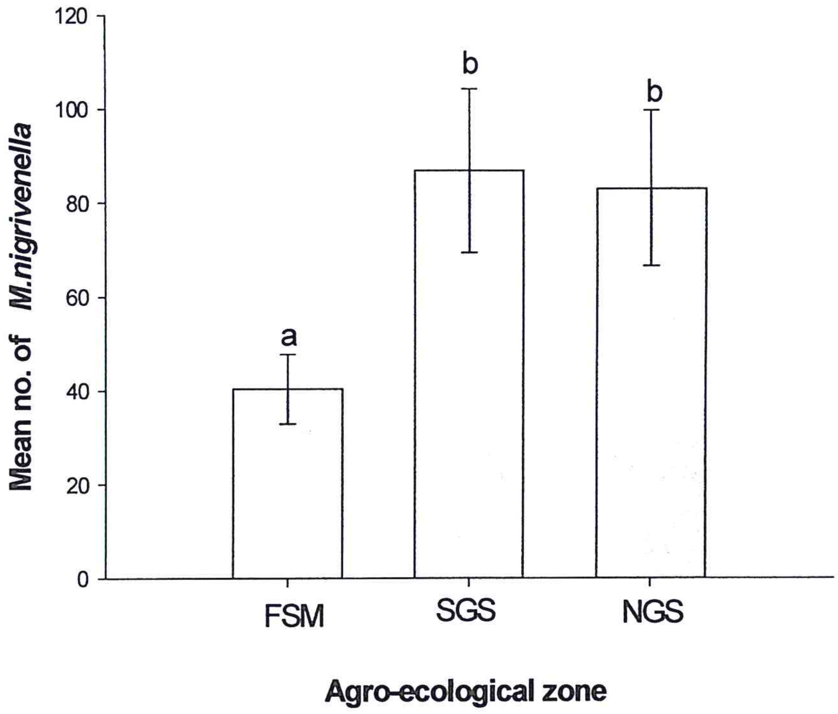

Fig. 7-4 Mean monthly trap catches of *M. nigrivenella* in three agro-ecological zones of Benin, from June 1994 until November 1997 (FSM = Forest Savanna Mosaic, SGS = Southern Guinea Savanna, NGS = Northern Guinea Savanna).

For all stepwise regression analyses, interaction terms were not significant (P > 15%). In the FSM, wind speed was the dominant weather factor influencing trap catches of *M. nigrivenella*, as shown by the partial explained variance, followed by maximum relative humidity with negative relations for both variables.(Table 7.2). Host plant availability had more weight than climate (Table 7.2); significantly more moths were trapped during the fruiting periods of both maize and jackbean, *Canavalia enseiformis* (L.) DC. (Fabaceae) which explained about 40% of the variation in trap catches.

Table 7-2 Multiple regression analysis for the effect of weather variables, host plant on light trap cathes of *M. nigrivenella* adults in different agro-ecological zones of Benin, between June 1994 and November 1997.

Factor	Estimate	SE	R^2-value	*t*-value	*P*-value
		Forest Savanna Mosaic			
Intercept	7.230	3.860		1.875	0.068
Wind speed	-0.070	0.051	0.16	1.78	0.080
Max. relative humidity	-0.065	0.040	0.06	1.71	0.095
Z. mays	0.288	0.276	0.23	1.72	0.092
C. enseiformis	0.761	0.272	0.17	2.806	0.009
Total			0.62		
		Southern Guinea Savanna			
Intercept	0.603	1.459		0.413	0.68
Wind Speed	-0.702	0.181	0.24	3.89	0.001
Maximum temperature	0.066	0.043	0.09	2.59	0.012
Total			0.33		
		Northern Guinea Savanna			
Intercept	-1.054	2.356		0.857	0.340
Z. mays	1.628	0.314	0.09	5.29	0.0001
P. biglobosa	1.612	0.302	0.38	5.39	0.0001
Total			0.47		
		Southern and Northern Guinea Savannas combined			
Intercept	-0.894	1.606		0.56	0.234
Evaporation	-0.008	0.002	0.14	3.24	0.002
Wind speed	-0.633	0.188	0.08	3.36	0.001
Maximum temperature	0.126	0.054	0.03	2.34	0.022
Z. mays	0.377	0.238	0.04	2.51	0.020
P. biglobosa	0.649	0.256	0.02	2.53	0.013
Total			0.31		

In the SGS, only weather factors were significantly related to trap catches, no host plant had a significant effect (Table 7.2). Wind speed was the most important factor explaining about 24% of the variation in *M. nigrivenella* trap catches, and exerted negative effect on monthly catches. The trap catches were positively related to maximum temperature, but this factor explained only 9% of the total variance.

The availability of maize cobs and fruits of *Parkia biglobosa* (Jacq.) Benth. (Mimosaceae) were the main factors affecting trap catches in the NGS, and these two host plants explained approximately 47% of the variation in *M. nigrivenella* trap catches (Table 7.2). No weather variable was found to be significantly related to the borer flight activity. Because no significant differences were found in the monthly catches between the SGS and the NGS (Fig. 7.4), the data of these two zones were subsequently pooled and a common regression model was determined. For the pooled data of SGS and NGS, only 31% of the total variation in trap-catches of *M. nigrivenella* could be explained by the regression model (Table 7.2). Total evaporation, wind speed and maximum temperature, exerted significant effects on number of *M. nigrivenella* collected in light traps (Table 7.2). Wind speed and total evaporation reduced *M. nigrivenella* flight activity, whereas the trap catches increased with maximum temperature (Fig. 7.1). In addition, flight activity of *M. nigrivenella* was also closely related to fruiting periods of both maize and *P. biglobosa* with the two host plants having comparable contribution (Fig. 7.3, Table 7.2).

7.5 Discussion

In the FSM and NGS, a strong seasonality in flight activity of *M. nigrivenella* was observed, coinciding with the fruiting periods of three known host plants of the borer, namely maize, *P. biglobosa* and jackbean. Agro-ecological variation observed in trap catches corresponded with the variability in the presence of host plants of *M. nigrivenella* in the different zones. In the Guinea savannas, wild and cultivated host plants are diverse, abundant, and have overlapping fruiting periods, whereas in the FSM only crops, i.e., maize, and jackbean were recorded as major host plants (cf. Chapter 4.4)).

In the FSM, the flight activity of *M. nigrivenella* was strongly related to the availability of maize cobs in the fields. The first adults in the trap were encountered in May-June, corresponding with the cob formation period of maize. In this zone, the light trap was set up close to a major city where overlapping planting of maize is common. Also, the fact that *M. nigrivenella* attacks tree species (Moyal, 1988; Sétamou *et al.,* 1999c) shows that adult moths of the borer are good flyers, and could therefore be attracted to the trap from far away maize fields. By contrast, catches of the noctuids

Busseola fusca (Fuller), *Sesamia calamistis* Hampson and the pyralid *Eldana saccharina* Walker decrease drastically with height of the light trap (Schulthess, pers. communication). Presence of pods of jackbean had also a positive effect on trap catches in this zone. In a field study, Sétamou *et al.* (1999c) observed higher populations of *M. nigrivenella* larvae on jackbean than maize. Thus, emerging adults of *M. nigrivenella* from pods of jackbean could have contributed to the high trap catches. At present, jackbean is commonly grown only on the IITA campus, but the expansion of acreage of this cover crop throughout the country may influence the population dynamics of *M. nigrivenella*. Therefore, cover crops may have an unexpected negative effect on quality and quantity of maize yields if the hatching of *M. nigrivenella* adults coincides with cob formation of maize.

The all-year presence of *M. nigrivenella* adults in light trap in the SGS, may be the result of high diversity and overlapping fruiting periods of food plants which perennuate the borer as shown by Sétamou *et al.* (1999b).

In the NGS, adult flight commenced with the onset of the fruiting period of *P. biglobosa* trees (cf. Chapter 4.4), indicating the importance of this host plant for the population dynamics of *M. nigrivenella* in this region. In addition, availability of maize cobs from September to December (Sétamou *et al.,* 1999c) increased the flight activity of the borer. The overlapping in the fruit setting of maize and *P. biglobosa* (cf. Chapter 4.4), also permit a continuous flight period of the borer in these zones from April to December.

In the three agro-ecological zones, the peaks in flight activity of *M. nigrivenella* coincided with the maturity of maize. Apart from cassava, maize is the major staple in Benin (Miracle, 1966; CIMMYT, 1990), and is grown on about 45% of the cultivated land (CIMMYT, 1990). The large distribution of maize in Benin, coupled with high cob infestation levels by *M. nigrivenella* observed in fields in Benin (Sétamou *et al.,* 1999a), may allow development of large adult populations resulting in high flight activity of the moths.

The positive effect of temperature on trap catches observed in the Guinea Savannas has also been reported for many lepidopteran species (e.g., McGeachie, 1987).

In all zones, trap catches decreased with wind speed. Similarly, Camps (1986) and McGeachie (1987) found that stronger winds reduced light trap catches of many noctuid moths. Therefore, the differences in trap catches between the agro-ecological zones could partly be explained by varying wind speeds. In the course of the study, stronger winds were recorded in the FSM and the NGS (between 2-6 km/h) compared to the NGS (1-4 km/h).

Average maximum relative humidity reduced the number of individuals caught in the light trap in the FSM. Because relative humidity increased with rainfall ($r = 0.62$, $N = 42$, $P > 0.01$, in the FSM), the maximum relative humidity may have been reached during rainy days, and rainfall has been reported to negatively affect the number of lepidopteran moths caught in light traps (Williams, 1961).

Low numbers of trap catches correspond well to higher values of total evaporation especially in the NGS. High values of monthly evaporation are observed in the dry season, when major host plants did not bear fruits, thus explaining the negative effects of total evaporation on flight activity of *M. ni*grivenella observed in the Guinea Savannas.

Weather variables and host plant availability are important factors influencing the flight activity of *M. nigrivenella*. These findings will enable a better understanding of the borer abundance in different agro-ecological zones of Benin.

8 Effect of harvest time and drying on the damage caused by *M. nigrivenella*

8.1 Introduction

In tropical Africa, small-scale farmers use various cultural control practices against important agricultural pests. Sun-drying of the harvested crop prior to storage is one of the most important cultural control techniques, since artificial drying in most cases is beyond the economic scope of African farmers (FAO, 1980). In West Africa and especially in Benin, most of the maize farmers leave the crop standing in the field for a pre-harvest drying period, and about 25% of the farmers additionally sun-dry their maize prior to storage (Tanzubil *et al.*, 1997; Hell *et al.*, 1996). Their reasons for doing so are to reduce (i) the moisture content of the grains and thus prevent subsequent fungal infections of the commodity and (ii) the pre-harvest infestation of maize by pests, i.e., mainly by beetles and lepidopteras. However, little is known about the efficacy of this method in Benin. The maize cob borer *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) is one of the most important pests of maize in West Africa (Moyal, 1988; Atachi, 1987; Bosque-Pérez & Mareck, 1990; Moyal & Tran, 1991; Shanower *et al.*, 1991; Gounou *et al.*, 1994; Sétamou, 1996). Although the borer attacks the maize in the field, the damage continues during the first months of storage (Borgemeister *et al.*, 1998; Hell *et al.*, 1998). The objective of our study was to evaluate the efficacy of sun-drying maize cobs in reducing the damage caused by *M. nigrivenella*. Such information is crucial for the development of effective control strategies that combine cultural practices and other control strategies.

8.2 Materials and Methods

A field experiment was conducted at the International Institute of Tropical Agriculture (IITA) in Abomey-Calavi, Benin during the main growing season of 1995. The experimental set-up was a randomised block design with four blocks containing three plots each. The distance between the blocks was 4 m and within each block that between the plots was 2 m. Each plot consisted of ten rows, each 10 m long and at a distance of 0.75 m. The 4-months IITA maize variety Tropical *Zea* Streak Resistant (TZSR), susceptible to *M. nigrivenella* (IITA, 1994), was sown as a monocrop on April 22. Planting density per row was 0.40 m. Agronomic practices included application of NPK 15-15-15 fertiliser (200 kg/ha) at planting, and urea (50 kg/ha) 45 days after planting (DAP), and two manual weed-controls 15 DAP and 50 DAP, respectively. The plants were rain fed.

Three harvest dates were staggered three weeks apart starting from one week after the physiological maturity of the maize ('early harvest'), four weeks after physiological maturity ('recommended harvest') and seven weeks after physiological maturity ('late harvest'). At each harvest time, 20 cobs were randomly selected from the eight central rows of each plot to record *M. nigrivenella* infestation and damage levels. Thereafter, all cobs from these eight central rows were manually harvested. From each plot half of the cobs were immediately stored, and the other half was sun-dried for one week on a cemented surface prior to storage. For each plot, all cobs were kept with husks according to treatment (stored immediately after harvest and after sun-drying) in two different small basket-type stores. The mean capacity of each experimental store was about 45 kg (approximately 500 cobs). The baskets were cylindrical in shape (0.6 m in diameter and 0.9 m in height) and were made of bamboo. Each basket was placed on a wooden platform, supported by four wooden legs on the exterior. The platform was situated at a distance of approximately 0.8 m from the ground.

Three months after storage, 20 cobs were randomly sampled from each basket. All sampled cobs, i.e., at harvest and three months after storage, were dehusked and the cob weight was measured. Thereafter, the cobs were shelled and the number of cobs infested and the percentage of grain damaged by *M. nigrivenella* were recorded. The number of *M. nigrivenella* per cob was only counted at harvest. At harvest, five 1,000 grain samples were randomly selected from each replicate and used for moisture content analysis. The grain samples were weighed, transferred to paper bags, and dried for five days in an oven at 70°C. Thereafter the dry weight of each grain sample was recorded and thereby the moisture content determined.

The data was analysed by means of analysis of variance (ANOVA). In case the ANOVA yielded a significant *F*-value, means were compared with a t-test, using the Bonferroni correction (Sokal & Rohlf, 1995).

8.3 Results

Grain moisture content, infestation of and damage by *M. nigrivenella* at harvest

The moisture content of maize grain significantly decreased with harvest time (F-value = 22.17; DF = 2, 54; $P < 0.001$) (Table 8.1). In all harvest treatments, field infestation by various insects (both lepidopteran and beetles) was recorded, but *M. nigrivenella* was the most important pest species. The percentage of cobs infested by *M. nigrivenella* varied significantly with harvest time (F-value = 7.86; DF = 2, 7; $P < 0.01$) (Table 8.1). One week after physiological maturity only 40% of the cobs were infested by the borer. However, three weeks after physiological maturity, the cob infestation level rose to 90%, and in the late harvest treatment virtually all sampled cobs were infested by *M. nigrivenella*. Likewise, the mean percentage of grains damaged by *M. nigrivenella* significantly increased from 3% in the early to 7% in the late harvest treatment (F-value = 23.3; DF = 2, 234; $P < 0.001$) (Table 8.1). Mean number of *M. nigrivenella* per cob was significantly lower in the early compared to the subsequent two harvest dates, which had comparable borer loads (F-value = 12.45; DF = 2, 234; $P < 0.001$) (Table 8.1). The cob weight significantly decreased with harvest time (F-value = 26.73; DF = 2, 234; $P < 0.001$), most likely as result of lower moisture content and more grain damage by the borer as the grains dried-up in the field.

Table 8-1 Effect of harvest time on grain moisture content (MC), cob weight and *M. nigrivenella* infestation parameters at harvest (mean data ± SE).

Treatment	MC(%)	% cobs infested	% grain damaged	No. Mn/cob	cob weight (g)
Early	28.7±0.4 c	38.6±2.2 a	2.2±0.2 a	1.1±0.3 a	128.3±3.8 c
Recommended	22.3±0.5 b	86.7±1.9 b	3.9±0.4 b	1.4±0.5 b	108.5±2.9 b
Late	17.2±0.2 a	97.6±1.7 c	7.1±0. 3 c	1.9±0. c5	93.7±3.7 a
F-value	22.17	7.86	23.30	12.45	26.73
DF (treatment, error)	2,54	2,7	2,234	2,234	2,234
P-value	<0.001	<0.01	<0.001	<0.001	<0.001

Means followed by a same letter within a column did not differ significantly ($P < 0.05$, multiple t-tests with Bonferroni correction).

Grain moisture, infestation and damage of stored maize. After three months of storage, the grain moisture content varied between 10.3% to 11.2% and no significant differences between the three different harvest date treatments were recorded (Table 8.2). At that time, in addition to *M. nigrivenella*, many other insects, i.e., mainly beetles, were found in the stores. The level of cob infestation by *M. nigrivenella* was only affected by the time of harvest and was similar to that recorded at harvest (Table 8.2). No effect of drying was noticed on the percentage of cobs infested by the borer. However, both harvest date and drying significantly influenced the mean percent grain damage and cob weight (Table 8.2). Moreover, a significant interaction between harvest date and drying was recorded. The mean grain damage level due to *M. nigrivenella* after three months of storage increased with a delayed harvest but decreased with sun-drying after harvest (Fig 8.1). No further increase in the damage caused by *M. nigrivenella* was recorded when cobs were sun-dried before storage (Table 8.2). After three months of storage, the sun-drying after harvest had reduced the grain damage due to *M. nigrivenella* by 30%, 40% and 52% in the early, recommended and late harvest treatment, respectively. The mean cob weight decreased with harvest date, most likely as a result of higher grain damage levels. For the cobs harvested at the recommended and the late harvest date, sun-drying resulted in significantly heavier cobs three months after storage (Table 8.2, Fig. 8.1).

Table 8-2 Significance of *F* value from analysis of variance for grain moisture content, cob weight and *M. nigrivenella* infestation parameters three months after storage for three harvest dates and two sun-drying treatments.

Independence variable	Moisture Content	% cobs infested	% grain damaged	Cob weight
Block	> 0.05	> 0.05	0.005	> 0.05
Harvest date (HD)	> 0.05	0.02	< 0.001	< 0.001
Sun-drying (SD)	> 0.05	> 0.05	< 0.001	0.007
HD × SD	> 0.05	> 0.05	0.03	< 0.001

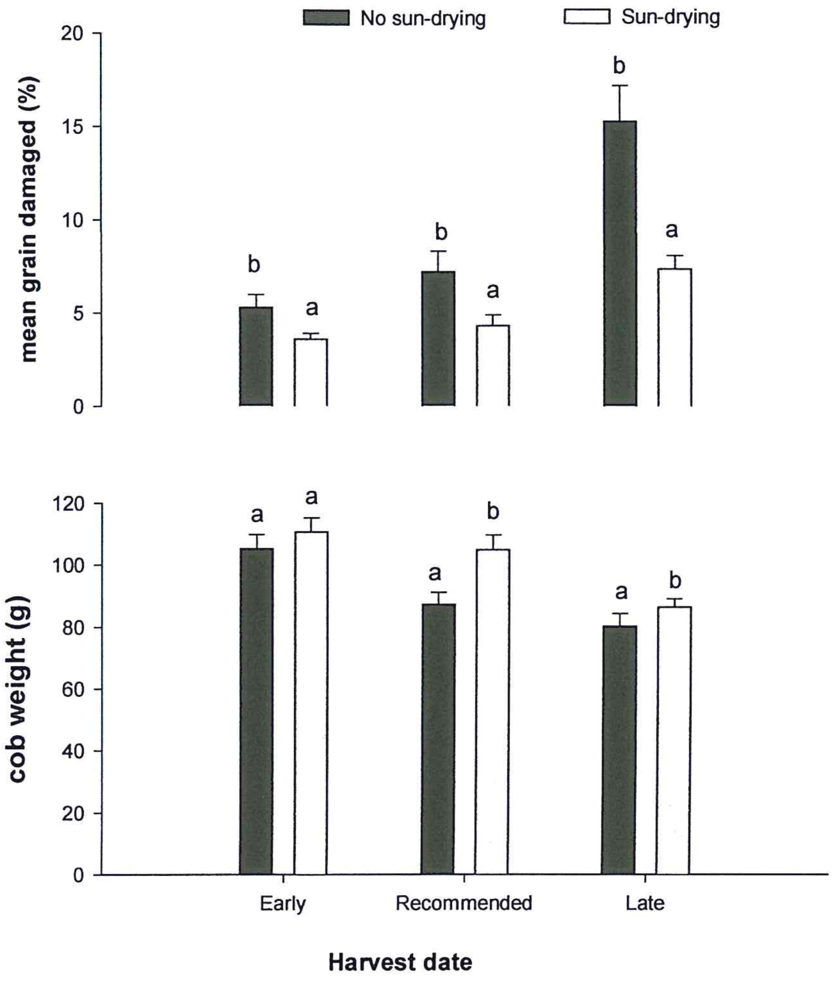

Fig. 8-1 Mean grain damaged by *Mussidia nigrivenella* and maize cob weight three months after storage for three harvest dates and two sun-drying treatments.

8.4 Discussion

Mussidia nigrivenella infestation and damage levels were related to the time of harvest. In early harvested maize, only low numbers of cobs were infested by *M. nigrivenella* and the grain damage levels were moderate. A delayed harvest led to significantly higher borer numbers and thus to increasing damage levels. In the Northern Guinea Savannas of Benin, farmers commonly leave their maize for extended drying periods in the field, resulting in a high incidence of *M. nigrivenella* in this zone (Hell *et al.*, 1998). In contrast, in region of low precipitation and low relative humidity delaying harvesting by up to four months after maturity had no significant effect on losses recorded at harvest (Santos *et al.*, 1997). The present study was however conducted in the southern part of Benin, characterised by high precipitation and high relative humidities.

A short period of additional sun-drying after harvest substantially reduced the damage due to *M. nigrivenella* after three months of storage. This reduction in damage following sun-drying suggests, that the borers continue their damage during the early months of storage. Sun-drying maize after harvest may expose the cobs to high temperatures in a relatively short period, which may lead to an increased mortality of the *M. nigrivenella* larvae feeding in the cobs. In field-dried maize however, the drying process may not be as rapid, thus not affecting the borers in the maize. The reduction of insect infestation following sun-drying has also been reported in cowpea (Ugwu *et al.*, 1999). In maize, a reduction in number of beetles counted 190 days after storage was recorded with sun-drying of the produce after harvest (Sheu, 1991).

In the early harvested maize, the moisture content of the grains was comparatively high, which could cause subsequent mould infections of the commodity in store. In a field study in central Benin, Borgemeister *et al.* (1998) observed a higher proportion of mouldy grains after six months of storage in maize, which had been harvested with a high moisture content one week after physiological maturity. In addition to higher grain damage by *M. nigrivenella* as observed in this study, Sétamou (1996) recorded higher levels of aflatoxin contamination in late harvested maize in Benin. Thus, a delayed harvest of maize can lead to both quantitative and qualitative losses. Although the level of cob infestation by *M. nigrivenella* did not differ between maize harvested four and seven weeks after physiological maturity, the mean grain damage level in the recommended harvest was lower compared to that of the late harvest treatment. Moreover, the additional sun-drying after harvest inhibited the further development of the borer, thus substantially reducing the in-store losses due to *M. nigrivenella*. Therefore, a combination of a well timed harvest and an additional sun-drying of the maize prior to storage can considerably reduce the losses caused by *M. nigrivenella*.

9 Natural enemies of *M. nigrivenella* in Benin[7]

9.1 Abstract

Surveys conducted in the different agro-ecological zones of Benin during 1994-1997 revealed one egg parasitoid, three larval parasitoids and one pupal parasitoid attacking the pyralid maize cob borer *Mussidia nigrivenella* Ragonot. Egg parasitism was scarce on all host plants sampled and in all agro-ecological zones. Parasitism by larval and pupal parasitoids was usually low (< 10%), and was varied with the different host plant species. Both larval and pupal parasitoids were rare or absent in maize fields. The solitary chalcidid pupal parasitoid, *Antrocephalus crassipes* Masi, was the predominant species, contributing to approximately 53% of the observed mortality. Logistic regression analysis suggested that this parasitoid was more prevalent on fruits of *Gardenia* spp. than on the other host plant species, and was abundant between February and September.

9.2 Introduction

In West Africa, *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) is a pest of maize cobs (Moyal, 1988; Bosque-Pérez & Mareck, 1990; Moyal & Tran 1991; Shanower *et al.*, 1991; Gounou *et al.*, 1994) and cotton balls (Staeubli, 1977; Silvie, 1990). Although reported from other regions in Africa, *M. nigrivenella* is known as a pest of annual crops from western African countries only. Typically, more than half of the cobs in the field are usually infested by the borer (Whitney, 1970; Sétamou, 1996), but reported yield losses varied from 5 to 15% only (Moyal & Tran, 1991; cf. Chapter 2.4). *Mussidia nigrivenella* damage, however, also predisposes maize to pre- and post-harvest infestations by storage beetles, *Aspergillus flavus* Lk. Fr. infections and subsequent aflatoxin contamination (Sétamou *et al.*, 1998; cf. Chapter 3.4).

Sétamou (1996) theorised that in a given ecozone, the seasonality and pest status of *M. nigrivenella* is mainly influenced by availability of suitable fruiting structures of both cultivated and wild host plants. Surveys in different agro-ecological zones of Benin,

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[7] To be published as M. Sétamou, F. Schulthess, H-M. Poehling, G. Georgen, and C. Borgemeister. Natural enemies of the maize cob borer, *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae) in Benin, West Africa. To be submitted to *Biocontrol, Science and Technology*.

conducted between 1993 and 1997, revealed about 20 plant species from 11 different plant families, most of them trees and bushes, hosting the borer, some of them more suitable for growth and development of the pest than maize (Sétamou *et. al.*, 1999; cf. Chapter 5.4).

Little is known about the natural enemies attacking this pest. Several country-wide surveys on maize in Ghana (Gounou *et al.*, 1994) and Benin (Shanower *et al.*, 1991) yielded no larval or pupal parasitoids. Likewise, Moyal (1988) working on maize in Côte d'Ivoire only found some unidentified trichogrammatid and scelionid egg parasitoids, causing between 2-20% parasitism. From Cameroon, Nonveiller (1984) reported the ichneumonids *Hemimetopius anguilitarsis* Benoit and *Syzeuctus* sp., and Ndemah (1999) the chalcidid *Antrocephalus crassipes* Masi, the braconid *Bracon sesamiae* Cameron and species of the eulophid *Tetrasticus atriclavus* complex, which are both parasitoids and hyperparasitoids, from larvae and/or pupae of *M. nigrivenella.* In general, occurrence of those larval and pupal parasitoids was rather anecdotal and parasitization rates exceedingly low. However, all these collections have been done on maize only, which due to its phasic growth is a rather unstable habitat for both borers and beneficials, and nothing is known about the natural enemy complex attacking *M. nigrivenella* on wild host plants. Preference for foraging on particular food plants of a polyphagous insect host is frequently found in parasitoids (Taylor, 1932; Vinson, 1981; Kouloussis & Katsoyannos, 1994).

In this study an attempt was made to establish a catalogue of natural enemies occurring on cultivated and wild hosts in the different agro-ecological zone of Benin. In addition, abundance of both the pest and its beneficials was followed up on selected host plants during two years.

9.3 Materials and Methods

A preliminary 10 days survey on pod and fruit-bearing herbaceous plants and shrubs, sampled in a haphazard manner, was carried out in Benin in autumn of 1991. Further country-wide surveys conducted from July 1993 to December 1995 at 3 months-intervals, and monthly from January 1996 to December 1997 concentrated on tree species mainly (cf. Chapter 4.3). In addition, data are used here from maize fields sampled throughout the country or on-station experiments (Sétamou *et al.*, 1995; Sétamou & Schulthess, 1995; Sétamou *et al.*, 1998; cf. Chapter 2.3 and Chapter

4.3). Maize and plant species with fruiting structures suspected to harbour *M. nigrivenella*, including known host plants were sampled. Whenever possible, a sample of 20 fruits was taken. All collected fruits were first visually examined for eggs or first instar larvae, and then dissected for borer collection. Because the immature stages are difficult to identify, eggs, larvae and/or pupae collected on the different hosts were brought to the laboratory. The eggs were incubated at 26 ± 2°C and 65 ± 5% RH, on moistened tissue paper until larval or parasitoid emergence. The emerged larvae as well as the collected larvae were reared on *C. enseiformis* pods, following the protocol developed by Sétamou *et al.* (1999) until pupation of parasitoid emergence. Pupae were kept individually in 30 ml transparent plastic capsules, until moth or parasitoid emergence. Parasitoid species were identified at the insect museum of the International Institute of Tropical Agriculture (IITA), Calavi, Republic of Benin, and *M. nigrivenella*. using the key established by Moyal (1988).

Non-parasitoid related mortality factors, such as desiccation, pathogens, mechanical damage and unknown mortality causes were not included in the analysis, thus leading to an underestimation of the impact of natural enemies in general and of parasitoids in particular. Percentage parasitism, calculated separately for each of the three immature stages and per host plant species, was expressed as the number of parasitoids emerged over the total number of *M. nigrivenella* in the respective developmental stage.

For the 1996/97 survey data on wild hosts, backward stepwise logistic regression models (Hosmer & Lemeshow, 1989) were used to evaluate the effects of sampling year and month and the different host plants as predictors of the level of parasitism in the different *M. nigrivenella* developmental stages. All predictor variables are coded as dummy variables, i.e., 0 for absence and 1 for presence. Hence, for months 11 dummy variables were derived, and three dummy variables for host plants, corresponding to the four host plants from which larval and/or pupal parasitoids were obtained during the surveys. Analyses were conducted using the PROC LOGISTIC of SAS (SAS institute, 1996), and the fit of the models was determined using the χ^2 value (Hosmer & Lemeshow, 1989).

9.4 *Results*

Species composition and distribution of parasitoids Only five parasitoid species were found on immature *M. nigrivenella* and with a few exceptions they were all obtained from tree species which are common in the savannas, and especially the southern Guinea savanna (SGS) but rare in the Forest Savanna Mosaic (FSM) in the south (Table 9.1). The scelionid *Telenomus* sp. was the only egg parasitoid and emerged mainly from samples collected on fruits of *Parkia biglobosa* (Jacq.) Benth. (Mimosaceae). No egg parasitoids were recorded from maize cobs. The braconid larval parasitoids *B. sesamiae* and *Apanteles* sp. were obtained from maize and some tree species. About 65% of the larval parasitism were due to *B. sesamiae* but from maize only seven specimens were collected during all surveys. A few specimens of *Perilampus* sp. (Hymenoptera: Perilampidae) also emerged from *M. nigrivenella* larvae, but species of this genus can be either primary or hyper-parasitoids (Varma, 1989).

From pupae, only one parasitoid species, the chalcidid *Antrocephalus crassipes* Masi (Hymenoptera: Chalcididae) was obtained (Table 9.1). This solitary parasitoid emerged mainly from pupae collected on fruits of wild host plant species with one specimen only from maize in the northern Guinea savanna (NGS). *Antrocephalus crassipes* emerged from pupae collected SGS, NGS, and in the Sudan Savanna (SS), but not from samples collected in the FSM (Table 9.1). Across all host plant species, *A. crassipes* was the predominant parasitoid, accounting for approximately 53% of all emerged parasitoids (Fig. 9.1).

No parasitoids were recorded on other herbaceous plants such as the cover crops jackbean, *Canavalia enseiformis* (L.) DC. (Fabaceae) and velvetbean, *Mucuna pruriens* DC. (Fabaceae), which are highly suitable for growth and development of *M. nigrivenella* (Sétamou *et al.*, 1999b).

Table 9-1 Species composition and distribution of parasitoids of *M. nigrivenella* collected on different host plants in Benin between 1994 and 1997.

Parasitoid species	Order: Family	Host plant	Agro-ecological zone
Egg parasitoid			
Telenomus sp.	Hym: Scelionidae	*P. biglobosa*	SGS, NGS
Larval parasitoids			
Bracon sesamiae	Hym: Braconidae	*A. digitata*	SGS
		Gardenia spp.	SGS, NGS,SS
		P. biglobosa	SGS, NGS
		X. americana	NGS
		Z. mays	FSM, SGS
Apanteles sp.	Hym: Braconidae	*Gardenia* spp.	NGS, SS
		P. biglobosa	SGS, NGS, SS
Perilampus sp.[1]	Hym: Perilampidae	*P. biglobosa*	SGS
		Z. mays	SGS
Pupal parasitoid			
Antrocephalus crassipes Masi	Hym: Chalcididae	*Gardenia* spp.	NGS, SS
		P. biglobosa	SGS, NGS, SS
		X. americana	NGS, SS
		Z. mays[2]	NGS

[1] Parasitoid of, or hyperparasitoid on many lepidopteran larvae
[2] Collected on one occasion in late harvested maize fields.

Incidence and levels of parasitism Egg parasitism was in general extremely low (< 0.1%) and thus not included in the subsequent analyses. Mean larval and pupal parasitism, and total parasitism across all sampling occasions on the different host plant species are presented in Figure 9.1. Larval parasitism ranged between <0.5% on *Ximenia americana* L. (Olacaceae) and *Adansonia digitata* L. (Bombacaceae) and 4-5% on *P. biglobosa* and *Gardenia* spp., respectively. A similar trend was observed for pupal parasitism, with highest level of nearly 10% on *Gardenia* spp., but no specimen was recovered from *A. digitata*. Total parasitism ranged from 0.2 % on *A. digitata* to 7.1% on *Gardenia* spp.; on maize it was < 0.1%. Incidence of larval and pupal parasitism varied with host plant species and time, thus, reflecting the phenology of fruit setting of a species, and the pattern was similar in both years (Fig.

9.1 and 9.2-9.5). On *X. americana* larval parasitoids were recorded only in September, and the pupal parasitoid *A. crassipes* was found in November and December (Fig. 9.5). Levels of pupal parasitism were also low on *P. biglobosa*, but larval parasitism was recorded throughout the whole fruiting period, with higher values towards the end (cf. Chapter 4.4, Fig. 9.3). On *Gardenia* spp., both parasitized larvae and pupae were found throughout the whole year, but levels of parasitism varied with time (Fig. 9.2).

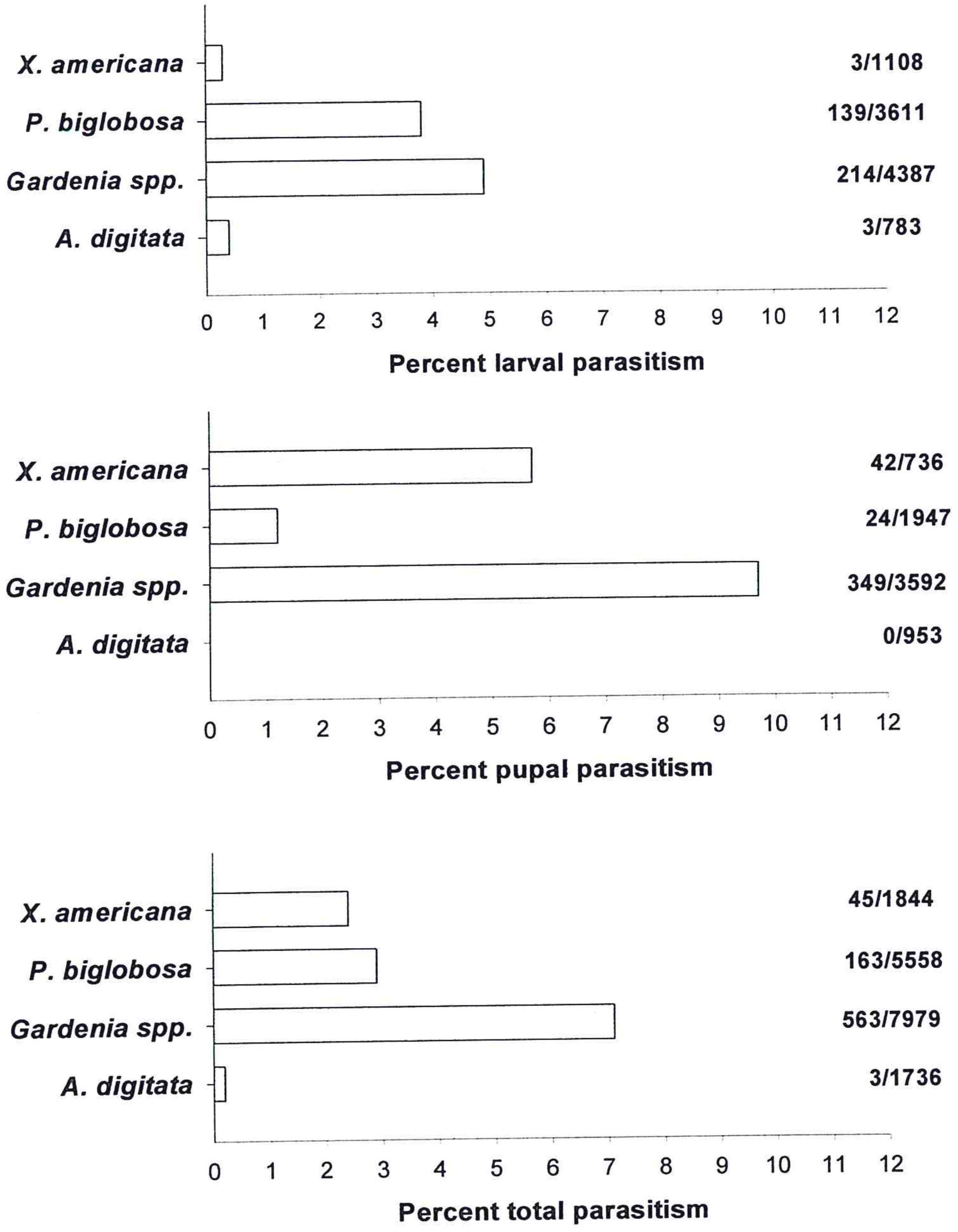

Fig. 9-1 Incidence of natural enemies on *Mussidia nigrivenella* populations on various wild host plants from January 1996 until November 1997 in Benin.

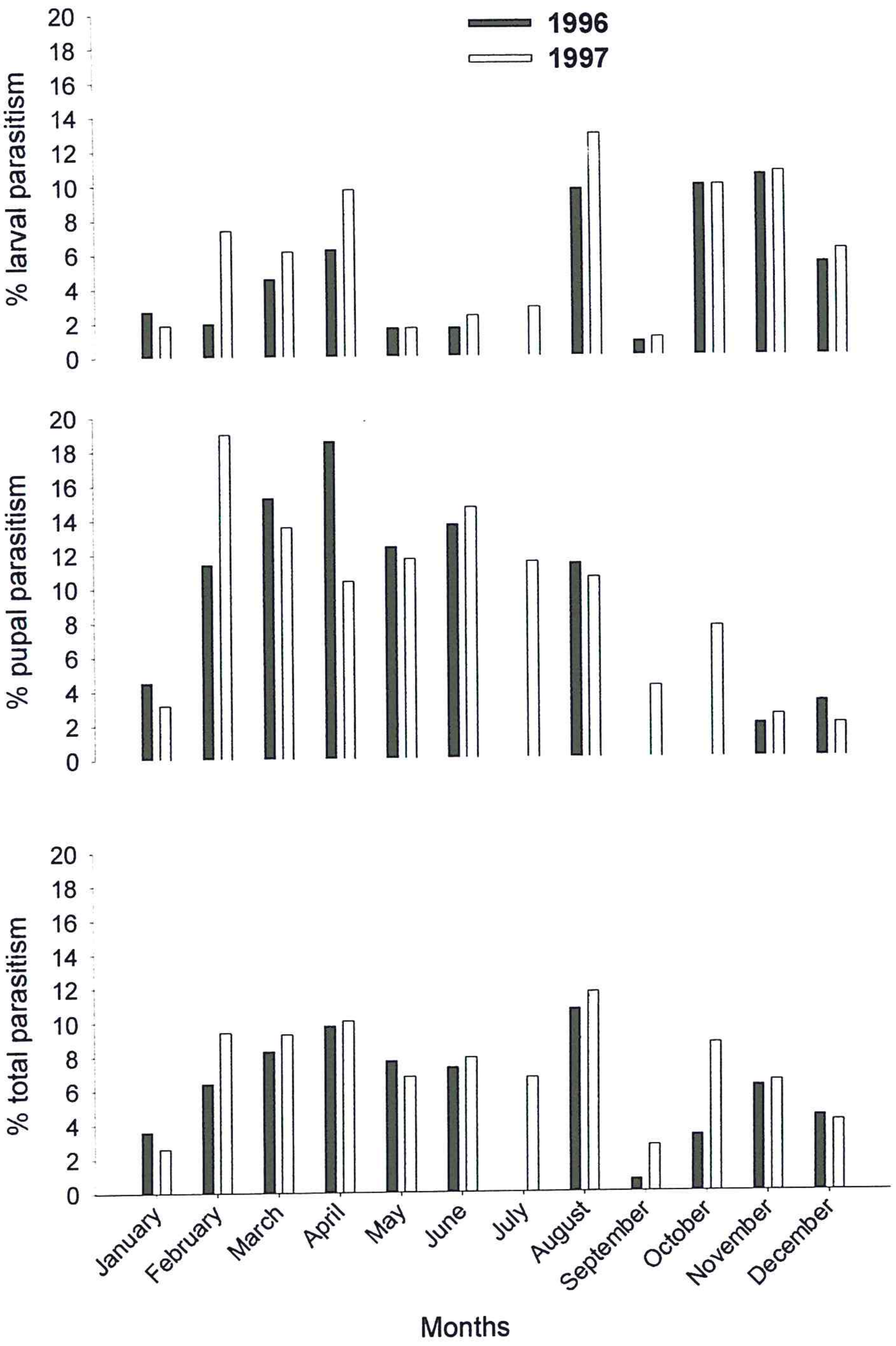

Fig. 9-2 Parasitism of *Mussidia nigrivenella* borers by larval and pupal parasitoids on fruits of *Gardenia* spp.

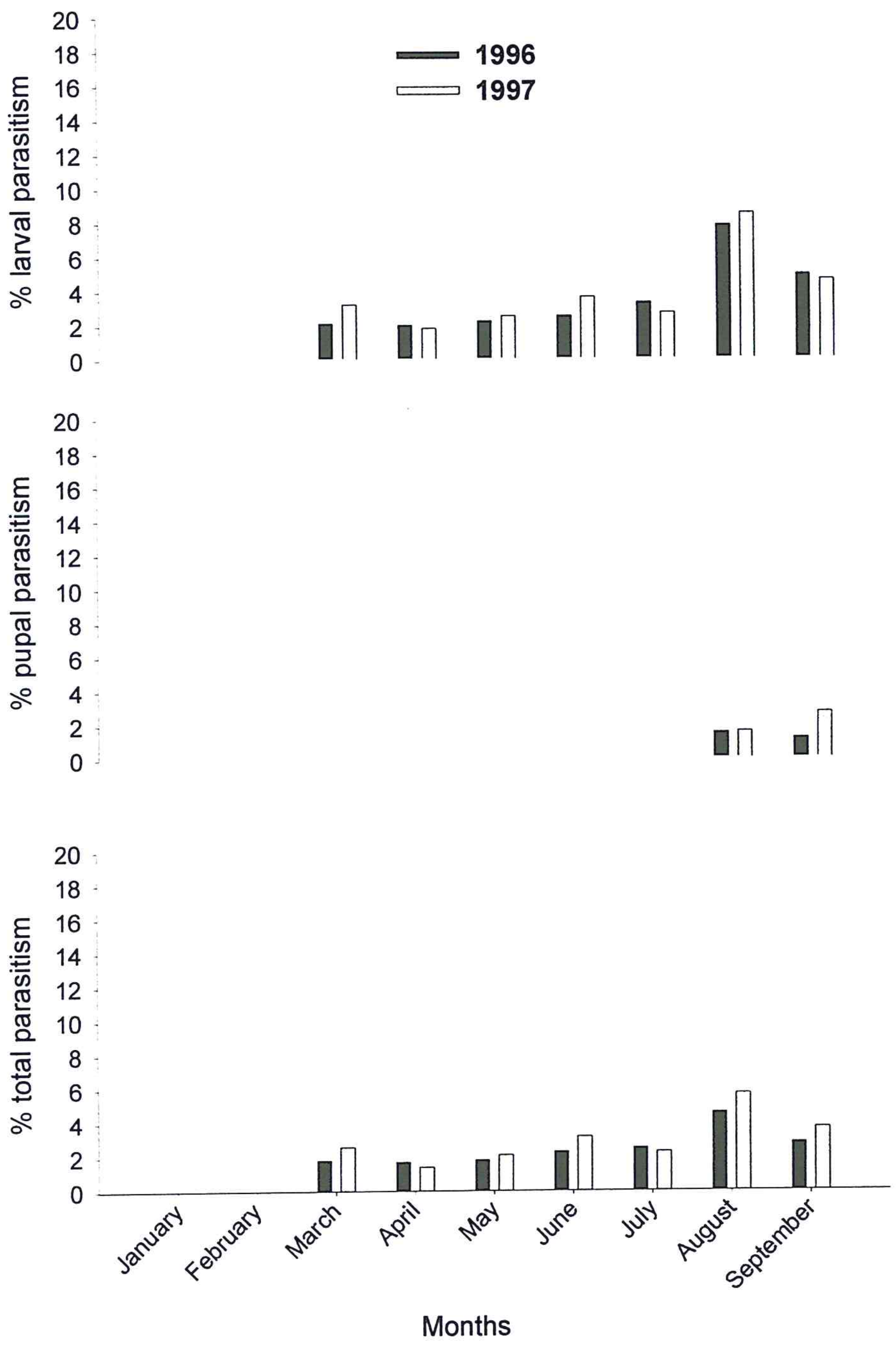

Fig. 9-3 Parasitism of *Mussidia nigrivenella* borers by larval and pupal parasitoids on fruits of *Parkia biglobosa*.

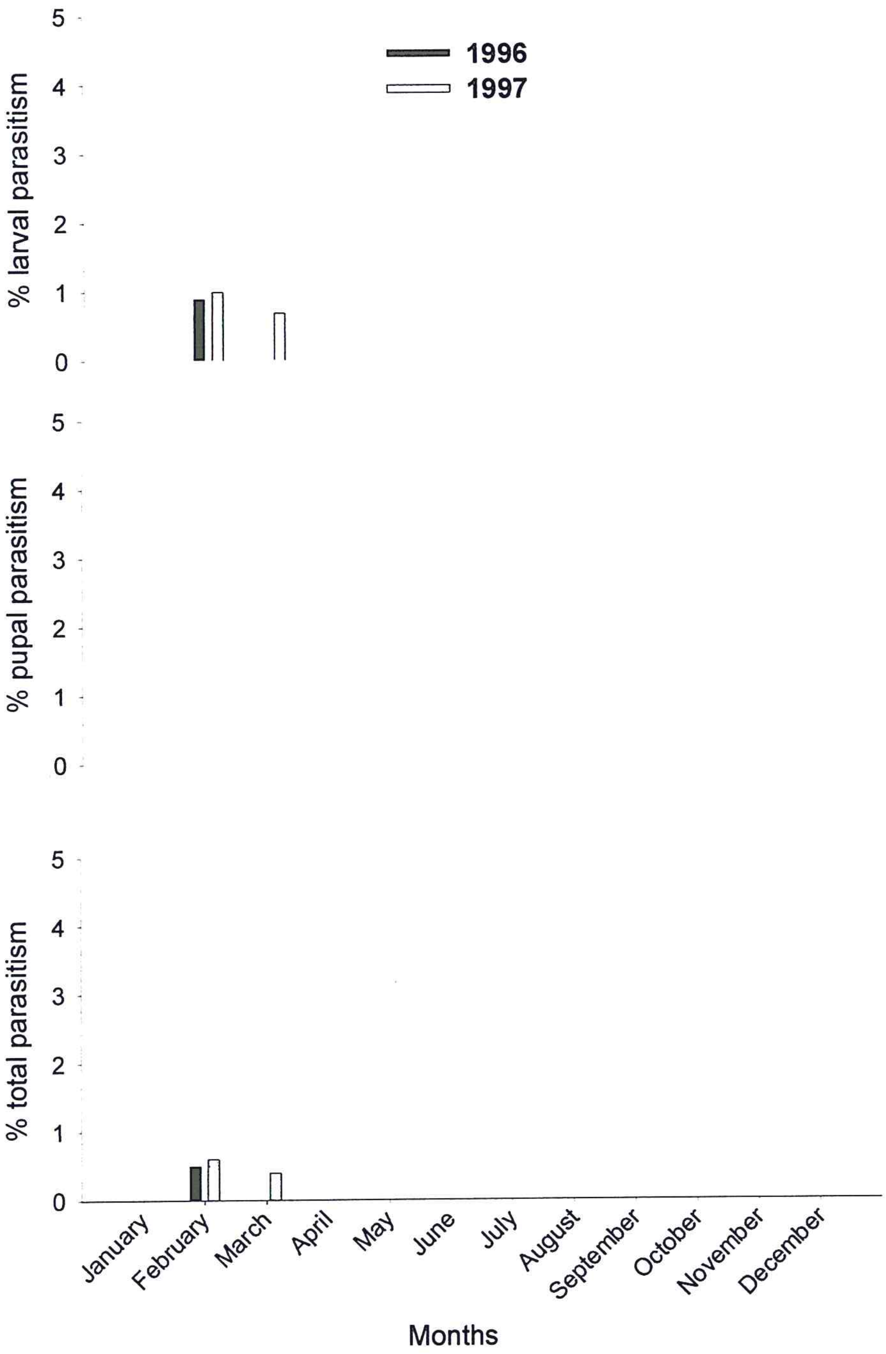

Fig. 9-4 Parasitism of *Mussidia nigrivenella* borers by larval and pupal parasitoids on fruits of *Adansonia digitata*.

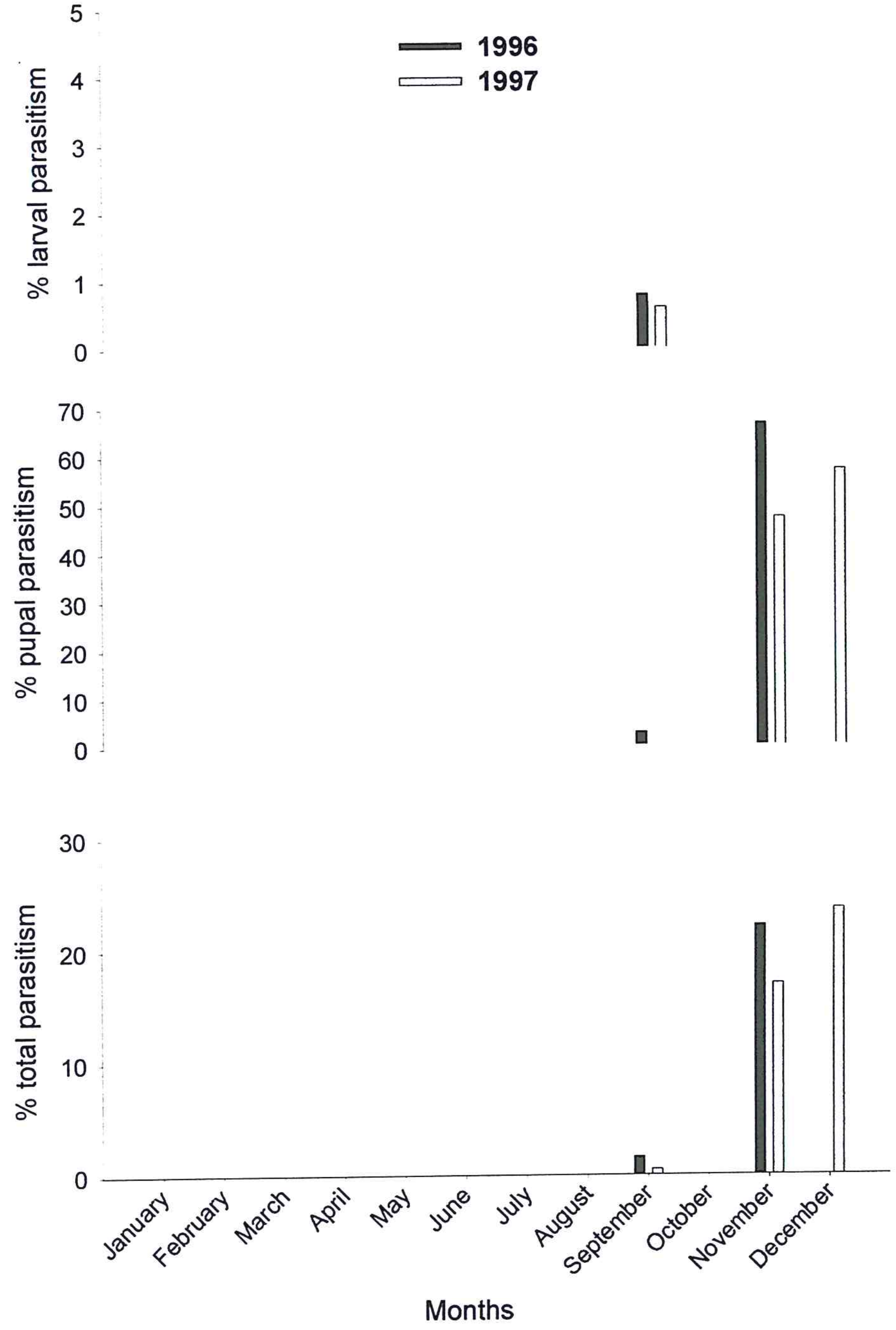

Fig. 9-5 Parasitism of *Mussidia nigrivenella* borers by larval and pupal parasitoids on fruits of *Ximenia americana*.

The logistic regression models yielded a clear association between both larval and pupal parasitism and host plants (Table 9.2 and 9.3). Likewise, time of the year had significant impact on the levels of parasitism. No significant effect of year of sampling was observed for both larval and pupal parasitism. The fit of both models was good

(χ^2 = 3.41; DF = 4; P = 0.49 and χ^2 = 4.90; DF = 7; P = 0.67 for larval and pupal parasitism, respectively). Larval parasitism was most likely to occur when larvae were collected on *P. biglobosa* and *Gardenia* spp., whereas the other host plants had no significant contribution (Table 9.2). The high odds ratios for *Gardenia* spp. and *P. biglobosa* (22.9 and 16.7, respectively) indicated a preference of the larval parasitoids for these host plant species (Table 9.2). Larval parasitism was significantly higher between August and November than during the other months (Table 9.2).

Table 9-2 Logistic regression analysis of the effect of sampling months and host plant species on levels of larval parasitism in *M. nigrivenella*.

Variable	DF	Parameter estimate	SE	Wald χ^2	*P*-value	Odds ratio
Intercept	1	-6.05	0.42	212.33	< 0.01	-
January	1	-0.81	0.25	10.95	< 0.01	0.44
May	1	-0.69	0.23	8.97	< 0.01	0.50
August	1	0.77	0.16	23.03	< 0.01	2.17
October	1	0.72	0.30	5.60	0.02	2.05
November	1	0.78	0.36	4.66	0.03	2.18
Gardenia spp.	1	3.13	0.42	55.70	< 0.01	22.92
P. biglobosa	1	2.81	0.42	45.07	< 0.01	16.67

The likelihood of parasitism of *M. nigrivenella* pupae by *A. crassipes* was significantly higher on *Gardenia* spp. than on other host plant species (Table 9.3). The high odds ratio for *Gardenia* spp. (= 9.7) indicated, that pupae on this host plant species are about ten times more likely to be parasitized by *A. crassipes* as those on the other host plant species. Likewise, the occurrence of *A. crassipes* was significantly higher between February and September, with the likelihood of parasitism being three to four times higher during this period than between October and January.

Table 9-3 Logistic regression analysis of the effect of sampling months and host plant species on levels of parasitism by *A. crassipes* in *M. nigrivenella* pupae.

Variable	DF	Parameter estimate	SE	Wald χ^2	*P*-value	Odds ratio
Intercept	1	-5.44	0.31	307.27	< 0.01	-
February	1	1.32	0.19	48.60	< 0.01	3.75
March	1	1.40	0.18	61.90	< 0.01	4.06
April	1	1.43	0.19	57.06	< 0.01	4.18
May	1	1.14	0.21	30.60	< 0.01	3.14
June	1	1.30	0.34	14.79	< 0.01	3.67
August	1	1.13	0.27	18.05	< 0.01	3.10
September	1	1.06	0.34	9.90	< 0.01	2.89
Gardenia spp.	1	2.27	0.28	65.13	< 0.01	9.72

9.5 Discussion

Only five out of the 20 host plants described for *M. nigrivenella* (Moyal, 1988; Sétamou, 1996; cf. Chapter 4.4) yielded parasitoids. The discrepancy in both parasitoid diversity and abundance between annual herbaceous plants and trees, as well as between the different tree species was striking. However, some of the most suitable and common annual host plants such as maize, the jack- and the velvetbeans are exotic to Africa and may not produce the chemical and physical cues needed by the natural enemy to detect its insect host (e.g. Smith *et al.*, 1993; Janz & Nylin, 1997). A similar example poses the natural enemy complex of the pyralid maize pest *Eldana saccharina* (Walker) on sugar cane in South Africa. On its most common natural host plant, the sedge *Cyperus papyrus* L. (Cyperaceae), the natural enemy fauna is quite diverse and the parasitization rates can be high (Conlong, 1990; Conlong, 1994). However, those parasitoid species do not attack the *E. saccharina* on adjacent sugar cane fields. Besides chemical or physical cues, accessibility of the host very likely plays a major role. *Mussidia nigrivenella* spends most of its life cycle within the cob, seed pods or fruit and most of the plant species show no external feeding damage until shortly before pupation, when the borer produces an exit hole. As a result, the most common parasitoid *B. sesamiae* attacking larvae belongs to the drill-and-sting guild (Smith *et al.*, 1993), and larval parasitism is generally considerably lower than pupal parasitism. In addition, the size and shape of the fruiting structure or thickness of the pericarp varies considerably with plant species which may affect accessibility of the host to the parasitoid. For example, the baobab fruits are large with strong pericarps whereas *Gardenia* spp. produces relatively small and thin-skinned fruits. Consequently, both larval and pupal parasitism was considerably higher on *Gardenia* spp.. The duration of fruit formation and the period that fruits are available to both pest and its beneficials also may play a major role. Mature maize cobs harbouring *M. nigrivenella* pupae are generally exposed to potential pupal parasitoid attack in the field for a maximum period of 30 days, thereafter the cobs are harvested. In contrast, the fruits of most wild host plant species, except for *P. biglobosa*, are never harvested and remain on the plants until they drop. Thus, the long exposure period of wild host plant fruits may allow the development of several *M. nigrivenella* generations per year (cf. Chapter 4.4), and thereby increase the likelihood of parasitization. In this respect, wild woody host plants are a far more stable habitat than the rather ephemeral maize plants. This, however, does not explain the differences in parasitism between tree species, and the fact that on most species beneficials are absent. According to Hare and Luck (1991), and Karowe and Schoonhoven (1992) those differences may also reflect the suitability of herbivorous hosts for the developing parasitoid, which may vary with the host plant fed upon. However, in the laboratory *A. crassipes* equally parasitized *M. nigrivenella* pupae stemming from different host plants, i.e., maize, jackbean, *A. digitata*, *P. biglobosa*, *Gardenia* spp., and *X. americana* (M. Sétamou, unpubl. results). The pupal parasitoid *A. crassipes* was the predominant parasitoid species, occurring in all three northern agro-ecological zones of Benin. Logistic multiple regression analysis indicated higher levels of pupal parasitism during the dry season. In olfactometer studies, *A. crassipes* showed a strong preference for low relative humidities (M. Sétamou, unpublished data). Similar humidity preferences have been reported for *Antrocephalus hakonensis* (Ashmead) (Hymenoptera: Chalcididae), a pupal parasitoid of *Opisina arenosella* Walker (Lepidoptera: Pyralidae) (Mohandas & Abdurahiman, 1995). *Antrocephalus crassipes* was only found on wild host plant species and only in the three northern agro-ecological zones, which reflects the diversity and abundance of wild host plants in these zones. In the south, the most common host is maize and to a lesser extent the jack- and the velvetbeans (cf.

Chapter 4.4). Similarly, in the forest zone of Cameroon, only one specimen of *A. crassipes* was ever obtained from maize (Ndemah, 1999). In NGS and SS of Benin, high levels of parasitism by *A. crassipes* were recorded between February and September, i.e., before and during cob formation in maize. Thus in those regions, biological control activity on wild host plants may have an impact on pest infestations on crops such as maize and cotton.

Egg parasitism was in general <0.1%, and was zero on maize, whereas in the savannas of Côte d'Ivoire Moyal (1988) found up to 20% of the *M. nigrivenella* eggs on maize parasitized. The most common parasitoid species belonging to the *Tetrastichus atriclavus*-complex reported from *M. nigrivenella* on maize in the forest zone in Cameroon (Ndemah, 1999) was never found on this pest in West Africa. In Cameroon, parasitization rates are generally below 10%, but as indicated by the present findings this pest has to be controlled on its wild hosts since maize is a relatively unstable habitat and not very attractive to parasitoids. However, the introduction and use of facultative parasitoids in biological control is highly controversial (Ehler, 1979).

Though described from East, Southern and Central Africa (Janse, 1941; Sorauer, 1925; Le Pelley, 1959; Buyckx, 1962; Entwistle, 1972; Waiyaki, 1973), *M. nigrivenella* was never reported as a pest of annual crops outside western Africa. This leaves the possibility that in other regions *M. nigrivenella* is controlled biologically in its wild habitats, thereby preventing the pest from moving onto maize and cotton. This opens opportunities for the re-distribution approach (i.e., to increase the geographical range of parasitoid species or strains of them; Hokkanen & Pimentel, 1984) or the 'new association' approach (use of natural enemies of closely related species occupying similar ecological niches; Hokkanen & Pimentel, 1984) as proposed by Schulthess *et al.* (1997) for lepidopterous cereal stem borers in Africa. Janse (1941) described eight *Mussidia* spp., five from the African mainland, two from Madagascar and Reunion, and one from Asia. Exploratory work should concentrate on East and Southern Africa, including the islands. Because of the exceedingly cryptic behaviour of this pest, emphasis should be given to egg and pupal parasitoids.

10 General Discussion

The main objectives of the here presented studies were to investigate the factors affecting the population dynamics of the maize cob borer *M. nigrivenella* in Benin. Such information is urgently needed for a better understanding of the fluctuation in pest status of this borer and is a prerequisite for the development of sustainable management strategies against this pest. Precise data on the borer distribution, infestation and damage levels in maize, host plant range, biology on natural host plants, spatial distribution, adult flight activity, the effect of farming practices, as well as the impact of parasitoids on *M. nigrivenella* have been presented and discussed separately in the respective chapters. In this general discussion, the relationships between the individual findings and their implications for the development of sustainable pest management options against the borer are presented.

The results from our various surveys clearly illustrate, that *M. nigrivenella* is abundant throughout Benin and that cob infestation levels are generally high. Whitney (1970) reported equally high cob infestation levels in Nigeria. Despite this high incidence, damage levels due to *M. nigrivenella* were rather moderate, the main reason probably being the short feeding period of larvae on maize cobs. In contrast to most other lepidopterous maize stem borers, which feed on the grains for up to 30 days (Shanower *et al.*, 1993; Bosque-Pérez & Mareck, 1991), larvae of *M. nigrivenella* have a relatively short developmental time of only 15 days (Bordat & Renand, 1987; Moyal & Tran, 1991b; Bolaji & Bosque-Pérez, 1998, Sétamou *et al.*, 1999b; cf. Chapter 5). Hence, the damage due to an individual *M. nigrivenella* larva is lower compared to other species such as *B. fusca* or *S. calamistis* (cf. Chapter 2.4) and as a result, only high larval densities of *M. nigrivenella* can lead to high grain damage levels. *Mussidia nigrivenella* densities per cob varied generally between two to three borer larvae (cf. Chapter 2.4), reflecting the aggregated egg laying behaviour of the adult female (Moyal, 1988). In life table studies, using maize cobs as food source, high mortality mainly occurred during the early larval instars (Sétamou *et al.*, 1999b; cf. Chapter 5). Correspondingly in field studies, Moyal (1988) observed up to 90% mortality before establishment of *M. nigrivenella* larvae in the maize cob.

In West Africa, small-scale farmers usually select big and healthy cobs from their harvest as seed source for the next cropping season. Since *M. nigrivenella* infests a high percentage of the cobs in the field, and preferentially attacks bigger cobs (Sétamou *et al.*, 1995), the borer may also threaten the subsequent maize crop by substantially reducing the viability of seeds.

The exit holes of the late instar larvae of *M. nigrivenella* in maize husks constitute entrance holes for many coleopteran storage pest species. In addition, the high mobility of borer larvae in maize cobs contribute to the spread of *A. flavus* spores on damaged grains, which can result in contamination of the commodity by aflatoxin. Thus, because of the positive association between *M. nigrivenella* and storage beetles on one hand, and the aflatoxin-producing fungus *A. flavus* on the other hand (Sétamou *et al.*, 1998; Chapter 3), the borer additionally reduces the quality of the maize and increases the risk of grain losses in storage.

Strong variation in the relative importance of *M. nigrivenella* was observed between the different agro-ecological zones of Benin. Sétamou (1996) theorised, that this variation may be due to host plant availability. Based on the detailed studies on wild and cultivated host plants of *M. nigrivenella*, the crucial role of individual host plant species for the population dynamics of the borer in Benin could be elucidated. In the Forest Savanna Mosaic (FSM), alternative host plants of the borer are scarce. Except for the two recently introduced cover crops *C. enseiformis* and *M. pruriens*, which are presently mainly grown as experimental plots, maize is the most common host plant of *M. nigrivenella* in this zone (cf. Chapter 4). As also shown by the light trap catches (cf. Chapter 7), *M. nigrivenella* populations are strongly influenced by the seasonality of maize cropping, and are low or crash when suitable development stages of maize cobs are not yet or not anymore available. The host plant range of *M. nigrivenella* includes tall tree species such as *P. biglobosa* and the baobab tree, *A. digitata* (cf. Chapter 4), which can reach up to 25-30 m in height (von Maydell, 1990), indicating that adult *M. nigrivenella* are good flyers. However, migration between regions probably plays a minor role in the population dynamics of this species. How fast critical infestation levels are reached in the next season depends to a large extent on the diversity and abundance of wild and cultivated host plants in a given area. Consequently, in the FSM it takes more than one cropping season to achieve peak pest infestations. By contrast, host plants are diverse and abundant in the Guinea Savannas of central and northern Benin (cf. Chapter 4). The overlapping fruiting periods of these host plants permit a continuous development of the borer. In these zones, *M. nigrivenella* populations are therefore maintained throughout the year and high numbers of females can infest maize fields, thus explaining the higher damage levels in maize recorded in the Guinea Savannas. Weather conditions have little effect on *M. nigrivenella* flight activity in these zones. However, the long dry season from November to March in the Northern Guinea Savanna (NGS), affects fruit formation of many plants and thus indirectly influence the flight activity of the adults.

The on-going propagation of jack- and velvetbeans as new cover crops may subsequently change the pest status of the borer in different agro-ecological zones, because both plants are highly suitable for *M. nigrivenella* development (cf. Chapter 5). Infestation and damage levels in maize could increase if the planting of the cover crops is not properly timed by avoiding that their fruiting periods precede that of maize. In field studies (cf. Chapter 4), *C. enseiformis* was more attractive to ovipositing *M. nigrivenella* females than maize. Consequently, this crop may draw the females from maize fields if its fruiting period and cob formation of maize crop coincide.

As shown by our field trials, leaving maize cobs in the field for an extended field drying period increases the infestation by and damage of *M. nigrivenella*. However, early harvest, i.e., one week after physiological maturity can increase the risk of mould development during storage (Borgemeister *et al.*, 1998). An additional sun-drying of the maize prior to storage not only reduces the subsequent damage of the borer in the stores, but also decreases the risk of aflatoxin contamination of maize (Hell, 1998). Therefore, a combination of a well timed harvest and an additional sun-drying prior to storage can considerably reduce the losses caused by *M. nigrivenella*.

Overall, few parasitoid species were found attacking *M. nigrivenella* populations in Benin. Moreover, these parasitoids were not equally common on the different host plants of the borer, indicating a certain preference to forage on particular host plant species of *M. nigrivenella*. In our study, the incidence of egg parasitoids was in general < 0.1%, whereas in the savanna zone of Côte d'Ivoire Moyal (1988) found up to 20% of the *M. nigrivenella* eggs on maize parasitized. Larval and pupal parasitoids were strongly associated with wild and more stable habitats, and scarce on maize. Levels of parasitism were higher on *Gardenia* spp. and *P. biglobosa* compared to other host plant species. The accessibility of larvae by the parasitoids may be an important factor explaining these differences. The small fruits of *Gardenia* spp. and the thin pericarp of fruits of *P. biglobosa* may allow contact of the parasitoids with their host borers, whereas the tough maize husks may considerably protect the borers from their natural enemies. Thus, biological control efforts should concentrate on natural habitats where high levels of parasitism can be achieved. However, as shown by our results, an integrated approach which combines several management options appear to be the best strategy towards solving the *M. nigrivenella* problem in West Africa.

The difference in parasitization observed on various host plants may also indicate the possibility of different species or strains of *M. nigrivenella* attacking the different host plants. As pointed out by Maes (1997), many taxonomic problems in noctuids and pyralids remain unsolved in Africa.

With the insights provided by this study the ecology and population dynamics of *M. nigrivenella*, particularly the role and importance of wild host plants are now better understood. The findings on the preference for cover crops such as *C. enseiformis* may open up new avenues for control options. This cover crop could be used as trap plant, thus reducing the borer load on maize cobs. However, additional work in this field is essential. The low levels of natural parasitism of *M. nigrivenella* found in the present study contrasted with the relatively high pupal parasitism level reported on maize in Cameroon (Ndemah, 1999). Thus, the redistribution approach of natural enemies as suggested by Schulthess *et al.* (1997) could be further investigated to solve the *M. nigrivenella* problem in West Africa

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