POPULATION ECOLOGY OF THE LEGUME POD BORER, *MARUCA TESTULALIS* GEYER (LEPIDOPTERA : PYRALIDAE) IN RELATION TO ITS NATURAL ENEMIES ON COWPEA IN WESTERN KENYA

BY

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DECLARATION

I JOASH BARACK OKEYO-OWUOR hereby declare to the senate of the University of Dar-es-salaam, that this thesis is a result of my own work except where acknowledgement is in text. It has not been submitted nor is it being concurrently submitted for a similar qualification in any other University.

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ABSTRACT

Studies were conducted at the International Centre of Insect Physiology and Ecology, Mbita Point Field Station (MPFS) farm and the Lambwe Valley farmer's field during 1983 - 1985, to determine the natural population changes of Maruca testulalis Geyer (Lepidoptera; Pyralidae). The role of natural enemies, host plants and climatic factors on natural population, development and survival of M. testulalis was investigated. Further investigations on the biology of Tetrastichus sesamiae (Chalcididae, Eulophidae) a gregarious pupal endo-parasitoid as well as bioassays on Nosema sp., a protozoan pathogen of the pest were conducted in the MPFS laboratory. It was found that M. testulalis colonised the crop at least 15 days after plant emergence when the first adult moths were recorded in the pheromone traps. The egg and larval populations started increasing steadily at the flower initiation stage reaching a peak between 42 and 54 DAPE at both sites. Only one generation of M. testulalis occurred on each crop of cowpea.

From the partial ecological life tables it was found that total real mortality for the generations at MPFS and Lambwe ranged between 51.7 - 98.9% and 96.4 - 97.7% respectively indicating very low survival in this species. Several natural enemies were found associated with M. testulalis, including 7 parasitoids, five of which attacked pupae and 2 on larvae. No egg parasitoid was found. The

major pathogenic microorganisms found on dead M. testulalis larvae and pupae were Nosema sp. and Bacillus sp. Observable parasitism played negligible role in causing mortality on M. testulalis being only 0.02 - 0.09 and 0.04 - 0.06% at MPFS and Lambwe respectively. Pathogens especially Nosema sp. and Bacillus sp. contributed significantly to mortality of M. testulalis at both sites. Disappearance designated as other losses not due to either parasitoids or pathogens also accounted for a large proportion of mortality. Analysis using key factor and correlation methods revealed that disappearance at the egg stage (k_0) was the key-factor causing population change at MPFS, while in Lambwe, although, more observations are necessary for this analysis, the factor k_3, representing disease at 3rd instar larval stage, was identified as the key factor. Temperature and rainfall also affected seasonal abundance of M. testulalis under field conditions. Under laboratory conditions, temperature was found to be an important factor affecting development and survival of the pest.

Biological studies on T. sesamiae showed that the development period range from 14 - 18 days. Major factors identified to influence the biology and efficiency of the parasitoid include quality of food, age of host pupae and different host species. Results from bioassay for pathogens showed that Nosema sp. was the most virulent naturally occurring pathogen on M. testulalis.

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INTRODUCTION

The legume pod borer, Maruca testulalis Geyer belongs to the family Pyralidae of the order Lepidoptera. According to Taylor (1978), the species was first described by Hubner, but the last part of its taxonomy was finalised and published by Geyer. Thus, the description of M. testulalis is currently ascribed to Geyer by modern taxonomists (Taylor 1978). The adult of this species is greyish-brown in colour with dark greyish wings bearing distinct white and brown marks which are more conspicuous on the hind than the fore wings (Plate 1). The female has a brown abdomen which becomes larger when the moth is gravid and ends in a bipid and hairy abdominal tip. In the male, the abdomen is dark-grey, especially the last 4-5 segments and has a sharp posterior end. According to Okeyo-Owuor and Ochieng' (1981) the female and male moths are of the same size and measure 11.0 $\pm$ 0.12 mm from head to abdominal tip and the wing span at full spread measures 24.2 $\pm$ 0.14mm (n=50). The moths are nocturnal in activity and during the day they usually rest with their wings fully spread on the lower leaves of host plants. The eggs are small in size (0.695$\pm$0.024 by 0.498$\pm$0.013 mm) and oval in shape, but are dorsoventrally flattened while glued onto the plant surface. The eggs hatch in 2-3 days after oviposition. There are five larval instars in M. testulalis (Taylor, 1967; Koehler and Mehta, 1972; Akinfenwa, 1975; Odebiyi, 1981). The noenate first instar larva is light brown in colour and after 2 days it moults into a second instar larva which has light-dark spots.

The 3rd to 5th instar larvae are brown or brownish-green depending on the colour of food substrate ingested, with characterisitic black spots throughout the body. A full grown 5th instar larva measures 10.3 - 10.5 mm in length compared to only 2mm in first instar larvae.

Pupation occurs in the soil, although in India this was reported on leaves of Cajanus cajan L. Millsp. (Vishakantaiah and Babu, 1980). Freshly pupated M. testulalis is greenish brown in colour but soon turn darkish with light brown spots on the puparium. The pupa measure about 10mm in length and is surrounded by finely woven silken material which if in the soil is further enclosed in fine soil particles. Detailed field and laboratory studies on the biology of M. testulalis has been conducted by Taylor (1967), Usua (1976) in Nigeria, Vishakantaiah and Baby (1980) in India, Okeyo-Owuor and Ochieng (1981) in Kenya and Ke et al. (1985) in China. Ochieng' et al. (1981, 1983) developed methods for rearing this species on both natural and artificial diets at ICIPE's Mbita Point Field Station (MPFS).

M. testulalis is a cosmopolitan insect which is widely distributed throughout the tropical and subtropical regions of the world and is mostly associated with various cultivated and wild legumes. Wolcott (1933) gave a general account of the life history and habits of M. testulalis as one of the three podboring species on limabeans in Puerto Rico. Lever (1944, 1947) reported it as an important pest of C. cajan, Crotolaria sp. and cowpea in Fiji. Jepson (1948) reported M. testulalis as a pest of groundnuts in Uganda, while in Sierra Leone, M. testulalis was reported to attack Poinciana sp. and Phaseolus vulgaris L. (Hargreaves 1937).

In Asia and the Philippines, M. testulalis is an important pest of P. vulgaris and vegetable cowpea (Barroga, 1969). In Sri Lanka, it is a serious pest of C. cajan (Subasinghe and Fellowes, 1978). Dina (1978) reported M. testulalis as a pest of soybean in Nigeria. In Australia, the pest was recorded on cowpea and mungbeans, while the navy beans and soybean were less preferred (Anon., 1981). Taylor (1967) noted that during the off season M. testulalis fed on climbing beans, Sphenostylis stenocarpus L. Sunhemp, Crotolaria juncea and winged beans in Nigeria. In India the pest has been recorded as an important pest of C. cajan by Vishakantaiah and Babu (1980), while in China the insect was recently reported on long yard bean (Vigna sesquipedalis L.) by Ke et al. (1985). Singh and van Emden (1969) reviewed the distribution and host range of M. testulalis throughout the tropical region. Hill (1975) published a distribution map of M. testulalis in the world and listed a wide range of legumious host plants of pest.

M. testulalis has been reported by several workers as an important pest of cowpea, Vigna unguiculata L. Walp (Papilionoidae Leguminosae) in various parts of tropical Africa (Taylor, and Ezedinma, 1964; Booker, 1965; Taylor, 1967, 1978; Jerath, 1969; Bohmen, 1973; Summerfield et al., 1974; Hill 1975; Agayen-Sampong 1978; Muturi et al., 1979; and Okeyo-Owuor and Ochieng' 1981). The pest attacks the crop at pre-flowering stage and persists until pod maturity. The larvae of this pest are voracious feeders. In the vegetative growth stage, before flowering, they feed on tender shoots and stems of cowpea plant. The young larvae later attack buds and flowers, while the older ones feed on green pods.

During their feeding larvae burrow into various parts of the plant and only come out when the food is exhausted. Because the pest usually attacks different parts of the cowpea plant, its common name, the "legume pod borer", is misleading, as it seems to imply that M. testulalis only attacks the pods.

Taylor (1967, 1978) described the damage by M. testulalis on cowpea. He observed that the larvae on hatching eat their way into the centre of the flower without much wandering on the surface so that no external sign of attack is noticed. However, more recent observations by Okeyo-Owuor and Ochieng' (1981) revealed that on hatching the larvae initially feed around the oviposition site and then bore into tender buds and flowers. In the absence of flowers the larvae bore into terminal shoots causing damage similar to that shown in Plate 2, where the feeding is extensive. However, in the presence of flowers the first instar larvae bore into them and concentrate their feeding on the essential floral parts, i.e. anthers stigma and ovary (Taylor, 1967). Taylor (1967) observed that the phenomenon of flower-drop in cowpea is not necessarily associated with M. testulalis damage and that an open flower, whether attacked or not drops within 24 hours. As a matter of fact the attacked flowers rarely drop prematurely as is usually assumed, but when the flowers are attacked 2-3 days before they are due to open they never open (Taylor 1967, Okeyo-Owuor, unpublished data). The larvae show a distinct preference for the ovary, style, stigma, and anthers, and rarely feed on the inner parts of the corolla.

Damage by M. testulalis to cowpea is characterised by the faecal frass produced by the larvae on flowers and pods. The flowers and green pods are usually bound together by frass-covered webs (Plate 3). Plate 4 shows dry pod and seed damage by the pest.

According to Taylor (1967), two phenological stages of cowpea are important as far as pest attack is concerned. The first is the early leaf formation stage, when the leaves and growing points are attacked mainly by a beetle, Oothecs mutabilis Sahl. and other lepidopteran larvae. The second stage is the period of flower bud initiation, flowering and pod formation, in which attack by M. testulalis appear to be the most important. At this stage any damage caused by insect pests can hardly be copensated for by the plant and leads directly to seed yield loss.

Yield loss caused by M. testulalis larvae on copea crop is variable, though severe. Taylor (1968) reported yield loss on grain ranging from 30-70% on different cowpea varieties in Nigeria. In Kenya, yield loss on grain of up to 80% was reported by Okeyo-Owuor and Ochieng' (1981). Usua (1975) reported that susceptibility of cowpea to the pest was high in varieties in which pods touch any other parts of the plant. He found that pod damage increased by almost 100% in 'cv' prima in which pods were oriented closer than normal. According to Taylor (1978), M. testulalis is recognised as a key pest of cowpea in Africa because its attack is serious and perennial, and its population often remains above economic threshold. This is partly because the moth is able to establish itself on young growing parts of the plant in the pre-flowering stage and moves on to damage flower buds, flowers, green pods and seeds extensively. A survey conducted in 1982 by Okeyo-Owuor

unpublished data) showed that in all cowpea growing areas in Kenya, M. testulalis was the most predominant pest of crop during all cropping seasons, althgouh aphids, thrips and pod bugs may occasionally cause severe damage in localized hot dry areas. Thus in Africa it is widely felt that the low cowpea seed yields obtained by farmers (ca.350-500 kg/ha) is largely due to M. testulalis attack.

Attempts to control cowpea pests have yielded variable results. Booker (1965) showed that by controlling cowpea pest complex of which M. testulalis is the most important, seed yield may be increased to 1800 kg/ha in Nigeria. Although, the use of chemical insecticides has reduced yield losses, the damage by M. testulalis has always remained high unless early control is undertaken (Booker, 1965; Jerath, 1968; Taylor, 1968). Koehler and Metha (1972) reported that weekly spraying with insecticides provided a higher degree of protection on pods than flowers of cowpea in Uganda. In West Africa, especially in Nigeria, several insecticides have been tested and recommended for M. testulalis control on cowpea crop (Dina, 1976; Singh and van Emden, 1978 and Taylor, 1978; Jackai, 1983). However, in East Africa, use of chemical control methods would not be advisable since both leaves and seeds are used as food. Besides, the number of sprays required and the cost of the chemicals recommended would be prohibitive to the subsistence resource poor farmer. Furthermore, the farming systems involving intercropping cowpea with other crops such as cereals make the conventional spraying methods cumbersome. Unfortunately, control of M. testulalis by alternative methods, such as the use of resistant cowpea lines are still hard to come by, since no varieties have been found resistant to the pest on flowers

and pods. So far, only a low level of resistance in the stems has been reported on cowpea variety Tvu 946 (Jackai, 1982; Macfoy et al., 1983). Also studies in Nigeria showed that M. testulalis still remained a major factor limiting cultivation of cowpea in the region irrespective of attempts to use time of planting and manipulation of planting date as a cultural practice to control the pest (Ezueh, 1982). The use of biological control agents against M. testulalis still requires detailed studies to identify and evaluate promising pathogens, parasitoids and predators of this species. Taylor (1967) reported that parasitoids of M. testulalis play negligible role in its natural control, since less than 5% of the total larvae collected were found to be parasitized in Nigeria. Further studies to identify and determine the role of natural enemies in other agroecosystems is necessary.

Some of the factors that complicate control of M. testulalis are, (a) resting behaviour of the moths under crop canopy and their nocturnal predilection (b) the feeding of larvae inside the food material during most of its life time which makes it dificult for conventional synthetic insecticides to reach the desired target and (c) the difficulty in locating eggs and therefore, predicting the onset of infestation on the crop for a timely control intervention (Okeyo-Owuor and Ochieng', 1981). Jackai (1980) reported the use of oil soluble dyes in detecting M. testulalis egg distribution on cowpea plant. However, this technique is only possible on a limited scale but, is of limited use on large fields. Recent investigations on the use of pheromones in population studies of M. testulalis have shown that the female moth produce sex pheromones that attract males in the field (Okeyo-Owuor and Agwaro, 1982).

The use of pheromone traps for population studies, forecasting and control is well documented in other related groups of moths (Campion et al., 1977; Laster et al., 1978; Nasr et al., 1978 and Beroza et al. 1978). Silverstein (1981) reviewed the potential role of pheromones for integrated pest management (IPM), especially as a means of forecasting, mass trapping and distruption of certain essential behaviour patterns in reproduction of the pest in question. According to Silverstein (1981) the use of pheromones require a thorough understanding of the pests behaviour. Thus, population studies of M. testulalis incorporating pheromone traps would provide information for better understanding of its population ecology as well as forecasting its infestation for control purposes.

It is evident that aspects of biology and behaviour of M. testulalis have received considerable attention from workers in tropical Africa. A knowledge of the pest population ecology is vital for formulating effective control strategy. In the light of the current problems in controlling M. testulalis, studies on population ecology should provide information on biotic and abiotic factors influencing the natural population densities, their manipulation and effective utilization in control programmes, time of infestation on the crop, appropriate forecasting systems, critical crop stages of growth when pests attack would lead to economic damage and yield loss, etc. All this information would provide a natural basis for effective management of the pest.

Knowledge on population ecology on M. testulalis is scanty. The present studies have therefore been undertaken with the following major objectives:

1. To study and understand the changes in field population of M. testulalis under subsistence farming systems.

2. To determine the major factors that regulate population changes in M. testulalis, with special reference to the role of natural enemies.

3. To study aspects of the biology of selected natural enemies of M. testulalis.

The objectives were achieved by testing the following hypothesis: That:-

1. natural enemies, especially parasitoids, and pathogens are important mortality factors in M. testulalis;

2. climatic factors, especially changes in ambient temperatures, relative humidity and rainfall play an important role in determining M. testulalis population size and its natural enemies in cowpea crop;

3. infestation levels of M. testulalis on cowpea depends on survival of the pest on alternative host and seasonal

changes occurring at MPFS and the subsistence farms, and that these host plants also help in harbouring and perpetuating the pest as well as its natural enemies;

4. crop phenology has an important effect of M. testulalis growth and survival rates.

Plate 1. Adult *M. testulalis* moth resting on the lower leaf surface of cowpea plant.

Plate 2: Symptoms of M. testulalis damage on vegetative parts of cowpea plants:

A. Damage on terminal shoot

B Damage on stem.


A

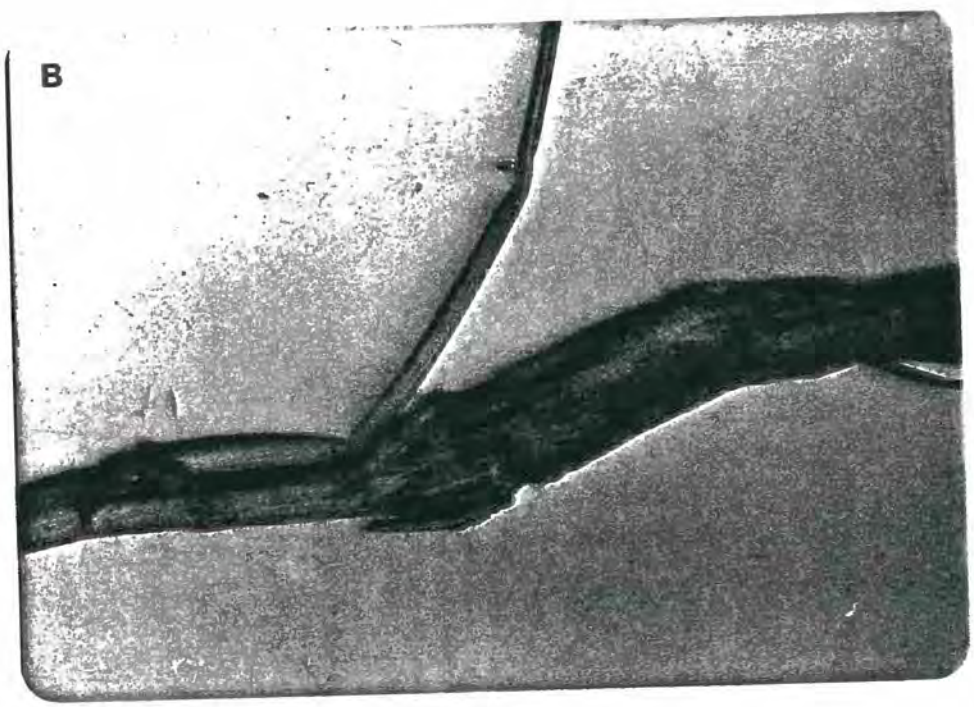

B

Plate 3. Symptoms of M. testulalis damage on flowers and green pods:

A. Dissected flower showing internal damage.

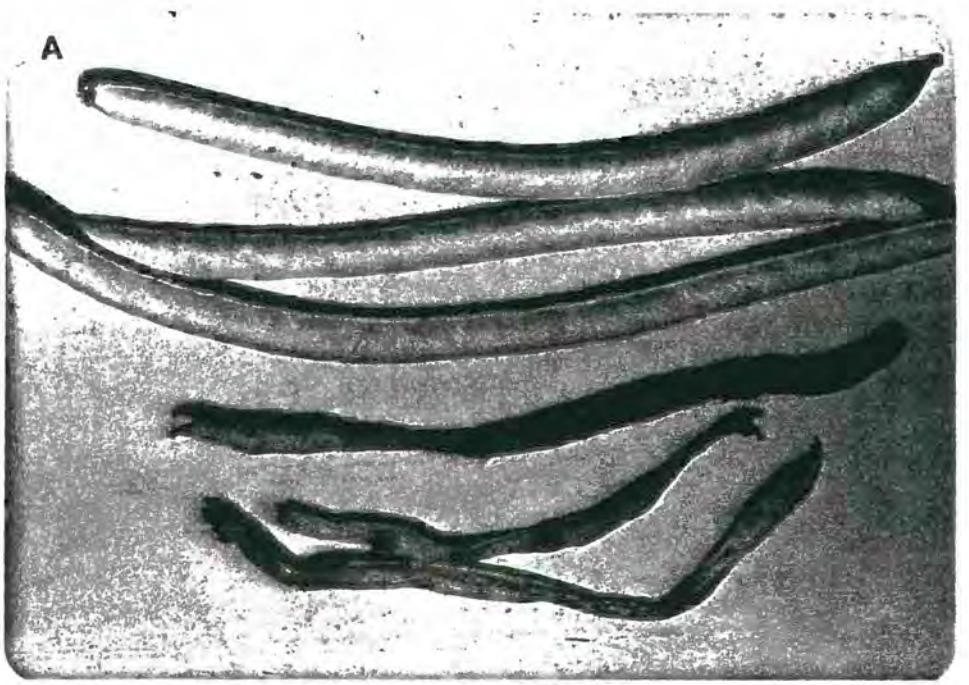
B. Green pods showing external damage symptoms.

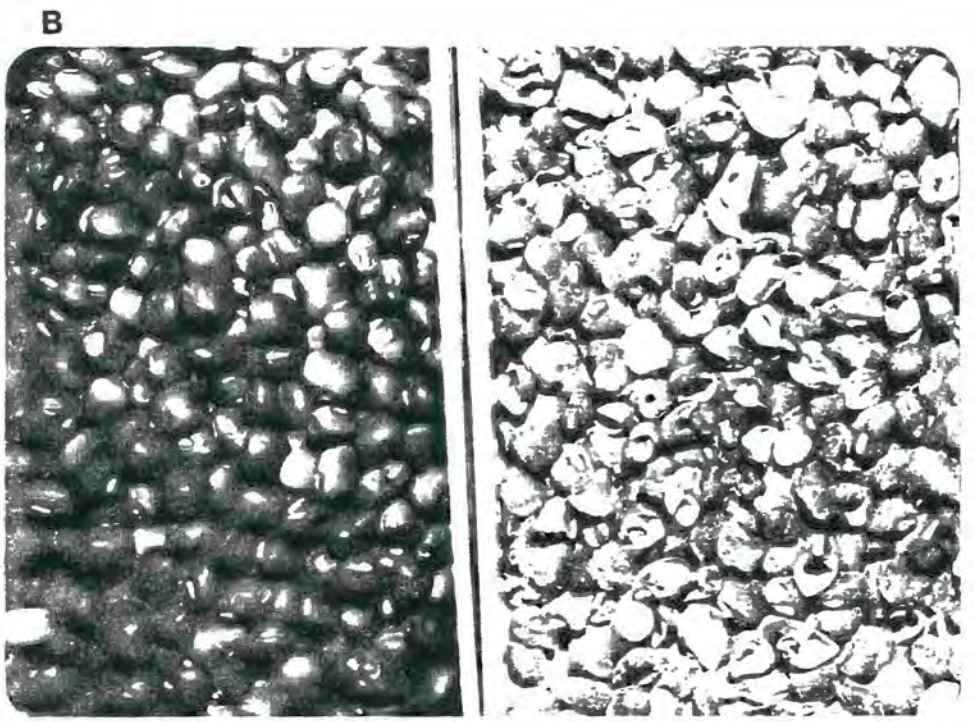
Plate 4. Symptoms of M. testulalis damage on dry pods and seeds of cowpea.

A. Damaged and Undamaged pods

B. Damaged and Undamaged seeds.

B


A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CHAPTER II

REVIEW OF LITERATURE

2.1 POPULATION ECOLOGY

The term "population" has been defined by several authors who, in general, refer to the term in relation to the environment (Andrewartha and Birch 1954; Nicholson, 1957; Milne 1957, 1962; Solomon, 1964, 1970). Milne's (1962) definition, which refers to the population as "the number of individuals ofa particular species existing in a particular place", is considered the most appropriate for purposes of the present study. Milne (1961) further stated that "Population changes with time", while Solomon (1949) stressed that population is an integral part of the ecosystem; hence the environment. According to Solomon (1970), the term "population dynamics or population ecology" is applied to the study of changes of the number of organisms in populations and of the factors influencing these changes. It also includes the study of the rates of loss and replacement of individuals and of any regulatory processes tending to keep the numbers stable or at least to prevent excessive change. This definition is similar to that of Begon and Mortimer (1981).

Although studies on population ecology of insect pests of crops provide the necessary basic information for formulating appropriate pest control strategies (Cock 1986), there is scanty literature on population dynamics of a number of these important

insect pests world wide, especially in the tropical region. Nevertheless, there are examples of well studied crop pests elsewhere, especially in the temperate region. Hughes (1962, 1963) studied population ecology of the cabbage aphid, Brevicoryne brassicae L. in Australia. Population ecology of the Colorado potato beetle, Leptinotarsa decemlineata (Say) was studied in Canada by Harcourt (1963, 1964) who determined sampling unit and used the unit to estimate population and mortality during the six age intervals of the beetle. Population ecology of the boll weevil, Anthomonus grandis Boheman, on cotton was investigated by Walker and Niles (1971), and Starling and Adkisson (1978). The important finding reported by Starling and Adkisson was that the percent damaged cotton squares follows a curvilinear model and may be used to estimate the number of adult weevils per hectare of cotton and, therefore, predict the extent of boll weevil damage on the crop.

Population studies on Lepidoptera pests of crops include those on the cabbage worm, Pieris rapae L. (Harcourt 1961b, 1962 and 1966), diamond back moth, Plutella maculipennis (Curt.) (Harcourt, 1960, 1961a), the European corn borer, Ostrinia nibilalis (Hubner) (Hudon, 1960; Hudon and Le Roux, 1961), H. zea (Hartstack Jr. et al., 1973), Anticarsia gemmatilis Hubner on soybean (Luna et al., 1982) and Epiphyas postvittana (Walker) on apples (Danthanarayana, 1976a, 1976b, 1980b, 1983). More recent studies on population ecology of lepidopteran crop pests have been reported by Thorvison et al (1985) on Plathypena scatra F (Noctuidae) on soybean, Plutella xylostella (L) (Yponomeutidae) on cabbage (Iga, 1985; Yameda and Yamaguchi, 1985), Earias vittella (Fab) on cotton (Bilapate 1985), Chilo

terrenella (Pyralidae) on sugar cane (Li, 1985) and Sesamia nonagrioides Lefebuvre (Noctuidae) (Al Salti and Gallichet, 1986). Studies are lacking on population ecology of lepidopteran pests of arable crops in the tropical world, especially in Africa. The only data available are scanty and represent only one life stage of the pests studied and therefore cannot be analysed to give a precise understanding of the pests' population ecology.

Literature on population ecology of M. testulalis is scanty and the reported studies have mainly concentrated on the colonization process and larval population build-up. Taylor (1967, 1978) studied the infestations and the larval dispersal of M. testulalis on cowpea in Nigeria. He reported that initial infestation of M. testulalis on cowpea arises from adults which emerge from alternative host plants at a time when the crop is in the most suitable state for oviposition; i.e flower-bud and flowering stage. He further, noted that in Nigeria, this first generation attacks the early crop during May and gives rise to a second generation that attacks a late cowpea crop planted between August and September. In his earlier studies, Taylor (1967) revealed that the incidence of M. testulalis was usually higher in the late than in the early crop and that a complete or partial second generation of pest may overlap with the first one during the months of July and August due to the extended flowering period of most cowpea varieties and short life cycle on the pest. He observed that during the off-season (January-May) low populations and breeding of M. testulalis occurred on volunteer cowpea plants and alternative hosts, particularly Phaseolus and Crotolaria species grown in gardens and farms. In subsequent studies Taylor (1978)

found that attack by larvae on flower buds leads to wide-spread infestation of flowers as they form and that usually more than one larva may be found in each flower at this stage. However, the larvae subsequently disperse to other open flowers, flower buds and peduncles, their movement being facilitated by the production of silken threads which they use as bridges between these parts. Further observations showed that peak damage coincides with peak flowering period suggesting that peak larval population density occurs during peak flowering period (Taylor 1978). This mode of infestation on cowpea crop leads to the extent of damage and yield loss similar to that reported by Booker (1963, 1965a), Taylor and Ezedinma (1964); Taylor (1967, 1978), Raheja (1976a), and Okeyo-Owuor and Ochieng' (1981). Further studies on M. testulalis population especially on larvae have been done by Jackai (1981) in Nigeria. He reported that larval infestation began in the terminal shoots in the early growth stage of the plant suggesting that adult females were attracted for oviposition about 21 days after planting. However, Wooley (1977) noted that moths were not attracted to the plant until flower buds were "large enough". Jackai (1981) compared larval infestation on different cowpea varieties during two seasons and found that infestation on terminal shoots were higher in the second than in the first season and that of the 5 varieties tested only Tvu 946, had lower numbers of larvae on the shoots. The rest were equally susceptible at the shoots. In the case of flower infestation Jackai (1981) found that, although the second season still had higher numbers of larvae than the first season, there was no significant difference in infestations of the flowers from different varieties. This finding suggests that

seasonal changes are important in determining population of M. testulalis larvae. He further, observed that larval density was lower in pods than in flower and flower buds, possibly due to larval mortality resulting from plant or some extraneous factors. He postulated that pod infestation rate may provide some insight into migration efficiency from, as well as crowding intensity at sites of primary infestation and larval survival. In Kenya, larval population on cowpea were studied by Okeyo-Owuor et al. (1983) and other workers (Higashi and Sato, unpublished data). Studies by Okeyo-Owuor et al (1983) revealed that at MPFS and neighbouring farms, M. testulalis larvae constitute 67.1 and 73.6% of the total borer population infesting pods and flowers respectively on cowpea crop. In this area M. testulalis occurred all the year round and their numbers on cowpea showed an increasing trend as the rainfall increased (Okeyo-Owuor et al., 1983). They further found that M. testulalis populations remained low even when the cowpea crop was maintained under irrigation during the dry period. Studies on the population density of the larvae under intercrop situation have revealed that the numbers of larvae on pure cowpea crop as compared to cowpea-maize intercrop are not significantly different. and that simultaneous planting of cowpea and maize as an intercrop tended to increase infestation by M. testulalis (Okeyo-Owuor et al. 1983: Ezueh and Tailor, 1984). Hagashi and Sato (Unpublished report) studied larval population of M. testulalis at Homa Bay Farmer's Training Center (FTC) in Western Kenya and suggested that the major

limitations in understanding its population ecology and making the life tables are the low numbers of eggs recovered during field samples and difficulty in sampling of pupae. Some preliminary investigations have been reported on the population of adult stage of M. testulalis by Taylor (1967) in Nigeria and Okeyo-owuor and Agwaro (1982) in Kenya. Taylor (1967) recorded M. testulalis adult population using a mercury vapour lamp light-trap while the studies by Okeyo-Owuor and Agwaro (1982) involved Pheromones traps using virgin females to monitor adult populations on cowpea crop.

Population studies reported so far on M. testulalis concentrates mainly on colonization process on the host plant and constitutes only part of the population ecology of this species. The present studies therefore contributes significantly to the knowledge on the pests population ecology by presenting a detailed population analysis as related to the different life stages and mortality factors.

2.2. FACTORS DETERMINING POPULATION SIZE

In recent literature on population ecology there has been a lot of debate on population regulatory mechanisms and which factors are responsible for the changes in population. Klomp (1964) reviewed opinions of various authors on the subject and recognized four mechanisms, namely:

1. Regulation through interaction with organisms of another kind other than food (i.e. natural enemies).

2. Regulation through interaction with organisms of the same kind, i.e. intraspecific (limited requisite) and mutual-interspecific or self regulation (no requisite in-short supply).

3. Regulation through environmental modifications, and,

4. Regulation through genetic feed-back mechanisms.

Solomon (1964) identified three categories of processes influencing population abundance, i.e. regulation by density dependent processes, density independent processes and modification of regulatory processes. He stated that the violent fluctuations in adundance are characteristic of many insect species as influenced by these factors and that the amplitude of fluctuation depends partly on the number of years or generations covered. However, the range of fluctuation is influenced by many different factors which include variability in climate, the reproductive capacity of the species, the degree of regulation and the number of different regulatory factors (Solomon 1964). There is a lot of literature dealing with the density dependent and density independent factors which regulate population abundance as is evident from the reviews by Klomp (1964, 1966) and Varley et al. 1973).

2.3 NATURAL ENEMIES IN POPULATION ECOLOGY

The role of natural enemies in causing mortality and population regulation in insects is well documented. According to Solomon (1970), the presence or absence of various natural enemies is an important factor in determining population abundance of an insect species. On the other hand, some authors such as Bess (1961) have argued that natural enemies such as parasitoids have negligible effect on population regulation. According to Campbell (1963), since any attack by parasitoids usually leads to death of the host and such deaths are not normally detected, estimation of parasitized hosts is usually lower than those attacked, resulting in an under-estimation of the effect of parasitism on population regulation. Driesche van (1982) and Cock (1986) also expressed similar views in assessing egg and larval parasitism in insect pests. Cock (1986) stated that rates of parasitism should always be related to host population density to be able to assess the regulatory role (density dependence) of the parasitoid. The same may be argued for other groups of natural enemies, such as predators and pathgenic microorganism. In the present work, the role of parasitoids and insect pathogens in population ecology of lepidoptera crop pest species has been reviewed.

The importance of studying parasitoids of crop pests not withstanding their significance in population regulation lies in formulating appropriate biological control strategies and hence integrated pest management (IPM). Hill et al., 1978) and Andreadis (1982) reported that, of the five introduced parasitoids of O. nubilalis only three established, but at too low a population density densities to control the pest effectively. It appears from the reports that there was inadequate basic knowledge of these exotic parasitoids, neither was there a thorough survey to determine presence and activity of indigenous parasitoids. Before any biological control methods are applied it is important to assess the presence and role of local natural enemies. Recently, Hokkanen and Pimentel (1984) compared the role of "new" and "old" associations in biological control, where old associations were considered as a species interaction between a pest and its natural enemies from indigenous range when the latter is re-established by introduction to areas where the pest has been introduced. New associations refer to the introduction of a natural enemy of a species closely related to the target species. The argument by these authors show that for biological control purposes, the new associations are more effective. However, the available evidence suggest that both associations are appropriate and that native pest association are more effective. However, the available evidence suggest that both associations are appropriate and that native pests are also suitable

for biological control (Carl, 1982; Cock, 1986). Murdoch et al. (1985) distinguished between two types of effective biological control agents, the first one being that which practices the strategy of lying-in-wait, such as polyphagous predators and the other which practises a search-and-destroy tactic. The second group are ideally monophagous and exhibit those characters of a suitable biological control agent predicted by workers such as Beddington et al. (1978); Hassell, 1978) and May and Hassell (1981). Cock (1986) recorgnised that the understanding of the dynamics of biological control agents is relevant to the selection of the most appropriate agent,, be they host-specific parasitoids or pholyphagous predators. He further concluded that population studies should be carried out to assess the importance of parasitoids and predators in their native areas and that such studies should consider what species occur, their biology, and their relative effciency in population regulation.

There are a number of reports from previous work on the role of parasitoids in population regulation and biological control of pests of crops. This has been clearly demonstrated in situations where synthetic pesticides have had adverse effects on natural enemies. For example, frequent application of insecticides to control Laspeyresia pomonella (L) on apple was observed to cause secondary outbreaks of the other pests as a result of destruction of parasitoids and predators in the orchards (Picket, 1959: Le Roux, 1959). Ferro et al. (1975) suggested that, since many organic

insecticides used in orchards destroy arthropod biota in the ecosystem, a more logical or less destructive approach was needed. He further reported high mortality in L. pomonella in orchards free of extensive insecticidal treatments. The mortalities were attributable to predators, an egg parasitoid, Trichogramma minutum Riley and larval parasitoid, Ascogaster quaridentata Wesmael which played a big role in regulating the numbers of this pest in the absence of chemical application. In Australia, predation by arthropods was identified as the key factor in determining submortalities of the different life stages from egg to pupa of Epiphyas postvattana, a pest of fruits and horticultural crops, alghough the role of parasitoids was found to be relatively unimportant (Danthanarayana, 1983). In Canada, several important parasitoids attacking the different life stages of diamond back moth, P. maculipennis and P. rapae were reported by Harcourt (1966). In these studies, larval parasitoids, such as Apanteles glomeratus and Phryxe vulgaris were responsible for 13% mortality of P. rapae, while Pteromalus puparum parasitized pupae causing 17% mortality on this species in Canada (Harcourt, 1966). In Brazil, efforts to control Diatraea saccharalis on sugarcane using mass reared larval parasitoids, Apanteles flavipes and Parantheresia clavipalpis was recently reported by Araujo et al. (1985) and Macedo et al. (1985). The results showed that by releasing 10,000 parasitoids per hectare satisfactory control of D. saccharalis was achieved on the crop. Parasitoids of Spodoptera frugiperda have

also been studied by Sales (1985) in Brazil and Rohlfs and Mack (1985) in Alabama on maize crop. Sales (1985) observed that leaving natural vegetation in close proximity to the crop provided a refuge to natural enemies and therefore reduced damage on the crop.

There is some evidence on parasitization of M. testulalis although the role of the parasitoids identified so far on either population regulation or their potential in biological control is not yet elucidated in the tropical world. In Nigeria, Taylor (1967) observed M. testulalis to be parasitized by a dipteran, (Musca domestica form callara Wlk), two Braconids (Braunsia sp. and Phanerotoma sp., and Ephydrid (Trypopsitopa sp.) Usua and Singh (1978) also recorded several predators and parasitoids of the pest in Nigeria. More recently, Don-Pedro (1983) reported M. testulalis parasitization in Nigeria to be upto 6.8% due to Phanerotoma sp. and Braunsia sp. in cowpea fields while in China Ke et al (1985) reported that M. testulalis larvae were parasitized by Cremastus sp. and Pseudoperichaeta insidiosa. In Fiji and Burma, Rao et al. (Unpublished reports) observed that the Braconid, Cedria paradoxa which was introduced in 170 localities to control Hapalia machaeralis Wlk (Lepidoptera: Pyralidae) and Hyblaea phera Cram. (Lepidoptera: Hybaeidae), was recovered from M. testulalis in two locations. Other parasitoids such as Apanteles etiellae Vier, Bracon cajani Mues, B. thurberiphagae (Muas), Phanerotoma bennetti Mues (all Braconidae), Perisierola sp. (Bethylidae) and Eiphosoma annulatum Cresson (Ichneumonidae) a parasitoid of a related pod

borer, Ancylostoma stecorea (Zell) were introduced to control M. testulalis in Fiji but their success was not recorded (Rao et al., Unpublished. report). In India, Vishakantaiah and Babu (1980), reported two Braconid parasitoids, Agathis sp. and Phanerotoma sp. on M. testulalis larvae on pigeon pea crop. Fellows and Amarasena (1977) reported 6-7% larval parasitism by Phanerotoma hundecasissella Cam and 12-30% pupal parasitism by Antrocephalus nr asubelongalus in Sri Lanka.

The role of pathogenic microorganisms in population regulation and control of various insects, especially those of lepidoptera species have received considerable attention by authors such as Jacques (1983). De Bach (1974) also reviewed in sufficient detail major pathogens related to crop pests, namely, bacteria, (Bacillus spp.), viruses (nuclear polyhedrosis), and microsporidia such as Nosema sp. Other reports in this field include those by Steinhous (1954), Hughes (1957) and David (1978). On lepidopteran pests Bacillus thuringiensis is well documented as an important pathogen of the larvae of Heliothis virescens, Cydia nigricana, C. pomonella (Burges, 1982). The relative susceptibility of six lepidopteran species attacking soybean to B. thuringiensis var kurstaki was studied by Ignoffo et al. (1977) and the results showed that susceptibility to this pathogen varied with insect species. Andreadis (1979) reported that the boring activity of H. zea and O. nubilalis reduced effectiveness of this bacteria in biological control, while Young et al. (1980) demonstrated a

synergistic control activity when B. thuringiensis was applied together with nuclear polyhedrosis virus (NPV) to control Trichoplusia ni on cabbage. Bacillus sp. was reported for the first time to infect and cause mortality in natural larval populations of M. testulalis in Kenya by Otieno et al. (1983).

Among crop pests in which virus diseases have been studied in relation to population regulation and biological control are Heliothis armigera (Hubner) (Coaker, 1958; Rogers et al., 1983), Trichplusia ni (Hall, 1957; Hofmaster, 1961; Ignoffo, 1964; Biever and Hostetter, 1971; Conerday, 1968; Jacques, 1969; Stacey, et al. (1981) reported on viruses causing mortality to Marastra brassicae L. while mortalities on P. rapae and P. brassicae caused by viruses were reported by David (1965), Hostetter et al. (1973), Payne et al (1981) and Crook (1981). Recent studies on Spodoptera exempta and S. littoralis revealed that these species suffer high mortalities due to NPV (Klein and Podoler, 1978; Odindo, 1981). The presence of NPV and granulosis virus (GV) in field population of M. testulalis was reported for the first time in Kenya by Otieno et al. (1983).

Microsporidia have gained much prominence in recent advances in crop pest pathology. According to De Bach (1973), this order contains many families of which Nosematidae contains the most important insect pathogens. The genus Nosema in this family is an important pathogen among the lepidopteran crop pests. Nosema

pyrausta is a known pathogen of the European corn borer, O. nubilalis and several workers have studied its effect on larval population and biological control potential on the pest (Zimmack and Brindley, 1957; Windels et al., 1976; Lewis and Lynch, 1976; 1978; Lublinkhof, et al., 1979; Lewis, 1978, 1982; Andreadis, 1984). N. pyrausta was also reported earlier on a pyralid moth Pyrausta nubilalis under the identity of Perezia pyrausta by Kramer (1959). In Kenya, Nosema sp. was observed to cause mortality in field populations of M. testulalis (Otieno et al., 1983) and Chilo partellus (M.O. Odindo, Pers Comm.), but detailed studies on the role of this protozoan in reducing natural populations of these two species are yet to be known.

2.4 CLIMATIC AND HOST PLANT FACTORS

The role of climatic and host plant factors in regulating insect populations has received much attention. Climate was singled out by Clerk et al. (1972) as a major factor in determining population abundance. Varley et al. (1973) reviewed in depth how climate and weather affect both insect development and population. According to these authors the annual, seasonal and diurnal changes in temperature, humidity, rainfall, etc. constitute climate and weather. These factors affect insects as individuals (independently of population density) and so acts as density independent or catastrophic factors. They further argued that if a population is

acted upon, both by density dependent factor and density independent variable factor such as weather, then the weather determines the changes, but the density dependent factor is primarily responsible for regulating the population about its average level of abundance Studies on the effect of climatic factors on life and population abundance of insect have been reported by authors such as Klomp (1962), Morris and Fulton (1970), and Baker and Miller (1974).

Host plants may affect the biology and population abundance in any ways. Under normal conditions, preferred host plants attract their pest species at a suitable time when oviposition, and development is favoured resulting into population build up. Phytophagous insects depend on specific oviposition or feeding stimuli and usually respond to similar stimuli in related plant species of variable nutritional value as illustrated by the study of Hsiao and Fraenkel (1968) on the host selection and growth response of Leptinotarsa decemlineata. The host plant phenology is an important factor in determining growth and development, survivorship, population build up and distribution of lepidopteran pest species as demonstrated by studies on Chilo partellus Swinhoe (Kalode and Pant, 1967), Lymantria dispar L. (Barbosa and Capinera 1977; Hough and Pimentel, 1978; Barbosa and Greenblatt, 1979), Diacrisia casignetum (Banerjee and Haque, 1985) and on H. zea, (Farrah and Brandley Jr. 1985). Studies by Taylor (1978),

Okeyo-Owuor and Ochieng' (1981) and Okeyo-Owuor et al. (1983), showed that infestation of cowpea by M. testulalis coincided with the flower initiation stage and the population of larvae builds up reaching its peak at maximum flowering stage, Further studies by Okeyo-Owuor and Okech (unpublished data) have revealed that flowers of cowpea are the most preferred plant stage by the pest and, therefore, support high larval populations of the species.

The role of alternative host plants in maintaining M. testulalis populations is well documented by Taylor (1967). Among other species, Crotolaria sp., C. juncea, Sphenostylis stenocarpus L. were reported as alternative host M. testulalis during the off-season in Nigeria (Taylor, 1967). Such host plants are important in perpetuating pest populations from one season to the other as well as determing the subsequent population size attacking the crop and the rate of population build up. Atsatt and O'Dowd (1976) argued that many plants that attract insects may also function as decoys, causing mortality or reducing fecundity due to the presence of toxins or absence, deficiency or imbalance of certain nutritional materials, thus reducing insect abundance. The same authors reviewed the role of host plants as insectary plants for predators and parasitoids of insect pests. They reported that, when nector production by neighbouring insectary plants or even host plants is synchronized with oviposition of these natural enemies, their efficiency may be significantly higher, causing reduced numbers in the pest. They illustrated this phenomenon by quoting some typical examples from several workers in their paper entitled "Plant Defence guilds" (Atsatt and O'Dowd 1976). More recent

investigations have revealed that wild or alternative host plants are important in enhancing the effect of natural enemies on insect pests (Salick, 1983; Altieri, 1983; and Cock, 1985). Cock (1985) observed that the cabbage budworm, Hellula phidilealis Wlk (Pyralidae) which attacks Brassica crops and Cleome spp. in the Carribean suffers almost no parasitism on the crop, while it is attacked by several parasitoids on Cleome spp. Thus, if these parasitoids were introduced to control other Hellule sp. on Brassica crops they might not succeed. However, if Cleome spp. are preferred hosts, then higher levels of parasitism in these plants might reduce the number of moths available to attack the crop. Sales (1985) found that the activity of natural enemies of S. frugiperda was enhanced by leaving natural vegetation in close proximity to maize crop. He showed that under such conditions defoliation on the crop was less than 2%, but attack by S. frugiperda increased significantly with the distance from natural vegetation. The importance of wild or alternative host plants in determining population abudnance of M. testulalis and their role on facilitating control by its natural enemies may therefore be expected.

2.5 POPULATION ESTIMATION, LIFE TABLE AND KEY FACTOR ANALYSIS

In studying population ecology of insects, many workers have described and used various techniqes in collecting and analysing data obtained from such investigations. To facilitate analysis from the data the number of individuals occurring in each life stage must be known or if cannot be directly sampled should be estimated.

Richard and Waloff (1954) and Dempster (1956) described methods of estimating population and mortality in each stage based on the calculation of the slope of the fall in the population after peak in numbers has been reached by extrapolating back to the origin of the generation. This method, which is based on logarithmic transformed data, is suitable for populations with rapid build-up and well defined peaks and is useful in estimating mortality and initial number of individuals. Southwood and Jepson (1962) used a graphical method for estimating the total population at the median age of the stage. This is a perfect method, if mortality occurs only at the end of the slope but under-estimates the population, if mortality is constant and high. Another method for estimating mortality and population in cases where there is prolonged build up in population and the peak is not well defined, was described by Richards et al. (1960). This method requires that the initial number of the population and the duration of each stage are known. Another technique described by Dempster (1961), is applicable to insects with any number of generations a year, provided they are distinct. The various methods of population and mortality estimations in insect ecology have been reviewed and compared by several authors (e.g. Southwood, 1978; Manly, 1974b; Birley, 1977). The method of Manly (1974b) is similar to that of Richard and Waloff (1954) and individuals, and the rate of entry into a stage do not have to be known. The method, however, assumes, that the time of entry into a stage follows a normal distribution. Whichever method is used, the purpose is to obtain reasonably accurate number of individuals in the different life stages of the species, to facilitate analysis and understanding of population change.

Data from regular population samples and estimates may be analysed and interpreted in a number of ways. According to Morris (1957), presentation of mortality data as high or low percentage contributes little to the understanding of population dynamics. Solomon (1964) described in detail four methods used to assess the role of any mortality factor in insect populations; namely, (a) direct inspection of the effects of mortality factor on population, (b) artificial reduction or exclusion of mortality factors, (c) life table analysis and (d) key factor analysis. The last two methods are common and often used together in analysing insect populations and are briefly reviewed below.

Life tables were originally used by students of human populations and were devised as a tool for demographical studies as well as for insurance purposes (Harcourt, 1969). According to Deevey (1947) life tables refer to "a concise summary of certain vital statistics of a population". Harcourt (1969), defined life tables as a condensed tabulation of the essential information pertaining to the schedule of mortality for a known cohort of individuals. Johnson (1978) stated that ecological life tables record a series of sequential measurements that reveal population changes throughout the life cycle of a species in its natural environment. Relationship of these measurements to mortality causes provide a budget of successive processes that operate in a given population (Harcourt, 1969). Solomon (1964) reported that for valid comparison of ranges of population fluctuations, one should consider the life stage most vulnerable to disturbing influences and life stage which is more closely regulated. For this purpose, Solomon (1964) pointed

out that census of the life stages and construction of life tables of the successive generations are necessary. The methods reviewed above on population and mortality estimates, especially that described by Birley (1977), enable complete reconstruction of life tables made from census data at irregular intervals and grouped by life-stage.

Deevey (1947) applied life tables for the first time in natural populations while Morris and Miller (1954) presented the first detailed example of a life table for natural populations in an insect species, the spruce budworm, Choristoneura fumiferana (Clam). Harcourt (1969) reviewed the development and use of life tables in natural insect population including sampling plans for developing such tables. Harcourt (1969) and Price (1975) presented a review on the insects and systems for which a number of ecological life tables have been developed. Other workers who have recently considered life table as being an important tool in analysing population census data in insects include, Varley and Gradwell (1971); Southwood and Reader (1976); Podoler and Rogers (1974), Hassell et al. (1976); Birley (1977); Chibuchi (1979) and Danthanarayana (1983). Among the crop pests of lepidopteran species, detailed life tables have been developed for P. rapae on cabbage in Canada and lesser corn stalk borer Elasmophalpus lignosellis in Texas (Johnson 1978). The uses of life tables in identifying density dependent mortality factors have been advocated by authors such as Southwood (1969, 1978) and Varley et al. 1973). Hassell, (1985) presented some problems of using life tables for this purpose. In general, life table construction, although useful

in anlysing data, requires collection of data of successive mortality factors within a generation from successive discrete generation, a situation which seldom arises in tropical Africa (Cock 1968). However, Cock (1986) stated that the key-factor analysis can then be used to identify a mortality factor most closely matching the total or generation mortality and hence can be considered the key mortality factor.

Key-factor is an important tool for analysing population census data. The term "Key factor" was introduced by Morris (1959) for mortality factors which "cause a variable mortality and are largely responsible for the observed changes in population" in successive generations. Using logarithmic equation Varley and Gradwell (1960) illustrated how key - factor may be used in population studies. This method is also discussed in detail by Clerk et al. (1972) and Varley et al. (1973). They observed that, the aim of key - factor analysis is to arrive at an equation that permits prediction of population density in the next or subsequent generation from data already available, and that this helps to provide a better understanding of population dynamics of the insect. According to Morris (1959) and Varley et al (1973) key -factor is that factor responsible for causing population change or one which is of most use in predicting population change. Since the last definition does not reveal the cause of change, Varley and Gradwell (1960) suggested the former as being the more accurate definition.

Among lepidopteran species, key -factor analysis has been used in studying population ecology of Epirrhoe brumata (L)

(Varley and Gradwell, 1960), Zeiraphera diniana (Auer, 1968), and Epypyas postvittana (Wlk) (Danthanarayana, 1983). In recent years key-factor anlysis has been used on a number of invertebrates to analyse population census data and also to compare life tables of the same species of insect in different places (Huffaker and Kennett, 1966; Varley and Gradwell, 1971; Clerk et al., 1972).

Several methods, including visual inspection may be used to determine key-factor in a population data. Hassell and Huffacker (1969) calculated key-factors using correlation coefficients between values of total generation mortality (K) and individual submortalities (k) and from graphical plots of these values they used the technique to determine key mortality factors from life table data. This technique was also used by Harcourt (1971) and, in this case, a high correlation indicated the key-factor. Development and comparison of key-factors from life-table data for different generations in insect species has been reported by Varley and Gradwell (1960; Luck (1971); Varley et al, (1973); Johnson (1978) and Danathanarayana (1983).

Although both life table and key-factor analysis are important in understanding population dynamics in insect species, they have mostly been used in studying forest and perennial crop pests in temperate regions. Insect pests of crops in the tropical regions, have received no attention in this respect.

CHAPTER III

MATERIALS AND METHODS

3.1 STUDIES ON NATURAL POPULATION OF MARUCA TESTULALIS

3.1. Locality

The studies were conducted at ICIPE's Mbita Point Field Station (MPFS) situated in a subsistence farming are in western Kenya. The Station is about 1240m above sea level and lies between 5°S and 5.5°S latitude and 3°E and 4°E longitude. At this Station, there is usually one rainy reason which occurs during the months of March to June, but sometimes short rains may occur between October and December but these are sporadic and unreliable. In some cases a long dry spell occurs which starts from July to September or even upto March the following year. Hence, there is only one cropping season a year in the area. The mean annual rainfall is about 900m, most of which falls in the long rainy season. The temperature and relative humidity are normally 24-30°C and 50-80%, respectively. The field Station has black cotton soil with poor drainage. Field studies were also conducted in a subsistence farm in Lambwe Valley (about 20 km east of the Field Station) where rainfall is more reliable and usually supports two cropping seasons in a year.

3.1.2 The Host plant

A large collection of local and exotic cowpea varieties exist at the Field Station and are being used for various research purposes. A local cowpea variety, ICV 6, popularly known as 'Ex-Luanda', was selected for the studies (Plate 5). This is an indeterminate and medium maturing (10-12 weeks) variety grown by many subsistence farmers for leaf vegetable and dry seed production in western Kenya. Studies at MPFS farm during 1980-1982 showed that the variety produces 35-45 flowers, 15-28 pods per plant and yields 300-600 kg/ha of grain if unprotected by chemical treatment, (Okeyo-Owuor, unpublished reports). The variety is susceptible to infestation by M. testulalis, especially on meristematic parts of the plant, flowers and developing pods.

3.1.3. Experimental layout

Experimental fields of size 2500m^2 were prepared at both MPFS and a subsistence farm in Lambwe Valley. The cowpea ICV 6, was planted at the spacing of 50 cm between and 30 cm within rows. The area was divided into 16 plots each of size 156.25m^2 to provide for a stratified layout for sampling purposes as described by Cochran (1963) and Snedecor and Cochran (1976). The experimental block was surrounded by a 2m wide guard row of the same cowpea variety.

Planting at both sites was synchronized with the onset of both rainy seasons. The studies were conducted during the short rainy seasons from 1983 to 1985 at MPFS and long rainy seasons from 1984 to 1985 at the subsistence farm. Crops were also planted durin the off-season at MPFS in 1984 and maintained under irrigation. No chemical insecticide was used to control pest throughout the study period.

3.1.4 Sampling Procedure

Samples were collected from each plot for the census of each life stage of M. testulalis using the technique described below.

Egg and Larvae:

Destructive sampling method was employed to sample for eggs and larvae of M. testulalis. Sampling was started two weeks after crop emergence since earlier studies at MPFS had shown that M. testulalis attacks the crop as early as between 21 to 30 days after plant emergence (DAPE) (Okeyo-Owuor and Ochieng' unpublished report). Random samples of 10 plants per plot were taken every three days so as to allow for recruitment of the different development stages from egg to fifth instar larva. The plants were uprooted as shown in Plate 5 and the different parts of the plant carefully searched for the presence of egg and larvae of M. testulalis. The larvae found were counted and sorted into different instars; both the eggs and larvae were then taken to the laboratory

where they were reared to recover adult moths or any parasitoids. Field collected larval cadavers were taken to Insect Pathology Unit at the Station to isolate and identify pathogenic microorganisms.

Due to the difficulty involved in examining eggs in field samples, several methods were tried. The methods by Jackai (1981) using oil soluble dye to determine oviposition sites of M. testulalis, which depends on artificial infestation of the plants by moths fed on dyed diet, was found unsuitable for detecting the oviposition sites or even locating eggs. Moreover, the technique is not applicable in natural populations. A direct egg dying method was also attempted without success. Laboratory tests with various dyes on M. testulalis eggs laid on clean cowpea leaves showed methylene blue to give the best dying results, as the eggs could clearly be seen and easily counted. However, in the field situation this method was found unsuitable for a number of resons. First, foreign objects on the plant surface were also stained, making it difficult to locate and count the eggs. Secondly, soil particles on the plant also made it difficult to detect the eggs, especially after a rainy day. Thirdly, the sample size was too large for applying the dye effectively. Lastly, the use of this dye to locate eggs for counting consumed just about the same time as direct searching and counting method. The direct inspection and counting method was therefore adopted for estimation of egg numbers.

Prepupae and Pupae

Although, Vishakantaiah and Babu (1980) reported that M. testulalis pupated on the pigeon pea plant in India, studies in Nigeria and at MPFS, Kenya, have shown that, in cowpea crop pupation occurs in the soil (Taylor, 1967; Okeyo-Owuor and Ochieng', 1981). Thus, in these studies a suitable techniqe to collect M. testulalis pupae from the soil was developed. Because of the type of cocoon surrounding M. testulalis pupae, direct sampling by soil collection and sieving was not appropriate, due to difficulties in recovering pupae as well as causing high mortalities. The use of corrugated paper sheets as pupal traps were found suitable for sampling of M. testulalis pupae from cowpea fields and was adopted throught the study periods. The corrugated paper sheets manufactured from local paper mills in Kenya for packing purposes were bought in rolls from wholesale shops in Nairobi, Kenya, and used for the study. The paper sheets were placed on top of the soil under the crop canopy; the mature larvae then descended from the plant, and crawled under the sheets where the prepupae prepared cocoons in the paper grooves for pupation (Plate 6). The pupae were collected by carefully lifting the sheets from the soil. The pupae were usually found lying attached along the grooves on the under surface of sheets. During the studies, 25 of such paper traps each measuring 30 cm x 30 cm were placed in randomly selected sites in each plot. The traps were checked every three days and the pupae and prepupae found were collected and taken to the laboratory for recovery of moths and parasitoids. Dead pupae collected from the field were diagnosed for insect pathogens.

Adults

To sample adults emerging from the field for the purposes of population estimation in experimental plots, emergence traps designed to cover an area (1.5 m^2) with 10 cowpea plants were used. To achieve this, steel frames measuring 100 cm wide, 150 cm long and 100 cm high, covered by a fine wire mesh on all sides except the bottom surface were used to recover adults emerging from pupation (Plate 7). In each plot out of a total of 16, four traps were placed from the onset of flowering to pod maturity and after harvest. The traps were regularly moved around in each plot and the moth emergence checked every morning. The number of M. testulalis moths emerging from the traps were collected and their number recorded.

To provide information on crop colonisation and the adult population fluctuation throughout the cropping and off season, pheromone traps using virgin females as baits were placed in each study area and the number of male moths trapped was recorded every morning (Plate 8). The pheromone trapping technique for M. testulalis was described for the first time by Okeyo-Owuor and Agwaro (1983).

3.1.5 Temporal distribution and Population analysis

Data from field samples were used to construct temporal distribution graphs for the different life stages of M. testulalis. The life stages whose temporal distribution graphs were consturcted were eggs, first and second instar larvae (Larvae I-II), 3rd instar larvae (larvae III), 4th instar larvae (Larvae IV), 5th instar larvae (Larvae V), pupae and adults from emergence traps. To construct the graphs the data for all the life stages were tranformed into density per hectare by multiplying the number of insect per sample by a constant, i.e. an inverse proportion of the hectare. In the case of eggs and larvae, the mean number of individuals per plant sampled was multipled by the number of plants per hectare, while for pupae and adults the density per hectare (N_A) was obtained by dividing the number of individuals per unit area sampled (N_t) by the area sampled (a) and multiplying by the area of the hectare (A) as follows:-

$$N_A = N_t \cdot A/a$$

Data on the first and 2nd instar larvae were pooled and presented graphically as one growth stage, since it ws not easy to separate them. The curves for the 3rd, 4th and 5th larval instars as well as pupae and adults were constructed separately. The curves for pupae and adults were constructed from the counts taken from pupal and adult emergence traps respectively.

Since the field samples failed to yield the correct values of egg population, the number of individuals in this stage was estimated to facilitate the construction of life tables and key-factor analysis. The various methods of estimating population from field samples have been reviewed in Chapter II. To estimate the number of eggs of M. testulalis occuring in each generation the method by Richard and Waloff (1954) and Manly (1974a) was preferred over the others. The method of these authors is based on the calculation of the slope of the fall in the population after peak in numbers has been reached by extrapolating back to the origin of the generation. This method may be used to estimate mortality and initial number of individuals in a life stage if the population has a well defined peak and a rapid-build up. Further, the method also assumes that the mortality rate is steady throughout the generation. Population trends of M. testulalis satisfied these requirements, hence, the choice to use this method to estimate egg numbers. To do this the individuals per sample per hectare were transformed into logarithm values and the logarithm values obtained after the peak population were plotted against time (days after plant emergence)using a "Wang Professional Computer" which gave lines of best fit. These lines were then extrapolated back to the origin of the generation. The respective values of logarithm at this point were read off from the Y axis and transformed back to their antilogs to give the number of M. testulalis eggs in each generation.

Standardised numbers were obtained by dividing the population of each life stage per heactare by the developmental time of the appropriate life stage.

$$\text{Standardized No./ha} = {}^{N_T}/_{t}$$

where t = mean developmental time obtained at 29°C under laboratory conditions at MPFS, and N_T = the number of individuals in each generation. The method described by Southwood and Jepson (1962) on plotting the area under the curve to give life-stage days per hectare and then dividing by the developmental gime gave more or less similar results as the method described above when one small square in the graph paper was considered to represent a unit of population per hectare.

The standardized values obtained were used to construct partial ecological age-specific life tables for M. testulalis for the various generations at both sites. The life tables were constructed using the format of Morris and Miller (1954). According to these authors the age interval, e.g. egg, larval, etc. are represented by x in the life-table, lx represents number of individuals alive at stage x, dxF - factors responsible for mortality, dx - number of individuals dying during x, 100qx - apparent mortality and 100rx - real mortality. The factors responsible for mortality were grouped into disappearance, parasitism and disease, where disappearance represented any loss in numbers caused by factors which were not directly examinable such as predation, dispersal, etc.

The values from life tables were used to construct partial mortality budgets and used for key-factor analysis as described by Varley and Gradwell (1963) and Southwood (1978). The method involves transforming the values in the lx column into logarithms and then substracting the log values to give k-values as follows $\log l_{xo} - \log l_{x1} = k_o$, $\log l_{x1} - \log l_{x2} = k_1$, etc, etc. The various k- values obtained signified the various mortality factors occurring at the different life stage the sum of which represented the total generation mortality (K).

$$K = k_o + k_1 \text{ ——— } k_i$$

The k - values including the generation mortality were plotted against generation, and by inspection the various graphs were compared with that of K. The k - value graph that appeared more similar to K than the others was considered as the key-mortality factor. Correlation analysis was also conducted between the k - values which appeared similar to K against K to confirm the key mortality factor as described by Hassell and Huffacker (1969) and Harcourt (1971). The k - value which showed high correlation to K was the key factor. The various mortality factors which showed positive relations to K were then analysed for density depenced by plotting k - values against log of population density (lx) entering the age interval on which it acts (Varley and Gradwell 1963). A slope of unity (1.0) indicates that the density-related mechanisms are operating and completely compensating for changes in host density, while a slope of less than 1.0 suggests that the factor undercompensates for the change. A negative slope indicate inverse density dependence.

3.2 SURVIVAL AND DEVELOPMENT OF M. TESTULALIS ON HOST PLANTS

Survival and development were investigated on the main host plant, cowpea, and wild host plants under natural and artificial infestation.

3.2.1. Survival and Development on Cowpea

During the field studies, data was collected on the various aspects of plant phenology, such as, growth pattern, production of vegetative and reproductive parts of the plant. The number of leaves, flower buds, flowers, and pods were counted during each sampling date. The relationships between these units and the natural population density of M. testulalis was analysed using correlation/regression programmes in the "Wang Professional" computer. The information obtained was used to determine the effect of plant phenology on natural population density of the pest.

Further studies were conducted in screenhouses, open field and on potted plants to determine the effect of cowpea plant phenology on the survival, development and population changes of the known cohort of M. testulalis. These studies were conducted at MPFS and the cowpea plants (ICV6 variety) were artificailly infested with eggs of M. testulalis. Infestation on the potted plants performed poorly due to poor development of the plants resulting into mass dispersal of larvae after egg hatch.

In screen house experiments (screen house size 84 m^2, divided into 4 plots, 18 m^2 each) the ICV6 variety was planted and managed from the beginning of the long rainy season 1984 according to the recommended agronomic practices described above. The plants were irrigated regularly. The experiment was repeated four times. At 25 DAPE the plants were artificially infested with eggs at black head stage at the rate of 20 eggs per plant. A cowpea leaf containing eggs was pinned onto each plant in the evening to avoid dessication of the eggs. A total of 60 plants were infested per plot an alternate row of cowpea was left unifested.

In open field experiments artificial infestation was also done following a similar procedure but this case some plots were left open in the field (uncovered) and the others covered by a nylon mosquito netting just before artificial infestation. While the crop in the screenhouse was irrigated, the field crops were rainfed.

The plants were checked every 12 hours for egg hatch until no more viable eggs were detected. The number of unhatched eggs were recorded. Sampling for larvae started 3 days after infestation and samples were collected every 3 days to take care of recruitments into the different development stages. During each sampling day 10 plants were sampled from each plot, five each from the infested and unifested plants. The unifested plants were sampled to recover those larvae which might have dispersed from the infested ones. The plants were carefully searched for the presence of larvae and those recovered were recorded. However, the larvae were returned into the crop to restore original number of larvae before sampling. Any larvae found dead were examined for the presence of parasitoids and pathogens as described earlier.

Pupae were sampled by using the cardboard pupal traps as described before. In each plot 26 traps each measuring 30 cm x 30 cm were placed under the crop canopy. The traps were checked every 3 days and the pupae were then placed back and no pupae were removed from the traps. The number of adults emerging in the screen house and in the plots covered by the nylon netting was estimated by searching the plants and taking adult counts until no more emergence was observed. In all the treatments, especially in the open plots the number of empty pupal cases on pupal traps was used to estimate the number of adults emerging.

Further studies were conducted in the laboratory to determine the suitability of different cowpea parts for survival and development of M. testulalis. Cowpea plants (ICV6 variety) at 45-55 DAPE were used for the study. At this stage, the different parts of the plant (i.e. stems, leaves, terminal buds. flower buds, flowers, tender and mature green pods) were used for rearing the larvae First instar larvae were planced singly per glass vial containing the different parts of the plant and left to feed ad lib. The tops of the vials were covered with a piece of cotton wool and the diet was changed every 2-3 days during which time the number of larvae surviving, and their weights were recorded. At pupation stage the number of pupae, larval period, pupation period and pupal weights were recorded. The number of adults emerging was recorded and the survival and life cycle of the insects were computed.

3.2.2. The role of Wild Host Plants on Population of M. testulalis

Field studies were conducted to search for possible wild host plant of M. testulalis and determine their role in sustaining the pest and its natural enemies. Studies were conducted at the following sites:

1. MPFS area
2. Rusinga Island (7 km from MPFS)
3. Lambwe Valley (site 1) near the farmer's experimental field.
4. Lambwe Valley (site 2) about 15 km from site 1. (Cowpea is not grown in this area)
5. Rangwe area; a cowpea growing area 60 km from MPFS and 45 km from Lambwe site 1).

These sites were selected on the basis of the variation of weather condition as well as farming systems. At MPFS and Rusinga there is only one reliable rainy season, supporting one cropping season (semi-arid), while at the other 3 sites both the long and short rains occur, and support 2 crops. Areas 1, 2, 3 and 5 were also selected as sites because of the agroecosystem which normally includes cowpea crop cultivated as intercrop with other cereals and wild hosts may provide an important source of M. testulalis on cowpea crop. There is limited agricultural activity in area 4 which lies partly in the Lambwe game reserve. Since it is a stable

ecosystem, (except for occasional fires) this site is a potential source of crop pests such as M. testulalis and their natural enemies.

Weakly search of wild host plants were conducted during the short rains from November 1984 through the 1984/85 off season to the end of long rains, July, 1985. Several leguminous plants were collected and searched for eggs and larvae of M. testulalis. Any larvae found were brought back to the laboratory and reared on cowpea flowers and green pods until pupation. The dead larvae and pupae found on the plants and those dying during rearing were examined for parasitoids and pathogens. Those suspected of containing parasitoids were kept until the parasitoids emerged. The parasitoids were then preserved and identified as described later.

3.3 EFFECT OF SOME CLIMATIC FACTORS ON M. TESTULALIS

3.3.1 Field Recording of Climatic data

During the field studies, changes in temperature, relative humidity (R.H.) and rainfall were recorded using thermohygrograph (model Wilh. Lambrecht, type 253) placed in a Stevenson's screen (Plate 9). Rainfall was recorded with the standard rain gauge distributed in the study area. Facilities were not available for recorded other climatic factors. The data on population estimates from field samples were analysed in relation to changes in temperature, rainfall, and R.H.

3.3.2 Optimum Temperature for Survival and Development of *M. testulalis*

The objective of this study was to determine the optimum temperature for survival and development of this pest. Under natural conditions at MPFS and Lambwe temperatures fluctuate between 15°C and 35°C. Thus, the temperature used in these investigations were selected within this range.

The experiment was conducted in growth chambers (Model B & T cooled incubators) with constant temperature set at 18°C, 21°C, 23°C, 26°C, 29°C and 35°C.

A known number of freshly laid eggs of *M. testulalis* were place in a small perforated petridish and each of which was placed in separate growth chambers set at different constant temperatures for 18 hours. A thermohygrograph was placed in the chambers to monitor temperature and R.H. conditions, as power supply in the laboratory is switched on only for 18 hours in a day.

The eggs were checked for hatching daily and the number of first instar larvae recorded. The larvae were then placed singly in glass vials with tops covered with a fine cloth to prevent escape. They were fed on fresh clean cowpea flowers and left under similar temperature conditions as the eggs. Their food was changed every two days until they pupated. Any dead larvae were recorded and removed from the chamber every day. The pupae were weighed and left in the chamber to develop to adults. Records were taken on egg incubation pe : od, % eclosion, survival in the larval and pupal stages, pupal weight, % pupation and adult emergence, and life cycle duration.

3.4 STUDIES ON NATURAL ENEMIES OF M. TESTULALIS

During the field population studies described above, observations were conducted on the occurrence of natural enemies of M. testulalis with special emphasis on parasitoids and pathogens and their effect on the pest population. Incidence of and mortality due to predators were difficult to quantify; hence, their contribution to generation mortality was pooled under disappearance in life tables. The nocturnal habit and hiding behaviour of M. testulalis made it difficult to directly observe predation in the field. Predators as a group are also general feeders, although some such as Rhodolia cardinalis are specific to Iceria purchasi.

3.4.1. Parasitoids: Field Studies and Identification

Field collected larvae and pupae were placed singly in sterilised plastic vials and their tips covered with a fine nylon mesh to provide ventilation but not to allow escape of any larva or parasitoid. Larvae were fed on fresh ICV6 cowpea flowers by the rearing methods developed by Ochieng' et al. (1981). Any parasitoid emerging from the vials was collected for rearing and identification. The parasitoids were sent to the International Insitute of Entomology, Britain, for identification and confirmation.

During the sampling period the proportion of larvae and pupae of M. testulalis parasitized by the various parasitoids and the number of parasitoids recovered per sample were recorded.

3.4.2. Biology of Tetrastichus sesamiae Risbec (Eulophidae), a pupal endoparasitoid.

Laboratory Culture

During the field studies of M. testulalis at both sites, several larval and pupal parasitoids were recovered and identified. Due to sporadic nature of their occurrence, all except Tetrastichus sesamia proved difficult to culture in the laboratory. T. sesamiae is a gregarious pupal endoparasitoid and was more frequently collected from the MPFS study plots.

A laboratory colony of this parasitoid was estabished from parasitized pupae obtained during field samples. A laboratory culture of M. testulalis reared on cowpea flowers was used as a source of host pupae for maintaining the parasitoid colony. The progeny and sex ratio were recorded on parasitoid emergence. Adult parasitoids were kept in transparent perspex cages (measuring 25 cm width x 25cm length x 22 cm high) where they were fed on 20% honey syrup soaked in cotton wool. Zero day old pupae were introduced into the cage and exposed for 48 hours for parasitoid oviposition. This was repeated until all parasitoids died. The pupae were then removed and placed singly in small plastic vials with tops securely covered with fine nylon mesh. A large laboratory colony of the parasitoid was established by this method to provide material for studies on its biology and behaviour. These studies were conducted under laboratory room conditions, with a range of temperature of 22-28°C and relative humidity of 55-70%. The rooms had 12 hours light and 12 hours darkness throughout the study period.

Behaviour of T. sesamiae

Plastic vials (30 ml in volume) with secure tops were used to hold one pair freshly emerged female and male parasitoids for mating behaviour and longevity studies. A completely randomized design (CRD) was used to evaluate the effect of absence or presence of host pupae on longevity of the parasitoid. The effect of commercial honey and sucrose solutions in water (5%, 10%, 15%, 20%, w/v) as food source on longevity and survival of the parasitoid was also studied. The experiment was laid out in a completely randomised block design (RBD) replicate 30 times. Mating and oviposition behaviour of the parasitoid as well as its life cycle were observed. Studies were also conducted to determine time of parasitoid emergence from 30 parasitized pupae.

Reproduction and Development on M. testulalis

Potential fecundity and progeny production were studied under the laboratory condition specified above. Potential fecundity was estimated by teasing gravid young females to release eggs on a drop of water on a slide and counting the eggs under a Wilde M5 dissecting microscope. Progeny production of females was estimated by counting the number of parasitoids emerging from all the pupae parasitized by one females. The influence of food quality on reproduction and development was studied using sucrose and honey as

described above. One pair of freshly emerged male and female parasitoids were placed in each vial and supplied with a food source. One host pupa was placed in each vial and the parasitoids were allowed to oviposit over a 48-hour period after which the pupa was removed and kept in separate vial. The parasitoid was then offered another fresh pupa. This was continued until the female parasitoid died. The pupae were kept separately until the adult parasitoids emerged. The experiments were laid in an RBD with 30 replications.

The suitability of the different stages of M. testulalis pupal development for parasitization was determined using 20 pupae of each age group (From prepupae to days 8 old pupae). The prepupae and pupae were exposed for 48 hours for parasitoid oviposition in the vial after which they were kept separately for parasitoid development and emergence. The effect of host age on period of development and rate of parasitization was determined by comparing the duration of development to adult parasitoid after exposure, the progeny production and the percent pupae parasitized in each age group.

The influence of pupal size on parasite development and host selection was studied. Pupae of weights ranging from 2.5 mg to 5.1 mg. selected from a laboratory colony were weighed using a 'Sartorius' electronic analytical balance 'type, 1972 MP8'. Ten pupal sizes were were selected and the pupae were placed singly in

labelled 30 ml. vials. A pair of freshly emerged male and female parasitoids were introduced into each vial and left for 48 hours. After exposure the pupae were kept separately for parasitoid development and emergence. The number of parasitized pupae, the number of parasitoids emerging per pupae and the duration parasitoid development in each pupae were recorded.

Host preference of T. sesamiae

Further studies were conducted to determine the alternative hosts and their effect on development of the T. sesamiae especially among the lepidoptera pests of crops in western Kenya. The pests tested were Busseola fusca, Chilo partellus, Eldana saccharina, and Spodoptera exempta all of which attack cereal crop grown as intercrops with cowpea. Freshly emerged parasitoids were exposed to one day old pupae of these pests in the same manner as described above and the rate of parasitism, progeny production and the development of the parasitoid in each host pupae recorded.

3.4.3 Incidence, Pathogenicity and Virulence of Microorganisms on M. testulalis

Field Collection, Isolation, and Identification

During the field studies, larval and pupal cadavers as well as feable looking larvae were collected to isolate and identify insect pathogens present. The different groups of pathogens were determined by external symptoms and examination under light microscopy. The material was macerated in a drop of distilled water placed on a microscope slide. The suspension obtained was covered

with a coverslip, and examined under a compound microscope (Leitz Dialux 20EB).

With the assistance of insect pathologists at the ICIPE' Insect Pathology Unit at MPFS, and various reference books on insect pathology including that by Poiner and Thomas (1984), the microorganisms were tentatively identified.

Culturing and Purification of the Microorganisms

The various microorganism isolated and identified namely bacteria, protozoa and fungi (except viruses which occurred in negligible proportions) were cultured using the following techniques.

To culture the bacteria (Bacillus sp. and Coccus sp.) recovered from cadavers of M. testulalis, a standard nutrient agar (NA) medium was used. The medium is a powder with a composition of 'Lab m' peptone 5.0 g, 'Lab m' beef extract 3.0 g, sodium chloride 8.0g and 'Lab m' agar 21.0g at pH 7.3. To formulate the medium, 28g of the powder was added to 1 litre of distilled water and boiled while frequently being stirred. The mixture was then sterilized in an autoclave for 15 minutes at 121°C; it was then dispensed into clean sterilized glass petri-dishes and allowed to cool to room temperature under sterile conditions. This medium was also used to purify, isolate and culture the various types of bacteria obtained from dead M. testulalis. Dead larvae containing bacteria were

examined under the microscope and kept in separate vials. To innoculate the medium, pieces of the dead insect were macerated in distilled water on a sterilized glass slide and, using a sterile wire loop, the innoculum was streaked into the culture medium. This was done for each group of bacteria. The petridishes with the innoculum were placed in a growth chamber maintained at 30°C for 48 hours. Clones of bacterial cultures formed were harvested, purified further by repeating the same procedure as described above. The resultant cultures were used in bioassays to determine pathogenicity as described by Poiner and Thomas (1984).

Fungi recovered from field samples were cultured in Sabouraud Dextrose Agar (SDA), a nutrient medium formulated for culturing saprophytic and pathogenic dermatophytes. The powder medium contains 40 g dextrose, 10.0 g 'Lab m' balanced peptone No. 1 and 12.0g 'Lab m' agar No. 2 at pH 5.6. To prepare the medium 62g of the powder was mixed with 1 litre of distilled water and boiled with frequent stirring until the powder dissolved. The solution was sterilized in the autoclave for 15 minutes at 121°C and then dispensed in clean sterilized glass petridishes which were then covered and left to cool to room temperature under sterile conditions. The medium in each petridish was innoculated with fungal suspension from macerated cadavers as described for bacteria. The culture was maintained in a growth chamber at 30°C for 48 hours after which it was harvested, purified further and used in pathogenicity tests.

Live M. testulalis larvae were used to culture Nosema as there is no known artificial medium for the protozoan. Cadavers observed under the microscope to contain a high concentration of Nosema spores were macerated and used as source of innoculum. Three methods were tried for innoculating the protozoa into live 3rd instar M. testulalis larvae. In the first technique, the larvae were introduced into a watch glass containing a suspension of the innoculum in distilled water and left for about 1-2 minutes to get contaminated by the suspension. This method was found to be time consuming and unsuitable as it resulted in larval mortality through drowning. The 2nd method involved dipping cowpea flowers into the the prepared innoculum solution and feeding larvae on them. However, since the flowers collected from the field also contained contaminations of other microorganisms this method was also not preferred for culturing. The last method using a nutrient agar gel (NAG) as a carrier for the innoculum was developed. Earlier studies at MPFS by Okech (unpublished data) showed that M. testulalis larvae fed well on the nutrient agar gel. The NAG was prepared by mixing the following ingradients; 4.0 g agar, 1.0 g cellulose, 3.4 g sucrose and 91.6 ml distilled water. The mixture was boiled with frequent strirring and then dispensed into sterilized petridishes. The NAG was left to set at room temperature. Using a cork borer (diameter 0.5 mm) equal quantities of the NAG were dipped into a suspension of Nosema in distilled water and then transferred into a

dry sterile vial (75 mm long; 25 mm in diameter). Healthy 3rd instar M. testulalis larvae were offered NAG contaminated with Nosema and left to feed for 24 hours. This method minimized larval mortality due to handling and ensured free ingestion of the innoculum by the larvae. The larvae were then fed on clean flowers of the ICV6 cowpea variety until mortality occurred. A clean sterile vial was used each time to minimise contamination in the process of changing diet and transfer of larvae. The dead larvae were then used for culturing, isolation and pathogenicity studies.

Bioassay for Pathogenicity

Bioassays were conducted to determine pathogenicity and virulence of the microorganisms isolated from dead M. testulalis using the same innoculation procedure as described above. During these studies only four groups of microorganisms (protozoan, Nosema sp.; bacteria, Bacillus sp., Coccus sp.; and fungi, unidentified) were isolated and tested. Live healthy larvae were innoculated and placed singly on clean sterilized vials and fed on fresh clean flowers of the ICV6. The five treatments tested against 3rd instar larvae were, (1) Nosema, (2) Bacillus, (3) Coccus, (4) Fungus and (5) Control (with distilled water).

Treated larvae were maintained by the normal rearing methods. The following observations were made: (a) mortality and survival, (b) development period or time taken to die, (c) weight gained by larvae, (d) pupal weight, (e) fecundity of emerging females and (f) presence of pathogenic microorganisms in dead larvae from treated and live larvae from untreated (control) groups. The experiment was set in an RBD replicated 30 times (one larva constituting one replication per treatment). The presence of microorganisms on the cadavers from treated and control tests were examined on a glass slide under the compound 'Lietz' microscope at a magnification of 40 x and rated as follows: 0=absent, +=rare, ++=moderately abundant, and +++=abundant.

From the results obtained from the pathological tests above, further bioassays were conducted to determined the effect of Nosema sp. on the development and survival of M. testulalis larvae. The third innoculation method as described above for this protozoan was used in these tests. Larvae from 1st to 5th instar stage were used in experiments laid in a CRD and replicated 20 times. Healthy larvae reared on natural diet of cowpea flowers as described by Ochieng' et al. (1981) were used for the study. Before the experiment the larvae were kept singly in clean vials and starved for 12 hours.

Plate 5. The ICV6 cowpea plant showing the various parts of the cowpea plant on which M. testulalis may be found during sampling.

Plate 6. A trap designed for field sampling of M. testulalis pupae, showing pupae and prepupae trapped.

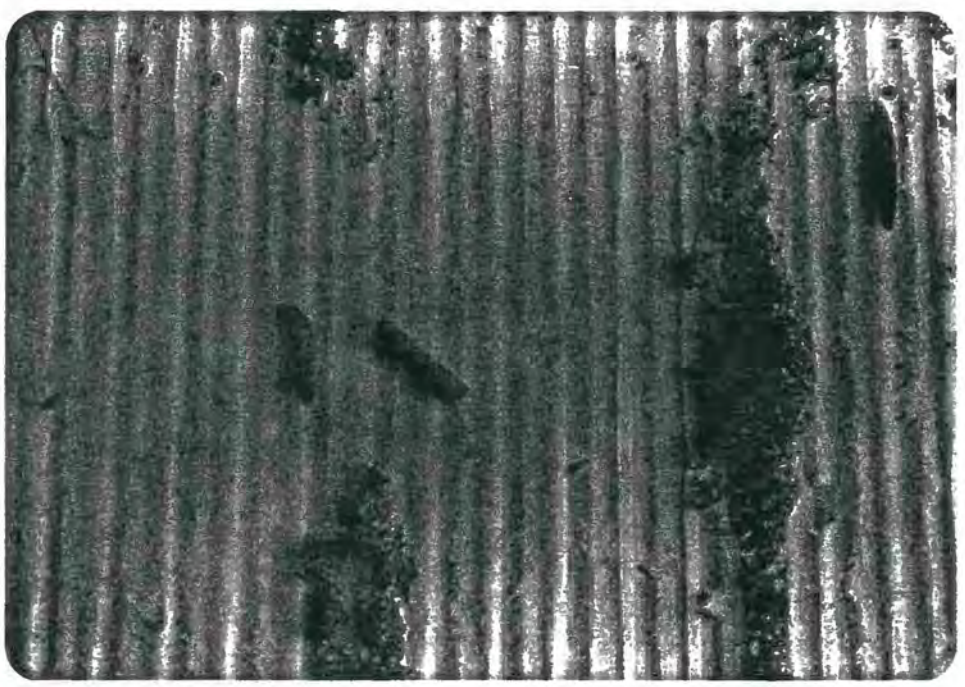


Plate 7. An emergence trap designed for sampling M. testulalis moths emerging from pupae in cowpea crop.

Plate 8. A pheromone trap used for monitoring male M. testulalis in cowpea crop.

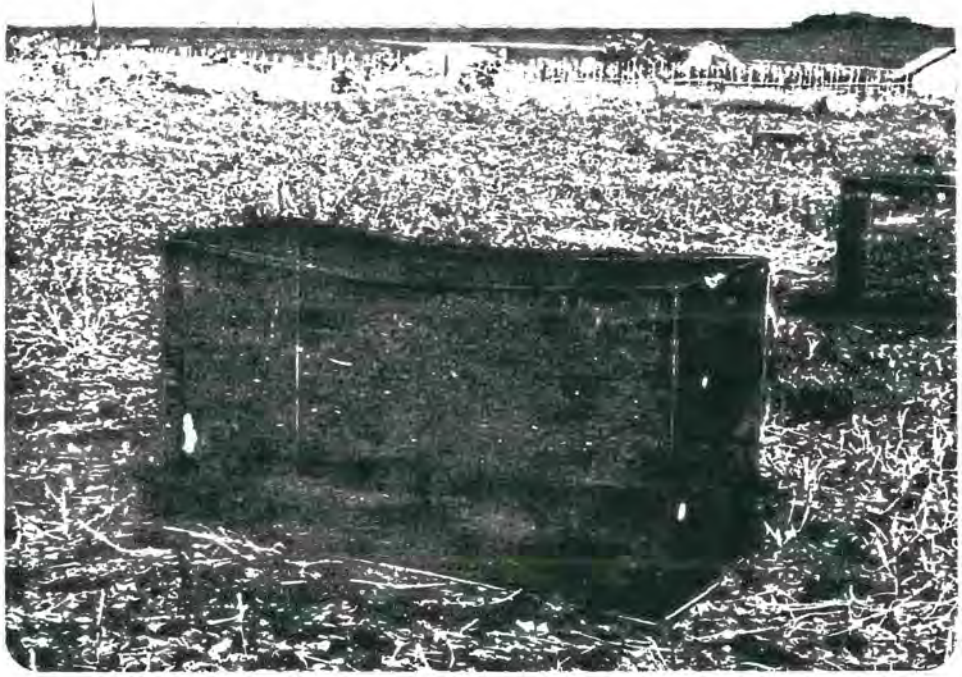


Plate 9.A thermohygrograph placed inside Stevenson's screen for recording ambient temperature and relative humidity on cowpea crop.

CHAPTER IV

R E S U L T S

4.1. NATURAL POPULATIONS OF M. TESTULALIS ON COWPEA CROP

4.1.1. Colonization and Temporal distribution

Mbita Point Field Station

1983: Studies at MPFS during the short rainy period showed that M. testulalis moths first appeared on the pheromone trap 15 days after plant emergence (DAPE) (Figure 1-2). Peak population density occurred 36 DAPE when the highest number of male moths were collected in the pheromone trap (Figure 1A). The moth population declined after this peak reaching zero level at 60 DAPE, but rose to a second peak 12 days later (Figure 1A).

Temporal distribution of the M. testulalis life stages is presented in Figure 3 for 1983 short rainy season. Eggs were first examined on the crop about 25 DAPE. This occurred at the time the first flower buds were formed on the cowpea plants. The eggs were s arcely distributed on the plants sampled at this stage and their numbers are not reflected in Figure 3. From 33 DAPE, the number of eggs rose to a peak 42 DAPE after which the number declined sharply to zero (Figure 3). The one peak observed represented only one generation during the crop development stage. There was considerable overlapping of stages within this generation throughout the crop development period (Figure 3). Temporal distribution of

the other life stages also showed only one peak which in the case of larvae occurred at peak flowering while those of pupae and adults occurred later (Figure 3).

1984: Initial colonization of cowpea crop by M. testulalis moth during the long rainy season is shown in Figure 1B The first male moths were attracted to the pheromone trap 15 DAPE, but the population remained extremely low and started increasing to a peak between 33 and 39 DAPE after which the population dropped and remained low but stable (Figure 1B). Another peak was observed after pod maturity (Figure 1B). Figure 4 shows the temporal distribution of the pest's life stages during early 1984 long rainy season. Eggs were found on the crop 30 DAPE, but due to heavy rainfall and poor weather conditions, the counts were considered unreliable (Figure 4), since the number of eggs recovered was lower than expected. The number of 1st and 2nd instar larvae were much higher than the number of eggs recovered from direct counts (Figure 4), indicating that the method of egg sampling under-estimated egg population during this season. Thus, for construction of the generation life table for this season the number of eggs were estimated by methods described earlier. As in the case of the 1983 populations at the field station, only one generation was recorded, showing considerable overlap of stages. However, in all stages only one peak was observed on this crop (Figure 4).

During the long rainy season 1984, a late crop was planted at MPFS next to the early crop of 1984 whose infestation is discussed above. The temporal distribution of the different stages on this second crop is shown in Figure 5. The pheromone trap results on this crop were inconsistent and not presented.

Due to bad weather and contamination of the plants by soil particles the egg counts were unreliable and not presented in Figure 5. However, eggs were detected on the crop as early as 15 DAPE and the first larvae were observed 21 DAPE. This suggested an early colonization and hence early peak density on the crop (Figure 5). Again only one generation was observed in this crop as evidenced by one peak in each development stage (Figure 5). The overlap of the stages in this generation was also observed.

The results of the off season and short rainy period of 1984 are not presented, since no complete generation of M. testulalis was observed due to severe early attack by thrips, white flies and aphids despite irrigation. The crop did not set any flowers and pods and did not last to normal maturity. Only a few eggs were found and the small numbers of early instar larvae observed died before pupation. Figure 1C and 1D shows pheromone trap records for the off season and short rain crops at MPFS during 1984. During these periods low catches of M. testulalis males were registered in the traps (Figure 1C and 1D).

1985: Colonization by adult moths as observed from pheromone trap results showed a similar trend as those already described for 1983 and 1984 at the same site (Fig. 1E). Figure 6 shows temporal distribution of the life stages during the long rainy season. In this study, egg counts were hampered by heavy rains and the numbers were lower than expected and not shown in Figure 6. However, the first eggs were found on the crop 24 DAPE. Early instar larvae started appearing on the crop 30 DAPE and the numbers increased rapidly to a peak 42 DAPE followed by a rapid decline

(Figure 6). The other later stages followed more or less similar trends, but with reduced numbers (Figure 6). Only one pronounced peak was observed in all cases, indicating a single generation with overlapping stages in this crop.

In the short rainy period, the rainfall was low and the crop was irrigated at the post flowering stage. The crop was also poor due to attack by aphids and M. testulalis population was low. Data from pheromone traps are presented in Figure 1F. Temporal distribution of the different life stages is presented in Figure 7. The 1st instar larvae showed a sharp population rise from 33 DAPE to a peak 39 DAPE followed by a rapid decline and a low peak between 48 and 51 DAPE (Figure 7). Only one peak was observed in the later instar larvae as shown in Figure 7.

Lambwe Farmer's Field

1984: Three crops were planted at Lambwe, the first during the long rainy season, the second in the off season and the last one during the normal short rainy period. The last two crops resulted into a total crop failure due to inadequate precipitation and severe attack by thrips, white flies and aphids at the vegetative stage. As a consequence, very low M. testulalis populations were observed and are, therefore, not presented here. In the 1984 long rainy season, infestation by adult moths of M. testulalis at Lambwe started 20 DAPE but remained low, rising to a peak 57 DAPE (Figure 2A). The first eggs and early instar larvae were observed 27 DAPE. Egg counts were poor due to heavy rains. The initial population build up on the crop was slow resulting into late occurrence of population peaks as shown in Figure 8. This was,

however, followed by a rapid build up of the early instar larval population reaching a high peak at the same time as the egg stage (Figure 8). The population density of the various life stages overlapped, but only one peak was observed in all stages throughout the cropping season suggesting that only one generation occurred at this site (Figure 8). The plants continued to produce flowers and pods after the normal maturity time (70 - 75 days) resulting into persistence of M. testulalis infestation (Figure 8). Pupae were recovered from the crop 63 DAPE and the population rose steadily to peak 81 DAPE, then started declining to zero at 105 DAPE (Figure 8). The adults started to emerge after 69 DAPE. Adults emerged daily, with a peak catch being recorded 99 DAPE but after 105 DAPE no more adults emerged from the field (Figure 8). Figure 8 shows the temporal distribution of M. testulalis life stages at this site during the season.

1985: During the long rainy season two crops were planted. Population build up on the earlier crop started 15 DAPE when the first moths were caught in the pheromone trap and eggs were recorded on the plant (Figure 2B). The pheromone trap catches were low but rose steadily to a low peak 84 DAPE. A low peak in male population was also observed 108 DAPE. Temporal distribution of the different life stages on the crop is presented in Figure 9. Although, the first eggs appeared on the crop as early as 15 DAPE, the first early instar larvae were observed much later, 39 DAPE and

the initial population build up was slow until after 67 DAPE. However, there was a sharp increase in the numbers of this stage reaching a high peak 75 DAPE (Figure 9). The slow initial population build-up was interrupted by an abrupt decline at 63 and 69 DAPE in all the larval stages, which was followed by rapid build-up of M. testulalis numbers to a peak 75 DAPE (Figure 9). Similarly, there was a slow build-up of pupal and adult population in the traps, but only one pronounced peak was observed in all cases (Figure 9). In this crop, M. testulalis persisted for a long period and possibly 2-3 generations may have occurred possibly due to prolonged rainy season. However, only the generation shown in Figure 9 was important as it occurred during the reproductive phase of the crop and the population in this generation was high.

The temporal distribution of the different M. testulalis life stages from the late crop of 1985 long rains are presented in Figure 10. Male moths first appeared in the pheromone traps 25 DAPE signifying a late infestation by adults as shown in Figure 2C. This gave rise to a later first peak in adult population occurring 54 DAPE and a second peak 78 DAPE (Figure 2C). The first early larval instars of the pest were recorded on the crop 30 DAPE after which population build-up was rapid, reaching the highest peak 66 DAPE (Figure 10). Two other peaks were also observed earlier in the early instar larvae. In the other stages the peaks were diffuse especially in the 3rd to 5th instar larvae (Figure 10).

Figure 1. Number of Maruca testulalis males caught in pheromone traps at MPFS during 1983-1985:

A. Trap catches during 1983 short rains

B. Trap catches during 1984 long rains

C. Trap catches during long rains - 1984 (late crop May - July)

D. Trap catches during 1984 - off season 1984

E. Trap catches during 1985 long rains

F. Trap catches during 1985 short rains.

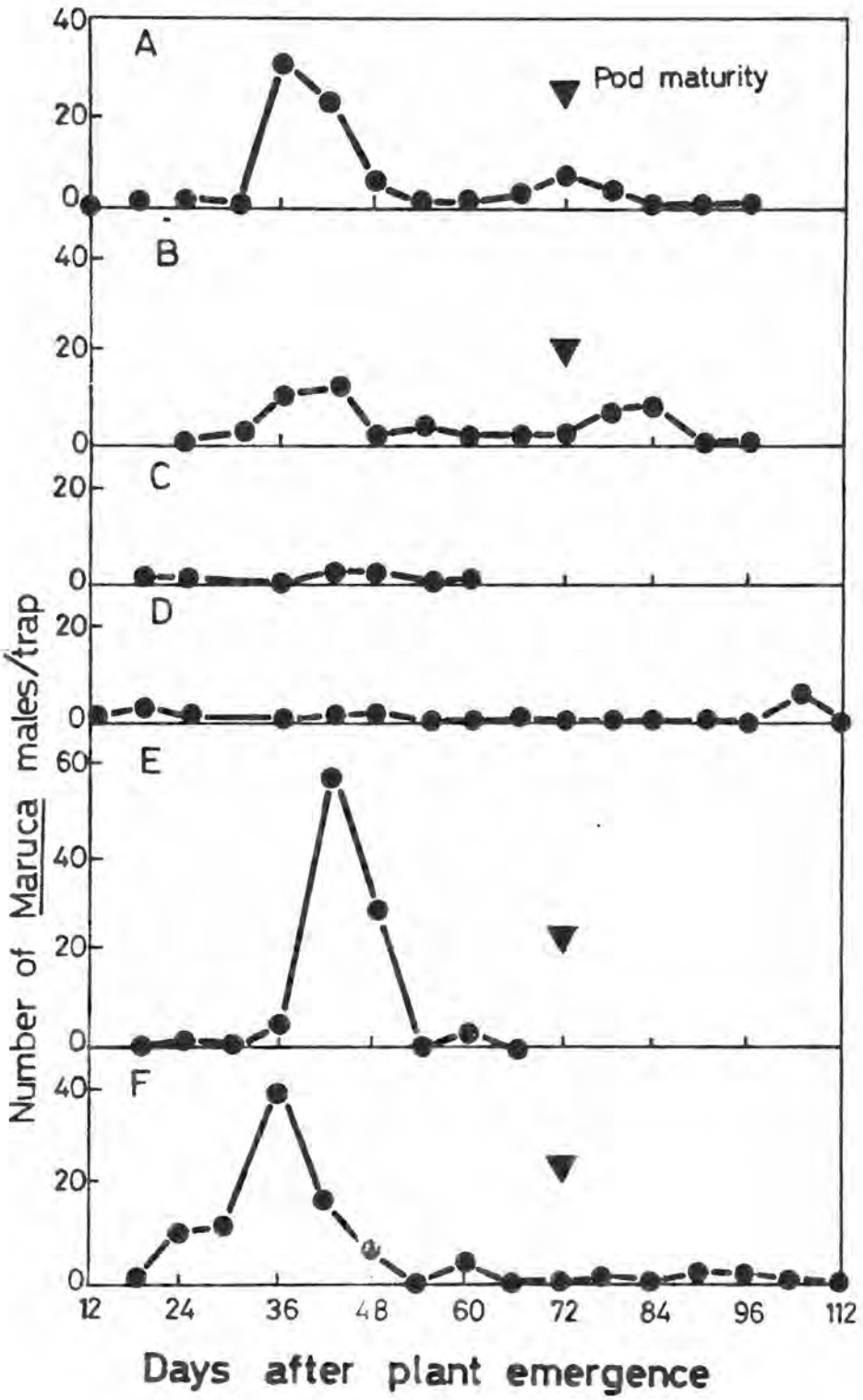

A
B
C
D
E
F
Pod maturity
40
20
0
60
12
24
36
48
60
72
84
96
112
Number of Maruca males/trap
Days after plant emergence

Figure 2. Number of Maruca testulalis males caught in pheromone traps at Lambwe during 1984 - 1985.

A. Trap catches during 1984 long rains

B. Trap catches during 1985 long rains

C. Trap catches during 1985 late crop.

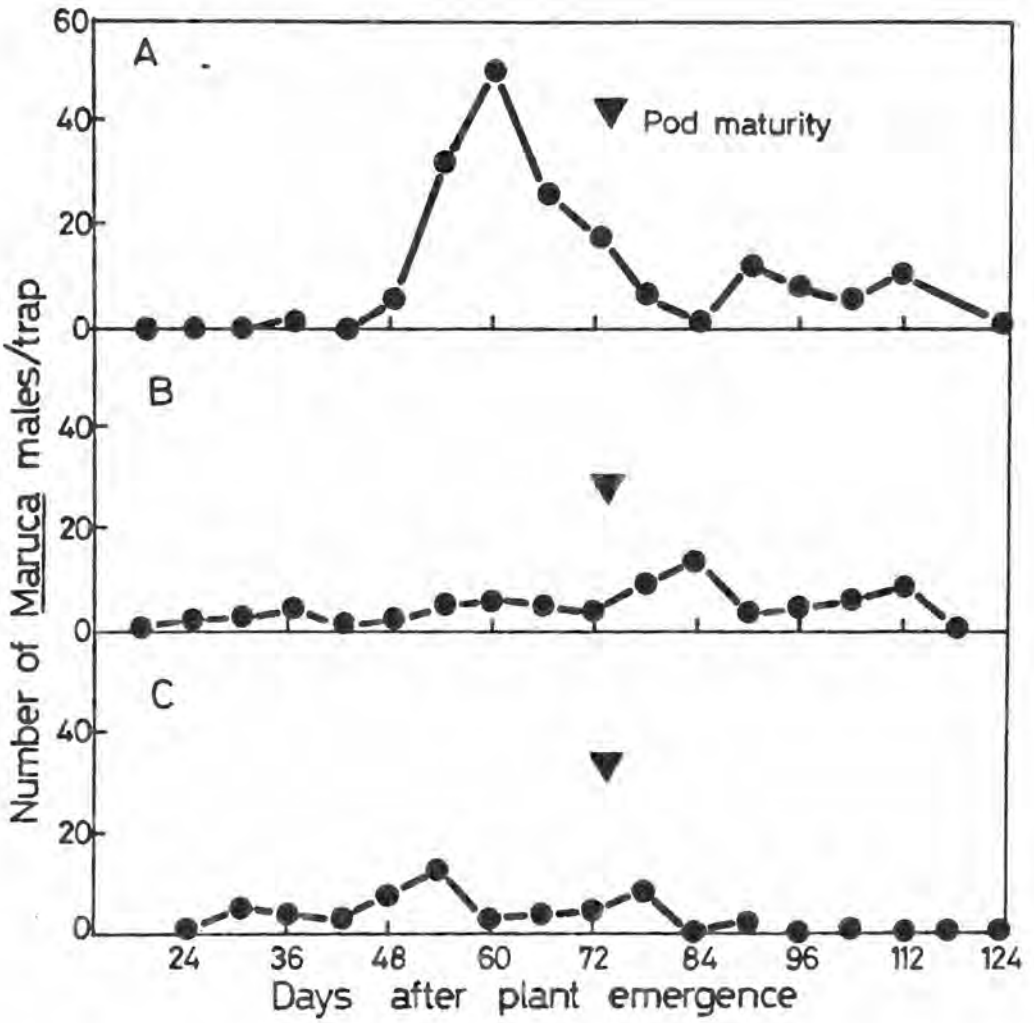

A
B
C
Pod maturity
60
40
20
0
Number of Maruca males/trap
24
36
48
60
72
84
96
112
124
Days after plant emergence

Figure 3. Temporal distribution of M. testulalis life stages on cowpea crop at MPFS during short rainy season 1983.

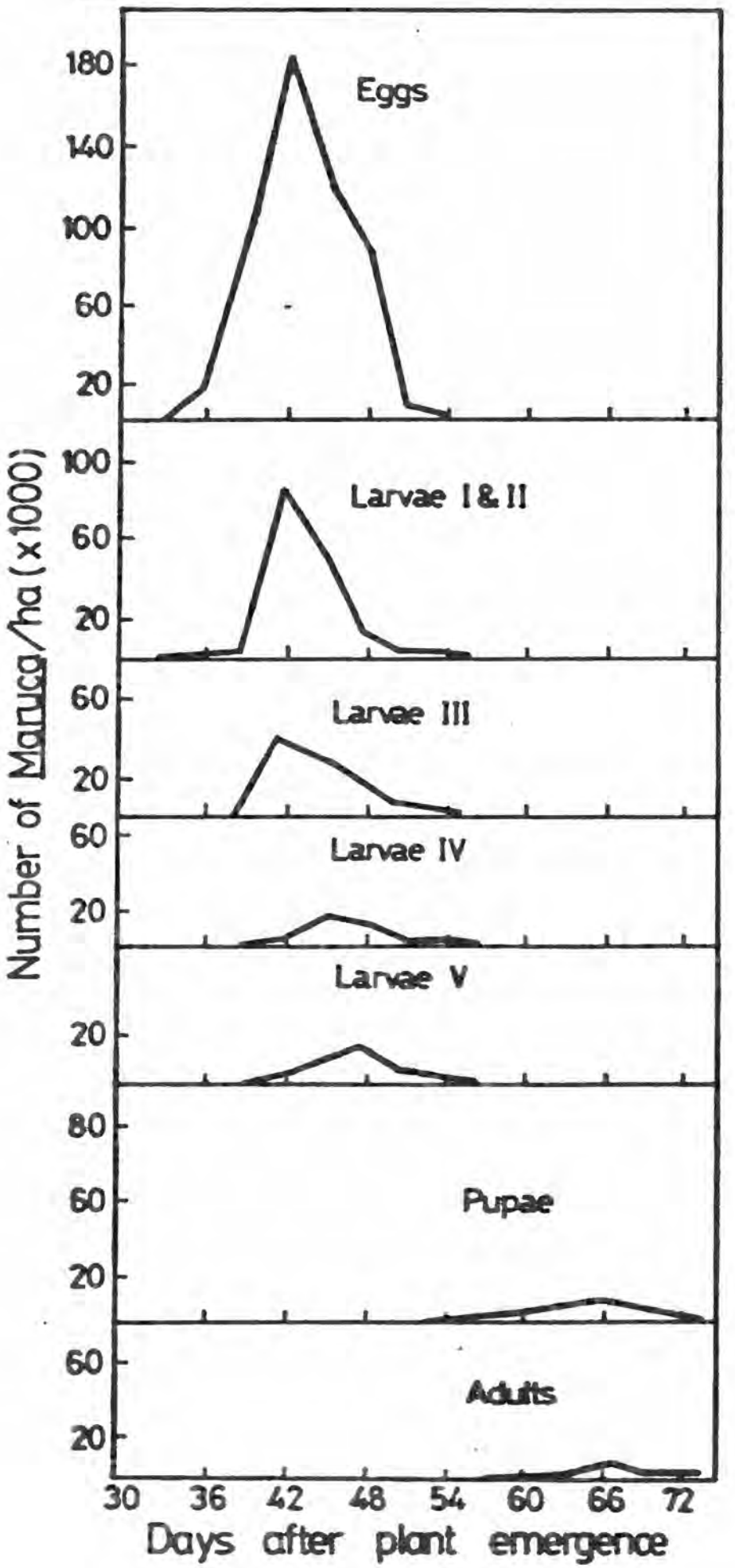

Eggs
Larvae I & II
Larvae III
Larvae IV
Larvae V
Pupae
Adults
Number of Maruca/ha (x1000)
Days after plant emergence
180
140
100
60
20
80
30
36
42
48
54
60
66
72

Figure 4. Temporal distribution of M. testulalis life stages on cowpea crop during long rainy season, 1984.

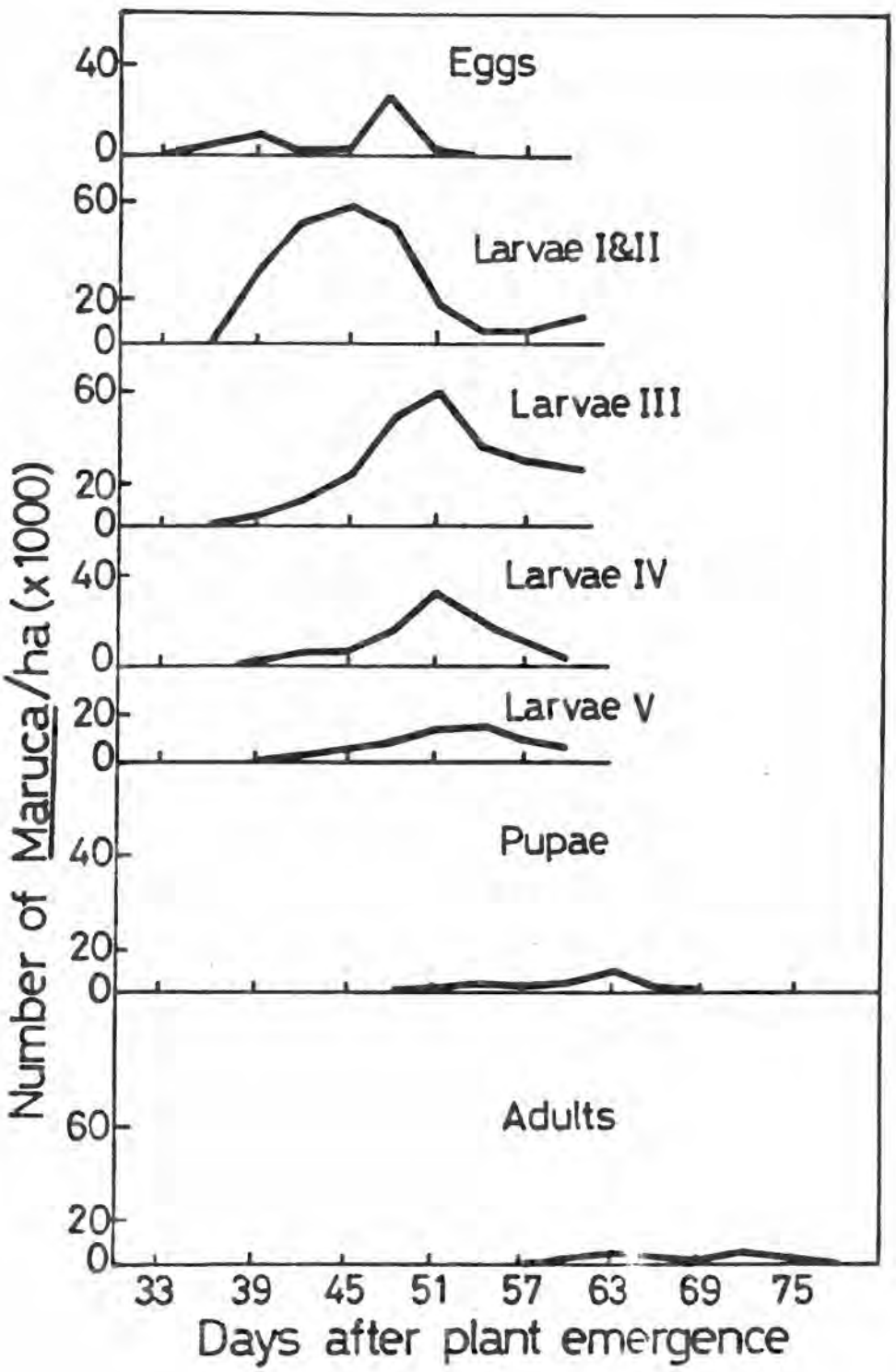

Eggs
Larvae I&II
Larvae III
Larvae IV
Larvae V
Pupae
Adults
40
0
60
20
0
60
20
0
40
0
20
0
40
20
0
60
20
0
33
39
45
51
57
63
69
75
Number of Maruca/ha (x1000)
Days after plant emergence

Figure 5. Temporal distribution of M. testulalis life stages on cowpea crop during long rainy season 1984 (late crop).

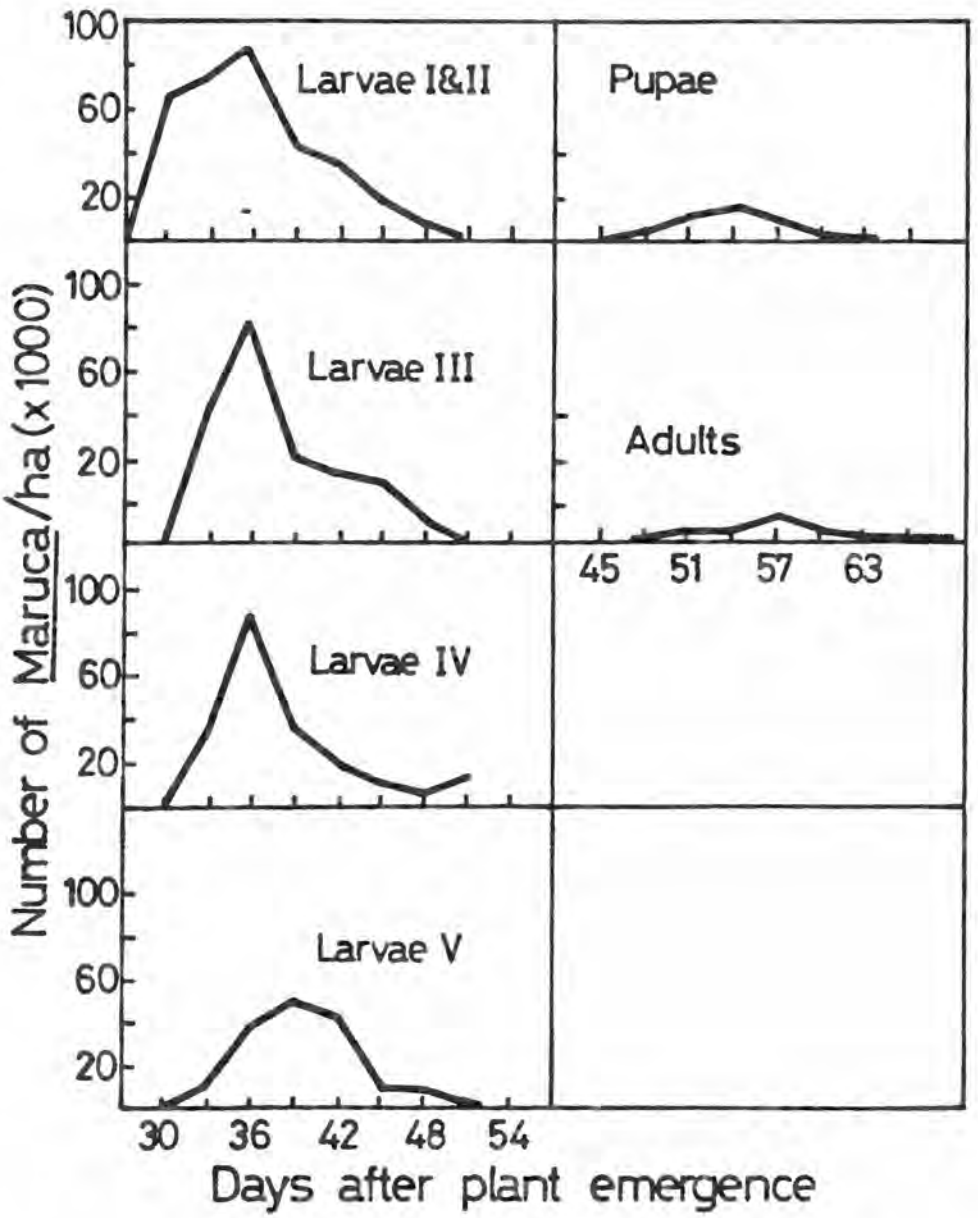

Larvae I&II
Pupae
Larvae III
Adults
Larvae IV
Larvae V
100
60
20
45
51
57
63
30
36
42
48
54
Number of Maruca/ha (x 1000)
Days after plant emergence

Figure 6. Temporal distribution of M. testulalis life stages on cowpea crop at MFFS during long rains 1985.

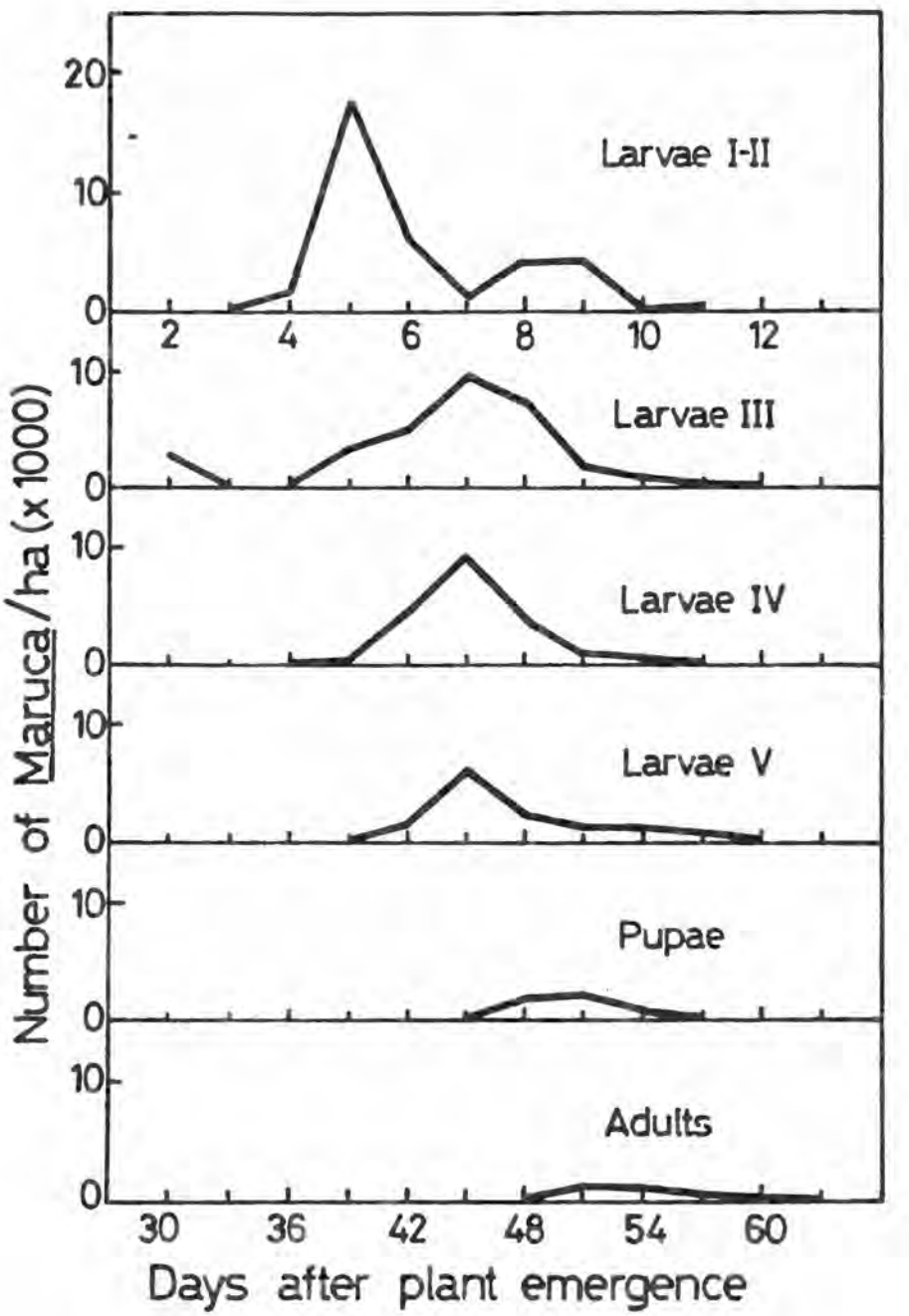

Larvae I-II
Larvae III
Larvae IV
Larvae V
Pupae
Adults
20
10
0
2
4
6
8
10
12
30
36
42
48
54
60
Number of Maruca/ha (x 1000)
Days after plant emergence

Figure 7. Temporal distribution of M. testulalis life stages on cowpea crop at MPFS during short rainy season, 1985.

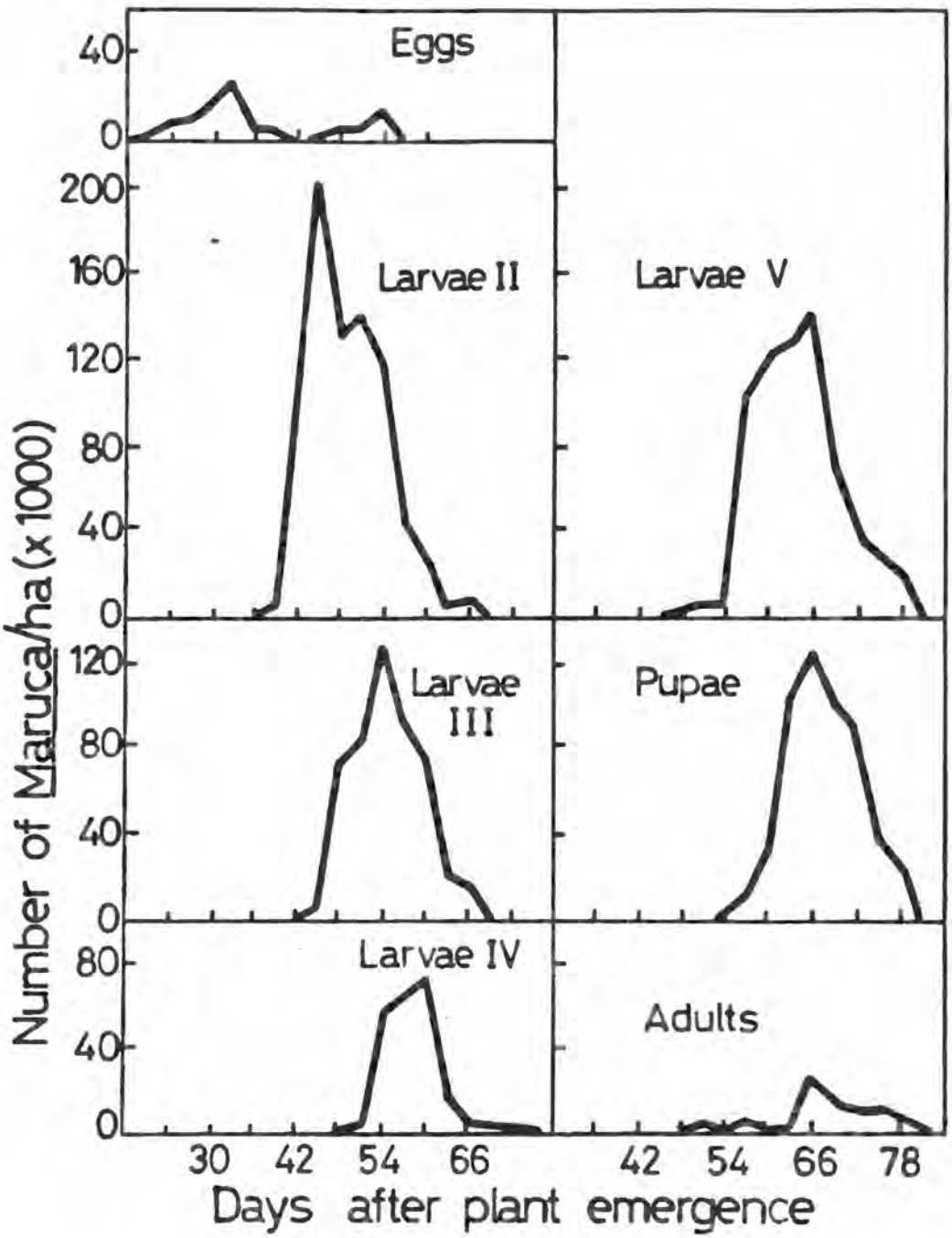

Eggs
Larvae II
Larvae V
Larvae III
Pupae
Larvae IV
Adults
Number of Maruca/ha (x 1000)
Days after plant emergence
40
0
200
160
120
80
40
0
120
80
40
0
80
40
0
30 42 54 66
42 54 66 78

Figure 8. Temporal distribution of M. testulalis life stages at Lambwe during long rainy season, 1984.

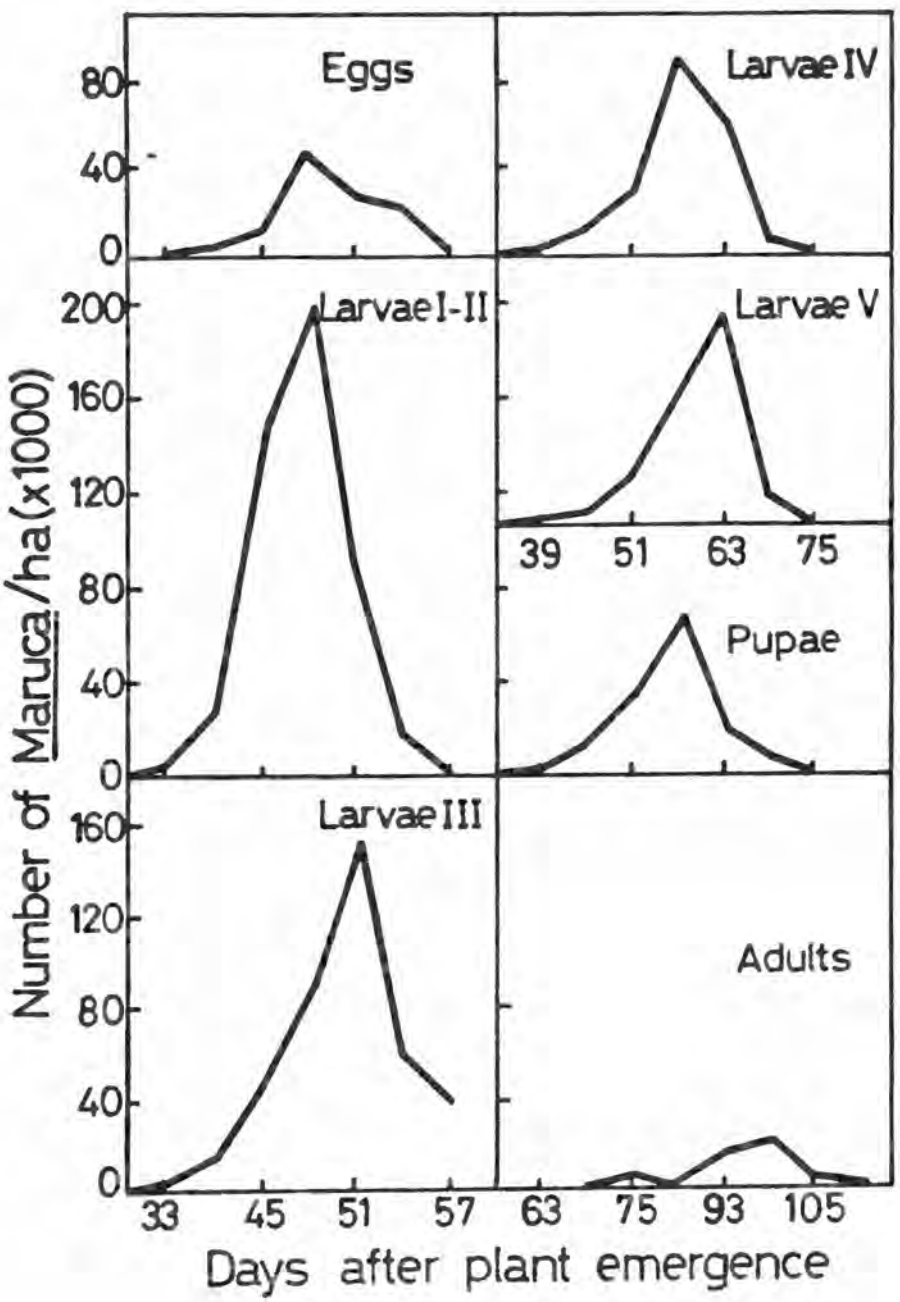

Eggs
Larvae IV
Larvae I-II
Larvae V
Pupae
Larvae III
Adults
Number of Maruca/ha (x1000)
Days after plant emergence
0
40
80
120
160
200
33
39
45
51
57
63
75
93
105

Figure 9. Temporal distribution of M. testulalis life stages on cowpea crop at Lambwe during long rainy season, 1985.

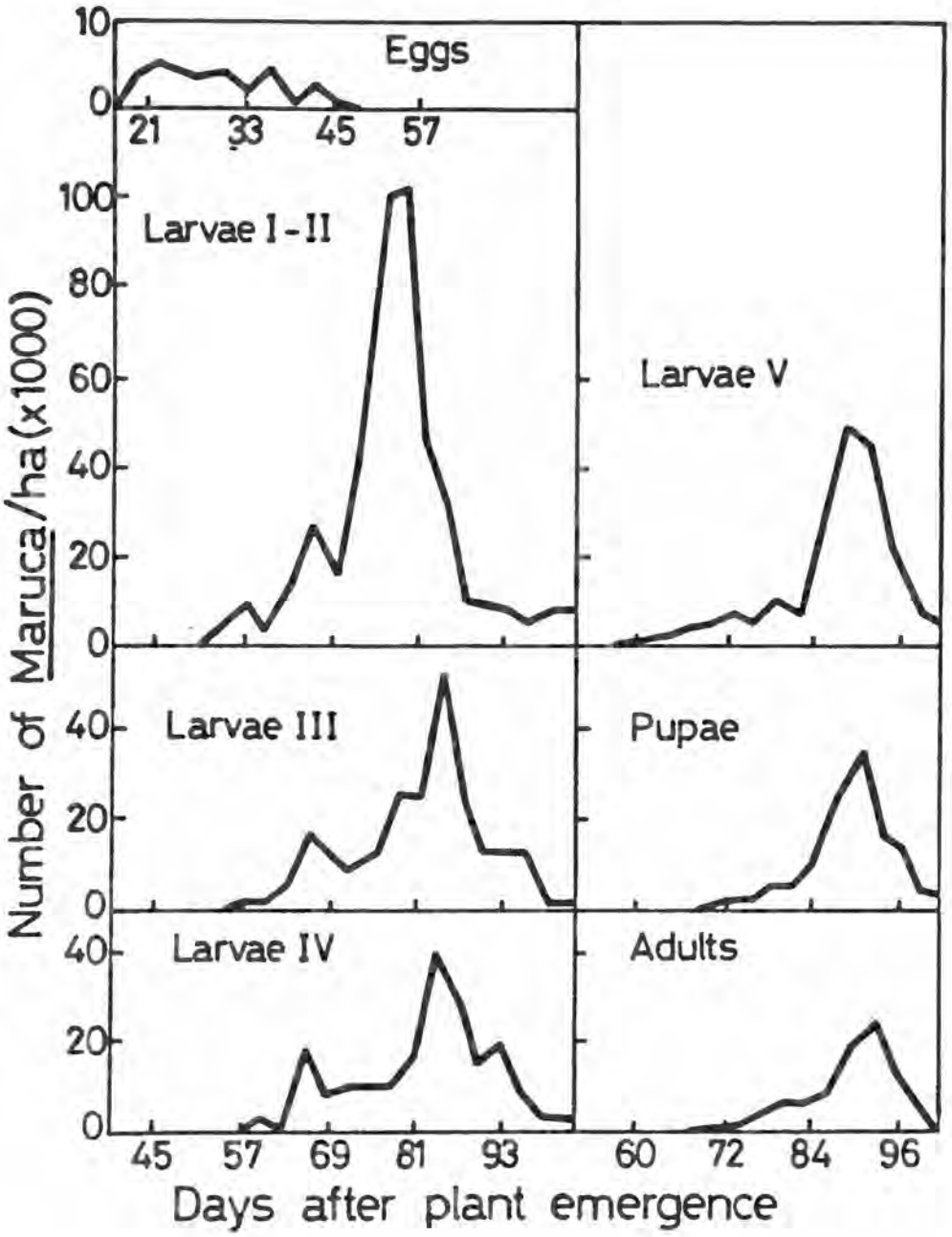
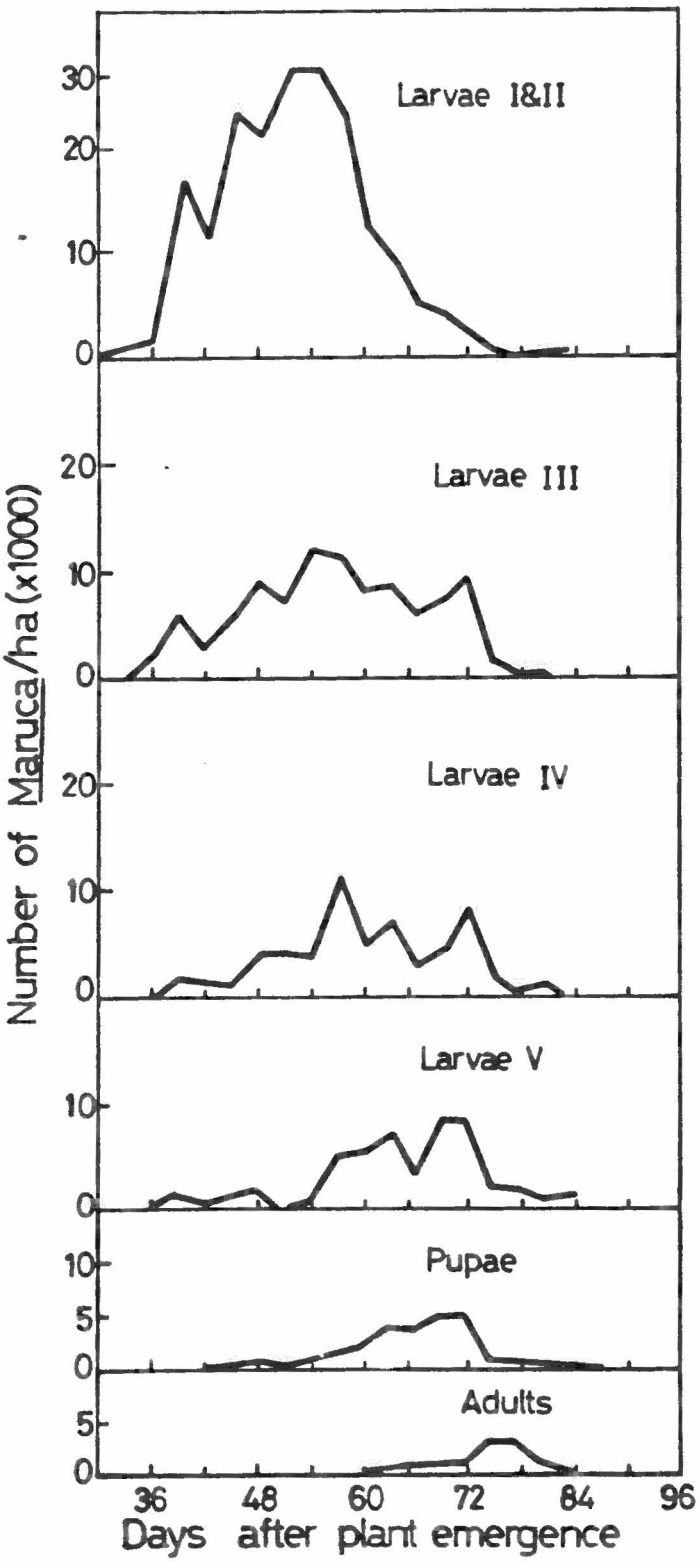

Eggs
Larvae I - II
Larvae V
Larvae III
Pupae
Larvae IV
Adults
Number of Maruca/ha (x1000)
Days after plant emergence
10
0
21
33
45
57
100
80
60
40
20
0
40
20
0
40
20
0
45
57
69
81
93
60
72
84
96

Figure 10. Temporal distribution of M. testulalis life stages on cowpea crop at Lambwe during long rainy season 1985 (late crop).


Larvae I&II
Larvae III
Larvae IV
Larvae V
Pupae
Adults
Number of Maruca/ha (x1000)
Days after plant emergence
36
48
60
72
84
96

4.1.2. Partial Ecological life tables and survivorship curves

Partial ecological life tables for five generations of M. testulalis at MPFS during 1983 - 1985 and 3 generations at Lambwe during 1984 - 1985 are presented in Table 1-8. The various life tables also give the real and apparent mortalities for M. testulalis in columns 100qx and 100rx respectively. The mean mortalities for the five generations at MPFS and three generations at Lambwe are presented in Figure 14A and 14B.

Survivorship curves for M. testulalis at MPFS and Lambwe during the whole experimental period are given in Figures 11 and 12, respectively, and the mean generation survivorship for the respective sites are presented in Figure 13. At MPFS, the mean real egg mortality was 28.5 $\pm$ 9.1% while those of other stages were 11.0 $\pm$ 2.6% in early instar, 20.7 $\pm$ 4.4% in 3rd instar, 10.2 $\pm$ 4.7% in 4th instar, 11.4% $\pm$ 5.6% in 5th instar larvae, and 0.02 $\pm$ 0.01% in pupae (Tables 1-5 and Figure 14). In Lambwe the respective mean real mortalities were 27.0 $\pm$ 6.2%, 27.8 $\pm$ 4.7%, 15.9 $\pm$ 3.8%, 1.1 $\pm$ 0.7%, 24.3 $\pm$ 4.2% and 1.1 $\pm$ 0.09% from egg to pupal stage (Table 6-8 and Figure 14). The results show that at MPFS the lowest real mortality occurred in pupal stage, and the highest mortality occurred at egg stage at MPFS (Figure 14). Also at this site real mortality was low at 4th instar stage. At Lambwe, the lowest real mortality occurred at the pupal as well as the 4th larval instar stages, while the highest mortality was at the egg and early instar stages (Figure 14).

The results show considerable variation in the inter-generation mortality expressed as % real mortality for all the life stages at both sites (Tables 1-8 and Figure 14A). The total % real mortalities for the generations at MPFS and Lambwe ranged between 51.6 - 99.9 ($x \pm SE = 82.2 \pm 8.8$) and 95.7 - 97.6 ($x \pm SD = 96.5 \pm 0.36$), respectively (Table 1 - 8). Figure 14B shows the mean apparent mortality occurring at different life stages of M. testulalis at both sites. The results show that, at MPFS the lowest apparent mortalities occurred at the early instars (Larvae I and II) and the 4th instar larval stage while the highest mortality was observed 5th instar larval stage (Figure 14B). In the case of Lambwe the lowest apparent mortality was observed at 4th instar larval stage while the highest was at the 5th instar stage (Figure 14B).

Table 1. Partial ecological life table of Maruca testulalis for the generation on cowpea at MPFS during short rainy season 1983

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
Eggs	258893	Disappearance*	177330	68.5	68.5
Larvae I-II	81563	Parasitism	0	0.0	0.0
		Disease	0	0.0	0.0
		Disappearance	3102	3.8	1.2
		TOTAL	3102	3.8	-
Larvae III	78461	Parasitism	0	0.0	0.0
		Disease	34680	44.2	13.4
		Disappearance	21504	27.4	8.3
		TOTAL	25184	71.6	8.3
Larvae IV	22277	Parasitism	0	0.0	0
		Disease	0	0.0	0
		Disappearance	0	0.0	0
		TOTAL	0	0.0	-
Larvae V	23417	Parasitism	0	0.0	0.0
		Disease	16103	68.8	6.2
		Disappearance	5960	25.4	2.3
		TOTAL	22063	94.2	-
Pupae	1354	Parasitism	139	10.3	0.0005
		Disease	276	20.4	0.001
		Disappearance	177	13.1	0.0007
		TOTAL	592	43.8	-
Adults	762	-	-	-	-
			TOTAL	99.9	

*Disappearance includes losses due to predator, emigration, and any other unknown causes.

Table 2. Partial ecological life table of Maruca testulalis for the generation on cowpea crop during 1984 long rainy season at MPFS

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
Eggs	(132639)	Disappearance*	(22482)	17.0	17.0
Larvae I-II	110157	Parasitism	0	0.0	0.0
		Disease	7601	0.9	5.7
		Disappearance	6169	5.6	4.7
		TOTAL	13770	12.5	-
Larvae III	96387	Parasitism	0	0.0	0.0
		Disease	40579	42.1	30.6
		Disappearance	11856	12.3	8.9
		TOTAL	52435	54.4	-
Larvae IV	43953	Parasitism	0	0.0	0
		Disease	12481	28.4	9.4
		Disappearance	7516	17.1	5.7
		TOTAL	19997	45.5	-
Larvae V	23954	Parasitism	0	0.0	0.0
		Disease	9964	41.6	7.5
		Disappearance	10891	45.5	8.2
		TOTAL	20855	87.1	-
Pupae	1354	Parasitism	313	10.1	0.002
		Disease	599	19.3	0.005
		Disappearance	87	2.8	0.001
		TOTAL	999	32.2	-
Adults	762	-	-	-	-
			TOTAL	97.7	

Figures in parentheses are estimated. *Disappearance include losses due to predation, emigation and any other unknown causes.

Table 3. Partial ecological life table of Maruca testulalis for the generation on cowpea crop during 1984 (Late crop) long rainy season at MPFS

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
Eggs	(232019)	Disappearance*	(59569)	25.2	25.5
Larvae I-II	172450	Parasitism	0	0.0	0.0
		Disease	15311	8.9	6.6
		Disappearance	23108	13.4	10.0
		TOTAL	38419	22.3	-
Larvae III	134031	Parasitism	0	0.0	0.0
		Disease	24549	18.2	10.6
		Disappearance	11527	8.6	5.0
		TOTAL	36076	54.4	-
Larvae IV	97955	Parasitism	0	0.0	0
		Disease	8718	8.9	3.8
		Disappearance	9763	10.0	4.2
		TOTAL	18481	18.9	-
Larvae V	79474	Parasitism	0	0.0	0.0
		Disease	42942	54.0	0.2
		Disappearance	30070	38.8	0.1
		TOTAL	73012	92.8	-
Pupae	6462	Parasitism	298	4.6	0.0001
		Disease	908	14.1	0.0004
		Disappearance	1519	23.5	0.0007
		TOTAL	2725	42.1	-
Adults	3737				
			TOTAL	65.7	

Figures in parentheses are estimated. *Disappearance include losses due to predation, emigation and any other unknown causes.

Table 4. Partial ecological life table of Maruca testulalis for the generation on cowpea crop during 1985 long rainy season at MPFS

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
Eggs	(478597)	Disappearance*	(93150)	19.5	19.5
Larvae I-II	385447	Parasitism	0	0	0
		Disease	0	0	0
		Disappearance	83866	21.8	17.5
		TOTAL	83866	21.8	-
Larvae III	301581	Parasitism	0	0.0	0.0
		Disease	20206	5.2	4.2
		Disappearance	47608	12.4	9.9
		TOTAL	67814	17.6	-
Larvae IV	237767	Parasitism	0	0.0	0
		Disease	0	0	0
		Disappearance	0	0	0
		TOTAL	-	-	-
Larvae V	238822	Parasitism	1622	0.7	0.0003
		Disease	92449	38.7	0.20
		Disappearance	118714	49.7	0.25
		TOTAL	212785	89.1	-
Pupae	26037	Parasitism	2623	10.0	0.01
		Disease	9418	36.2	0.02
		Disappearance	10259	39.4	0.02
		TOTAL	22300	85.6	0.02
Adults	3737	-	-	-	-
			TOTAL	51.6	

Figures in parentheses are estimated. *Disappearance include losses due to predation, emigation and any other unknown causes.

Table 5. Partial ecological life table of Maruca testulalis for the generation on cowpea crop during 1985 long rainy season at MPFS

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
ggs	(19906)	Disappearance*	2404	12.1	12.1
Larvae I-II	17502	Parasitism	0	0	0
		Disease	1033	5.9	5.1
		Disappearance	884	5.1	4.4
		TOTAL	1917	11.0	-
Larvae III	15585	Parasitism	0	0.0	0.0
		Disease	2123	13.6	10.7
		Disappearance	405	2.6	2.0
		TOTAL	2528	16.2	-
Larvae IV	13057	Parasitism	0	0.0	0
		Disease	1110	8.5	5.6
		Disappearance	4446	34.1	22.3
		TOTAL	5556	42.6	-
Larvae V	7501	Parasitism	0	0	0
		Disease	1665	82.2	31.0
		Disappearance	606	8.1	3.0
		TOTAL	6771	90.3	-
Pupae	730	Parasitism	70	09.6	0.003
		Disease	245	33.6	0.01
		Disappearance	143	19.5	0.01
		TOTAL	458	62.7	-
Adults	272	-	-	-	-
			TOTAL	51.6	

Figures in parentheses are estimated. *Disappearance include losses due to predation, emigation and any other unknown causes.

Table 6. Partial ecological life table of Maruca testulalis for the generation on cowpea crop during 1984 long rainy season in Lambwe Valley farmer's field

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
Eggs	(327793)	Disappearance*	85006	25.9	25.9
Larvae I-II	242787	Parasitism	0	0	0
		Disease	17238	7.1	5.3
		Disappearance	46858	19.3	14.3
		TOTAL	64096	26.4	-
Larvae III	178691	Parasitism	0	0.0	0.0
		Disease	55751	31.2	17.0
		Disappearance	25017	14.0	7.6
		TOTAL	80768	45.2	-
Larvae IV	97923	Parasitism	0	0.0	0
		Disease	6561	6.7	2.0
		Disappearance	2742	2.8	0.8
		TOTAL	9303	9.5	-
Larvae V	88620	Parasitism	3300	3.7	0.01
		Disease	46205	52.1	14.1
		Disappearance	24203	27.3	7.4
		TOTAL	73708	83.1	-
Pupae	14912	Parasitism	0	0	0
		Disease	6527	43.7	2.0
		Disappearance	4289	28.8	1.3
		TOTAL	10816	72.5	-
Adults	4096	-	-	-	-
			TOTAL	51.6	

Figures in parentheses are estimated. *Disappearance include losses due to predation, emigation and any other unknown causes.

Table 7. Partial ecological life table of Maruca testulalis for the generation on cowpea crop during 1985 long rainy season in Lambwe Valley farmer's field (early crop)

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
ggs	(264223)	Disappearance*	38741	14.7	14.7
Larvae I-II	225482	Parasitism	0	0	0
		Disease	0	0	0
		Disappearance	101859	45.2	38.6
		TOTAL	101859	45.2	-
Larvae III	123623	Parasitism	0	0.0	0
		Disease	9149	7.4	3.5
		Disappearance	14221	11.5	5.4
		TOTAL	23369	18.9	-
Larvae IV	100254	Parasitism	0	0	0
		Disease	0	0	0
		Disappearance	0	.0	0
		TOTAL	-	-	-
Larvae V	108433	Parasitism	2323	2.2	0.009
		Disease	40423	37.3	15.3
		Disappearance	49322	45.5	18.7
		TOTAL	92068	84.0	-
Pupae	16365	Parasitism	418	2.6	0
		Disease	2407	14.7	0.002
		Disappearance	3259	19.9	0.01
		TOTAL	6084	37.2	0
Adults	10281	-	-	-	-
			TOTAL	51.6	

Figures in parentheses are estimated. *Disappearance include losses due to predation, emigation and any other unknown causes.

Table 8. Partial ecological life table of Maruca testulalis for the generation on cowpea crop during 1985 long rainy season in Lambwe Valley farmer's field (late crop)

X	lx	dxF	dx	100qx	100rx
Age interval	No.alive/ha.	Factor responsible for dx	No.dying during x	dxi as % of lxi	dxi as % of lx_1
Eggs	(145201)	Disappearance*	58844	40.5	40.5
Larvae I-II	86357	Parasitism	0	0	0
		Disease	0	0	0
		Disappearance	36447	42.2	25.1
		TOTAL	36447	42.2	-
Larvae III	49910	Parasitism	0	0.0	0
		Disease	8285	16.6	5.7
		Disappearance	12547	25.1	8.6
		TOTAL	20832	41.7	-
Larvae IV	29078	Parasitism	0	0	0
		Disease	495	1.7	0.3
		Disappearance	111	0.4	0.1
		TOTAL	606	2.1	-
Larvae V	28072	Parasitism	1714	6.1	1.2
		Disease	16942	59.5	4.4
		Disappearance	6416	22.5	11.7
		TOTAL	25072	88.1	-
Pupae	3400	Parasitism	331	9.7	0.002
		Disease	590	17.4	0.004
		Disappearance	866	25.5	0.006
		TOTAL	1787	52.6	
Adults	1613	-	-	-	-
			TOTAL	51.6	

Figures in parentheses are estimated. *Disappearance include losses due to predation, emigation and any other unknown causes.

Figure 11. Survival curves of M. testulalis generations, 1983-1985, at MPFS.

1-5 refers to different generations of the pest.

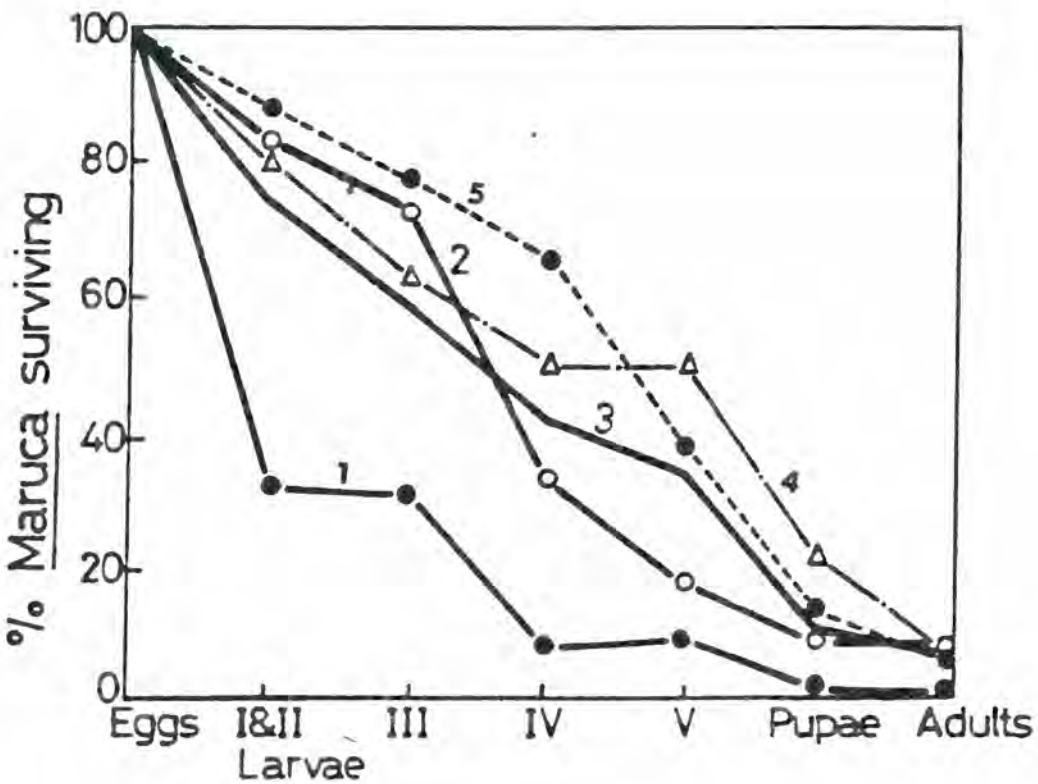

100
80
60
40
20
0
% Maruca surviving
1
2
3
4
5
Eggs
I&II
III
IV
V
Pupae
Adults
Larvae

Figure 12. Survival curves of M. testulalis generations, 1984-1985, at Lambwe farmer's field

1 - 3 refers to different generations of the pest.

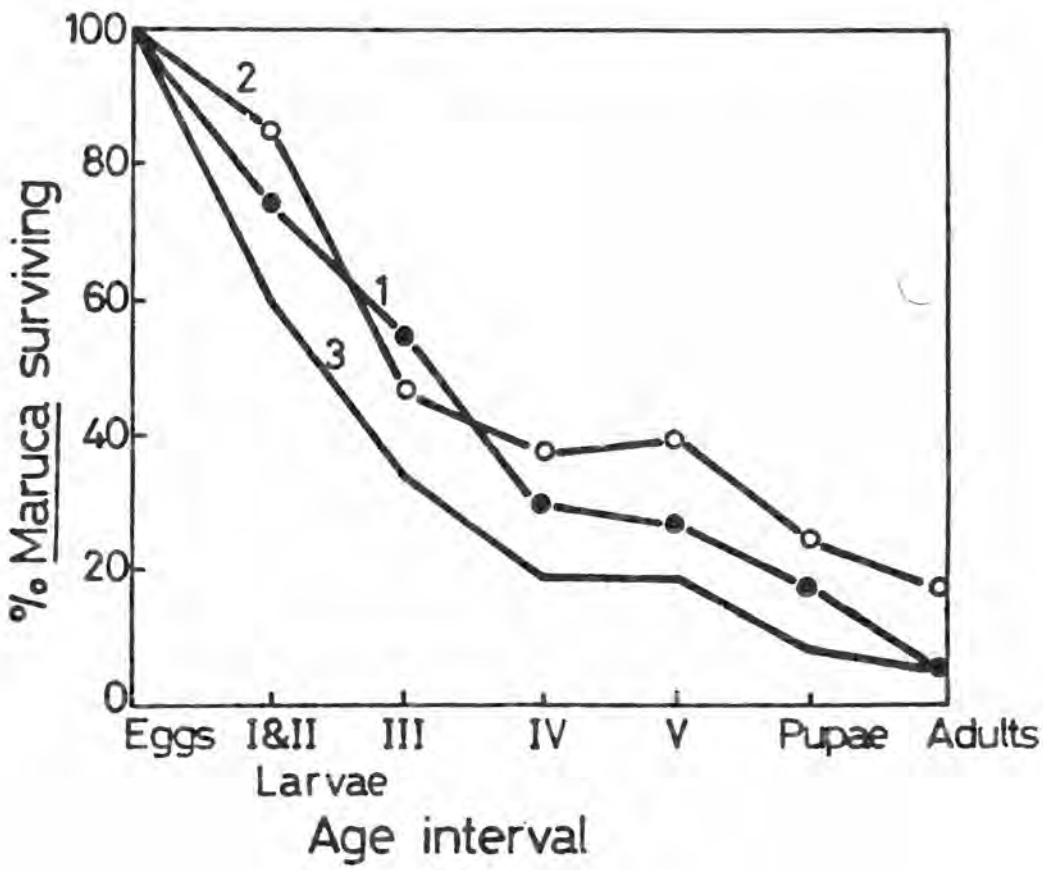

100
80
60
40
20
0
% Maruca surviving
1
2
3
Eggs
I&II
III
IV
V
Pupae
Adults
Larvae
Age interval

Figure 13. Mean survival curves of M. testulalis for all generations at MPFS and Lambwe Valley farmer's field, 1983-1985.

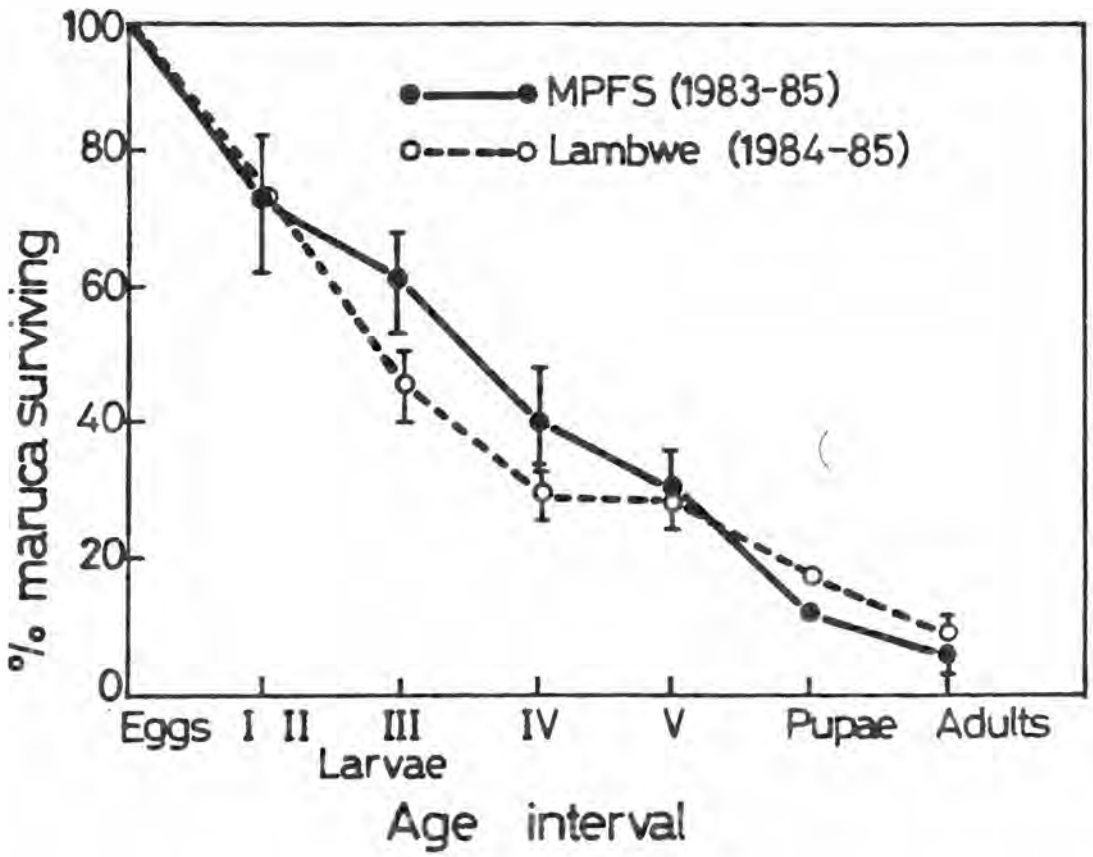
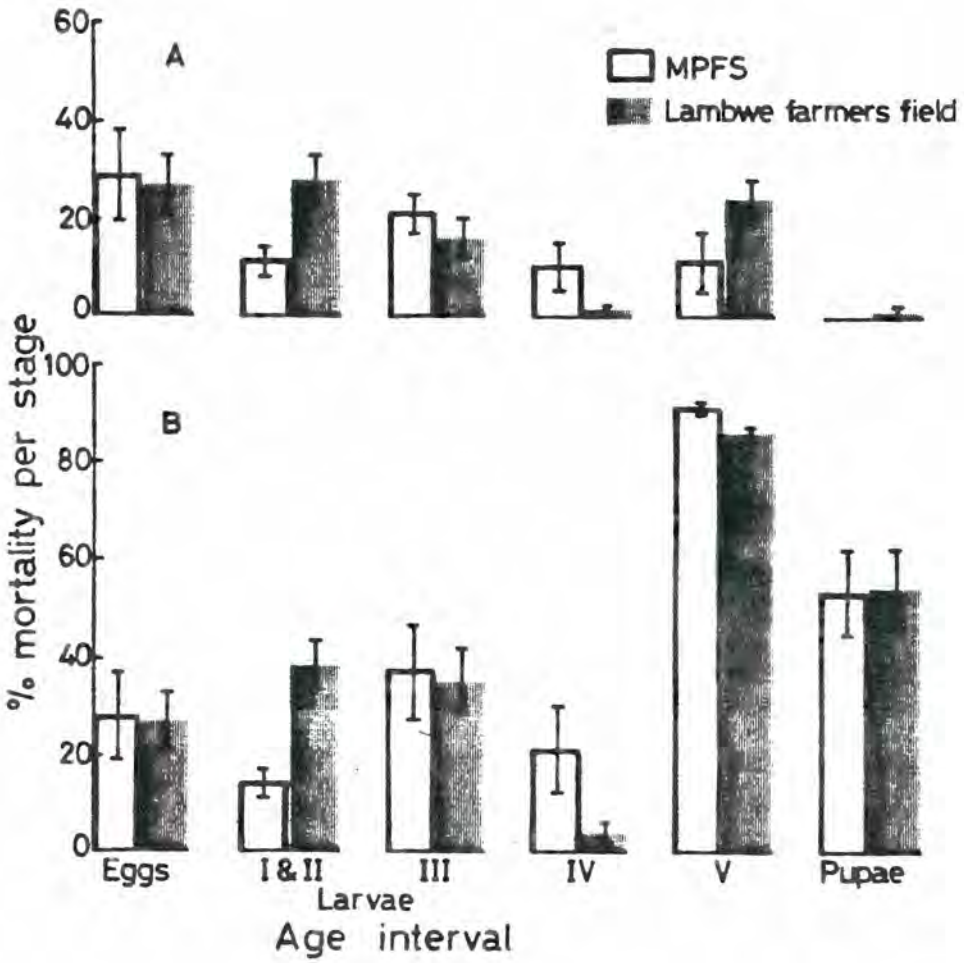

100
80
60
40
20
0
% maruca surviving
MPFS (1983-85)
Lambwe (1984-85)
Eggs
I
II
III
IV
V
Pupae
Adults
Larvae
Age interval

Figure 14. Percent mortality of M. testulalis at MPFS and Lambwe farmer's field 1983-1985.

A. Real mortality

B. Apparent mortality


A
B
MPFS
Lambwe farmers field
% mortality per stage
60
40
20
0
100
80
60
40
20
0
Eggs
I & II
III
IV
V
Pupae
Larvae
Age interval

4.1.3 Key factor analysis and density relationships

Life table values were used to construct partial mortality budget from which the various k values for M. testulalis were calculated. These are presented in Tables 9-16 for both sites. The relationship between the various k-values and K is presented in Figure 15.

At MPFS, the mortalities for k_0, k_4, and k_{12} showed positive relationships to K. The other k-values were unrelated to K and changes in their values were unlikely to contribute to changes in the values of K (Figure 15). The factors k_o, k_4 and k_{12} represent egg loss due to disappearance, disappearance at 3rd instar larva, and disappearance at the pupal stages respectively (Tables 9-13). The factors k_8 and k_{11} are small and represent the mortality due to parasitism. These results show that parasitoids contribute minimal mortality to M. testulalis. The trend of change in k_o is more similar to K than all the other k-factors in relation to magnitude of change (Figure 15). Thus, k_o which is a factor of disappearance operating at egg stage is the key factor causing population change as identified from the key factor method (Figure 15).

In Lambwe, although only three generations were examined, Figure 15 shows that, k_o, k_3, k_4, k_7 and k_{12} have close relationship with the total generation mortality, K, in terms of trend of change. The factor k_o represents

disappearance at egg stage while k_3 represents disease at 3rd instar larvae and k_4 represents disappearance at the same stage (Tables 14-16). The factor k_7 is disease at pupal stage and k_{12} is disappearance at the pupal stage. The results at this site show that k_3 resembles K more closely than the other k-factors in relation to magnitude of change, and thus, the key factor causing population change as identified by this method.

A further analysis of the relationship between the k-factors (k_o, k_4 and k_{12}) which showed close relations to the generation mortality, (K) was conducted by correlation methods. The results are shown in Figure 16 for the generations at MPFS. It was found that k_o ($r = 0.87$) and k_4 ($r = 0.830$) had higher positive correlation to K. The values for k_o had the highest positive correlation to K which was also significant at $P = 0.05$. The relationship between k_{12} and K was low ($r = 0.169$) and not significant. Thus, from this method k_o was confirmed the key mortality factor (Figure 16). A similar analysis was not possible for the Lambwe generations because the number of generations (3) observed were too few for a correlation analysis.

The density relationships between k_o, k_4 and k_{12}, for the MPFS generations, were tested by plotting their values against the log of the population density (lx) entering the age

interval on which it acts. This technique was used by Varley and Gradwell (1963) in describing density dependence in insect populations and indicated that a slope of 1.0 (unity) shows density related mechanisms which completely compensate for changes in host density, but that less than 1.0 indicates that the factor under compensates for the changes. A negative slope shows an inverse density dependence.

Figure 17 shows that k_4 (b = 0.006) and k_o (b = 0.1) are not dependent on the density of M. testulalis while k_{12} (b = 0.349) is only slightly positively density dependent.

Table 9. Partial mortality budget for Maruca testulalis at MPFS during sho rainy season's crop, 1983.

	No./ha	Log.No./ha	K.value
Eggs laid	258893	5.4131	
k_o (egg loss)			0.502
Larvae I-II	81563	4.9115	
k_1 (disease)			0.00
(Larvae I-II surviving disease)	81563	4.9115	
k_2 (disappearance)			0.017
Larvae III	78461	4.8947	
k_3 (disease)			0.253
(Larvae III surviving disease)	43781	4.6413	
k_4 (disappearance)			0.293
Larvae IV	22277	4.3478	
k_5 (disease)			0.00
(Larvae IV surviving disease)	22277	4.3478	
k_6 (disappearance)			0.0
Larvae V	23417	4.3695	
k_7 (disease)			0.050
(Larvae V surviving disease)	7314	3.8642	
k_8 (Parasitism)			0
(Larvae V surviving parasitism)	7314	3.8642	
k_9 (disappearance)			0.733
Pupae	1354	3.1316	
k_{10} (disease)			0.099
(Pupae surviving disease)	1078	3.0326	
k_{11} (Parasitism)			0.060
(Pupae surviving parasitism)	939	2.9797	
k_{12} (disappearance)			0.091
Adults emerging	762	2.8820	
		K =	2.553

Table 10. Partial mortality budget for Maruca testulalis at MPFS during lo rainy season 1984 (early crop).

	No./ha	Log.No./ha	K.value
Eggs laid	132639	5.1227	
k_o (egg loss)			0.081
Larvae I-II	110157	5.0421	
k_1 (disease)			0.031
(Larvae I-II surviving disease)	102556	5.0110	
k_2 (disappearance)			0.027
Larvae III	96387	4.9840	
k_3 (disease)			0.237
(Larvae III surviving disease)	55808	4.7467	
k_4 (disappearance)			0.104
Larvae IV	43953	4.6430	
k_5 (disease)			0.145
(Larvae IV surviving disease)	31470	4.4979	
k_6 (disappearance)			0.119
Larvae V	23954	4.3794	
k_7 (disease)			0.123
(Larvae V surviving disease)	13990	4.1458	
k_8 (Parasitism)			0
(Larvae V surviving parasitism)	13990	4.1458	
k_9 (disappearance)			0.655
Pupae	3099	3.4912	
k_{10} (disease)			0.093
(Pupae surviving disease)	2500	3.3979	
k_{11} (Parasitism)			0.058
(Pupae surviving parasitism)	2187	3.3398	
k_{12} (disappearance)			0.018
Adults emerging	2100	3.3222	
		K =	1.691

Table 11. Partial mortality budget for Maruca testulalis at MPFS during lo rainy season 1984 (late crop).

	No./ha	Log.No./ha	K.value
Eggs laid	232019	5.3655	
k_o (egg loss)			0.129
Larvae I-II	172450	5.2367	
k_1 (disease)			0.014
(Larvae I-II surviving disease)	157102	5.1962	
k_2 (disappearance)			0.069
Larvae III	134031	5.1272	
k_3 (disease)			0.088
(Larvae III surviving disease)	109503	5.0394	
k_4 (disappearance)			0.048
Larvae IV	97955	4.910	
k_5 (disease)			0.041
(Larvae IV surviving disease)	89237	4.9505	
k_6 (disappearance)			0.050
Larvae V	79474	4.9002	
k_7 (disease)			0.338
(Larvae V surviving disease)	36532	4.5627	
k_8 (Parasitism)			0
(Larvae V surviving parasitism)	36532	4.5627	
k_9 (disappearance)			0.752
Pupae	6462	3.8104	
k_{10} (disease)			0.066
(Pupae surviving disease)	5554	3.7446	
k_{11} (Parasitism)			0.024
(Pupae surviving parasitism)	5256	3.7207	
k_{12} (disappearance)			0.148
Adults emerging	3737	3.5725	
		K =	1.794

Table 12. Partial mortality budget for Maruca testulalis at MPFS during 1 rainy season, 1985.

Age interval	No./ha	Log.No./ha	K.value
Eggs laid	478597	5.6800	
k_o (egg loss)			0.094
Larvae I-II	385447	5.5860	
k_1 (disease)			0
(Larvae I-II surviving disease)	385447	5.5860	
k_2 (disappearance)			0.107
Larvae III	301581	5.4794	
k_3 (disease)			0.030
(Larvae III surviving disease)	281375	5.4493	
k_4 (disappearance)			0.073
Larvae IV	237767	5.3762	
k_5 (disease)			0
(Larvae IV surviving disease)	237767	5.3762	
k_6 (disappearance)			0
Larvae V	238822	5.3781	
k_7 (disease)			0.213
(Larvae V surviving disease)	146373	5.1655	
k_8 (Parasitism)			0.005
(Larvae V surviving parasitism)	144751	5.1606	
k_9 (disappearance)			0.745
Pupae	26037	4.4156	
k_{10} (disease)			0.195
(Pupae surviving disease)	16619	4.2206	
k_{11} (Parasitism)			0.075
(Pupae surviving parasitism)	13996	4.1460	
k_{12} (disappearance)			0.574
Adults emerging	3737	3.5725	
		K =	2.111

Table 13. Partial mortality budget for Maruca testulalis at MPFS during short rainy season, 1985.

Age interval	No./ha	Log.No./ha	K.value
Eggs laid	19906	4.2990	
k_o (egg loss)			0.056
Larvae I-II	17502	4.2431	
k_1 (disease)			0.026
(Larvae I-II surviving disease)	16469	4.2167	
k_2 (disappearance)			0.024
Larvae III	15585	4.1927	
k_3 (disease)			0.064
(Larvae III surviving disease)	13462	4.1291	
k_4 (disappearance)			0.013
Larvae IV	13057	4.1158	
k_5 (disease)			0.039
(Larvae IV surviving disease)	11947	4.0773	
k_6 (disappearance)			0.202
Larvae V	7501	3.851	
k_7 (disease)			0.749
(Larvae V surviving disease)	1336	3.1258	
k_8 (Parasitism)			0.0
(Larvae V surviving parasitism)	1336	3.1258	
k_9 (disappearance)			0.263
Pupae	730	2.8633	
k_{10} (disease)			0.178
(Pupae surviving disease)	485	2.6857	
k_{11} (Parasitism)			0.068
(Pupae surviving parasitism)	415	2.6180	
k_{12} (disappearance)			0.183
Adults emerging	272	2.4346	
		K =	1.865

Table 14. Partial mortality budget for Maruca testulalis at Lambwe farmer field during long rainy season, 1984.

Age interval	No./ha	Log.No./ha	K.value
Eggs laid	327793	5.5156	
k_o (egg loss)			0.130
Larvae I-II	247287	5.3852	
k_1 (disease)			0.032
(Larvae I-II surviving disease)	225549	5.3532	
k_2 (disappearance)			0.101
Larvae III	178691	5.2521	
k_3 (disease)			0.162
(Larvae III surviving disease)	122940	5.0897	
k_4 (disappearance)			0.099
Larvae IV	97923	4.9909	
k_5 (disease)			0.030
(Larvae IV surviving disease)	91362	4.9608	
k_6 (disappearance)			0.013
Larvae V	88620	4.9475	
k_7 (disease)			0.320
(Larvae V surviving disease)	42415	4.6275	
k_8 (Parasitism)			0.035
(Larvae V surviving parasitism)	39115	4.5923	
k_9 (disappearance)			0.419
Pupae	14912	4.1735	
k_{10} (disease)			0.250
(Pupae surviving disease)	83855	3.9235	
k_{11} (Parasitism)			0
(Pupae surviving parasitism)	8385	3.9235	
k_{12} (disappearance)			0.311
Adults emerging	4096	3.6124	
		K =	1.902

Table 15. Partial mortality budget for Maruca testulalis at Lambwe farm field during long rainy season, 1985 (early crop).

Age interval	No./ha	Log.No./ha	K.valu
Eggs laid	264223	5.4220	
k_0 (egg loss)			0.069
Larvae I-II	225482	5.3531	
k_1 (disease)			0
(Larvae I-II surviving disease)	225482	5.3532	
k_2 (disappearance)			0.261
Larvae III	123623	5.0921	
k_3 (disease)			0.033
(Larvae III surviving disease)	124475	5.0587	
k_4 (disappearance)			0.058
Larvae IV	100254	5.0011	
k_5 (disease)			0
(Larvae IV surviving disease)	100254	5.0011	
k_6 (disappearance)			0
Larvae V	108433	5.0352	
k_7 (disease)			0.203
(Larvae V surviving disease)	68010	4.8326	
k_8 (Parasitism)			0.015
(Larvae V surviving parasitism)	65687	4.8175	
k_9 (disappearance)			0.604
Pupae	16356	4.2139	
k_{10} (disease)			0.069
(Pupae surviving disease)	13958	4.1448	
k_{11} (Parasitism)			0.013
(Pupae surviving parasitism)	13540	4.1316	
k_{12} (disappearance)			0.120
Adults emerging	10281	4.0120	
		K =	1.445

Table 16. Partial mortality budget for Maruca testulalis at Lambwe farmer' field during long rainy season, 1985, (late crop).

Age interval	No./ha	Log.No./ha	K.value
Eggs laid	146201	5.1620	
k_o (egg loss)			0.226
Larvae I-II	86357	4.9363	
k_1 (disease)			0
(Larvae I-II surviving disease)	86357	4.9363	
k_2 (disappearance)			0.238
Larvae III	49910	4.6982	
k_3 (disease)			0.079
(Larvae III surviving disease)	41625	4.6194	
k_4 (disappearance)			0.156
Larvae IV	29078	4.4636	
k_5 (disease)			0.008
(Larvae IV surviving disease)	28584	4.4561	
k_6 (disappearance)			0.002
Larvae V	28472	4.4544	
k_7 (disease)			0.393
(Larvae V surviving disease)	11530	4.0618	
k_8 (Parasitism)			0.070
(Larvae V surviving parasitism)	9816	3.9919	
k_9 (disappearance)			0.460
Pupae	3400	3.5315	
k_{10} (disease)			0.063
(Pupae surviving disease)	2810	3.4487	
k_{11} (Parasitism)			0.054
(Pupae surviving parasitism)	2479	3.3943	
k_{12} (disappearance)			0.187
Adults emerging	1613	3.2076	
		K =	1.956

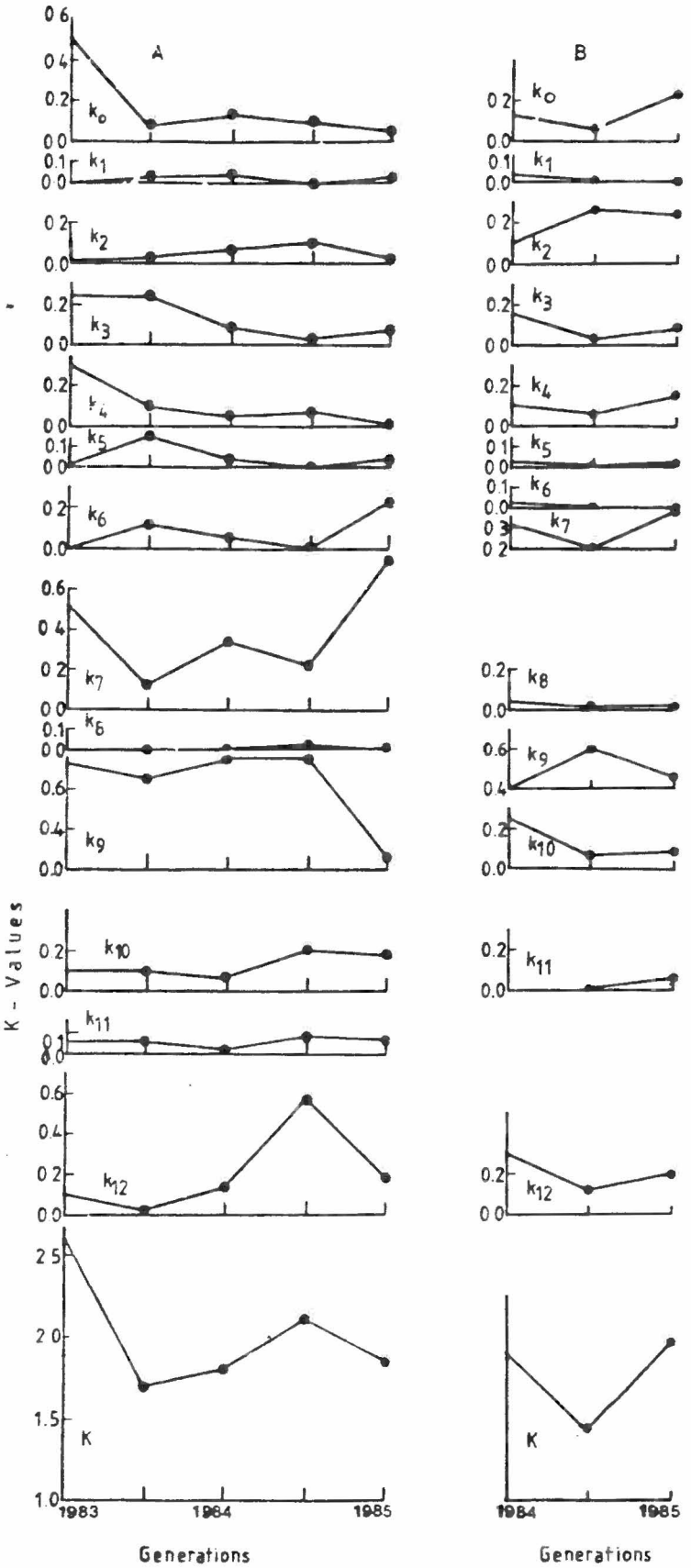
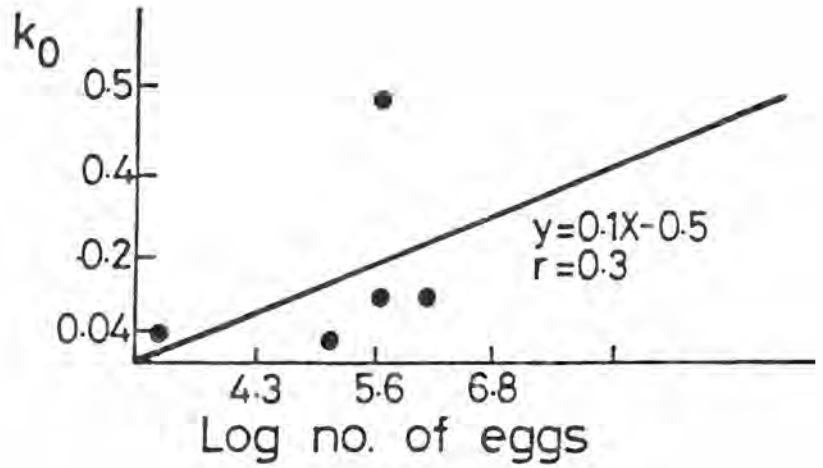
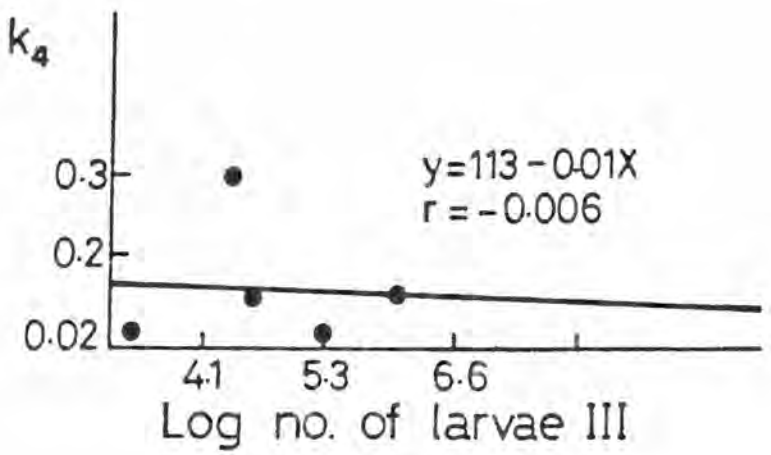

A
B
K - Values
k_0
k_1
k_2
k_3
k_4
k_5
k_6
k_7
k_8
k_9
k_{10}
k_{11}
k_{12}
K
1983
1984
1985
Generations
Generations

Figure 15. Key-factor analysis of M. testulalis life table data for MPFS (A) and Lambwe farmer's field (B).


k_0
0·5
0·4
0·2
0·04
y=0·1X-0·5
r=0·3
4·3
5·6
6·8
Log no. of eggs


k_4
0·3
0·2
0·02
y=113-0·01X
r=-0·006
4·1
5·3
6·6
Log no. of larvae III

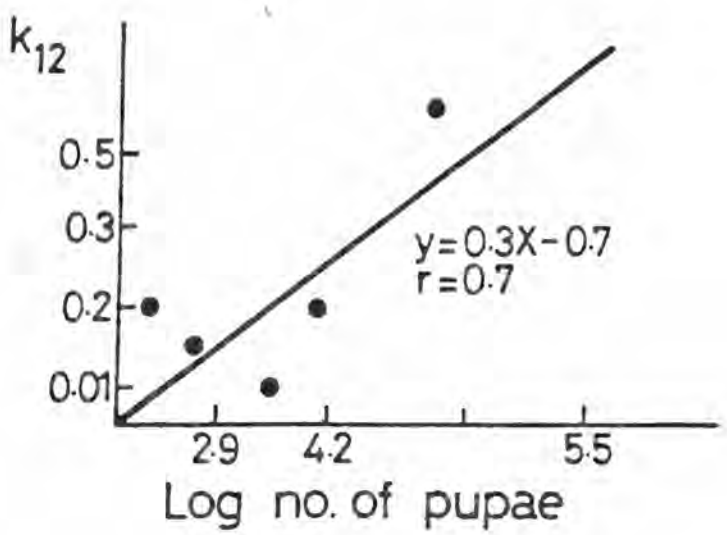
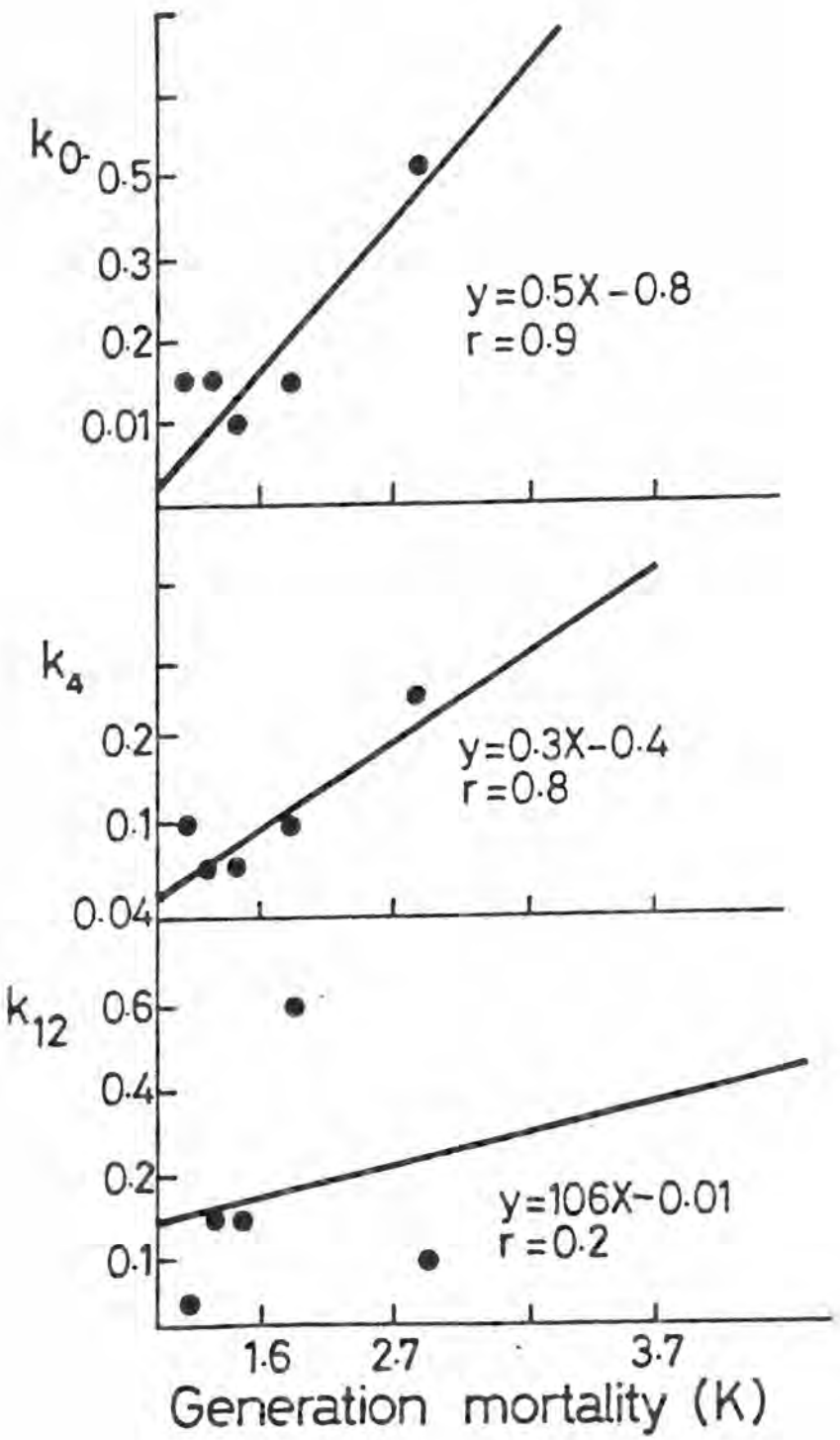

k_{12}
0·5
0·3
0·2
0·01
y=0·3X-0·7
r=0·7
2·9
4·2
5·5
Log no. of pupae

Figure 16. Correlation of the various k-values on generation mortality, K, for M. testulalis life stages at MPFS.

Figure 17. Relationship between morality factors (k-values) and density of M. testutalis life stages at MPFS.


k_0
0·5
0·3
0·2
0·01
y=0·5X−0·8
r=0·9
k_4
0·2
0·1
0·04
y=0·3X−0·4
r=0·8
k_{12}
0·6
0·4
0·2
0·1
y=106X−0·01
r=0·2
1·6
2·7
3·7
Generation mortality (K)

4.1.4 Factors causing mortality

Mortality of M. testulalis occurring at the various development stages are shown in the various life tables presented in Tables 1-8. Several factors were identified as causes of mortality at the various development stages. The term mortality is used here to designate reduction in numbers due to disappearance (predation, emigration, climatic and unidentifiable factors), parasitoids and pathogens directly or indirectly observed in field samples. Thus, disappearance signifies any losses in numbers which could not directly be attributable to either parasitoids or pathogenic microorganisms. The common parasitoids and pathogenic microorganisms recovered from M. testulalis are presented in Plates 11-13. Plate 10 shows the larvae of M. testulalis infected by pathogenic microorganisms.

Egg

Due to the problems in field already stated earlier in sampling eggs, direct causes of mortality in this stage was not identified and the reduction in egg numbers were grouped under disappearance (Tables 1-8). No evidence of egg parasitism was observed and viability o fertility could not be quantified under field conditions.

Larvae

Larval mortality at the two sites was caused by pathogenic microorganisms (disease), parasitoids and disappearance. Various microorganisms were recovered from dead M. testulalis larvae. Of these, the bacteria, Bacillus sp. and Clostridium sp., protozoa, Nosema sp. and Mettesia sp., an unidentified nematode, and viruses (nuclear polyhedrosis and granulosis) were pathogenic to M. testulalis larvae (Table 17). Nosema sp. and Bacillus sp. were the most common disease agents in this stage of the pest and were recovered from all the larval instars in all the generations at both study sites (Table 17). The incidence of these two pathogens contributed significantly to mortality in M. testulalis (Tables 1-8). Plate 11 shows Nosema sp. spores recovered from M. testulalis cadavers. Also an unidentified endoparasitic nematode was recorded on dead larvae and pupae of M. testulalis at both sites during 1984-1985 cropping periods but the incidence was negligible (Plate 12).

Four larval parasitoids were recovered from M. testulalis at both sites (Plate 13). At MPFS no larval parasitoids was recovered during 1983 and 1984 cropping seasons. During the long rainy season of 1985, however, hymenopteran parasitoids, Apanteles sp. and Bracon sp. (Braconidae) were recorded from only 0.6% M. testulalis 5th instar larvae throughout the generation. In the Lambwe site three larval parasitoids both hymenoptera, Apanteles sp., Chelonus sp. and an unidentified Braconidae were recorded on M. testulalis larvae during 1984 long rainy season. These were also recovered from 5th instar larvae and together

contributed to 3.7% mortality in this stage, representing only 0.01% real generation mortality. The results show that, although larval parasitoids of M. testulalis existed in natural populations at both the study sites, their contribution to natural mortality and subsequent effect on population change of the pest was low (Tables 1-8).

Other mortality factors which were not directly examined in the field included predation on larvae, dispersal or emigration, all grouped as disappearance. Mortality due to these factors was high but variable for different life stages and generations at both study sites. The results are given in various life tables for the generations studied (Table 1-8).

Pupae

As in the case of larvae, causes of pupal mortality were considered as being due to pathogens, parasitoids and disappearance (Table 1-8). The pathogenic microorganisms recovered from the pupae were similar to those of the larvae and their contribution to pupal mortality was variable in this stage (Table 1-8). Nosema sp. and Bacillus sp. were the most common pathogens (Table 17).

Five pupal parasitoids were recovered from field samples at the study sites (Plate 14). These were, Antrocephalus sp. (Chalcididae, Hymenoptera), Tetrastichus sesamiae Risbes (Eulophidae, Hymenoptera) Bracon sp. (Braconidae, Hymenoptera), Braunsia sp. (Braconidae, Hymenoptera) and an identified Tachinid (Diptera). Apart from T. sesamiae, the other parasitoids occurred at both sites, although,

the level of observed parasitism on pupae was low. Their contribution to real generation mortality ranged from only 0-0.02% at both sites (Table 1-8). Antrocephalus sp. was the most common parasitoid at both sites, although attempts to raise a laboratory colony failed. A gregarious pupal endo-parasitoid, T. sesamiae was recorded only at MPFS and its colony was easily raised under laboratory conditions. Bracon sp. was observed to parasitize both late instar larvae and pupae of M. testulalis, under laboratory conditions, but due to lack of mating, attempts to rear this parasitoid only yielded male adults and the colony was terminated.

The incidence of parasitoids and pathogens on dead M. testulalis collected from field samples at MPFS and Lambwe is presented in Table 17 for all the generations studied. The term "unknown" indicates that the cadaver was examined through microscopic and direct techniques and showed no symptom of any pathogen or parasitoid, although mortality occurred. Considering all the generations together at each site Nosema sp. contributed to the highest mortality in M. testulalis, being 34.3 $\pm$ 12.6% at MPFS and 41.8% in Lambwe, while parasitism contributed 5.3 $\pm$ 2.8% and 7.3 $\pm$ 3.6% of the total mortality at MPFS and Lambwe, respectively (Table 17).

Table 17. Percent incidence of parasitoids and pathogens on dead Maruca testulalis from field samples at MPFS and Lambwe farmer's field during 1983-1985 cropping seasons

	% INCIDENCE PER GENERATION (YEAR)												
	MBITA POINT								LAMBWE				
ORGANISM	1(83)	2(84)	3(84)	4(84)	5(84)	6(85)	7(86)	MEAN ± SD	1(84)	2(84)	3(84)	4(84)	5(84)	MEAN±SD
Parasitoids	6.4	3.5	1.0	-		8.9	6.8	5.3± 2.8	3.4			6.6	12.0	7.3± 3.6
Bacillus sp	16.2	42.6	27.3	-	-	21.0	15.3	24.5 ±10.0	15.0	-	-	42.9	8.0	21.7±14.7
Nosema sp	45.3	15.5	24.4	-	-	37.1	49.1	34.3±12.6	46.7	-	-	34.6	44.0	41.8± 5.2
Nematodes	0.0	0.0	0.0	-		4.3	0.0	0.9± 1.7	2.8	-	-	0.0	14.0	5.6±6.10
Fungi	3.4	9.1	6.7	-		1.8	6.8	5.6± 2.6	12.1	-	-	1.6	8.0	7.2± 4.3
Viruses	8.5	3.2	6.1	-	-	0.0	3.4	4.2± 2.9	0.4	-	-	0.0	0.0	0.1.±0.2
Other bacteria	0.0	1.6	0.3	-	-	0.0	0.0	0.4± 0.6	0.0	-	-	0.0	0.0	0.0
Unknown	20.2	24.5	34.2	-	-	26.9	18.6	24.9± 5.5	19.6	-	-	14.3	14.0	16.0± 2.6

Plate 10. M. testulalis larva infected by pathogenic microorganisms.

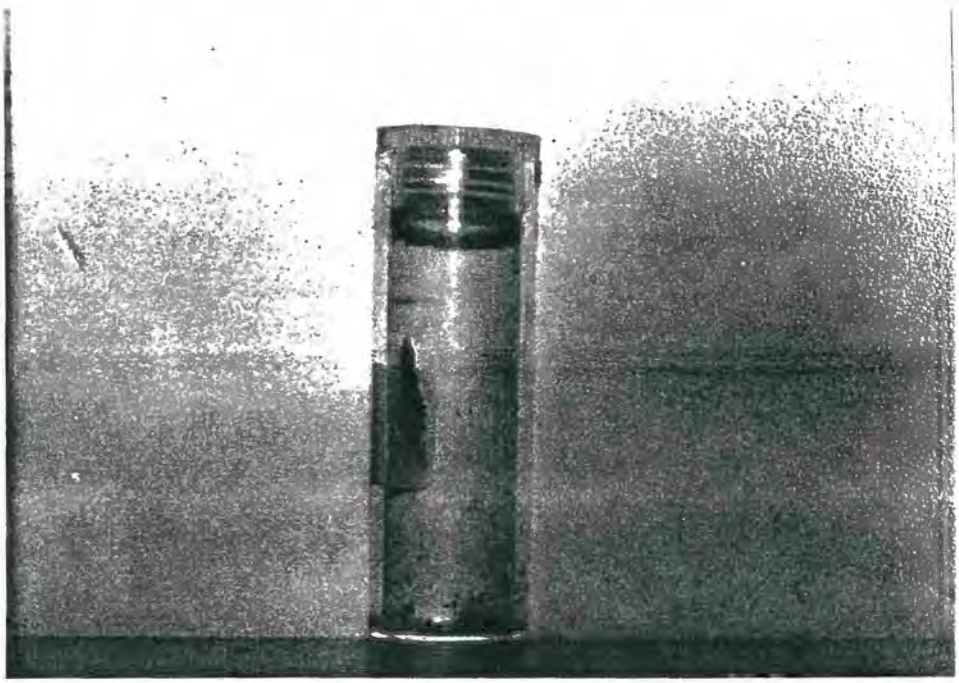
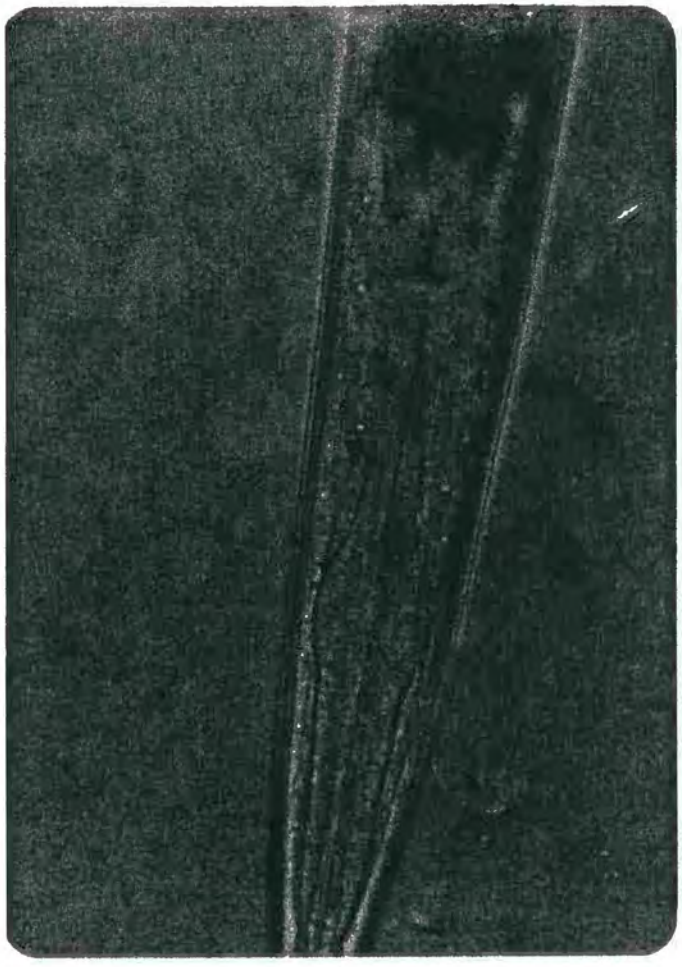


Plate 11. Nosema sp. a microorganisms recorded on cadavers of M. testulalis larvae at MPFS and Lambwe.

Plate 12. An unidentified endoparasitic nematode recorded on M. testulalis cadavers at MPFS, 1984-1985.



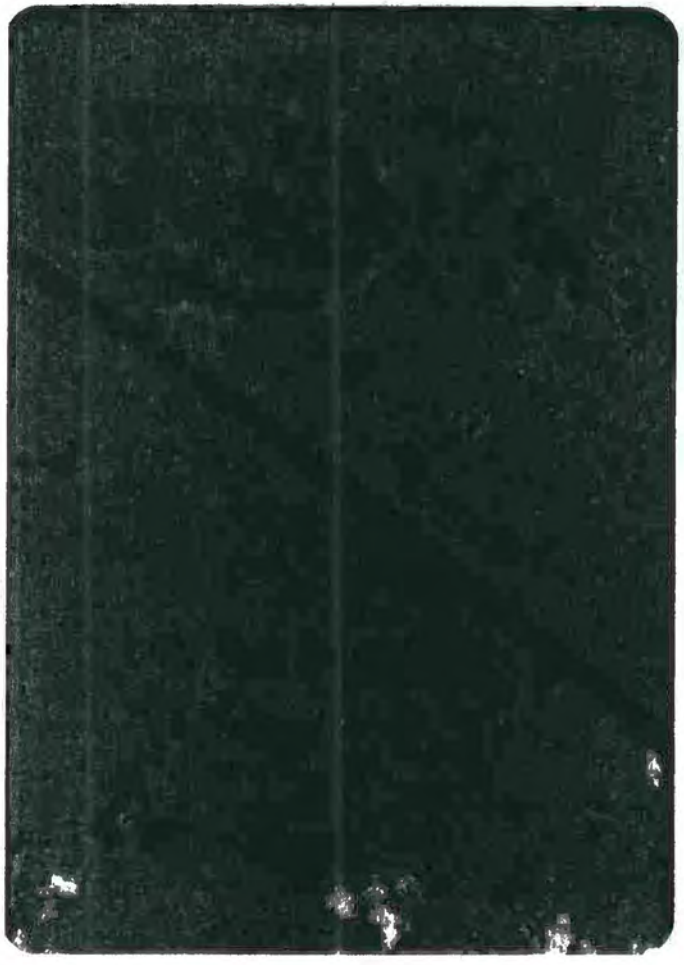


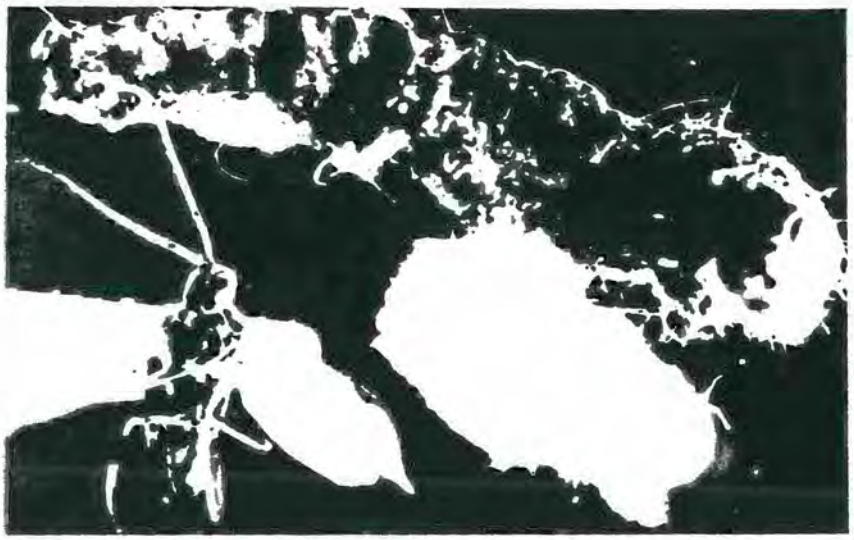
Plate 13. Parasitoids of M. testulalis larvae recorded at MPFS and Lambwe, 1983-1985.

A. Chelonus sp. (Braconidae, Hymenoptera)

B. Apanteles sp. (Braconidae, Hymenoptera)

C. Bracon sp. (Braconidae, Hymenoptera).

А



Б

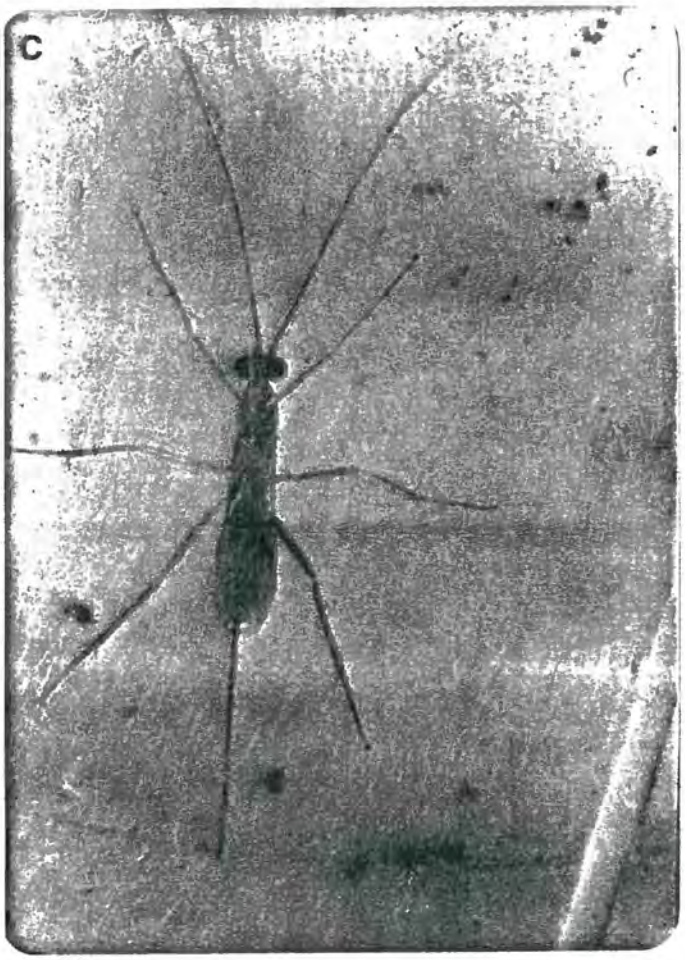
Plate 14. Parasitoids of M. testulalis pupae recorded at MPFS and Lambwe, 1983-1985.

A. Testrastichus sesamiae (Eulophidae, Hymenoptera)

B. Antrocephalus sp. (Chalcididae, Hymenoptera)

C. Braunsia sp. (Braconidae, Hymenoptera)

D. An unidentified Tachinid (Diptera)


C

C

D

4.2. SURVIVAL AND DEVELOPMENT OF M. TESTULALIS ON HOST PLANTS

4.2.1 Survival and distribution on cowpea plants in the

Studies on the distribution of the different life stages of M. testulalis on cowpea plant in the field showed that 79.6% of the eggs were laid on cowpea leaves and especially on the lower surfaces of the leaves (Figure 18). The rest of the eggs were recovered from stems and rarely on flowers and pods (Figure 18). Figures 19-26 show the distribution of M. testulalis larvae on the different cowpea plant parts from the period the first larvae were detected on the crop (30-33 DAPE) to crop maturity at both study sites. These results, show that the distribution of this stage changed with changing crop phenology. At the initial stages, just before flower initiation the majority of the larvae were found on the vegetative parts of the plant especially on terminal buds, tender parts of the stems, and young leaves, (27-36 DAPE) (Figures 19-26). When more flowers were formed on the plants, between 36 and 51 DAPE, a definite shift in larval distribution occurred on the plants with 90-100% of the larvae being found on flowers and later on pods (Figures 19-26).

The larval population was terminated when the mature pods were dry in the case of all the generations studied at MPFS (1983-1985) and that at Lambwe during 1984 long rains (Figures 19-23). In the case of the Lambwe, during 1985 long rainy season, normal crop, the rainfall

period was extended resulting into plant rejuvenation and hence continued attack by M. testulalis larvae (Figures 24-25). The late crop gave very few pods and flowers at this site and the larvae were mostly found on vegetative plant parts after 70 DAPE (Figure 26).

Further, analysis to determine the relationship between some plant characters especially, flower bud, flowers and pod production and natural populations of M. testulalis were conducted. The results are presented in Figures 27-29. It was found that the mean larval population per generation was positively correlated to the number of flower buds (r = 0.506), flowers (r = 0.788) and pods (r = 0.733). This relationship was significant (P = 0.05) in the case of flowers and pods (Figures 28 and Table 18). There was no significant correlation (P = 0.5) between the mean number of eggs laid per plant per season and the number of flower buds, flowers or pods per plant (Figure 27 and Table 18). Similar results were also observed in the case of pheromone trap catches of male moths (Figure 29 and Table 18).

4.2.2. Survivorship and development in screen house

Studies initiated to determine the effect of cowpea plant on M. testulalis survivorship and development on potted plant proved unsuccessful due to high migration in the larvae and poor growth of the plants in pots and were therefore abondoned.

The survivorship of M. testulalis on the cowpeas directly planted in screen house and open field conditions and artificially infested with M. testulalis eggs are shown in Figure 30. From the data obtained, it was found that the egg hatch under both conditions were

similar being 78.8% in screen house as compared to 73.0% in the open field (Table 19). The survivorship curves for both screen house and open field were also similar (Figure 30). The results also show that there were high mortalities in the early development stages of M. testulalis (Figure 30). A summary of the number of M. testulalis surviving in both screen and open field conditions from eggs to adult stage is presented in Table 19. The results show low generation survivorship, 3.0% in screen house and 1.2% in open field.

Observations on the development period from egg to adult stage in the screen house and open field showed similar results (Table 2). The eggs hatched in 2-3 days, larval period was 9-14 days in screen house and 10-14 days in open field, while the range in pupal period were 6-11 days and 7-12 days respectively (Table 20). In the screen house the total life cycle lasted 17-26 days and that in open field was 19-29 days (Table 20).

4.2.3 Survival and development on different parts of the cowpea plant

The effects of feeding M. testulalis larvae on stems, terminal buds, green mature pods, tender green pods and flowers of the ICV6 cowpea plants are presented in Figure 31. Survival of the

larvae to pupation and adult emergence were significantly lowered (P=0.05) by feeding them on stem and terminal buds as compared to soft leaves, pods and flowers (Figure 31A). The larvae failed to feed on old leaves and there was no survival even to pupation stages. The best survivorship occurred when the larvae were fed on tender green pods and flowers whose performance were not different significantly (P = 0.05) (Figure 31A). Considering larval development period, the reproductive plant parts (mature and tender pods and flowers)gave significantly lower development period than the vegetative parts (stems, terminal buds and leaves) all of which were not different (P = 0.01) (Figure 31B). Figure 31C shows that feeding M. testulalis larvae on the different parts of the ICV6 variety had no significant effect on the pupal period. However, pupal weights of M. testulalis were adversely affected by feeding on the vegetative parts of the cowpea plant (Figure 31D). High pupal weights were observed in larvae fed on tender pods, mature green pods which performed significantly better than flower fed larvae (Figure 31D).

The effect of the different parts of the cowpea plant on the life cycle of M. testulalis is presented in Figure 31E. The total development period of this species was shortest on tender green pods (17.7 ± 1.2 days) followed by green mature pods (18.0 ± 1.4 days) all of which were not significantly different, (P = 0.05)

(Figure 31E). The longest life cycle occurred in the case of stems (20 days) followed by leaves (19.1 ± 1.9 days) and then terminal shoots (18.5 ± 1.5 days) which were also not significantly different (Figure 31D).

4.2.4. Role of wild host plants on population of M. testulalis

The wild hosts of M. testulalis found in the various study sites are shown in Table 21. Of the many wild legume species searched, M. testulalis larvae were recovered from only ten species all belonging to the family Papilionoidae. The relative abundance of M. testulalis larvae on each plant species at every locality are designated as: (-) for absent, (+) for rare (less than 5 larvae/100 flowers), (++) for moderately abundant (5-10 larvae/100 flowers) and (+++) for abundant (more than 10 larvae/100 flowers) as shown in Table 21. The results of these ratings showed that M. testulalis was most abudant on Sesbania sesban L. followed by Vigna vexillata L. and V. luteola (Jacq) Benth (Table 21). Lambwe valley area B yielded the highest number of M. testulalis larvae in each wild host plant followed by Rusinga and then MPFS and the lowest number of larvae was obtained from Lambwe area A surrounding the farmers experimental plot and Rangwe area (Table 21). Plate 15 shows S. sesban a wild host plant on which M. testulalis larvae were found to be most abundant in western Kenya.

In Rusinga Island and Lambwe area B parasitoids were recorded on M. testulalis collected on wild host plants (Table 21). These were Bracon sp. on larvae and Antrocephalus sp. (Chalcidiae), on pupae of M. testulalis. At three localities, Rusinga, Lambwe B and MFFS direct larval mortality due to pathogens especially, Nosema sp. and Bacillus sp. was also observed (Table 21).

Table 18. Correlation Coefficient (r) of natural populations of M. testulalis versus mean number of varius cowpea plant parts produced during different cropping seasons at MPFS (1983-1985).

	Adult males	Eggs	Larvae
Flower buds	0.055 ns	-0.257 ns	0.506 ns
Flowers	0.678 ns	0.375 ns	0.788*
Pods	0.598 ns	0.086 ns	0.733*

*- Significant at 0.05 level, ns - non significant

Table 19. Number of M. testulalis surviving at each development stage in screen house and open field after artificial infestation of cowpea plants with eggs

Age Interval	NO. OF MARUCA RECOVERED			
	Screen house		Open field	
	No.	%	No.	%
Eggs	1200	100	1200	100
Larvae 1st Instar	945	78.8	876	73.0
3rd Instar	264	22.0	228	19.0
Pupae	169	14.1	101	8.4
Adults	36	3.0	14	1.2

Table 20. Development time and life cycle of M. testulalis in screen house and open field conditions after artificial infestation of cowpea with eggs.

Age Interval	Development period (days)	
	Screen house	Open field
Eggs	2 - 3	2 - 3
Larvae	9 - 12	10 - 14
Pupae	6 - 11	7 - 12
Total	17 - 26	19 - 29

Table 21. Incidence of Maruca testulalis and its natural enemies on wild host (samples taken at 5 locations between November 1984 and March 1985). (- = absent + = rate, ++ = moderately abundant, +++ = abundant)

Location & Host Plant on which Maruca were found	Maruca and enemies			
	Eggs	Larvae	Parasitism	Pathogens
1. MPTS				
Sesbania sesban L.	-	++	-	N+
Crotolaria deserticola L.	-	-	-	-
Vigna vexillata L.	-	++	-	-
Rhynchosia melacophylla (Spreng)	-	+	-	-
2. Lambwe farmers field (area A)				
Sesbania sesban L.	-	+	-	-
Crotolaria deserticola L.	-	-	-	-
Rhynchosia melacophylla (Spreng) Boj	-	-	-	-
Vigna vexillata L.	-	+	-	-
3. Lambwe (area B)				
Sesbania sesban L.	-	+++	-	+(N & B)
Crotolaria deserticola L.	-	+	-	-
Rhynchosia melacophylla (Spreng)	-	+	-	-
Vigna vexillata L.	-	++	-	+(N & B)
Rhynchosia sp. nr maxima (L) DC.				
4. Rusinga area				
Sesbania sesban L.	-	+++	-	+B
Crotolaria spp.	-	+	-	-
Vigna vexillata L.	-	++	+	-
5. Rangwa area				
Sesbania sesban L.	-	+	-	-
Vigna lutiola	-	++	+	-

N - Nosema sp.) recovered from dead M. testulalis larvae from
B - Bacillus sp.) field samples.

Plate 15. Sesbania sesban L. (Papilionoidae, Leguminosae) an important wild host plant of M. testulalis in western Kenya.

A

B

Figure 18. Distribution of M. testulalis eggs on various parts of cowpea plant under MPFS field conditions.

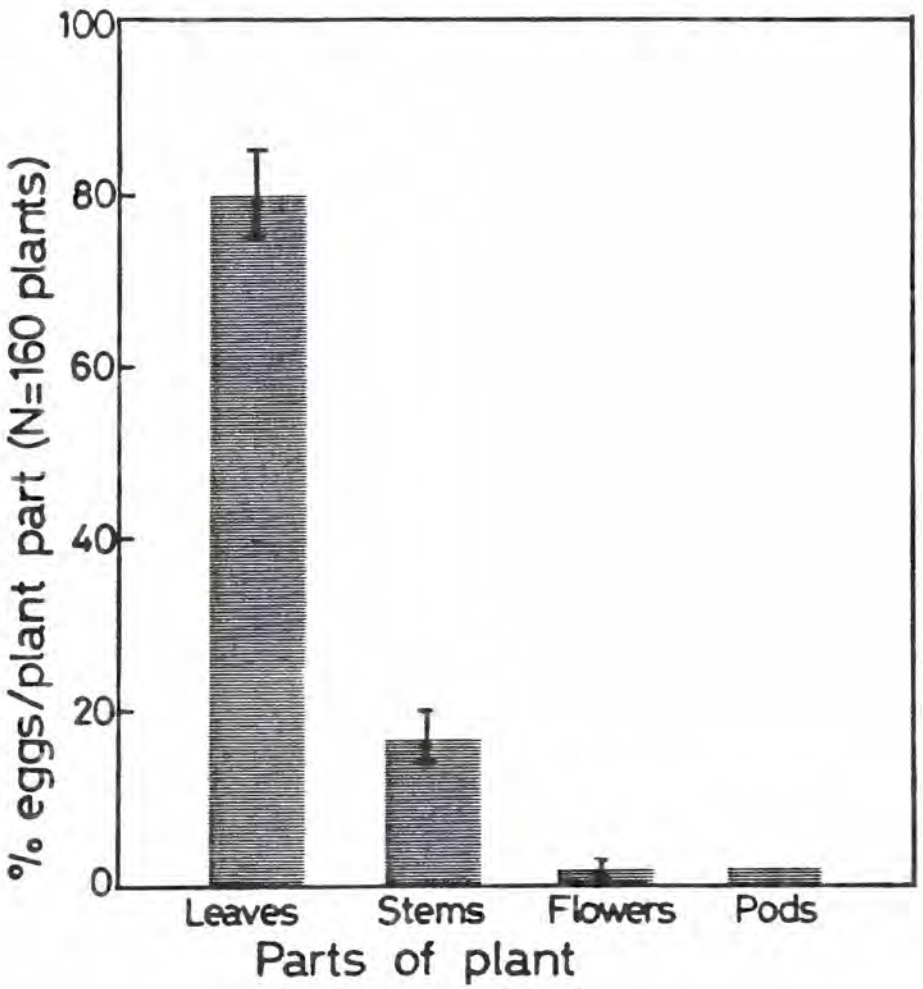

100
80
60
40
20
0
% eggs/plant part (N=160 plants)
Leaves
Stems
Flowers
Pods
Parts of plant

Figure 19. Per cent M. testulalis larvae found on different parts of cowpea plants during various phenological stages at MPFS, 1983 short rains.

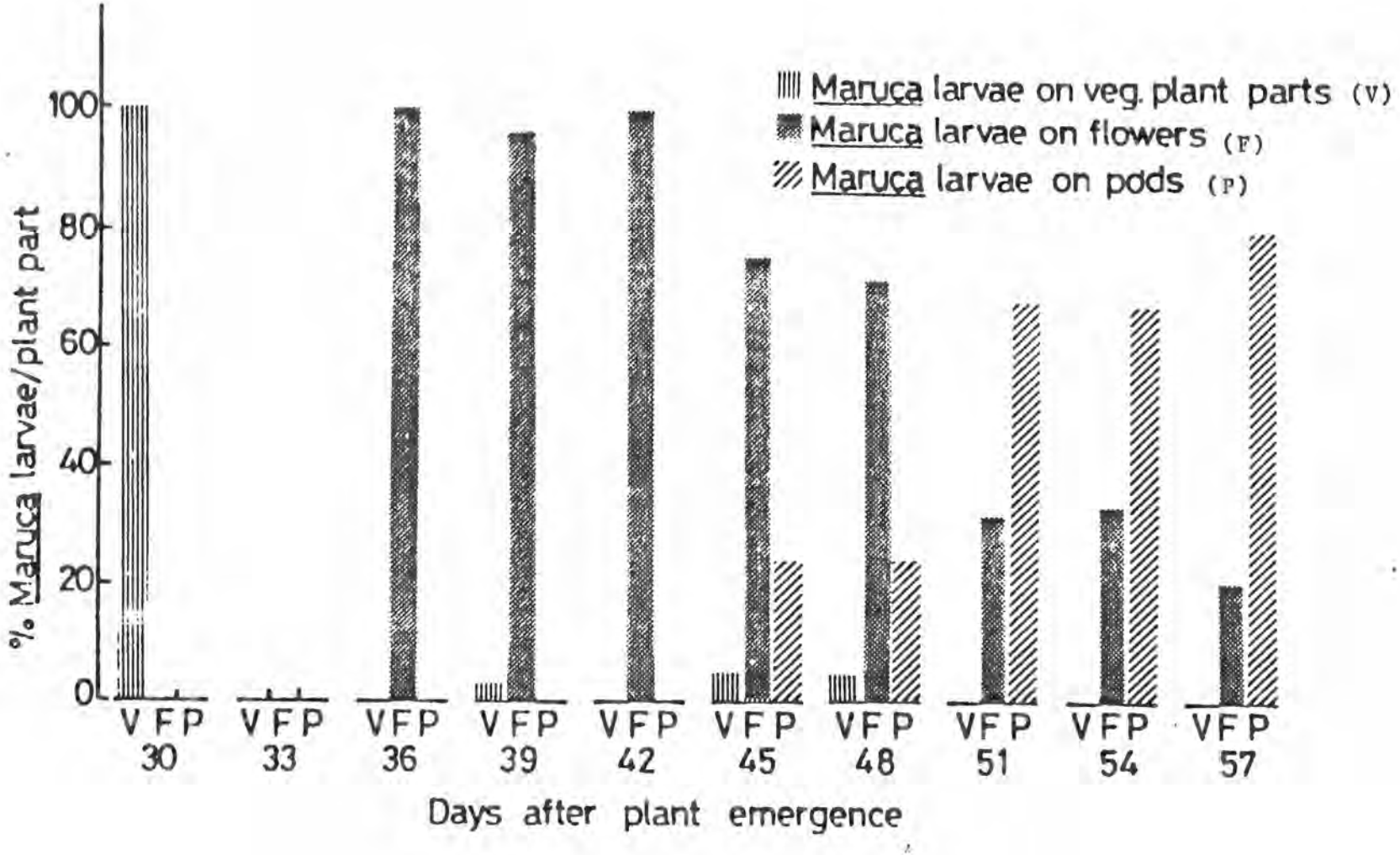

Maruça larvae on veg. plant parts (V)
Maruca larvae on flowers (F)
Maruça larvae on pods (P)
% Maruça larvae/plant part
100
80
60
40
20
0
V F P
30
33
36
39
42
45
48
51
54
57
Days after plant emergence

Figure 20. Per cent M. testulalis found on different parts of cowpea plants during the various phenological stages at MPFS, 1984 long rains.

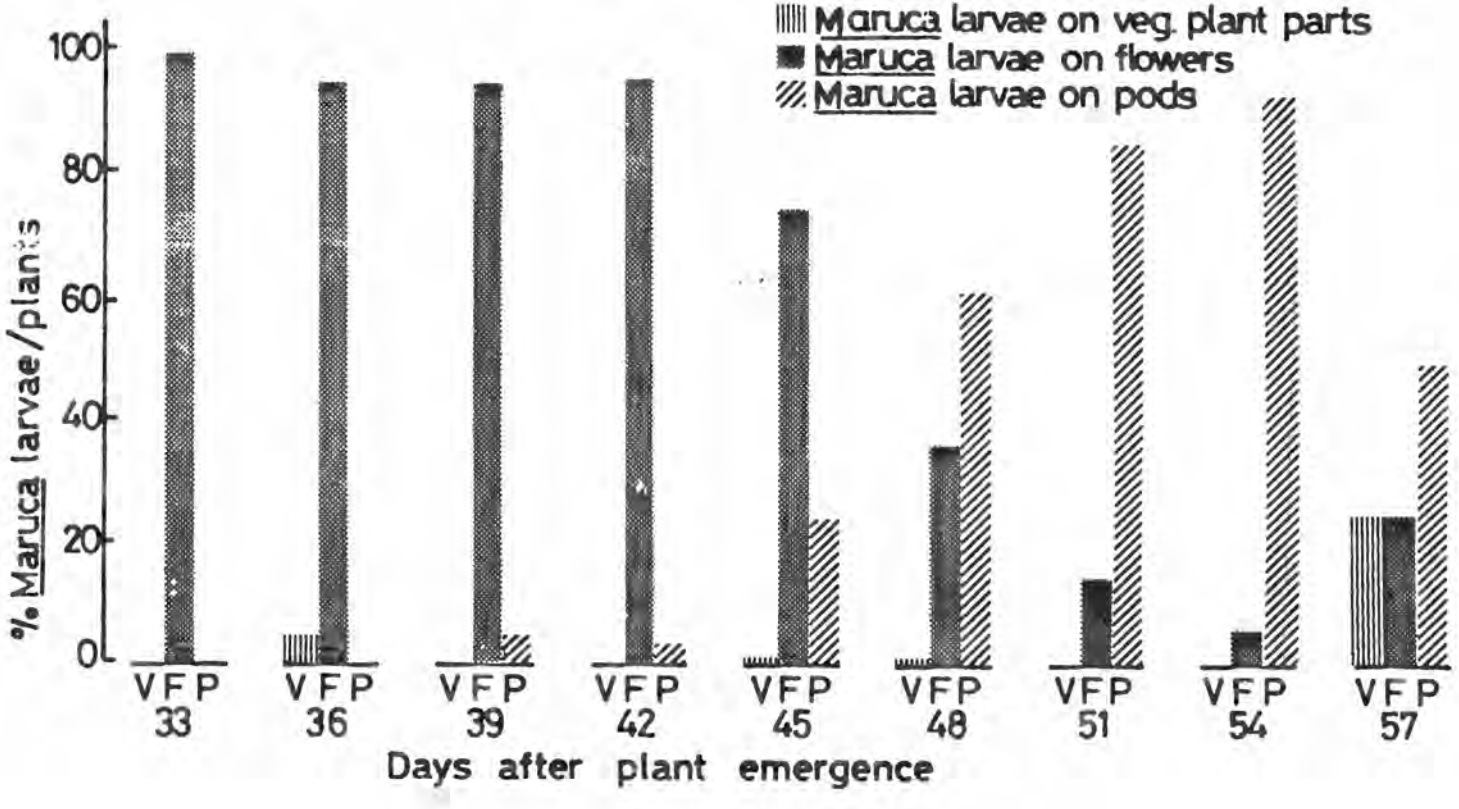

Maruca larvae on veg. plant parts
Maruca larvae on flowers
Maruca larvae on pods
% Maruca larvae/plants
100
80
60
40
20
0
VFP 33
VFP 36
VFP 39
VFP 42
VFP 45
VFP 48
VFP 51
VFP 54
VFP 57
Days after plant emergence

Figure 21. Per cent M. testulalis larvae on different parts of the cowpea plants during the various phenological stages at MPFS, 1984 long rains (late crop).

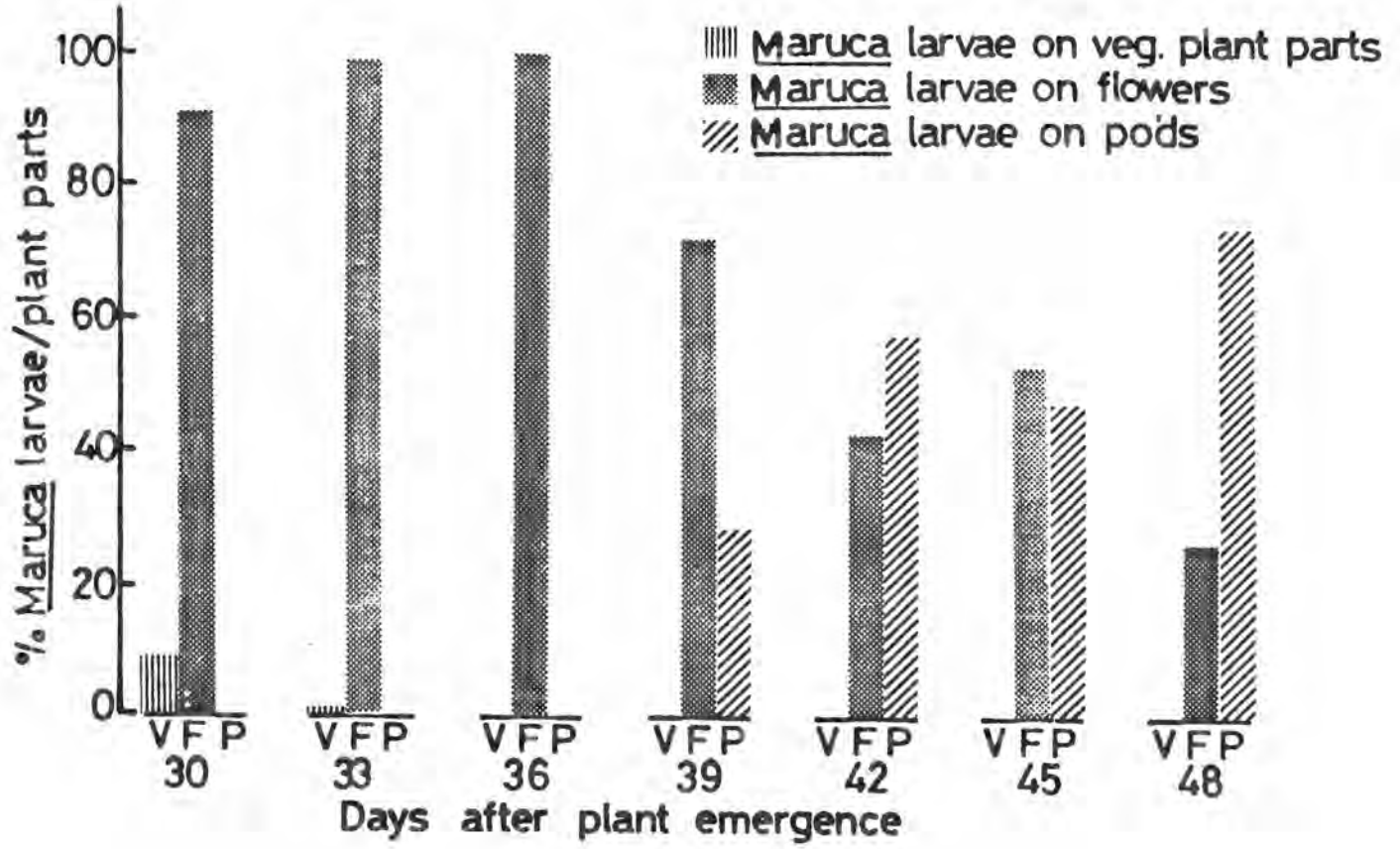

Maruca larvae on veg. plant parts
Maruca larvae on flowers
Maruca larvae on pods
% Maruca larvae/plant parts
100
80
60
40
20
0
V F P
30
33
36
39
42
45
48
Days after plant emergence

Figure 22. Per cent M. testulalis larvae found on different parts of cowpea plant during the various phenological stages at MPFS, 1985 long rains.

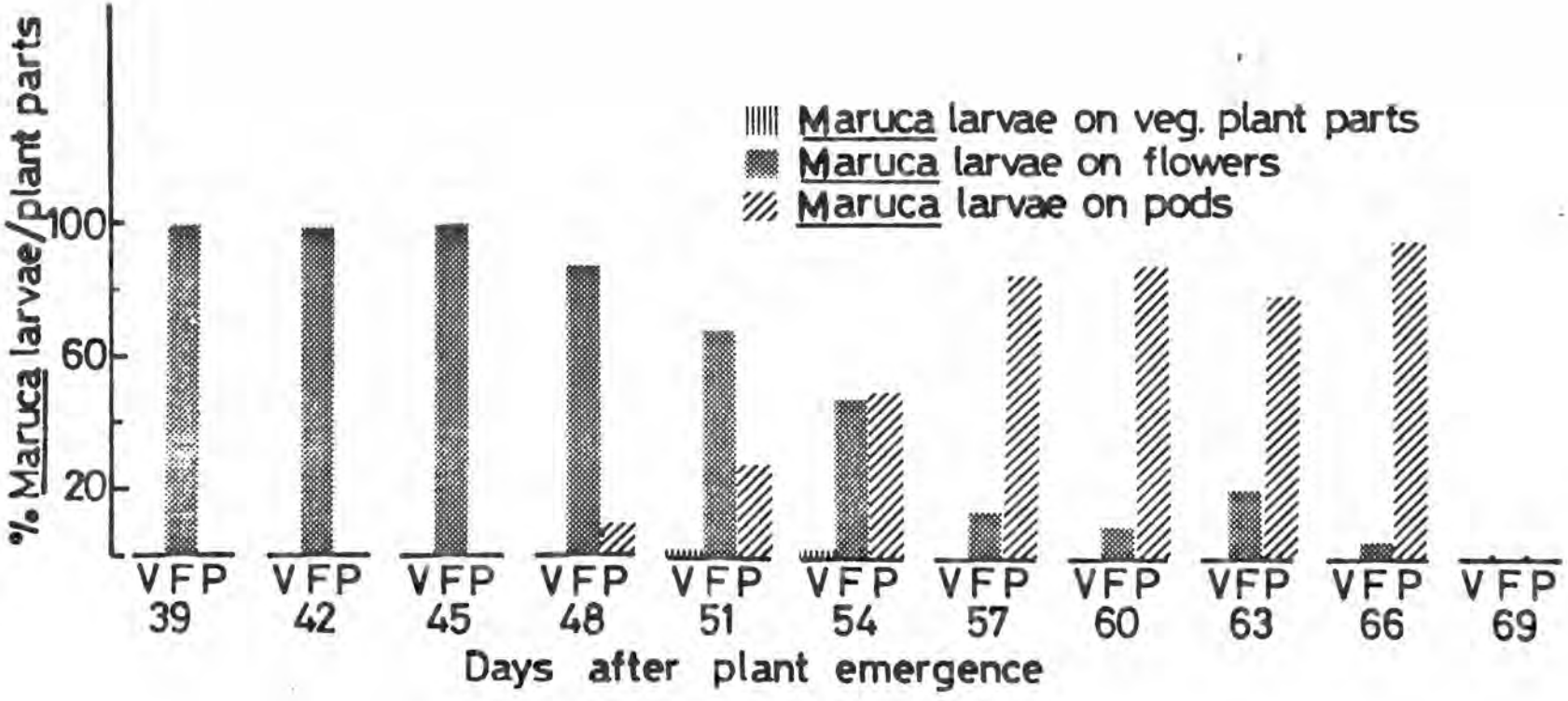

% Maruca larvae/plant parts
100
60
20
Maruca larvae on veg. plant parts
Maruca larvae on flowers
Maruca larvae on pods
VFP 39
VFP 42
VFP 45
VFP 48
VFP 51
VFP 54
VFP 57
VFP 60
VFP 63
VFP 66
VFP 69
Days after plant emergence

Figure 23. Per cent M. testulalis larvae found on different parts of cowpea plants during the various phenological stages at MPFS, 1985 short rains.

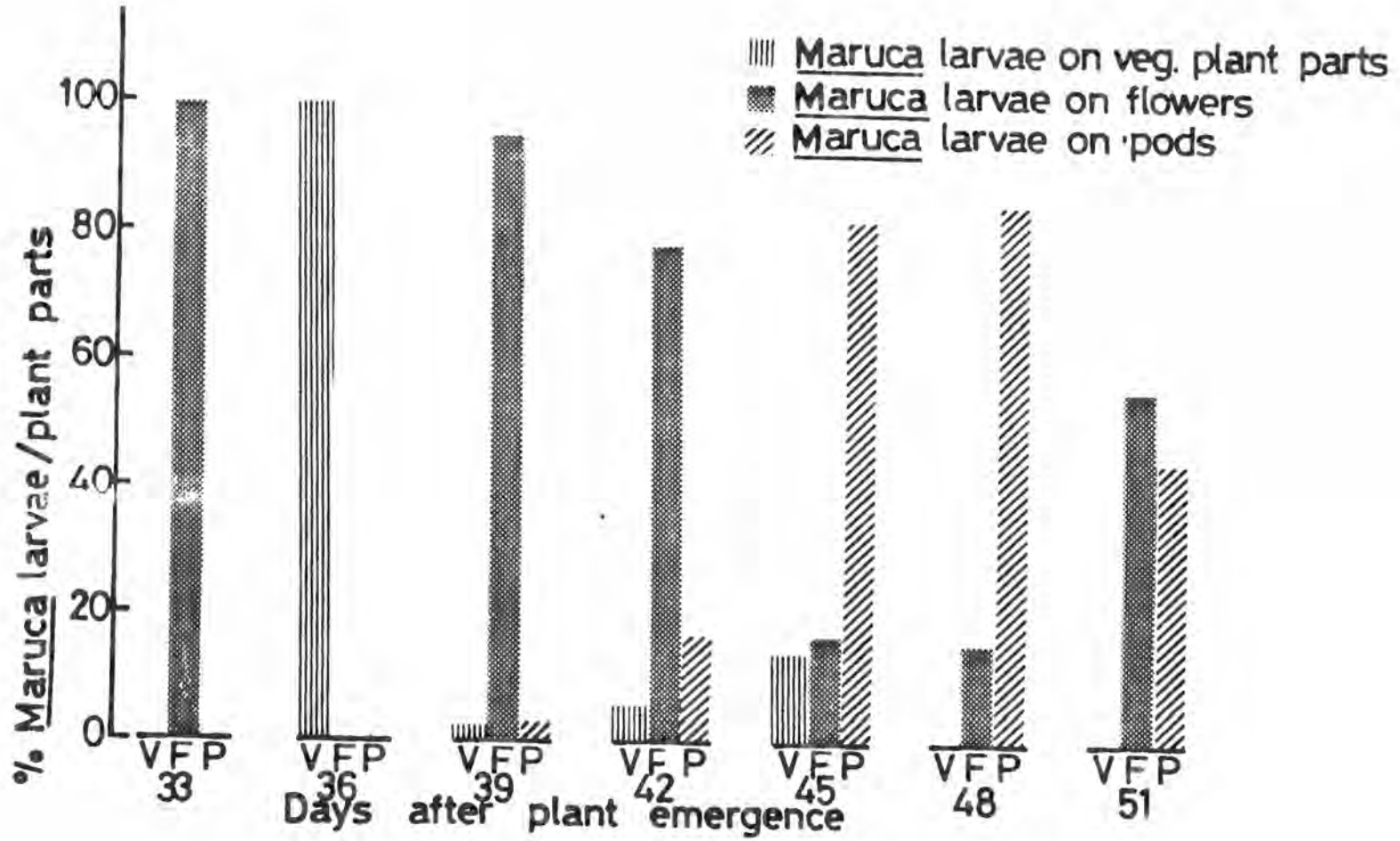

Maruca larvae on veg. plant parts
Maruca larvae on flowers
Maruca larvae on pods
% Maruca larvae/plant parts
100
80
60
40
20
0
V F P
33
36
39
42
45
48
51
Days after plant emergence

Figure 24. Per cent M. testulalis larvae found on different parts of cowpea plants during the various phenological stages in Lambwe, 1984, long rains.

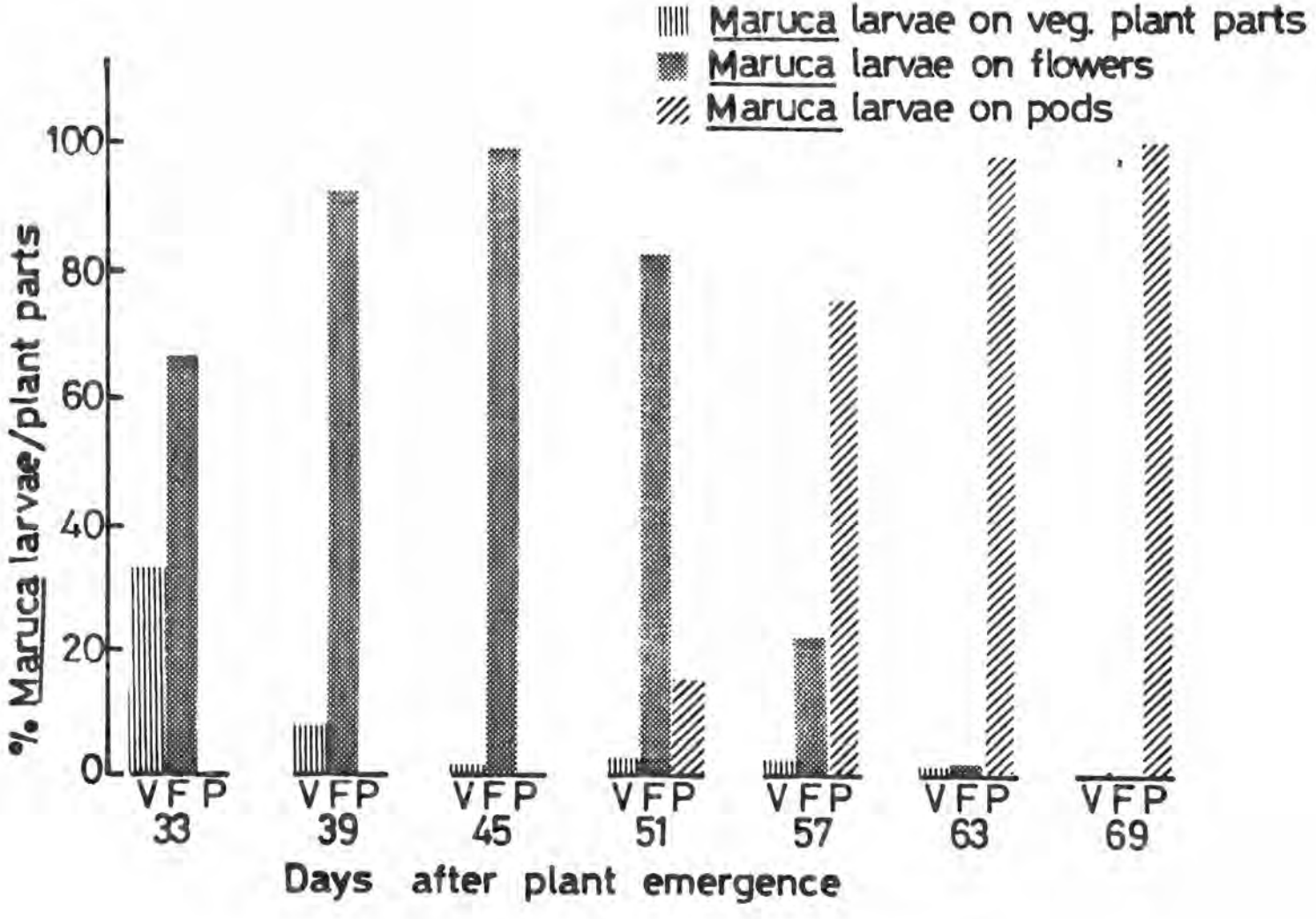

Maruca larvae on veg. plant parts
Maruca larvae on flowers
Maruca larvae on pods
% Maruca larvae/plant parts
100
80
60
40
20
0
V F P
33
39
45
51
57
63
69
Days after plant emergence

Figure 25. Per cent M. testulalis larvae found on different parts of cowpea plant during the various phenological stages in Lambwe, 1985 long rains.

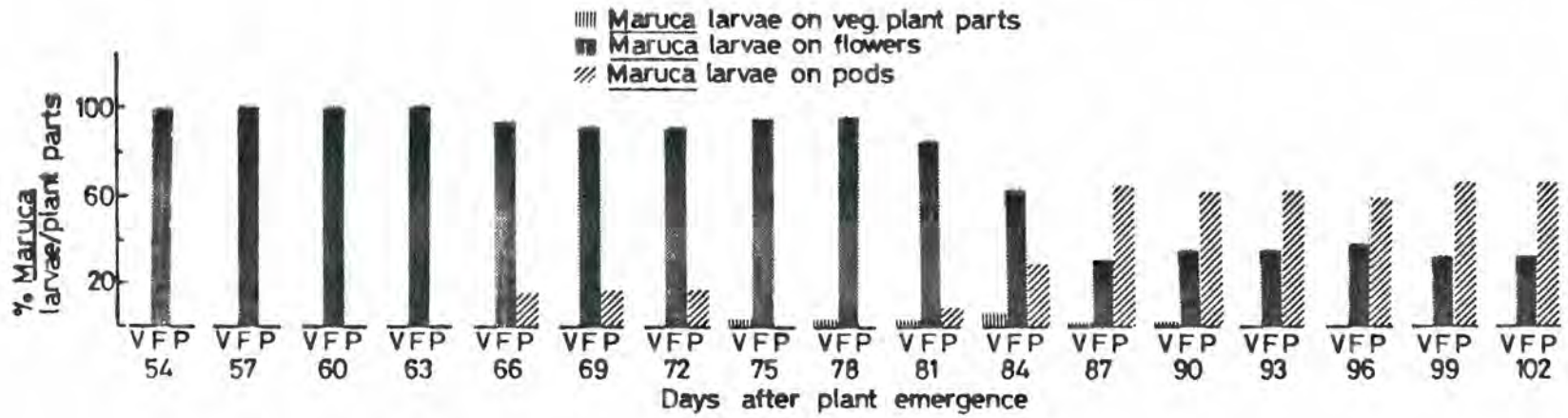

Maruca larvae on veg. plant parts
Maruca larvae on flowers
Maruca larvae on pods
% Maruca larvae/plant parts
100
60
20
VFP
54
57
60
63
66
69
72
75
78
81
84
87
90
93
96
99
102
Days after plant emergence

Figure 26. Per cent M. testulalis larvae found on different parts of cowpea plants during the various phenological stages in Lambwe, 1985 long rains (late crop).

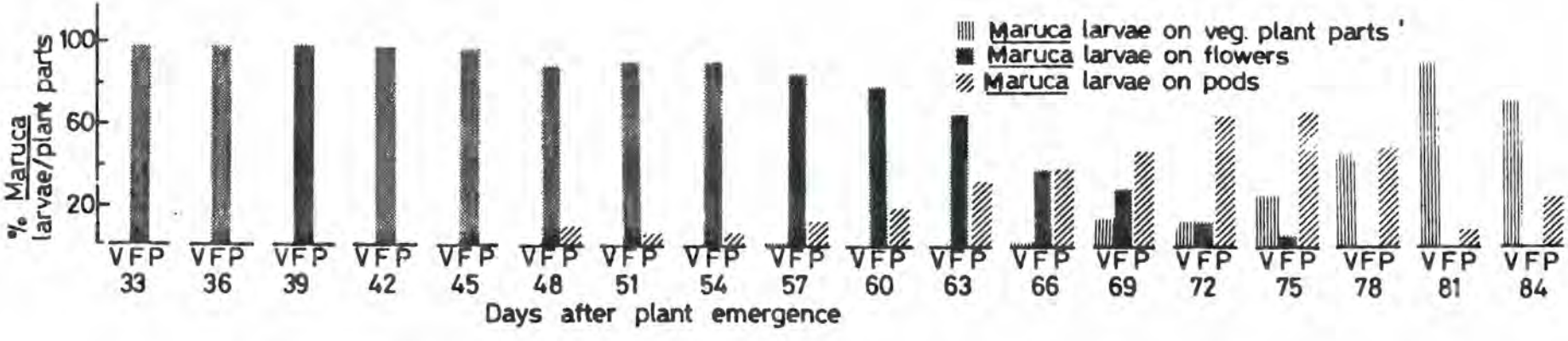

% Maruca larvae/plant parts
100
60
20
Maruca larvae on veg. plant parts
Maruca larvae on flowers
Maruca larvae on pods
V F P
33 36 39 42 45 48 51 54 57 60 63 66 69 72 75 78 81 84
Days after plant emergence

Figure 27. Correlation analysis of mean number of M. testulalis eggs on the number of various plant parts produced on the cowpea plant per season at MPFS.

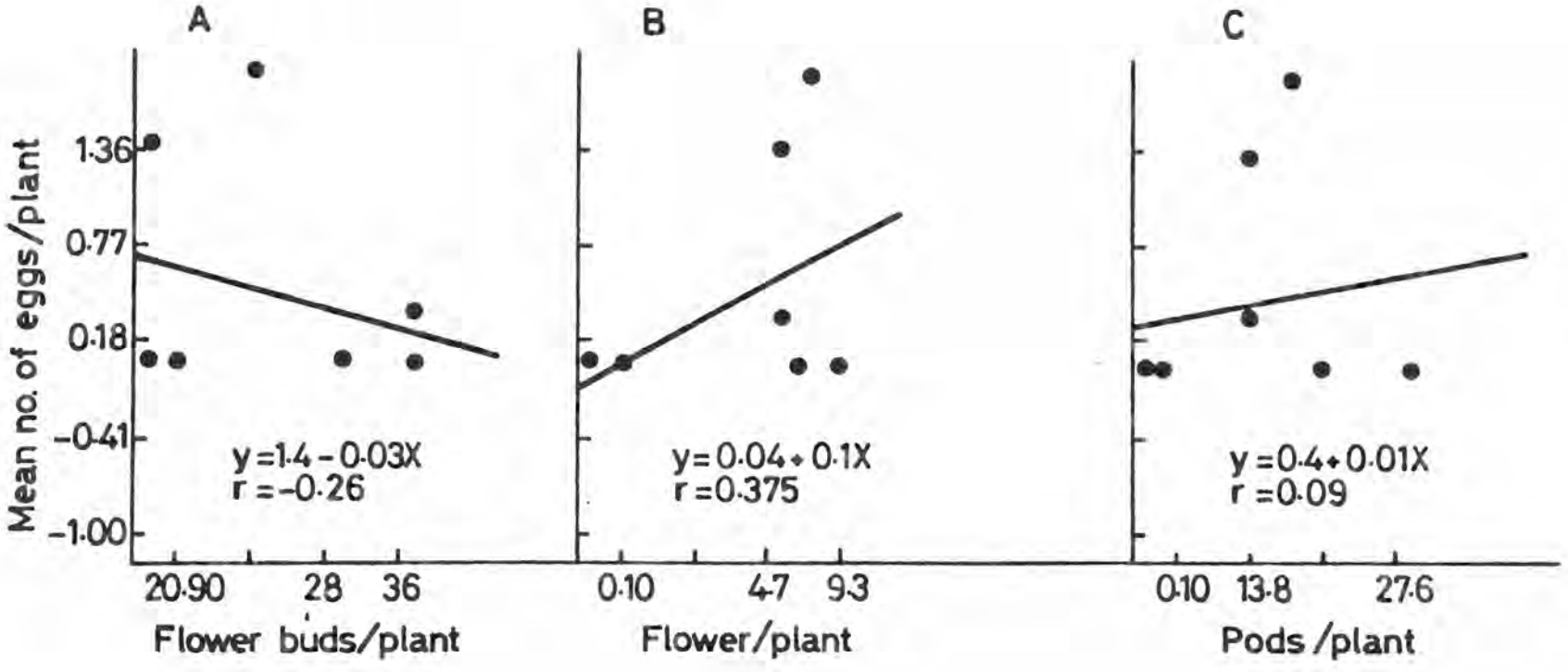

A
B
C
Mean no. of eggs/plant
1·36
0·77
0·18
-0·41
-1·00
y =1·4 - 0·03X
r = -0·26
y= 0·04 + 0·1X
r =0·375
y =0·4 + 0·01X
r =0·09
20·90
28
36
0·10
4·7
9·3
0·10
13·8
27·6
Flower buds/plant
Flower/plant
Pods /plant

Figure 28. Correlation analysis of mean number of M. testulalis larvae on various parts produced on the cowpea plant per season at MPFS.

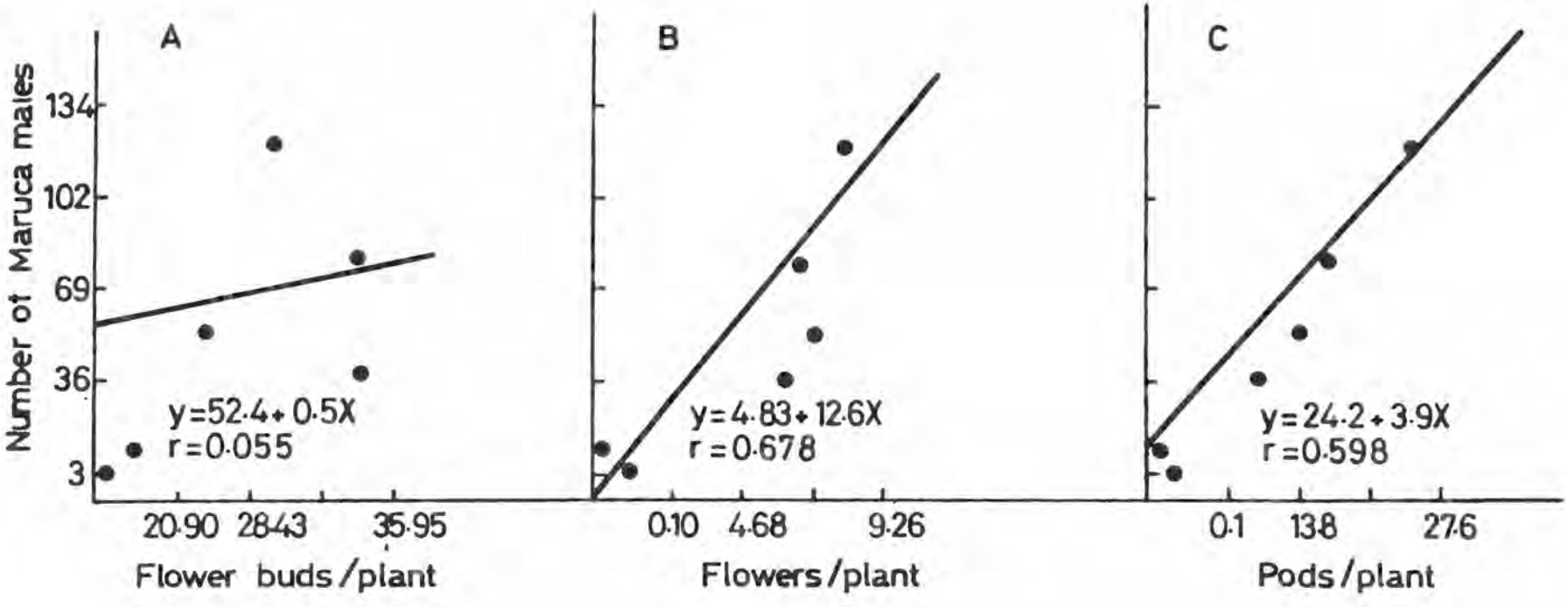

A
B
C
Number of Maruca males
134
102
69
36
3
y=52·4+0·5X
r=0·055
y=4·83+12·6X
r=0·678
y=24·2+3·9X
r=0·598
20·90 28·43 35·95
Flower buds/plant
0·10 4·68 9·26
Flowers/plant
0·1 13·8 27·6
Pods/plant

Figure 29. Correlation analysis of mean number of M. testulalis male moths on the number of various plant parts produced on the cowpea plant per season at MPFS.

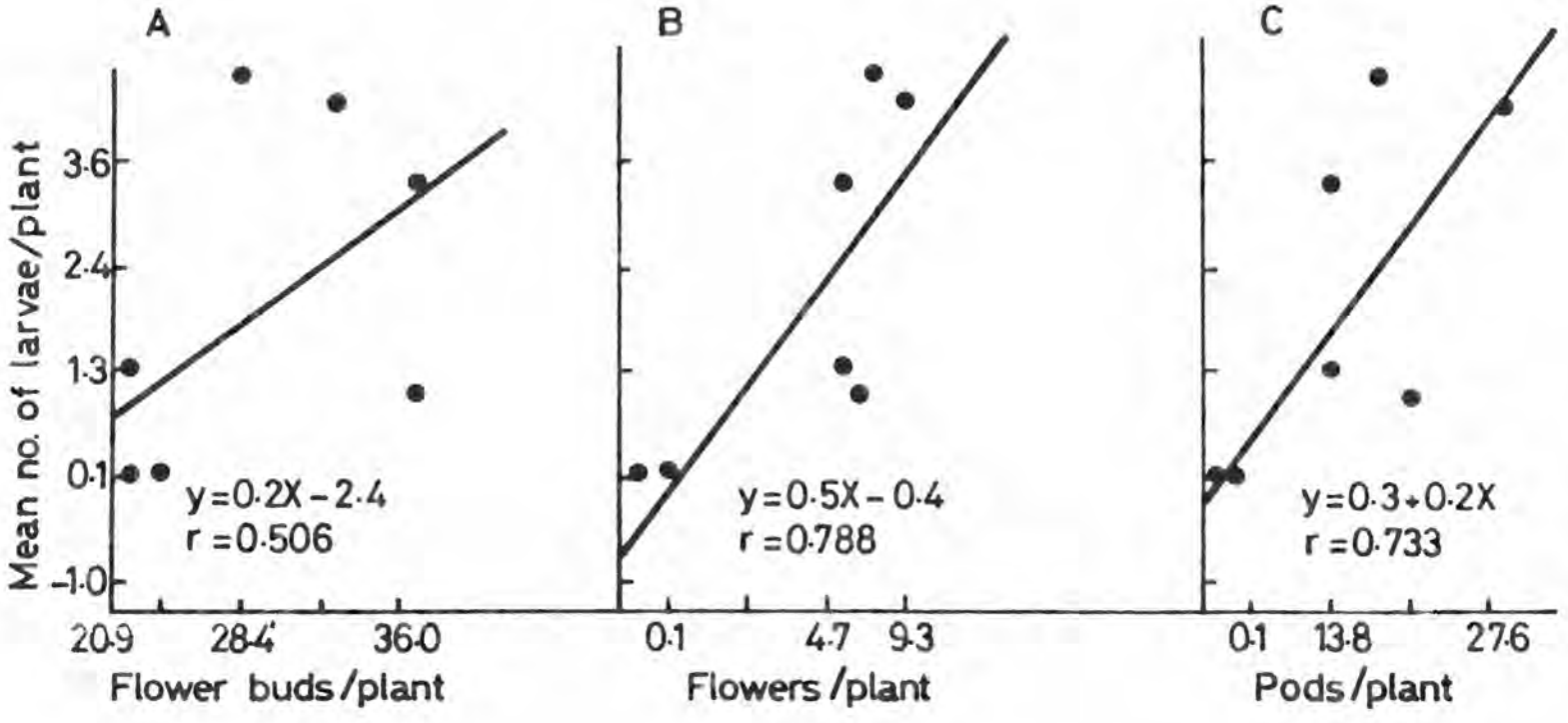

A
B
C
Mean no. of larvae/plant
3·6
2·4
1·3
0·1
-1·0
y=0·2X-2·4
r=0·506
y=0·5X-0·4
r=0·788
y=0·3+0·2X
r=0·733
20·9
28·4
36·0
Flower buds/plant
0·1
4·7
9·3
Flowers/plant
0·1
13·8
27·6
Pods/plant

Figure 30. Per cent M. testulalis larvae surviving in screen house and open cowpea plots artificially infested with eggs.

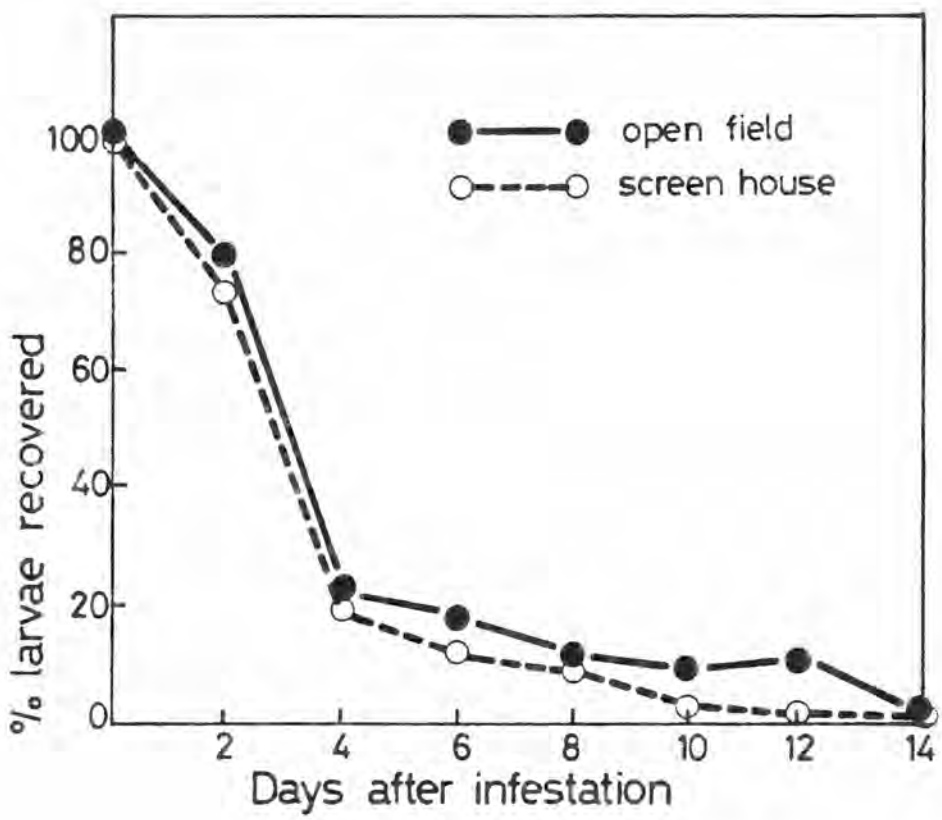

open field
screen house
% larvae recovered
100
80
60
40
20
0
2
4
6
8
10
12
14
Days after infestation

Figure 31. Survival and developmnet of M. testulalis larvae on different parts of the cowpea plant under MPFS laboratory conditions.

A. Effect on survival of M. testulalis

B. Effect on larval period

C. Effect on pupal period

D. Effect on pupal weight.

E. Effect on life cycle duration

% Maruca surviving
0
20
60
100
S.T
T.B
LV
G.M
T.G
F.L
A
Mean larval period (days)
0
8
16
S.T
T.B
L.V
G.M
T.G
F.L
B
Mean pupal period (days)
0
8
16
S.T
T.B
L.V
G.M
T.G
F.L
C
Mean pupal wt. (mg ± SD)
0
20
40
60
S.T
T.B
L.V
G.M
T.G
F.L
D
Mean duration of life cycle (days)
0
8
16
24
S.T
T.B
L.V
G.M
T.G
F.L
E
S.T - Stems
T.B - Terminal buds
L.V - Leaves
G.M - Green mature pods
T.G - Tender green pods
F.L - Flowers

4.3. EFFECT OF SOME CLIMATIC FACTORS ON POPULATION CHANGES AND SURVIVAL OF M. TESTULALIS

4.3.1. Rainfall

The logarithm of total (sum of eggs, larvae, pupae and adult numbers) M. testulalis population densities during the various sampling periods were plotted together with the weekly rainfall data for each cropping period at MPFS and the results are presented in Figures 32. Results for Lambwe are not presented since the rainfall records were not taken. No clear relationship existed between the amount of rainfall per week and M. testulalis population density (Figure 32). The amount of weekly rainfall did not seem to influence population build up (Figure 32). In cases where the crop was supported by irrigation the pest density remained low suggesting little or no influence of irrigation water on natural populations of the pest (Figure 32E-D). The total rainfall per cropping season was also correlated against population mean density of eggs and larvae per plant as well as adult males caught in pheromone traps per season and the results are presented in Figure 33, but the relationship although positive were not significant ($P = 0.05$).

4.3.2 Ambient Temperatures and Relative Humidity

The R.H. data was inconsistent in some seasons which had very heavy rainfall and the summaries were unreliable and hence the effect of ambient R.H. on M. testulalis is not presented. Also temperature changes within the season did not show any relationship with population trends of the different development stages of M. testulalis and are not presented. However, a correlation analysis of the relationships between M. testulalis population in each generation and mean ambient temperatures at MPFS per season is presented in Figures 34-36. Table 22 shows the correlation coefficient values and the levels of significance as analysed by students t-test. The results showed that population density of eggs per plant was highly correlated to the difference between mean maximum and minimum temperatures ($r = 0.84$) and the relationship was significant ($P = 0.05$) (Figure 34). Similar results were observed in egg numbers versus mean day-night temperatures ($r = 0.78$) (Figure 34F). In the case of larvae only mean minimum temperatures showed high positive correlation ($r = 0.74$) to larval population which was significant ($P = 0.1$) (Figure 35). The other temperature parameters showed no significant relationships with larval density. Figure 36 and Table 22 shows the relationships between male moths caught in the pheromone trap and the various temperature measurements. The positive correlations observed between the moth numbers and mean maximum temperature ($r = 0.58$) as well as mean day-night temperatures ($r = 0.51$) were not significant even at 0.1 level (Table 22).

4.3.3 Optimum temperature for survival and Development.

The results on the effect of constant temperature studied under MPFS laboratory conditions on M. testulalis survival and development are presented in Tables 23-24 and Figure 37-40. The results show that the temperature regimes affected the growth and development of M. testulalis significantly (P = 0.01). Further correlation analysis was conducted on the various development and survival parameters on eggs, larvae and pupae against the temperature regimes and the results are shown in Figures 41-42 and Table 24. The results show that the temperature regimes ranging from 21 - 32°C had little influence on egg incubation period and % egg hatch (Figure 38, 41A and 42A). However, at temperatures below 21°C and that above 34°C eggs did not hatch. In the case of larvae, the effect of temperature regimes on survival and development was highly significant (P = 0.05) between temperatures 21° - 35°C (Table 24). The survival was however, not significantly affected between temperatures 23-32°C (P = 0.05) although the variations in development period was still significant at these temperature regimes (Table 24). Figures 38-40 show that the optimum temperature for the development and survival of M. testulalis larvae was 29°C. Figure 37 shows the effect of temperature regimes (21-35°C) on pupal weight as a developmental parameter. These results indicate that the temperature regimes significantly affected pupal weight (P = 0.05) (DMRT). Correlation analysis show that temperature regimes between 21 - 32°C did not affect the pupal survival(r = 0.17), although the pupal duration and

weight were significantly affected (P = 0.05) (r = 0.91, and 0.94), respectively (Table 24). At 35°C no pupae survived and hence no adults were obtained. Figures 37-40 illustrate that the optimum temperatures for pupal development and survival were between 26-29°C.

The various temperature regimes (21-35°C) significantly affected the total life cycle duration of M. testulalis (Figures 38 and 41D, Table 24) (P = 0.01). At 35°C the life cycle was not completed as all the insects died before or during pupation. The optimum temperature for M. testulalis development and survival was between 23-26°C. It was observed that between temperatures 21-32°C, the growth and development of this species was favoured by increase in temperature, the survivorship was enchanced and that the generation time was significantly shortened as the temperatures increased between these ranges (r = 0.9) (Figure 41D).

Table 22. Correlation coeffecients (r) of Maruca testulalis population versus temperature variations during different cropping seasons at MPFS (6 obs), 1983-1985.

Age interval	Temprature parameters (Mean values)	r-values	Significance levls 0.01	0.05	0.1
Eggs	Minimum	-0.25	ns	ns	ns
	Maximum	0.64	ns	ns	ns
	Maximum-Minimum	0 84	ns	*	**
	Daily	0.55	ns	ns	ns
	Day	0.61	ns	ns	ns
	Night	0.45	ns	ns	ns
	Day-Night	0.78	ns	*	*
Larvae	Minimum	0.74	ns	ns	*
	Maximum	0.38	ns	ns	ns
	Maximum-Minimum	-0.21	ns	ns	ns
	Daily	0.48	ns	ns	ns
	Day	0.38	ns	ns	ns
	Night	0.59	ns	ns	ns
	Day-Night	0.26	ns	ns	ns
Adults males (Peromone catches)	Minimum	-0.12	ns	ns	ns
	Maximum	0.58	ns	ns	ns
	Maximum-Minimum	0.23	ns	ns	nn
	Daily	-0.07	ns	ns	ns
	Day	0.17	ns	ns	ns
	Night	0.32	ns	ns	ns
	Day-Night	0.51	ns	ns	ns

* - significant at the levels shown, ns - not significant.

Table 23. Survival of Maruca testulalis from eggs through to adults under different temperature regimes.

	% SURVIVAL PER TEMPERATURE REGIME					
Stage	21°C	23°C	26°C	29°C	32°C	35°C
Egg - Larvae	47.4(47.4)	68.0(68.0)	63.3(63.3)	60.0(60.0)	50.0(50.0)	64.0(64.0)
Larvae- Pupae	44.7(44.7)	58.8(40.0)	57.9(36.7)	75.8(63.6)	63.6(31.8)	24.3(15.0)
Pupae - Adults	86.7(17.1)	70.0(28.0)	90.9(33.3)	92.0(41.8)	69.1(22.0)	0.0(0.0)

Figure in parenthses ( ) are cumulative % survival calculated from the initial number of eggs used.

Table 24. Correlation coefficients (r) of Maruca testulalis growth and development versus temperature (range tested 21°C - 32°C) (5 c

Development parameters	r-values	Significance levels		
		0.01	0.05	01.
Eggs:				
Hatching period (days)	-0.61	ns	ns	ns
% Hatchability	-0.12	ns	ns	ns
Larvae				
Larval period (days	0.91	ns	*	*
% Larvae surviving	0.73	ns	ns	ns
Pupae				
Pupal period (days	0.91	ns	*	*
% Pupae surviving	0.71	ns	ns	ns
Pupal weight (mg)	0.94	*	**	**
Total life cycle period (days)	0.92	*	**	**

* - significant at the levels shown, ns - not significant

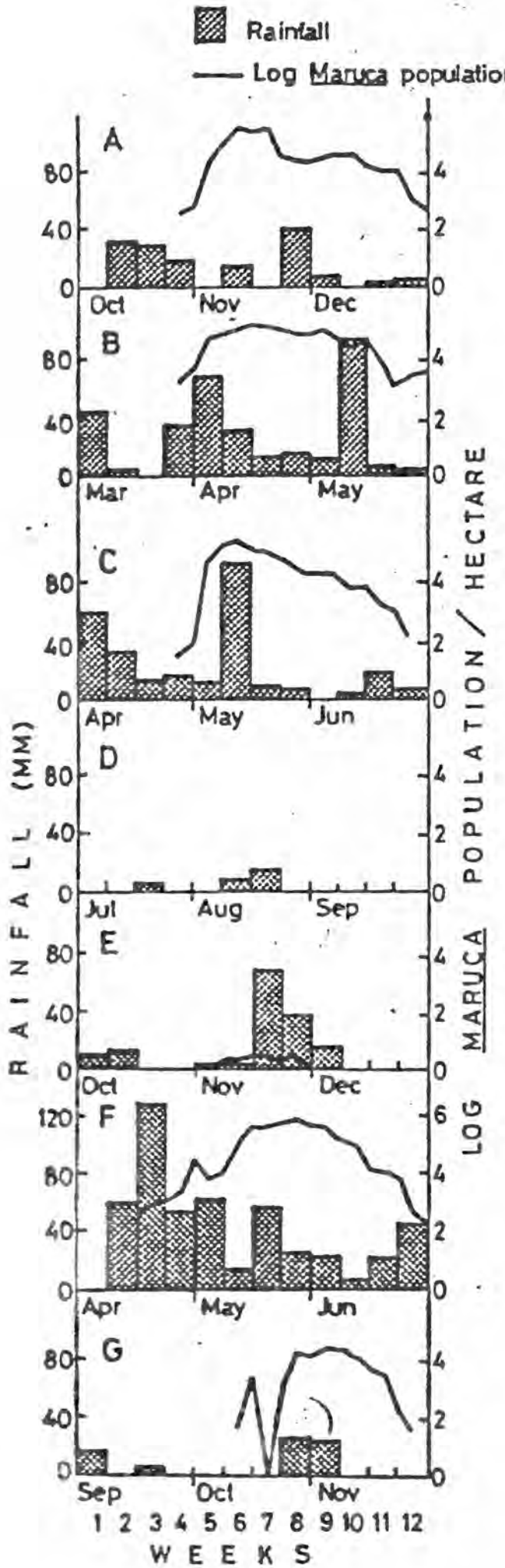

Rainfall
Log Maruca population
A
B
C
D
E
F
G
Oct
Nov
Dec
Mar
Apr
May
Jun
Jul
Aug
Sep
RAINFALL (MM)
LOG MARUCA POPULATION / HECTARE
WEEKS
1 2 3 4 5 6 7 8 9 10 11 12

Figure 32. Weekly incidence of M. testulalis population on cowpea crop and the rainfall pattern at MPFS, 1983-1985.

A. Short rains, 1983

B. Long rains, 1984

C. Long rains, 1984 (late crop)

D. Off season, 1984

E. Short rains, 1984

F. Long rains, 1985

G. Short rains, 1985

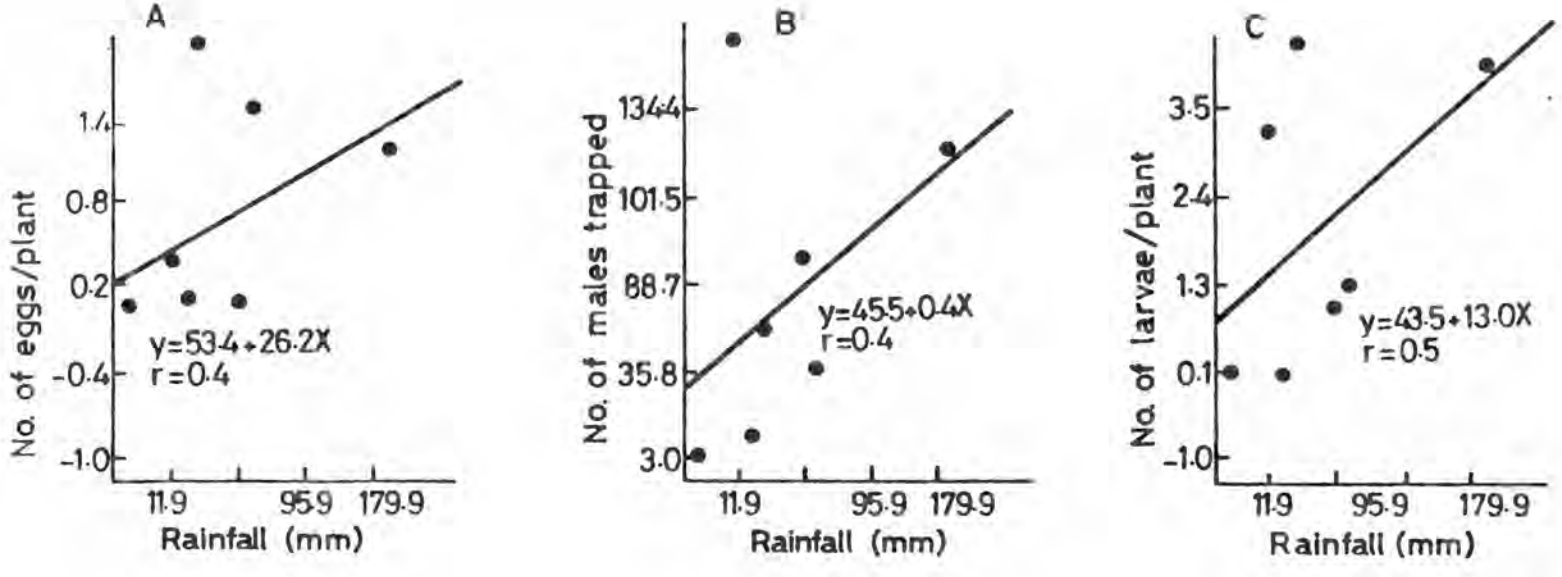

A
No. of eggs/plant
1.4
0.8
0.2
-0.4
-1.0
y=53.4+26.2X
r=0.4
11.9
95.9
179.9
Rainfall (mm)
B
No. of males trapped
134.4
101.5
68.7
35.8
3.0
y=45.5+0.4X
r=0.4
11.9
95.9
179.9
Rainfall (mm)
C
No. of larvae/plant
3.5
2.4
1.3
0.1
-1.0
y=43.5+13.0X
r=0.5
11.9
95.9
179.9
Rainfall (mm)

Figure 33. Correlation analysis of the number M. testulalis on the amount of seasonal rainfall at MPFS during 1983-1985.

A. Number of eggs per plant vs rainfall (mm)

B. Number of larvae per plant vs rainfall (mm)

C. Number of males per trap vs rainfall (mm)

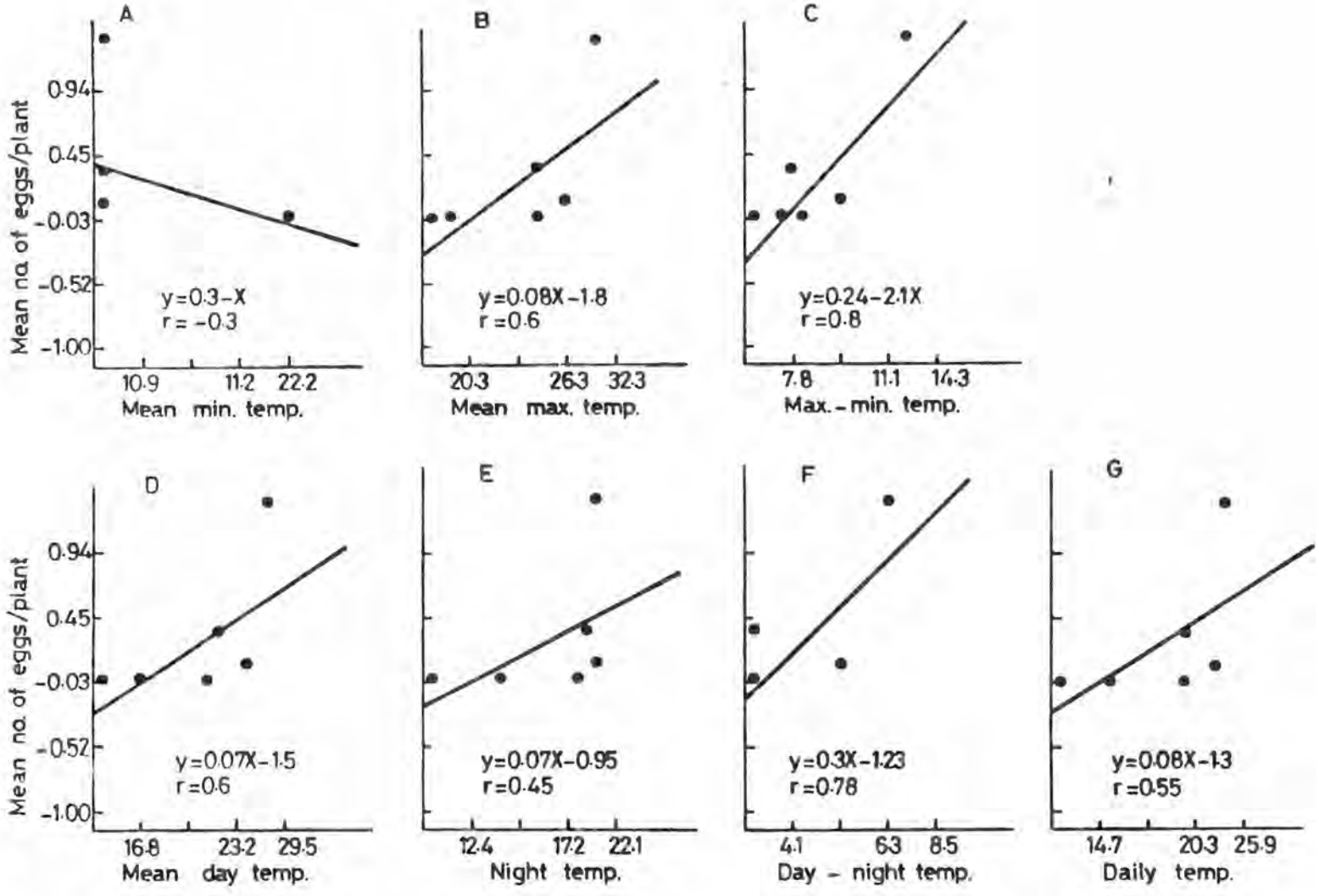

A
B
C
D
E
F
G
Mean no. of eggs/plant
0.94
0.45
-0.03
-0.52
-1.00
y=0.3-X
r=-0.3
10.9
11.2
22.2
Mean min. temp.
y=0.08X-1.8
r=0.6
20.3
26.3
32.3
Mean max. temp.
y=0.24-2.1X
r=0.8
7.8
11.1
14.3
Max.-min. temp.
y=0.07X-1.5
r=0.6
16.8
23.2
29.5
Mean day temp.
y=0.07X-0.95
r=0.45
12.4
17.2
22.1
Night temp.
y=0.3X-1.23
r=0.78
4.1
6.3
8.5
Day - night temp.
y=0.08X-1.3
r=0.55
14.7
20.3
25.9
Daily temp.

Figure 34. Effect of seasonal temperature variations on mean number of M. testulalis eggs per plant at MPFS, 1983-1985

A. Mean minimum temperature vs number of eggs

B. Mean maximum temperature vs number of eggs

C. Mean max-min. temperature vs number of eggs

D. Mean day temperatures vs number of eggs

E. Mean night temperatures vs number of eggs

F. Mean day-night temperatures vs number of eggs

G. Mean daily temperatures vs number of eggs.

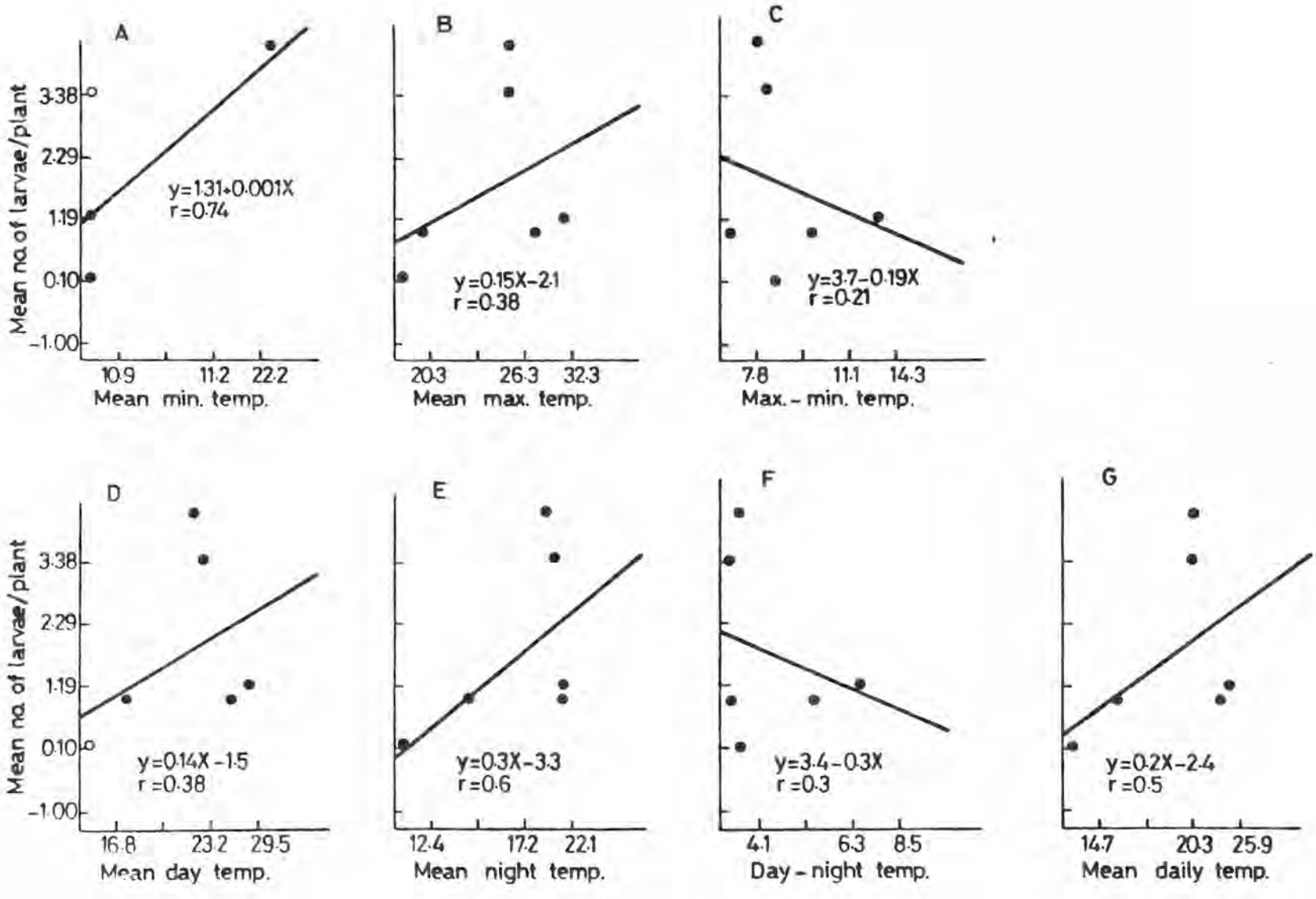

A
B
C
D
E
F
G
Mean no. of larvae/plant
3·38
2·29
1·19
0·10
-1·00
y=1·31+0·001X
r=0·74
10·9
11·2
22·2
Mean min. temp.
y=0·15X-2·1
r=0·38
20·3
26·3
32·3
Mean max. temp.
y=3·7-0·19X
r=0·21
7·8
11·1
14·3
Max.-min. temp.
y=0·14X-1·5
r=0·38
16·8
23·2
29·5
Mean day temp.
y=0·3X-3·3
r=0·6
12·4
17·2
22·1
Mean night temp.
y=3·4-0·3X
r=0·3
4·1
6·3
8·5
Day-night temp.
y=0·2X-2·4
r=0·5
14·7
20·3
25·9
Mean daily temp.

Figure 35. Effect of seasonal temperature variations on mean number of M. testulalis larvae per plant at MFTS, 1983-1985.

A. Mean minimum temperatures vs number of larvae

B. Mean maximum temperatures vs number of larvae

C. Mean max-min. temperatures vs number of larvae

D. Mean day temperatures vs number of larvae

E. Mean night temperatures vs number of larvae

F. Mean day-night temperatures vs number of larvae

G. Mean daily temperatures vs number of larvae.

Figure 36. Effect of seasonal temperature variations on M. testulalis male moth population per trap at MPFS, 1983-1985.

A. Mean minimum temperatures vs number of moths

B. Mean maximum temperatures vs number of moths

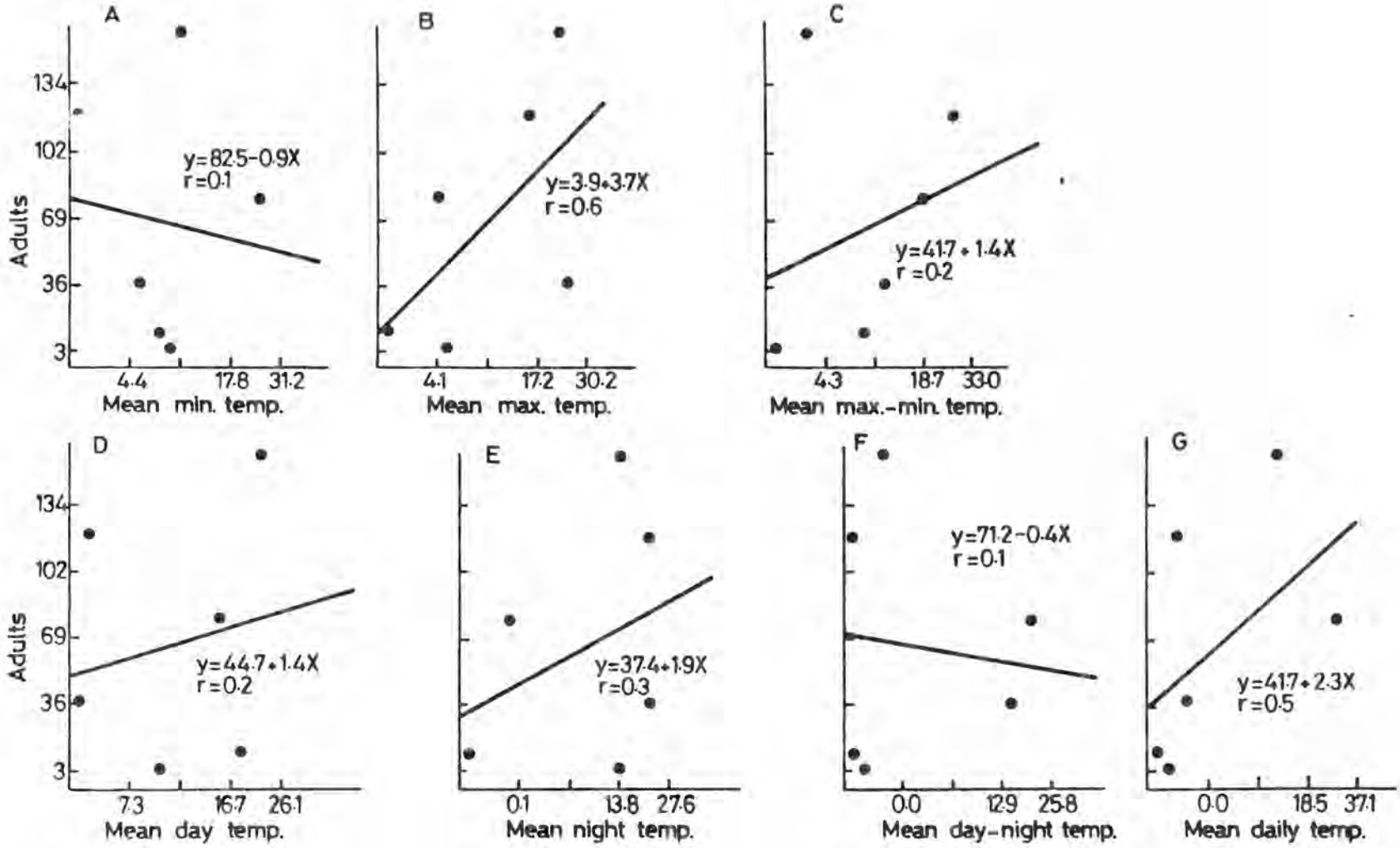
C. Mean max-min. temperatures vs number of moths

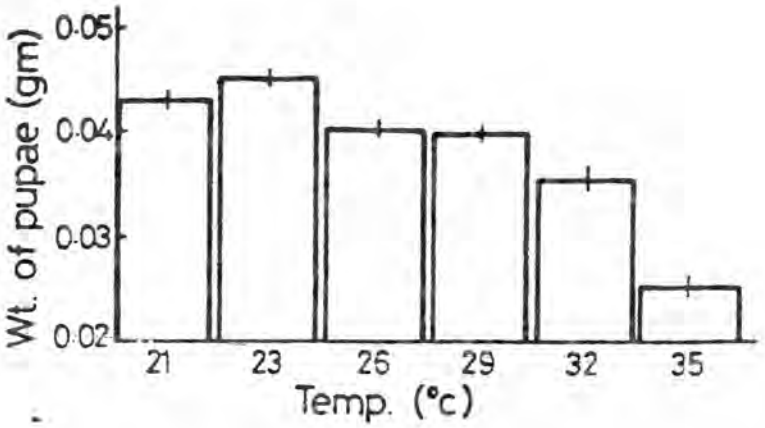
D. Mean day temperatures vs number of moths

E. Mean night temperatures vs number of moths

F. Mean day-night temperatures vs number of months

G. Mean daily temperatures vs number of moths


A
B
C
D
E
F
G
Adults
134
102
69
36
3
y=82·5-0·9X
r=0·1
y=3·9+3·7X
r=0·6
y=41·7+1·4X
r=0·2
y=44·7+1·4X
r=0·2
y=37·4+1·9X
r=0·3
y=71·2-0·4X
r=0·1
y=41·7+2·3X
r=0·5
4·4 17·8 31·2
Mean min. temp.
4·1 17·2 30·2
Mean max. temp.
4·3 18·7 33·0
Mean max.-min. temp.
7·3 16·7 26·1
Mean day temp.
0·1 13·8 27·6
Mean night temp.
0·0 12·9 25·8
Mean day-night temp.
0·0 18·5 37·1
Mean daily temp.


Wt. of pupae (gm)
0·05
0·04
0·03
0·02
21
23
26
29
32
35
Temp. (°c)

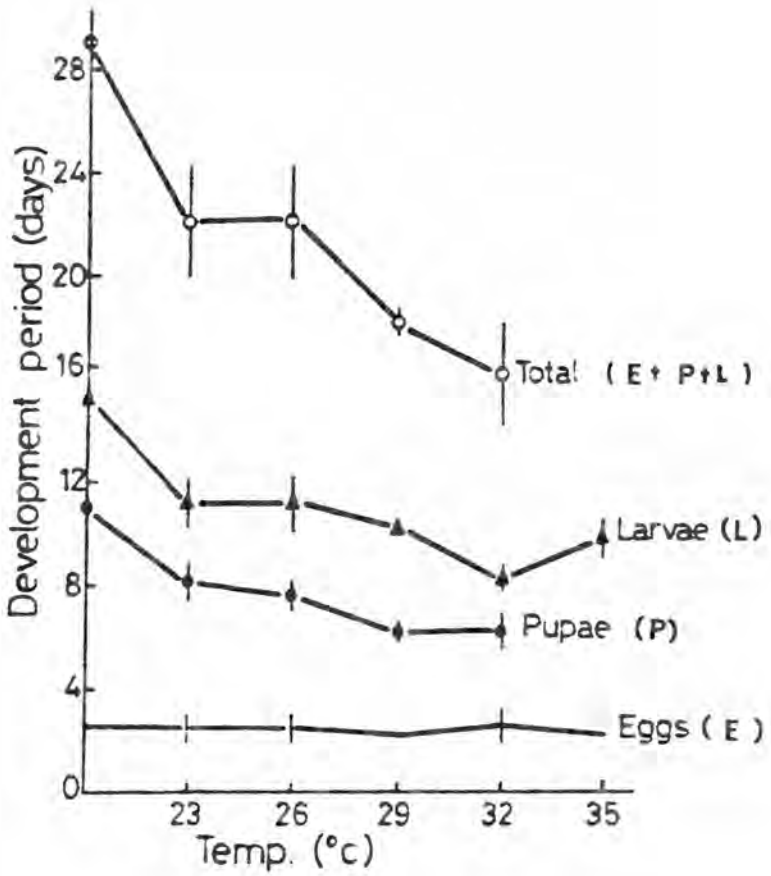
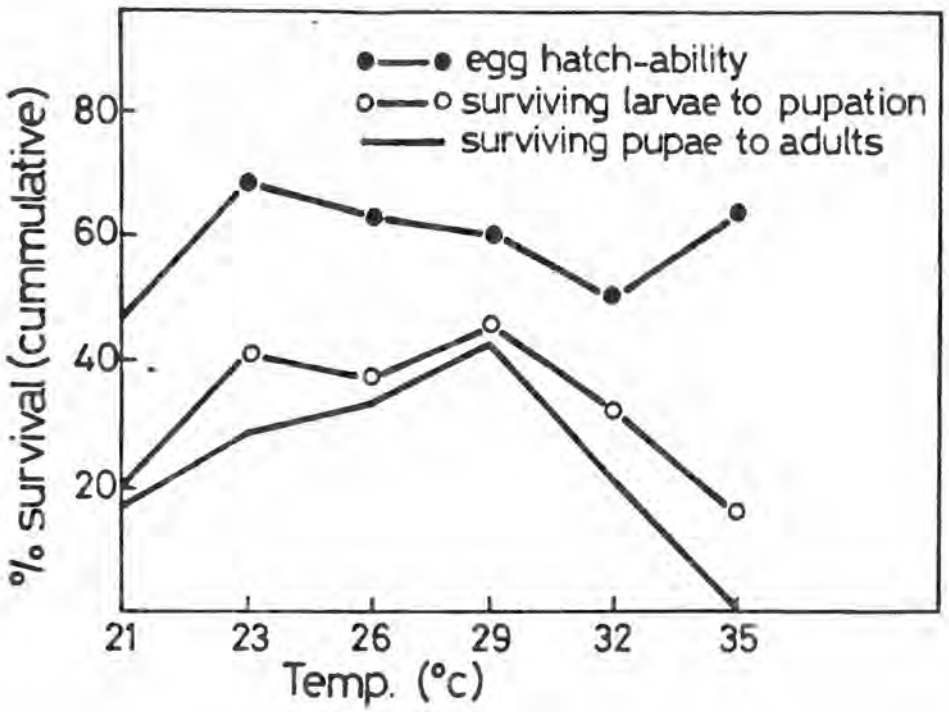

Development period (days)
28
24
20
16
12
8
4
0
Total (E + P + L)
Larvae (L)
Pupae (P)
Eggs (E)
23
26
29
32
35
Temp. (°c)

Figure 37. Effect of constant temperature regimes on weight of M. testulalis pupae.

Figure 38. Effect of constant temperature regimes on development period of different M. testulalis life stages.

Figure 39. Percent survival of M. testulalis under constant temperature regimes, expressed as proportion of the initial number of eggs used.

Figure 40. Percent survival of M. testulalis under constant temperature regimes, expressed as proportion of the preceeding life stage.


egg hatch-ability
surviving larvae to pupation
surviving pupae to adults
% survival (cummulative)
80
60
40
20
21
23
26
29
32
35
Temp. (°c)

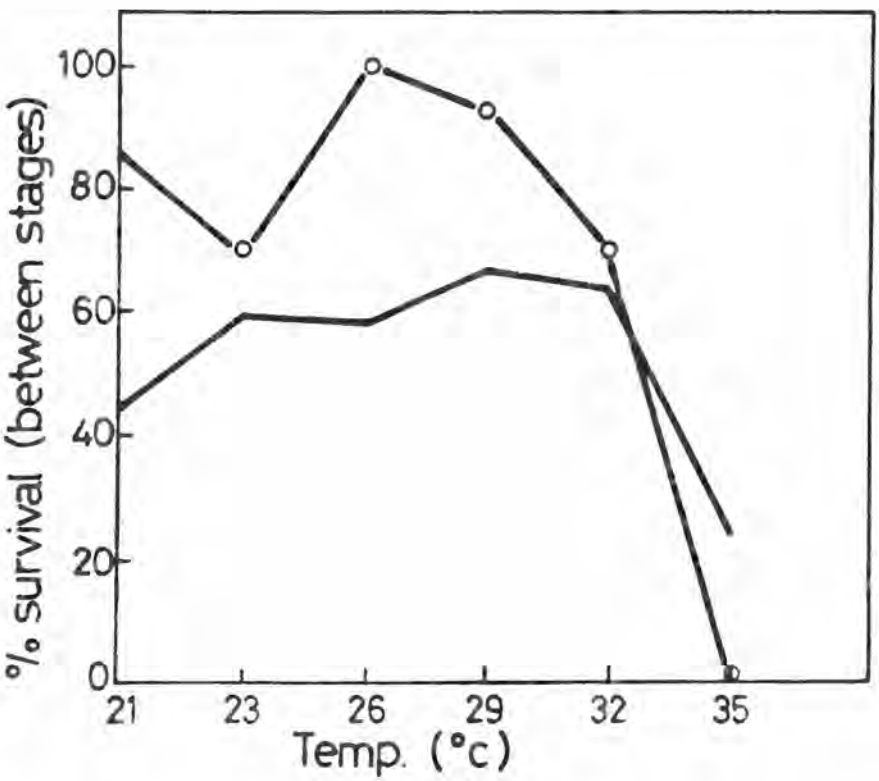

% survival (between stages)
100
80
60
40
20
0
21
23
26
29
32
35
Temp. (°c)

Figure 41. Correlation analysis of temperature regimes on development period of different M. testulalis life stages.

A. Temperature regimes vs duration hatch of egg (days)

B. Temperature regimes vs pupal period (days)

C. Temperature regimes vs larval period (days)

D. Temperature regimes vs life cycle duration (days)

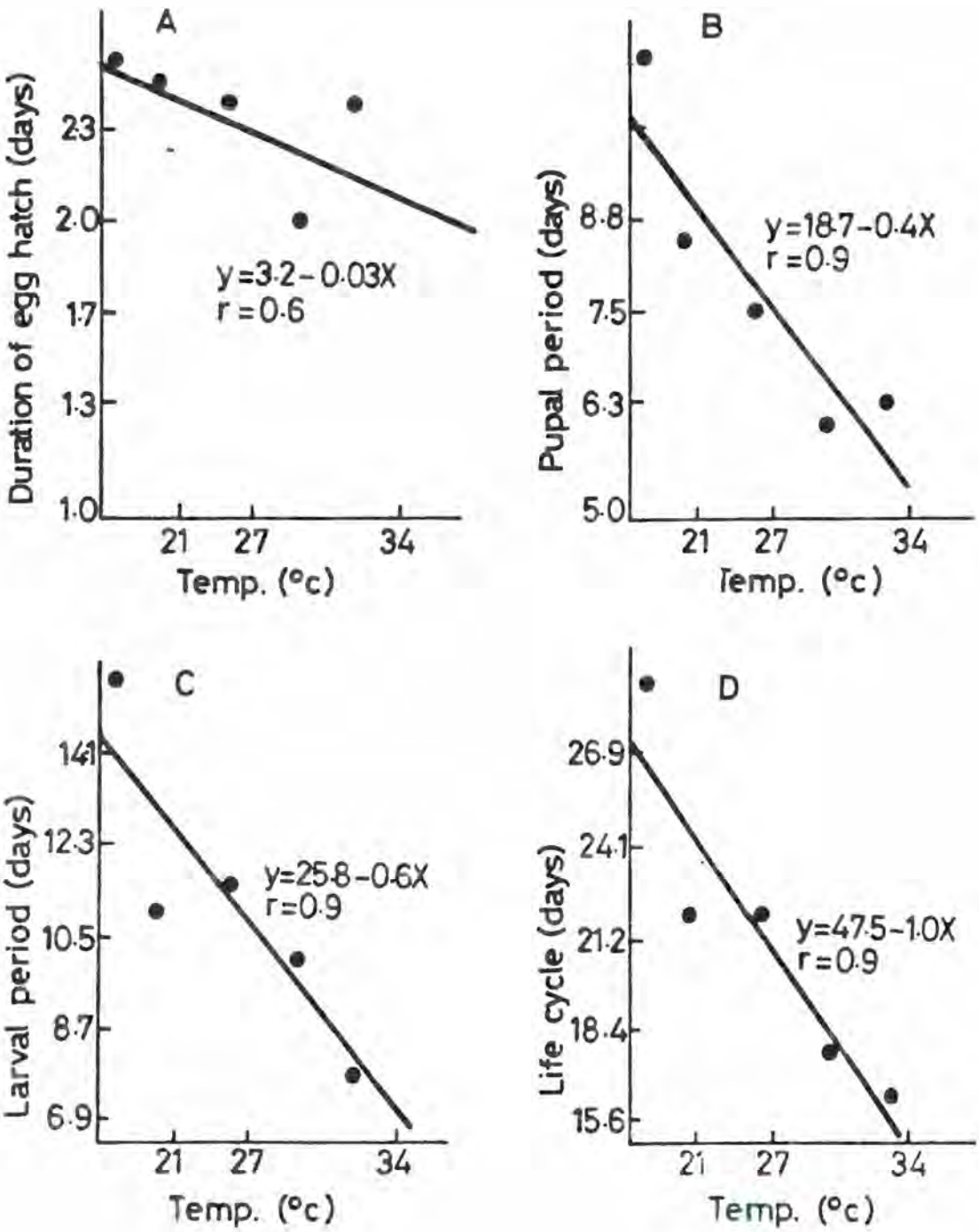

A
Duration of egg hatch (days)
2·3
2·0
1·7
1·3
1·0
y=3·2–0·03X
r=0·6
21
27
34
Temp. (°c)
B
Pupal period (days)
8·8
7·5
6·3
5·0
y=18·7–0·4X
r=0·9
21
27
34
Temp. (°c)
C
Larval period (days)
14·1
12·3
10·5
8·7
6·9
y=25·8–0·6X
r=0·9
21
27
34
Temp. (°c)
D
Life cycle (days)
26·9
24·1
21·2
18·4
15·6
y=47·5–1·0X
r=0·9
21
27
34
Temp. (°c)

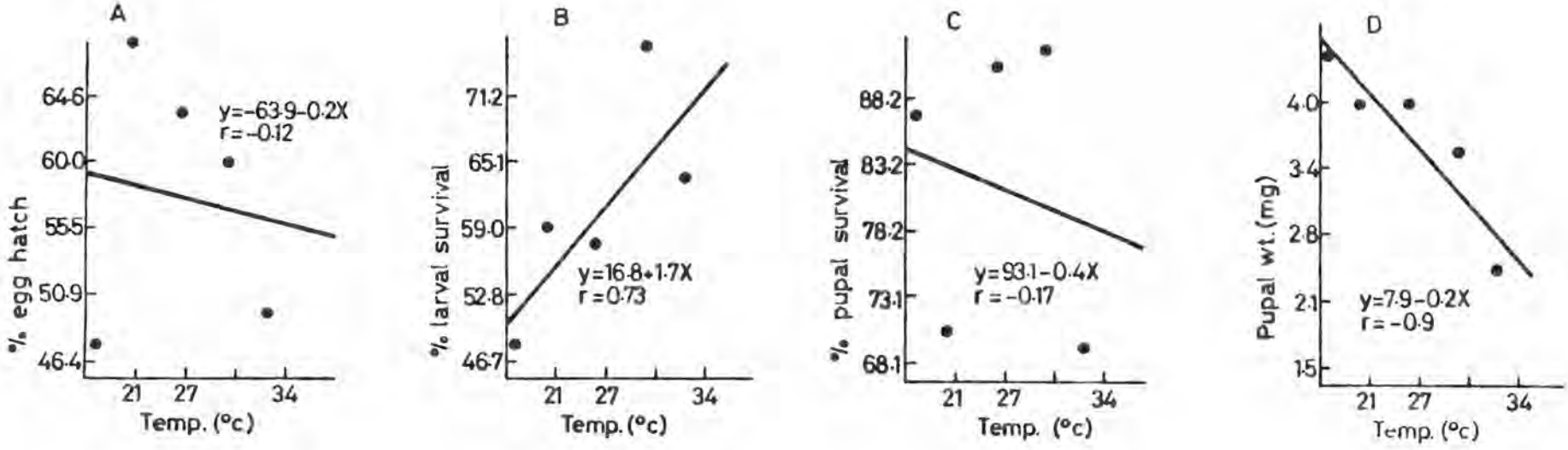
Figure 42. Correlation analysis of constant temperature regimes on survival and development of M. testulalis.

A. Temperature regimes vs egg hatch

B. Temperature regimes vs % larval survival

C. Temperature regimes vs % pupal survival

D. Temperature regimes vs pupal weight.


A
% egg hatch
64·6
60·0
55·5
50·9
46·4
y=-63·9-0·2X
r=-0·12
21
27
34
Temp. (°c)
B
% larval survival
71·2
65·1
59·0
52·8
46·7
y=16·8+1·7X
r=0·73
21
27
34
Temp. (°c)
C
% pupal survival
88·2
83·2
78·2
73·1
68·1
y=93·1-0·4X
r=-0·17
21
27
34
Temp. (°c)
D
Pupal wt. (mg)
4·0
3·4
2·8
2·1
1·5
y=7·9-0·2X
r=-0·9
21
27
34
Temp. (°c)

4.4. BIOLOGY OF SOME SELECTED NATURAL ENEMIES OF M. TESTULALIS

4.4.1. Tetrastichus sesamiae, a Parasitoid of M. testulalis

During the field studies seven parasitoids were recovered and identified from M. testulalis, but only one, Tetrastichus sesamiae Risbec (Eulophidae, Hymenoptera), was successfully reared in the laboratory at MPFS. T. sesamiae is a gregarious pupal endo-parasitoid. The insect is a small chalcid, typical of the family Eulophidae. The species is black with brownish white legs and the males are smaller and more active than the females.

Behaviour, Reproductive and Development on M. testulalis.

Studies under the MPFS laboratory conditions, showed that T. sesamiae started emerging from M. testulalis pupae from 8.00 hours and continued to 16.00 hours (Figure 43). However, the highest number of parasites emerged between 8.00 - 9.00 hours after which the number of parasitoids emerging diminished to zero at 12.00 hours (Figure 43). Some late emergence occurred between 15.00 - 16.00 hours, but the number was negligible (Figure 43). T. sesamiae adults started mating immediately after emergence from host pupae and one female was mated several times by either one or several males. Oviposition occurred in both mated and unmated females and there was no distinct time lapse between mating and oviposition. The females were active in searching for the host pupae and one female parasitoid ovipisited on upto 5 host pupae (Figure 44). This phenomenon was affected by feeding the parasitoid on different food sources (Figure 44).

The best results were obtained on feeding the females on 20% sucrose solution (Figure 44).

Longevity of T. sesamiae adults was variable but the mean ranged from 4.3 ± 0.6 to 13.9 ± 4.2 days depending on the quality of food substrate (Figure 45). Studies on the effect of aqueous solutions of sucrose and honey at different concentrations showed that the adult parasitoid lived for a significantly longer period when fed on 20% honey solution as compared to lower concentration of the same and 0-20% sucrose solution (Figure 44). The presence or absence of host pupae did not affect longevity (P = 0.05) but rather, if the adults were unfed they died within 4-6 days of emergence. The mean development period of T. sesamise on M. testulalis pupae was 16.8 ± 2.6 (N = 100 pupae). It was found that in freshly emerged unfed female parasitoids fecundity was variable depending on the age of the female (Table 25). The results showed that the fecundity was highest in one day old parasitoids which gave a mean egg count of 69.5 ± 7.5 per female compared to 42.8 ± 5.4, 37.8 ± 8.2. and 29.6 ± 4.7 in the case of day zero, 2 and 3 old parasitoids (Table 25). Examination of the ovaries of dissected females of various age groups showed that ovulation in T. sesamiae continued to occur even after adult emergence.

Further, studies on the parasitoid revealed a variable progeny production per female, ranging from 0-263, depending on the food quality (Figure 46). It was found that feeding the parasitoids on 20% sucrose solution resulted into the highest progeny production (Figure 46). The various concentrations of honey solution did not affect the progeny production of T. sesamiea females and the results were similar to

those of 5-10% sucrose solutions, but significantly lower than that of 20% sucrose solution (P = 0.05) (Figure 46). When the parasitoids were offered distilled water, tap water or no food at all, progeny production was drastically lowered (Figure 46). It was further observed that when host pupae were exposed to T. sesamiae the pupal mortalities caused by the parasitoids were much higher than the successful parasitization since the parasitiods did not always deposit egg in all attacked host pupae (Figure 47).

The results of the effect of pupal age on parasitization, progeny production and development period of T. sesamiae are shown in Table 26. Parasitization and progeny production were high when the parasitoids were exposed to zero day old M. testulalis pupae (Table 26). On such pupae 100% parasitism and a progeny of 142.5 ± 11.3 per female parasitoid was recorded (Table 26). M. testulalis pupae were parasitised upto when they were day 5 old. However, table 26 shows that progeny production was progressively decreasing with the age of the host pupa. The development period of T. sesamiae was not affected significantly by host pupae of day 0-5 (Table 26). However, when the parasitoids were exposed to pupae of day 6 and above, no progeny was produced and on dissecting such pupae 25 days after exposure it was found that in some cases oviposition occurred but the parasitoids failed to develop and dead malformed adult T. sesamiae were found (Table 26).

Host Preference of T. sesamiea

The results on parasitization and performance of T. sesamiae on pupae of five pest species M. testulalis, B. fusca, E. saccharina,

C. partellus and S. exempta are presented in Table 27. The highest parasitization was observed on C. partellus 84.4% followed by M. testulalis (78.0%) (Table 27). In all cases the number of females emerging from parasitised pupae were higher than the number of males (Table 27). S. exempta produced the highest number of females to males as well as the largest progeny per female (202.5 ± 79) compared to the pupae of the other species (Table 27). The sex ratio was lowest in the case of M. testulalis. There was a wide variation in progeny production in all cases. Except in the case of B. fusca which produced significantly low progeny (41.0 ± 18) per female parasitoid, the rest were not significantly different (P = 0.05) (Table 27). The duration of T. sesamiae development (or life cycle) in pupae of the different lepidopteran species were not significantly different (P = 0.05) and the means in the species studied ranged from 14.0 ± 2.7 to 16.8 ± 2.8 days (Table 27).

Table 25. Potential fecundity of unfed female Tetrastichus sesamiae measured on different days after parasitoid emergence.

Age (days)	No. of females	Eggs/female ± SE
0	50	42.8 ± 5.4 a
1	50	69.5 ± 7.5 a
2	50	37.8 ± 2.6 ab
3	50	29.6 ± 4.7 b
4	48	23.0 ± 6.6 b

The same letters indicate no significant difference (P = 0.05), analysed by Duncans Multiple Range Test (DMRT).

Table 26. Effect of age of M. testulalis pupae on performance of Tetrastichus sesamiea

Pupal age (days)	Pupae tested	% Mortality	% Parasitism	Development period of	Mean progeny/female
0	15	100	100	18.5±1.0a	142.5±11.3a
1	15	75	75	19.6±0.7a	83.3±17.8ab
2	15	50	64	18.0±1.3a	84.7±16 ab
3	15	75	42	17.8±0.9a	60.0±10.1 b
4	15	100	40	19.6±1.1a	77.8±14.4 b
5	15	100	25	19.7±1.3a	67.4±15.5 b
6	16	25	0	0	(41)
7	15	0	0	0	(57)
8	15	0	0	0	0

The same letters indicate no significant difference at P = 0.05 (DMRT). Figures in Parenthesis () indicate the number of dead parasitoids recovered in pupae after dissection of the pupal cadavers.

Table 27. Performance of Tetrastichus sesamiae on pupae of some lepidoptera pests species under laboratory conditions at MPFS.

Host species	Pupae tested	% Parasitism	Parasitoid		
			Sex ratio M: F	Progeny per female (± SD)	Life cycle (days) (± SD)
Maruca testulalis	30	78.0	1: 4.7	93.1 ± 64.8 b	16.8 ± 2.8 a
Busseola fusca	25	28.6	1: 6.2	41.0 ± 18 a	15.0 ± 3.5 a
Eldana saccharina	24	71.4	1: 7.0	99.6 ± 48 b	14.1 ± 3 a
Spodoptera exempta	35	50.0	1:12.5	202.5 ± 79 b	14.0 ± 1.7 a
Chilo partellus	30	84.4	1: 9.9	147.4 ± 45 b	15.9 ± 3.6 a

The mean followed by different letters are significantly different (P = 0.05)

Figure 43. Per cent emergence of T. sesamiea from M. testulalis pupae during different times of the day under MPFS laboratory conditions.

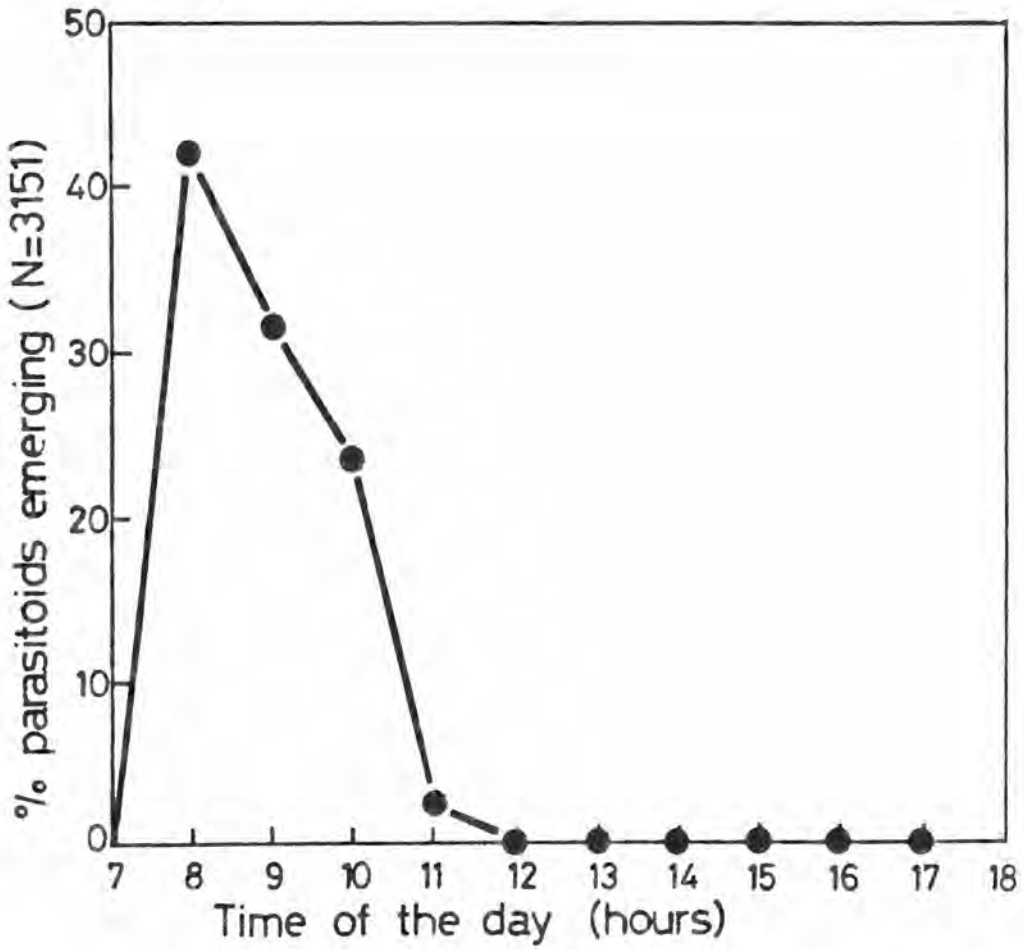
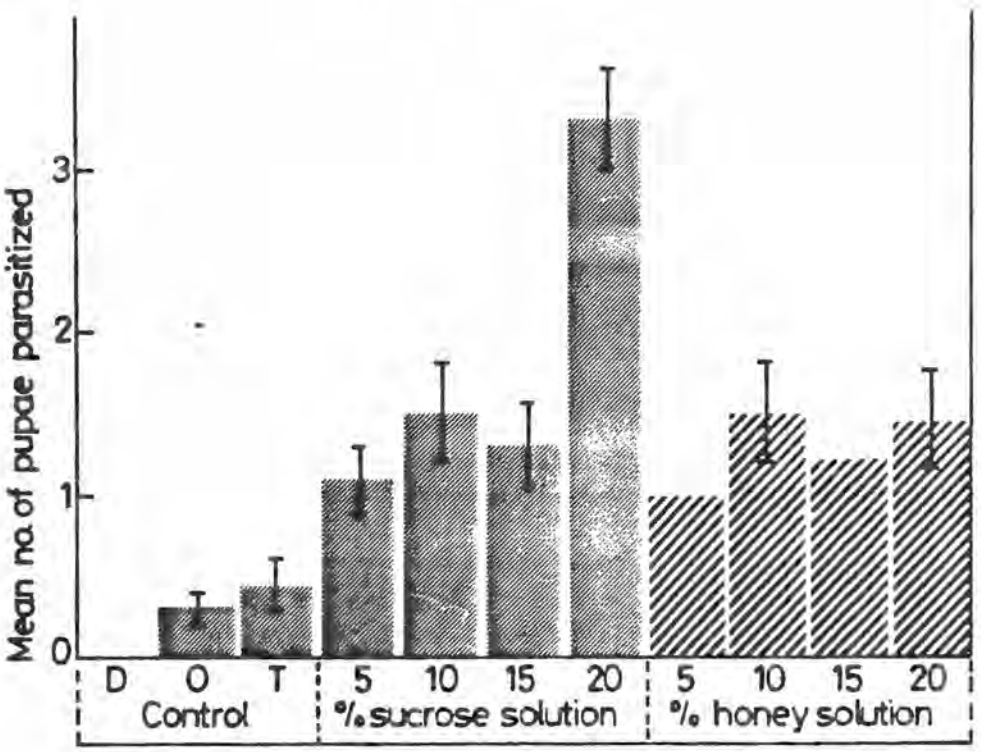

50
40
30
20
10
0
% parasitoids emerging (N=3151)
7
8
9
10
11
12
13
14
15
16
17
18
Time of the day (hours)

Figure 44. Mean number of M. testulalis pupae parasitized by T. sesamiea reared on different food substrates (D - Distilled water, O - no food, T-tap water).

Figure 45. Longevity of T. sesamiae adults when reared on different food substrates.


Mean no of pupae parasitized
0
1
2
3
D
O
T
Control
5
10
15
20
% sucrose solution
5
10
15
20
% honey solution

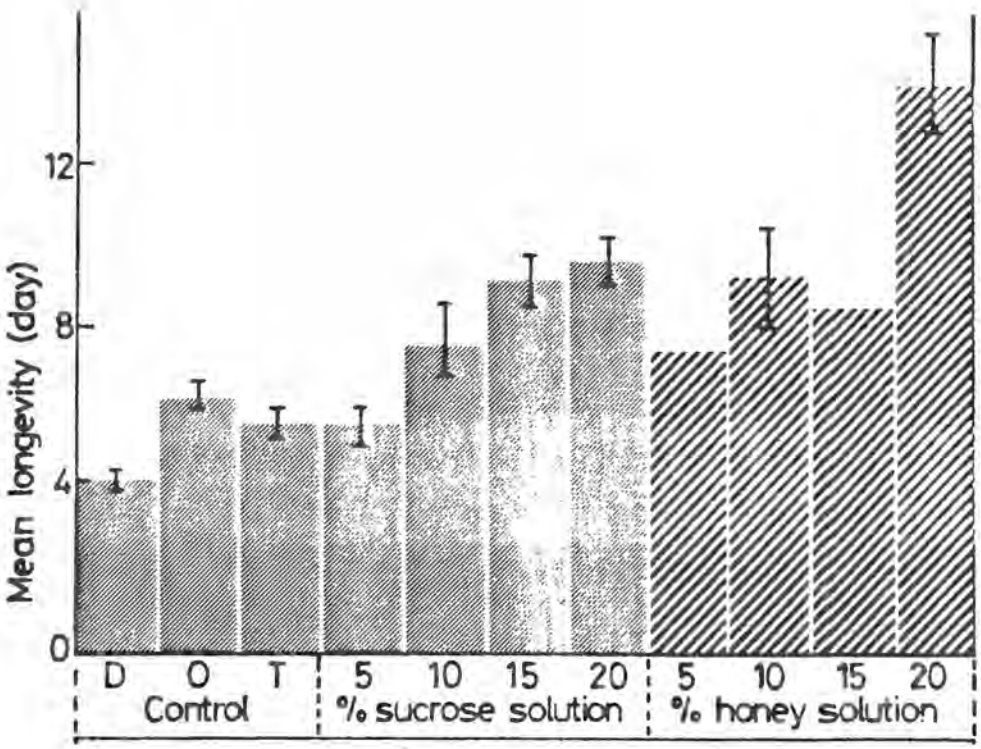
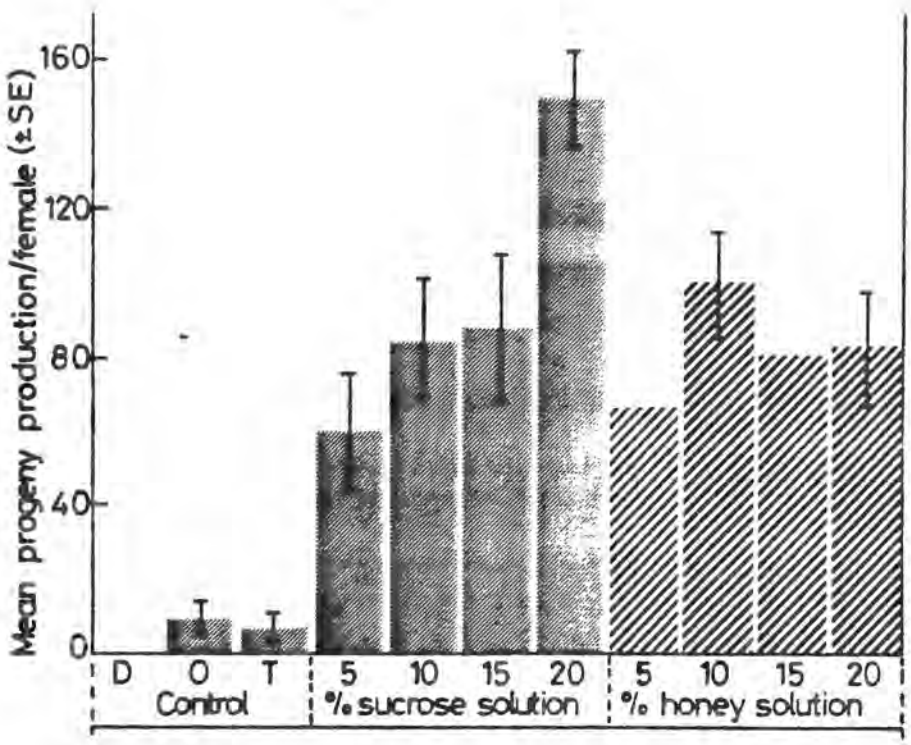
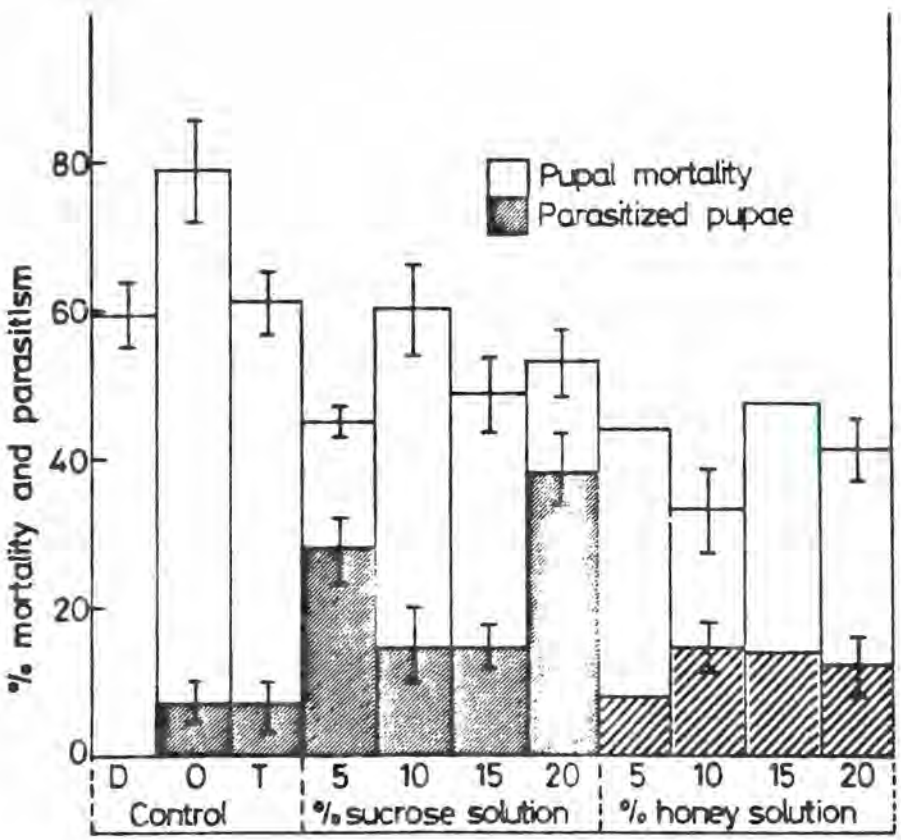

Mean longevity (day)
0
4
8
12
D
O
T
Control
5
10
15
20
% sucrose solution
5
10
15
20
% honey solution

Figure 46. Progeny production per female T. sesamiae on M. testulalis pupae when the parasitoids fed on different food substrates.

Figure 47. Per cent mortality and parasitism of M. testulalis exposed to T. sesamiea adults fed on different food substrate.


Mean progeny production/female (±SE)
160
120
80
40
0
D
O
T
5
10
15
20
5
10
15
20
Control
% sucrose solution
% honey solution


% mortality and parasitism
80
60
40
20
0
Pupal mortality
Parasitized pupae
D
O
T
5
10
15
20
5
10
15
20
Control
% sucrose solution
% honey solution

4.4.2. Pathogenicity and virulence of microorganisms on *M. testulalis*

Mortality due to the different microorganisms tested on *M. testulalis* under laboratory conditions larvae are shown in Table 28. High mortalities occurred in the larvae innoculated with *Nosema* sp. and *Bacillus* sp. The first larval mortality was observed after 48 hours, when the larvae were in the 4th instar stage, during which 40% of the larvae were found dead in both treatments (Table 28). At 5th instar stage 60% of the larvae treated with *Nosema* sp. had died, while in the case of *Bacillus* sp., the mortality remained at 40% (Table 28). All the larvae innoculated with *Nosema* sp. died before pupation. Thus, 100% mortality was observed within 4 days of innoculation with *Nosema* sp. The highest mortality examined in the case of *Bacillus* innoculated larvae was 60% (Table 28). The rest of the larvae (40) pupated and developed normally to adult stage. Microscopic examination of larval cadavers revealed high concentrations of *Nosema* and *Bacillus* spores in larvae innoculated by these microorganisms, confirming that these microorganisms were pathogenic to and were responsible for the larval mortality.

Before death the larvae innoculated with *Nosema* sp. and *Bacillus* sp. became moribund within 36 hours. They showed loss of appetite characterized by their negative orientation towards the food substrate. The *Nosema* infected

larvae, showed a yellowish colour change, with the distinct black marks characteristic to M. testulalis larvae, disappearing. The colour of the dead larvae remained light yellow after death and did not disintegrate for about one week. In the case of larvae infected with Bacillus no colour change was examined and the black marks did not disappear until after death. However, after mortality, the larvae quickly became darker in colour and within 1-2 days the body ruptured and a milky haemolymph oozed out of the larval cadaver showing a characteristic bacterial infection.

Fungus and Coccus sp. recovered from M. testulalis during field samples and cultures in the laboratory did not prove pathogenic to M. testulalis in laboratory assays. The mortalities observed in fungus (44%) and Coccus sp. (42%) innoculated larvae were similar to that of control (uninnoculated larvae) (45%) (Table 28). Microscopic examination of the dead larvae from this treatment showed neither Coccus sp. spores nor fungal hyphae, mycelia or fruiting bodies in the haemolymph. But rather some of the dead larvae were found to contain high concentration of Nosema.

4.4.3. Effect of Nosema on development and Survivorship of M. testulalis

It was found that when the different larval instars were challenged with Nosema sp. innoculum, mortalities were

highest in 1st and 2nd instars (Table 29). Mortality of these instar larvae were 100% and 86% respectively. Fourth instar larvae suffered the lowest mortality. When innoculation was done at 4th instar stage or the stages preceeding it, the larvae normally died before reaching pupal stage. However, if the 5th instar larvae were innoculated mortality was observed at the pupal stage.

The time taken by the different larval instar before death after infection by Nosema is presented in Table 29. The results show that the first instar larvae were the most vulnerable and died in significantly less time ($P = 0.05$) than the other larval stages (Table 29). The mean duration taken by the first instar larva to die was 2.7 ± 1.6 days, while those of the other stages ranged from 6.2 ± 3.0 to 6.9 ± 2.9 days (Table 29).

Attempts to use weight loss as an index of the effect of Nosema infection on M. testulalis yielded inconsistent results. Thus, this factor was neglected and as such the data are not presented. Studies on the effect of Nosema of fecundity of adult moths which survived the disease were also discontinued because the adults emerging from the bioassays tests were too few to warrant any meaningful tests. Detailed bioassay on Nosema sp. were not conducted due to lack of sterile conditions at MPFS during the study.

Table 28. Per cent mortality of 3rd instar M. testulalis larvae innoculated with different microorganisms under laboratory conditions at MPFS.

	No. of	% Mortality at (cumulative)				
	larvae	4th inst.	5th inst.	prepupae	pupae	TOTAL
Coccus sp.	30	0	0	23.6	42	42
Nosema sp.	30	40	60	100	-	100
Bacillus sp.	30	40	40	60	60	60
Fungus	30	0	10	30	30	44
Control	30	0	20	20	45	45

Table 29. Mortality and survival of different stages of M. testulalis larvae innoculated with Nosema spores under laboratory conditions at MPFS.

Development Stage	No./Test	% Mortality	% surviving to Pupae	% surviving to Adults	Days survived ± SD
Larvae I	30	100	0.0	0.0	2.7 ± 1.6 a
II	30	86.7	30.0	13.3	6.3 ± 3.0 b
III	30	83.3	16.7	16.7	6.2 ± 3.0 b
IV	30	56.7	53.3	43.3	6.7 ± 2.1 b
V	30	73.3	26.7	26.7	6.9 ± 2.9 b

The means followed by different letters are significantly different (P = 0.05) (DMRT)

CHAPTER V

DISCUSSION

Population studies on M. testulalis at MPFS and Lambwe provided a more detailed biological knowledge on the pest, especially on the seasonal population changes, and the factors responsible for such changes on host cowpea plant. This information is significant for a better understanding of population ecology and for future control strategies of this important legume pest. During the study period, 5 and 3 generations of M. testulalis were studied in detail at MPFS and Lambwe Valley, respectively, in the 1983-1985 cropping seasons.

It was found that adult colonisation on the crop in most cases started as early as 15 DAPE at both sites. These observations were obtained from pheromone trap catches of male moths during each season. Since the cowpea crop was newly planted during each cropping season, the initial attack on the crop by the moths was from other sources. However, the initial population of moths caught remained low for every generation studied until the flower initiation stage (30 DAPE) after which the population started rising to a peak 36-48 DAPE (Figures 1 and 2). There was very little variation in the time of occurrence of these peaks in the generations studied. The peaks appeared to coincide with crop flowering resulting

into high infestation by the larvae at both sites. This peak in moth population probably signified the time of peak pheromone production and mating activity. Furthermore, since this peak always coincided with the flowering period of the plants it suggested that, at this stage, the plants emitted some chemical cues which were attractive to the moths resulting into increased populations of moths migrating into the crop. Taylor (1967, 1978) also reported that M. testulalis were attracted to the cowpea crop when the plants were at the flowering stage. Studies by Okeyo-Owuor and Agrwaro (1983) revealed that the peak pheromone activity of the moths coincided with the mating activity which seems to support the earlier suggestion. From these observations, it may be concluded that both plant chemical cues and pheromone activities of the moths could contribute to this high peak observed on the crop at the peak flowering stage. Jackai (1981) also observed an early attack on the crop (21 DAPE) followed by a rapid population build up during flowering stage in Nigeria, although his data did not include moth population. Taylor (1967) studied the incidence of M. testulalis moths on cowpea using mercury vapour light traps and reported that the numbers were high during the cropping season. He observed that the high moth incidence coincided with the peak flowering and fruiting cycle of the two cowpea crops planted in Nigeria during the early and late season. He, further, observed that the moth population was low but active on both volunteer crop and wild host plants during the off season.

From the pheromone and adult emergence traps it was observed that in a number of generations a second but low peak in moth population occurred after crop maturity (70 DAPE). This peak represented the moth population emerging from pupae in the experimental plot and was presumably the source of the subsequent M. testulalis generations on either volunteer crops or wild host plants as discussed by Taylor (1967, 1978).

During the study period it was found that M. testulalis female moths oviposit most (79.6%) of their eggs on leaves. This observation confirms the earlier findings by Okeyo-Owuor and Ochieng' (1981). Okech (Unpublished data) also recorded more eggs on cowpea leaves than on any other part of the plant in both laboratory and field experiments at MPFS, although earlier observations by Taylor (1967) and Jackai (1981) in Nigeria showed that eggs were mostly laid on flowers buds and flowers of the plant. Egg population at MPFS and Lambwe Valley showed that oviposition occurred on the plant before flower initiation stage but like in the case of adults the egg population remained low and started rising only after the onset of flowering. Figure 3 shows that the peak egg population, during the short rainy season in 1983, coincided with peak flowering as well as that of moth population. Data for the other seasons (1984-1985) did not give reliable trend and were neglected in the construction of the temporal distribution. Because of the problems encountered during sampling for eggs, the number of eggs for these generations had to be

estimated using the methods described by Richards and Waloff (1954) and Dempster (1956) for the purposes of constructing ecological life tables. The problems of sampling for M. testulalis eggs in the field have been highlighted earlier by Taylor (1978), Jackai (1981), Okeyo-Owuor and Ochieng' (1981) and Higashi and Sato (Unpublished reports).

Population changes of M. testulalis larvae on cowpea crop have been reported by Taylor (1967, 1978) and Jackai (1981) in Nigeria and by Okeyo-Owuor, et al., (1983) and Higashi and Sato (Unpublished data) in Kenya. The results obtained in the present study confirm the findings of the previous authors on the distribution and population density of this stage on the crop. On distribution of M. testulalis larvae, Taylor (1967) reported that the first instar larvae after hatching eat their way into the centre of flowers without much wandering on the plant surface and that several such larvae may be found in one flower. However, at a later stage the larvae disperse from infested flower into other flowers or pods by means of the silken threads. Taylor (1967) and Jackai (1981) studied population of M. testulalis on several cowpea varieties and reported that the highest damage by larvae occurred at peak flowering stage. This observation and the present studies show that the highest incidence of larvae occur at peak flowering stage resulting into high damage of flowers.

Studies at MPFS and Lambwe Valley revealed that the field sampling technique developed for pupal sampling was useful in providing a good estimate of pupal population density. This method was developed and used for the first time for studying populations of this pest. So far, there is no record on a sampling technique for this pupae in the literature and the problems of sampling for this stage was recently highlighted by Higashi and Sato (Unpublished report). However, the disadvantage of this method was that the corrugated paper sheets had to be replaced frequently as they got soaked by rains and were often eaten up by termites. However, the results showed that the number of pupae in each generation was low indicating poor survival between the larval and pupal stage (Figure 6-10). It is also possible that the method used in sampling for pupae gave some inaccurate results. Pupation started to occur in the field after 48 DAPE and continued to a peak just before the pod maturity for every generation studied. Pupae were not recovered 3 weeks after pod maturity and harvest in the ICV6 variety, at both sites.

The temporal distribution for the pupal stage for each generation at MPFS and Lambwe Valley (Figures 6-10) and the results from the pheromone traps (Figures 1-2) suggest that the second peak in moth incidence resulted from a resident population on the crop. Since adult emergence started in the field 5-8 days after the first pupae were recorded in the trap and continued until 2-3 weeks after harvesting in cases where the crop growth did not extend beyond this

period, it was concluded that no aestivation/diapause occurred in M. testulalis either at the larval or pupal stage and that any adults found on a crop planted several weeks after harvest were presumably immigrating from other sources. Volunteer cowpea and wild host plants were observed to be an important source of infestation of the new crop by M. testulalis (Taylor 1978). There is no evidence of diapause in this species from previous studies in Nigeria and Kenya and mature larvae pupate and emerge normally throughout the year (Taylor, 1978; and Okeyo-Owuor, 1981). However, recent studies in China revealed that overwintering occurred in pupal stage (Ke et al., 1985).

By planting the crop also in the off season, it was found that M. testulalis development continued and several generations occurred throughout the year. However, although the pest was active throughout the year, only the generations on the cowpea crop occurring during the long rainy periods (March-July) and the short rainy seasons (October-December) cause much concern as far as crop damage and seed yield losses are concerned. During the cropping seasons only one generation was completed on the ICV6 variety which was selected for the study. In some cases in Lambwe Valley, when the rains were prolonged beyond the normal crop maturity period, a second low generation was also observed but this was often incomplete and not important. Since, the two rainy seasons were separated by a 3 month dry spell at Lambwe Valley and even by a longer period at MPFS the other generations during the period were

possibly completed on the wild host plants. This situation was different from that in Nigeria in which the late crop was attacked by the colony from previous early crop resulting into higher populations in the late than the early crop (Taylor, 1967, 1978). In other tropical countries, several generations of M. testulalis have been observed throughout the year (Taylor 1967, Ke et al. 1985) and population flunctuation seems to be similar to that observed during this study period. However, for the purposes of crop protection, control strategies should be directed towards the generations whose peaks coincide with peak flowering on cowpea crop during the cropping seasons.

Observations on mortality factors and their role on population regulation as presented in the life tables (Tables 1-8) and Figure 14 showed that the highest mortality occurs at the early life stages (between egg and 3rd instar larvae) and is attributable to disappearance. The total real generation mortality ranged between 51.7 - 98.9% (Mean = 82.0%) at MPFS and 96.4 - 97.7% (Mean = 97.2%) at Lambwe, showing that, from the initial cohort of eggs a range of only 1.1 - 48.3% were expected to survive to adult stage under field conditions. In case of mortalities occurring at different life stages (apparent mortality), the lowest mortality occurred at the 4th instar stage at both study sites. At MPFS low apparent mortalities were also observed at the early instar stage (Larvae I-II) as illustrated in Figure 14. These results suggest that the larvae at these stages were secure from mortality factors,

resulting into relatively higher survival than the other life stages. During field sampling it was found that the early instar (Larvae I-II) and the 4th instar larvae burrowed and concentrated their feeding inside the food substrate and because of this behaviour these stages could be in minimal contact with the various mortality agents occurring in the field. The other stages were relatively exposed. For instance, the eggs were laid on leaf surfaces and were usually unprotected. The 3rd instar larvae often moved about the plant looking for fresh food sites, while the 5th instar larvae at full growth came out of the plant to pupate in the soil. During this time of movement on the plant and pupation, these stages are exposed to parasitoids, predators, disease and adverse climatic factors. Considering apparent mortality, it was found that the 5th instar suffered the highest mortality followed by the pupal stage and then the 3rd instar larvae. Again as in the case of apparent generation mortality, the lowest apparent mortality was observed in the 4th and early (Larvae I-II) instar larvae, confirming an earlier discussion on possible factors responsible for the variation in mortality in the different life stages on M. testulalis.

The results on M. testulalis mortality are better illustrated in the survival curves presented in Figures 12-13. The shape of survival curves obtained in M. testulalis are not similar to any of the three types of general survival curves (Types I, II

and III) described for animals by Price (1975). However, he further described two basic types of survival curves obtained from life tables of 19 phytophagous insect species which may be useful in explaining M. testulalis survival curves. These he termed A and B. Type B is characterised by a concave shape in which very high mortalities (more than 70% by mid larval stage) occur in the early stages and is usually exhibited by free living and exposed species, although some may be protected by webs or buds. Members of type A have a convex survivorship curves with less mortality (40% or less) by midlarvae and the majority of the species are protected apparently by their burrowing habits or colonial defence behaviour. Survival curves of M. testulalis seem to be intermediate between type A and B curves but more similar to A and therefore satisfy the description of a typical insect survivorship curve as discussed by Price (1975). The mean survivorship curves obtained from generations at MPFS and Lambwe Valley, were more or less similar in shape and therefore either one of them may be used to describe survival of M. testulalis (Figure 13). Also the similarity between survival curves in field and screen house support the idea that parasitoids might be playing negligible role on the pest population since the tests in screen house excluded these mortality agents. According to Price (1975), the shape of insect survivorship curves are of interest in understanding the reproductive strategies of parasitoids that attack these insects and in applied control.

Although life tables have rarely been used in studying insect populations on arable crops in the tropical world, their construction for M. testulalis has proved useful in understanding

the population dynamics of this species. In the present study, life-tables were constructed for five generations as MPFS and three generations for Lambwe Valley from which the role of various mortality factors were derived. Mortality due to parasitoids and disease agents was not observed in M. testulalis eggs and the reduction in egg numbers were grouped under disappearance. Since the eggs were difficult to examine under field conditions due to sampling problems stated earlier, the number of eggs used in the construction of life tables and to culaculate mortality due to disappearance was estimated as described Chapter III. From the life tables it was found that larval real mortality due to the various causative agents was quite variable within and between the generations studied. For example, in the case of larvae I-II, real mortalities due to disease and disappearance ranged from 1.2 - 17.5% (mean = 11.02) at MPFS and 14.7 - 40.5% (mean = 28.8%) in Lambwe Valley. Thus, in this stage both disappearance and disease agents caused higher mortality in Lambwe Valley than at MPFS.

Disease contributed only 0-6.6% of the real generation mortality in Larvae I-II, while the rest was due to disappearance at MPFS. This observation suggests that the incidence of disease at this early stage of M. testulalis is negligible. Also no parasitism was observed on this life stage at this site. Similar results were also observed in Lambwe Valley, where only 0-5.3% real mortality in this stage was due to disease.

The life-tables, further revealed that real generation mortality in the 3rd instar larvae ranged from 14.1 - 39.5% of which disease contributed 4.2 - 30.6% at MPFS. The rest of the mortality was due to disappearance as no parasitism was observed in 3rd instar

larvae at this site. In Lambwe Valley, the range of real mortality in this stage was 8.9 - 28.6% of which 3.5 - 17.0% was caused by disease (mean = 13.9%), and the rest was attributable to disappearance (6.7%). In this site larval parasitism was not observed. Data from life tables reveal low real mortalities in the 4th instar larvae as compared to that of the other life stages at both sites. At MPFS mean real generation mortality due to disease was 3.8% compared to 6.4% for disappearance. In the case of Lambwe, the mortality was low and the contribution of the various mortality factors was negligible. No parasitism was observed at both sites in this stage.

In Larvae V low level of parasitism was observed, being only 0.04% at MPFS and 0.4% at Lambwe. Disease caused mean generation mortalities of 11.2% and 5.8% at both sites respectively while the respective real mortalities due to disappearance of larvae V were 6.8% and 4.4%. In this stage disease caused the highest mortality followed by disappearance and then parasitism. Life table data showed that parasitism caused by mean real mortality of 0.8% and 0.4% for the generations at MPFS and Lambwe respectively in M. testulalis pupae. These mortalities were low compared to those caused by disease (2.8% and 4.0% respectively) and disappearance (2.4% and 3.7% respectively). In this case disease and disappearance contributed equally to pupal mortality at both sites.

In the key-factor analysis k_o was found to be more similar to K than the other k-factors in relation to magnitude of change at MPFS. This was further confirmed by a correlation analysis of k_o,

k_4 and k_{12} on K. The results showed that there was high positive correlation (r = 0.87) between k_o and K followed by k_4 (r = 0.83). The value of k_{12} was not significantly related to K.

In the life tables, k_o which represents disappearance operating at the egg stage, was confirmed to be the key mortality factor identified by the method of Morris (1959), Varley and Gradwell (1960, 1968), Clerk et al. (1972), Varley et al. 1973, Johnson (1978) and Danthanarayana (1983). However, in the case of Lambwe Valley, although k_3 resembled K more than the other k-factors and was identified as the key mortality factor, the number of generations (3) was too few to warrant a meaningful statistical analysis on the factor. It is, therefore, possible that with more generations any other k-factor could have emerged as the key mortality factor at this site.

At both sites, sampling was regular, but due to difficulties of sampling and adverse weather for eggs, the density of eggs used in this analysis was estimated and such estimates could result into erratic causes of change with respect to some of the curves in the key factor analysis. Hence, this could give inaccurate estimation of the role of egg mortality agents on population changes of M. testulalis. From key-factor analysis it appears that disease contributed significantly to M. testulalis mortality. The two major pathogens observed, Nosema sp. and Bacillus sp., are potential candidates for biological control for this pest. From the values of k_8 and k_{11}, it appears that the

contribution of parasitoids to M. testulalis mortality and population change was low and negligible. This observation seem to agree with the view of some authors on the role of parasitoids in population regulation of insects (Bess, 1961). However, since any attack by parasitoids usually leads to death of the host and not normally easy to count directly, estimation of parasitized hosts my be lower than those attacked, resulting in an under-estimation of the effect of parasitism on population regulation (Campell, 1963; van Driesche, 1983 and Cock, 1986). Thus, the results on parasitism of M. testulalis found at MPFS and Lambwe Valley during 1983-1985, may give an under-estimate of the role of these mortality agents in view of the fact that a rich fauna of parasitoids were found at the sites and that laboratory studies on the pupal parasitoid T. sesamiae revealed even higher mortalities on M. testulalis pupae than actual parasitism (Figure 47). This was possibly due to stinging action of the parasitoids on pupae which though did not result into parasitoid oviposition caused wounds on the pupae resulting in death or mortality due to infection by disease agents.

The mortality factors at MPFS were further analysed for density relationship by plotting the values of k_o, k_4 and k_{12} against the log. of population density (l_x) according to the methods of Varley and Gradwell (1963). The results showed that k_{12} (b=0.3) was slightly density dependent. The regression value of k_{12} was high but not significant (P=0.05). From these results it is evident that the factors responsible for the major portions of the natural mortality of M. testulalis are not dependent on the population density of this insect species.

The field surveys revealed that M. testulalis is attacked by a wide range of natural enemies. The pathogens recorded on this insect were Nosema sp., Bacillus sp., Clostridium sp., Mettesia sp., and unidentified nematode and viruses (nuclear polyhedrosis and granulosis). Although, all these pathogens occurred at both study sites and appear to be widely distributed in cowpea growing areas of western Kenya, Table 17 shows that the most common disease agents were Nosema sp. and Bacillus sp. Mortality due to pathogens was mostly recorded in the age groups between 3rd and 5th instars. Although, pathogenicity tests under laboratory conditions at MPFS showed that those stages younger than the 3rd instar larvae were most susceptible, data from field studies suggested that field mortality at this stage was not due to these disease agents. In cases where microscopic examinations were made on 1st and 2nd instar larvae, found dead in the field, neither Nosema sp. nor Bacillus sp. were recovered. In a few cases where pathogens were observed, the spore concentration in the slide preparations was negligible. However, these pathogens played an important role as mortality agents on M. testulalis especially at the later stages. The existence and abundance of insect pathogens in lepidoptera crop pests have been studied in detail by several authors (De Bach 1974). Nosema pyrausta is an important pathogen of larvae of the European corn borer, O. nubilalis (Zimmack and Brindley, 1957; Raun, York and Brooks, 1960; Windels et al. 1976; Lewis and Lynch, 1976; Lynch and Lewis 1976 and Lewis 1978, 1982). Nosema sp. was also

recorded to cause mortality on C. partellus under natural field conditions in Kenya by M.O. Odindo (personal communication). This pathogen was first isolated on M. testulalis in Kenya by Otieno et al. (1983). Studies by Otieno et al. (1983) and the present results show that Nosema sp. is an important pathogen of M. testulalis and bears great potential for the biological control of this pest.

Although Bacillus sp. on M. testulalis was also abundant in the field, the strain found on the pest showed lower virulence than Nosema sp. when assayed in the laboratory. Under laboratory conditions at MPFS Nosema sp. caused 100% mortality on M. testulalis compared to only 60% in the case of Bacillus sp. Detailed field and laboratory studies on these species, Bacillus and Nosema, are necessary to a ascertain their potential in biological control of the pest.

A rich fauna of M. testulalis parasitoids were found to occur at both study sites on cultivated cowpea and wild hosts. Although no parasitoid was found on M. testulalis eggs, four hymenopteran parasitoids (Chelonus sp., Apanteles sp., Bracon sp. and an unidentified Braconid) were found to parasitize larvae. Of these only Apanteles sp. and Bracon sp. were found at MPFS, while at Lambwe Valley all these were recorded. The pupal parasitoids recorded at both sites were Antrocephalus sp., Braunsia sp. Bracon sp., T. sesamiae, (all Hymenoptera) and an unidentified Tachinid (Diptera). The Eulophid, T. sesamiae was found only at MPFS. Among

the parasitoids Antrocephalus sp. was the most common at both sites and was found to parasitize pupae during both seasons throughout the study period. It was also evident from the studies that the study site at Lambwe Valley was richer in parasitoids than at MPFS. Lambwe Valley as discussed in Chapter III, has two reliable rainfall seasons and supports a wide range of wild host plants and volunteer crops on which M. testulalis and its parasitoids survive during the dry period. On the other hand, MPFS usually has a long dry spell and short rains are only occasional. Hence, the few wild hosts on which the pest and its parasitoids survive are only found along the lake shores.

Several parasitoids have been recorded on M. testulalis in other cowpea growing countries. Taylor (1967), Usua and Singh (1978) and Don-Pedro (1983) reported a diptera (Musca domestica from Callara Wlk), Braunsia sp. Phanerotoma sp. as parasitoids of the pest in Nigeria. M. testulalis was also reported to be parasitized by Apanteles etiellae Vier, Bracon cajani Mues, B. thurberiphagae, Phenerotoma bennetti, Perisierola sp. Eiphosoma annulata and Cedria paradoxa in Fiji by Rao et al. (Unpublished reports). In India Agathis sp. and Phanerotoma sp. were reported to attack M. testulalis on pigeonpea crop (Vishakantaiah and Babu 1980); while more recently Ke et al. (1985) recorded two larval parasitoids namely Cremastus sp. and Pseudoperichaeta insidiosa on the pest in China. In the present study all parasitoid species, except Brausia sp. and Antrocephalus sp. were reported for the first time on M. testulalis. More detailed studies are necessary to determine the distribution of these parasitoids and identify others from other cowpea growing areas.

Host plants of M. testulalis were found to be important in determining biology and population trend of M. testulalis. For instance, at MPFS and in western Kenya cowpea is the most important host plant of M. testulalis. Data from the field studies revealed that cowpea was attacked by the pest at a specific time (15-30 DAPE) in crop growth stage and the population build up did not occur until flowering time. It was also observed that, although, cowpea leaves provided suitable oviposition sites, the larvae of M. testulalis survived best on flowers and tender green pods and that survival was low in the absence of these parts of the plant resulting into low populations of M. testulalis.

Field observations on the distribution of larvae on cowpea confirmed that the other parts of the plant such as leaves, shoots and stems were least prefereed for feeding. The larvae only fed on these parts whenever flowers and green pods were not available, such as during the preflowering stage and after the pods have dried up. The results showed a definite shift in larval feeding and distribution as the crop developed. For example, at the vegetation stage until flower initiation the few larvae found on the crop were feeding on plant shoots and soft parts of the stems. However, as more flowers formed, the larvae preferred to feed on flowers and the population shift was to these parts of the plant and later to green pods (Figure 19-26). Correlation analysis of the M. testulalis population data on the number of the various parts of the plant produced per season showed highly significant positive

relationships on flowers (r = 0.788) and pods (r = 0.733) (P = 0.05). These relationships confirmed the high preference by M. testulalis larvae for these parts of the cowpea plant and suggest that these parts are important in sustaining high populations of the pest on the crop. Furthermore, the results indicate that in seasons where the crop was affected by environmental conditions including weather, vegetative pests and diseases, resulting in reduced flower and pod production, M. testulalis survival and population build-up was greatly affected. This is indicated by the lack of significant correlation between the number of adults caught in the pheromone traps and eggs per plant against the various plant growth parameters (Figures 27 and 29 and Table 18). From this information it may be concluded that the success in M. testulalis establishment on cowpea crop depends on the availability of flowers and green pods on the plants and the success of the larvae in reaching and feeding on these preferred parts.

Preference of the flowers and green pods of the cowpea plant by M. testulalis larvae was reported in field studies by Taylor (1967, 1978). According to Taylor (1967), both young and advanced stage larvae concentrate their attack on the reproductive parts of the flowers. They initially consume the anthers, filaments, stigma and ovary before feeding on the internal components of corolla. However, the larvae later disperse to other parts of the plants, especially, flowers and fresh pods. He, further observed that, the successful establishment of

the pest at the flower initiation stage is significant in relation to subsequent damage, reduction in yield and difficulty often encountered in the control. He, further, observed that flower damage increases as the number of flowers per plant themselves increase, thus, reaching a peak about the same time as the peak flowering stage after which the damage on flower decreases, but the damage on pods increases rapidly until pod maturity. Similar observations were also reported by Usua and Singh (1978), Jackai (1981) and confirm the findings on the larval distribution and survivorship on the various parts of the cowpea plants studied at MPFS and Lambwe Valley. Further, investigations under laboratory conditions at MPFS confirmed that M. testulalis larvae survived and developed better on flowers and pods of the cowpea plants than on leaves, stems and terminal buds. These findings were also similar to that observed by Okech (Unpublished data) on different cowpea varieties. The laboratory studies also revealed that the duration of larval development was shorter and the pupal weight was heavier in the larvae fed on flowers and green pods than those fed on the vegetative parts of the plant. These observations suggest that, since the performance of M. testulalis was better on flowers and pods, the insect completed its life cycle earlier and the generation time was shorter on these parts; hence, higher chances of the generation survivorship. Thus, in some cowpea varieties which flower profusely and produce more pods as well as being medium to late maturing the pest may complete several generations leading to

severe damage on the crop and carry-over problems on the subsequent cowpea crop in areas with prolonged rainy periods and bimodal rainfall pattern.- In fact, in Nigeria, Taylor (1967, 1978) reported that the damage and losses due to M. testulalis on the late crop was higher than on the early crop, since the pest population tends to build up on the early crop and other cultivated legumes so that the late crop provides a focus of attack. This resulted into 40-50% loss of flowers and 20-40% damaged pods on copwea crop in Nigeria. Under such circumstances, at least 4 generations may be expected on both early and late crop. This situation in Nigeria may be considered similar to many parts of cowpea growing areas of western Kenya where there are two cropping seasons per year and M. testulalis has many cultivated legumes, including cowpea, and wild host plants to survive on. However, the Mbita conditions may be considered different because of its eratic short rainy season but survival of the pest is promoted by farmers' practice of planting irrigating small cowpea plots and the presence of wild host plants along the nearby lake shore.

M. testulalis was recorded from wild leguminous plants of the family Papilionoidae in all the five locations studied. Larvae of M. testulalis were found feeding mainly on flowers, but in some cases on pods of these plant species. Of the wild legumes from which M. testulalis was recorded, S. sesban supported the largest number of larvae (more than 10 larvae/100 flowers) followed

by V. vexillata and V. luteola (5-10 larvae/100 flowers). In the other legumes, R. melacophylla, Rynchosia sp. nr. maxima, Crotolaria sp. and C. deserticola, M. testulalis larvae were rare (less than 5/100 flowers). The survey results showed that S. sesban, V. luteolla and V. vexillata were common plant species at the study sites. In Lambwe Valley, Rangwe, Lambwe A and Lambwe B, these species of plants showed semi-perennial characteristics and were flowering throughout the year. Although flowering was less during the dry periods, M. testulalis larvae were still found feeding on the few flowers, green pods, and tender shoots and stems of the plants at low populations. The plants however, started flowering profusely soon after the onset of the rains and this was marked by an increase of M. testulalis larvae occurring on the wild hosts even before the cultivated cowpea crop was ready for infestation. Thus, from these studies it was evident that M. testulalis survived the dry period on the wild leguminous host plants and that as the cowpea crop grew, it was infested by the adult moths from the wild host plants after the onset of the rains. Such moths were trapped on pheromone traps as early as 15 DAPE. In the case of MPFS and Rusinga, the same wild hosts were found along the lake shore, where flowering also occurred throughout the year. These provided M. testulalis with a source of food supply during the dry period as well as acting as important source for cowpea crop infestation during the rainy periods.

In Nigeria, Taylor (1967) recorded seasonal occurrence of larvae on 36 host plant species and Taylor (1978) listed 26 host

plant species of M. testulalis in which several were wild species, and ornamentals belonging to the different families of Leguminosae. The role of wild host plants in sustaining M. testulalis populations during the dry seasons when the principal hosts is not cultivated have also been underscored by Taylor (1967, 1978), Usua (1975) and Jackai and Singh (1983).

An even more striking finding during the study on wild hosts of M. testulalis on the 5 sites was the fact that in some sites parasitoids and pathogens of the pest were also recovered from the larvae and pupae. For instance, in Rusinga, the parasitoids Bracon sp. and Antrocephalus sp. were found emerging from some dead larvae and pupae of M. testulalis respectively, while Nosema sp. and Bacillus sp. were microscopically examined from dead cadavers of M. testulalis larvae. These findings show that, apart from merely acting as wild hosts of the pest, these plants were also important in perpetuating the natural enemies of M. testulalis.

The role of alternative host plants in maintaining natural enemies of insect pests especially predators and parasitoids is well documented and therefore not unique to M. testulalis and its natural enemies. Recent investigations have revealed that alternative host plants are important in enchancing the effect of natural enemies on insect pests (Salick, 1983; Altieri, 1983; and Cook, 1985). According to Sales (1985) the activity of natural enemies on S. fugiperda was enhance by the presence of natural vegation in close proximity to maize crop and that under such conditions defoliation was less than 2%, while the crop damage by the pest increased significantly with distance from natural vegetation.

Although, in these studies some preliminary work was conducted to determine the effect of climatic factors such as rainfall, temperature and relative humidity on population ecology of M. testulalis, more detailed work is necessary to relate the various climatic parameters with the population changes of the insect. Furthermore, the kind of equipment used in collecting climatic data, especially, the thermohygrographs provided less accurate information on R.H. and temperature as they only measured those changes at the ambient level, but not the micro-climate surrounding the insect and within the host plant. Because of the frequent saturation of the apparatus data on R.H. at both sites were irregular and could not be used in determining the effect of this factor on population of M. testulalis. Furthermore, during the cropping season, the different stages of this pest resided in niches with high R.H. (between 90-100%) especially in the case of eggs, larvae and pupae and merely measuring the ambient R.H. changes might not prove useful and was not considered in the present study.

In the case of rainfall, two parameters were used to study its influence on population changes of M. testulalis. The first parameter involved comparison of weekly rainfall versus population density per sample within each cropping season at MPFS as shown in Figure 36. The results did not show that changes in rainfall pattern had any direct influence on population build up of M. testulalis possibly because of the lag phase between the rainfall and initial crop infestation by the pest. Population build up did not start on cowpea crop until 15-30 DAPE. Another parameter used was the effect of total seasonal rainfall on population development

of M. testulalis. Population densities of the pest per hectare per season was analysed against the total rainfall per season for all the generation seasons studied at MPFS (Figure 37). The highest correlation coefficient was found on rainfall versus larval density ($r = 0.49$), followed by male adult density ($r = 0.41$) and egg density ($r = 0.38$). Although the results showed positive relationships between the amount of precipitation per season and population density which to some extent suggested that M. testulalis population density was boosted by the increase in seasonal rainfall, these r-values were not significant ($P = 0.01$). However, from these studies it is evident that the total precipitation per season was more important in influencing the population density of M. testulalis expected on cowpea crop and could be a more important factor influencing seasonal population changes than mere rainfall within the season.

The total seasonal rainfall also influenced the growth and development in the host plant as well as changes in other abiotic and biotic factors which are to influence the seasonal population changes of the species. For instance, it was observed that high rainfall within the season favoured flower and pod production in the host plant thus, providing suitable food source for M. testulalis. In seasons where rainfall was low the crop was heavily attacked by thrips, aphids and white-flies at the vegetative phase. The low precipitation and attack by these pests on the crop adversely affected the flower and pod production on the plants. This resulted into poor establishment of M. testulalis larvae, low survival and subsequent reduction in population density of the pest throughout the cropping season. This phenomenon was more common at MPFS during

the August - January 1984 and 1985 when the rainfall was minimum and the crop development was retarded, resulting into low populations of M. testulalis (Figure 36). In 1983 the short rains (October - January) were high, the crop stand was good and the corresponding population of the pest was also high at this site. Although, the rainfall data at Lambwe were not recorded due to distance from MPFS station, the changes in seasonal population appeared to follow the same trend as that at MPFS and the relationship between the population and seasonal rainfall could be considered similar.

Previous studies in Nigeria showed that larval population of M. testulalis was favoured by longer and higher rainfall duration the type that occurred in the 2nd season (July to October) as compared to the population in the first season (May - July) which had lower rainfall (Taylor 1967; Jackai 1981). Okeyo-Owuor et al. (1983) also reported that the amount of seasonal rainfall was positively related to population density of M. testulalis larvae and that during the dry period the populations were low even though the crop was irrigated. Previous work on population dynamics have shown that factors such as rainfall are density independent or catastrophic and may only contribute towards insect population change rather than act as population regulation factors (Clerk et al., 1972; Varley, Gradwell and Hassell, 1975).

Ambient temperatures at MPFS and Lambwe fluctuated between 15°C at night and 35°C during the day, these being the highest recorded temperature on thermohygrograph readings at these sites. However, during the study period these extremes were rarely reached and the range in temperatures were mostly 18-21°C at night and 23-30°C during the day. The data at MPFS were used to study the

relationships between the temperature changes and population density of M. testulalis as shown in Figure 38-40. Results from correlation analysis revealed high positive relationships between maximum - minimum temperatures and egg density per plant (r = 0.84), mean day - night temperatures and egg density (r = 0.78) and mean minimum temperature and larval density (r = 0.74), all of which were significant. These temperature changes seemed to affect survival and development of M. testulalis under field conditions and hence determining the cause of population change of this species on a seasonal basis within the normal temperature ranges stated (18-21°C night and 23-30°C day). The observations suggest that the increase in ambient temperatures favoured faster development, infestation and successful establishment of M. testulalis resulting into increased populations on the crop. However, from the results it is was found that not all temperature changes measured contributed to seasonal changes in the pests population. For instance, Figures 34-36 show that, only the temperature parameters discussed above had significant correlations the various pest densities. The others were not related to population changes of the pest.

In the case of adult moths probably the lack of any significant effect of temperature on the population was because of the narrow range of temperatures (18-21°C) occurring during the night at the time when they are most active. The studies also suggest that in field populations seasonal changes in ambient temperature had significant effect on eggs than larval and adults stages. More detailed investigations especially on the effect of microclimatic factors on the insect are necessary in the field.

These were not measured due to lack of appropriate apparatus during the study period.

Investigations on the effect of constant temperature regimes on survival and growth of M. testulalis conducted under laboratory conditions showed that within 21°C - 32°C, the different life stages were favoured, especially in larvae and pupae, resulting into shorter life cycle of the pest and subsequently a shorter generation time. The optimum temperatures for M. testulalis survival and development was observed to lie within this range of temperatures. In the case of larvae the optimum temperature for survival was 29°C (Figures 43-44) and that for development was between 23-29°C (Figure 42). In the case of pupae the optimum temperature for survival and development was also found to be within the same range as that of the larvae. The heaviest pupal weights were observed when temperatures were maintained at 23°C showing that this temperature favoured pupal development best. The different temperature regimes, however did not seem to affect the egg hatchability and incubation period, except that at extreme temperatures, below 18°C and above 34°C no eggs hatched. The reason for this could be that these extreme temperatures affected egg development causing lack of egg viability or mortality. Similarly, in the case of larvae and pupae mortalities were high at temperatures below 18°C and above 34°C resulting into poor survival and development. In fact at 35°C neither larvae nor pupae survived.

The results observed in the laboratory studies confirm the observations under field conditions, that changes in temperature are significant in survival, growth and development of M. testulalis.

The temperature regimes tested under the laboratory conditions were similar to the normal range observed in the field. During the dry periods ambient temperature at MPFS and Lambwe ranged from 24-35°C in the day while during the rainy periods the range is 21-30°C, while in both seasons the temperatures fluctuated between 15-18°C during the night. The range of temperatures observed during the rainy season seem to be favourable to the pest and therefore under such conditions M. testulalis incidence was high at the study sites provided that the crop was in the field and in the right phenological stage. During the dry season temperatures are high and normally exceeded 30°C and temperatures reaching 35°C were not uncommon especially at MPFS. These high temperatures could be detrimental to egg, larval and pupal development and survival irrespective of whether the crop was maintained under irrigation, hence, partially contributing to the low population of M. testulalis observed during the off season.

The effect of temperature on survival and development of lepidopteran species is well documented. Recent, studies by Bues and Poitout (1984) revealed that temperature changes are important in terminating and inducing development in Arctia cajani (Lepidoptera, Arctiidae). Reynolds and Nottingham (1985) also showed that temperature was an important factor in growth and efficiency of food utilization in Manduca sexta and Fujiyoshi et al. (1984) showed that temperature was important in the development of Sesamia inference. Because temperature is an important factor influencing development and survival of insect species either indirectly or directly, its role in determining population changes as a density independent factor can not be underestimated on M. testulalis.

Studies on the biology of T. sesamiae a gregarious pupal parasitoid of M. testulalis showed that ovulation and development of eggs continued after female emergence and as such it was difficult to accurately determine their potential fecundity by teasing the female's abdominal parts. Thus, a better estimate of fecundity was done by observing the progeny production in the laboratory. The fact that this parasitoid had short development period (16.8 days), high progeny production (142.5 progeny per M. testulalis female) and that it can attack other cereal stem borers, such as C. partellus, B. fusca, and E. saccharina makes it a good candidate for biological control of these pests under traditional subsistence farming which are usually characterized by intercropping cereals and legume crops. It was also observed that one female parasitoid can parasitize and cause mortality of upto 5 pupae. The parasitoid was easy to rear on both M. testulalis and C. partellus under laboratory conditions. These pests species are well established in laboratory cultures at MPFS. Furthermore, the biological activity of this parasioid, such as, progeny production, longevity and parasitism was enhanced by improved nutrient supplies such as sucrose and honey solutions as shown in Figures 44-47. Thus, the parasitoid shows good prospects for mass rearing and use in a biological control programme.

T. sesamiae was not common in cowpea fields and was only recorded during one season at MPFS. The parasitoid was not found at Lambwe Valley throughout the study period. Although the species has not been reported on M. testulalis before, a number of species belonging to the genus Tetrastichus are known to parasitize several crop pests. For example, the sorghum earhead midge (Contarinia

sorghicola (Coquillet) was reported to be parasitized by T. diplosidis in Bukina Faso and Mali (Bonzi and Doumbia 1985) while T. blastophaga, T. venostus were reported on the midge in Texas (Brooks and Gilstrap 1985). On lepidopteran crop pests T. sokolowskii was released to control Plutella xylostella on cabbage in Fiji (Anon, 1985). T. sokolowskii was also among other parasitoids released to control P. xylostella in Cape Verde and they appear to have been established there (van Harten and Miranda 1985; Lima and van Harten 1985). On C. partellus attempts were made to release T. artriclavus among other parasitoids for control of this pest but with little success in Comoro Islands (Breniere et al., 1985).

SUMMARY

Investigations on population ecology of M. testulalis was conducted on cowpea crop (ICV6) at MPFS and Lambwe Valley farmer's field between the short rainy season (October-December 1983) and short rainy season (October-December 1985). During this period, five generations of the pest were studied at MPFS in detail and three in Lambwe Valley. The cowpea crop was planted at the beginning of each rainy season and all stages of M. testulalis were sampled for. Since, the short rains at MPFS were often unreliable, the crop was mostly maintained under irrigation. Crop was also planted during the dry periods of 1984 and 1985 at this site to assess the status of M. testulalis population in the off-season. The impact of parasitoids and pathogens as mortality factors was also determined through life-table and key-factor analysis. Bioassays on the most common disease agent, Nosema sp. and laboratory studies on the biology of the pupal endoparasitoid, T. sesamiae, were conducted at MPFS. The effect of climatic factors and alternative host plants on population changes of M. testulalis was investigated.

The results from these studies showed that:

1. Moths were first recorded on pheromone traps in cowpea crop at the pre-flowering stage (15 DAPE), but the population

remained low until after flower initiation stage (30 DAPE) when the trap catches rose to a peak. This peak population density coincided with peak flowering stage, which is most suitable for development of this insect.

2. The trend of egg population development on the crop was similar to that of adults, but the actual numbers sampled were low due to sampling problems stated earlier.

3. Larvae were first recorded on the crop at about 30 DAPE and the population increased sharply to a peak that coincided with peak flowering stage. The trend in larval population change was similar in all the generations at both sites for all the instars. Before flowering the larvae fed on tender shoots and stems of the plants, but later shifted to flowers and then to pods as soon as these parts were available on the plant.

4. Several generations of M. testulalis occurred throughout the year although at the study sites and in other areas of western Kenya only one complete generation occurred each on the long rainy and short rainy season's crop, causing substantial flower and pod damage and subsequent seed yield loss on cowpea crop. On the ICV6 cowpea only one generation of M. testulalis was successfully completed. Other generations occurred in low

numbers and survived either on leguminous crops cultivated under irrigation by farmers along the lake or on wild host plants existing within the vicinity of the study area.

5. Mortality and survival of M. testulalis on cowpea agroecosystem were determined through the contruction of life tables. The results showed considerable variation both in the intrageneration mortality of the life stages and the total generation mortality.

6. Survival curves of M. testulalis indicated that the survival of the pest was a typical insect one and was an intermediate between type A and B described by Price (1975). This survival curve is indicative of a constant rate of mortality with about 60% of mortality occurring by the 3rd (mediam) larval stage. Furthermore, survival of M. testulalis from egg to adult stage was low being less than 10% at both sites.

7. A rich fauna of natural enemies associated with M. testulalis occurred in the cowpea crop ecosystem as well as on wild host plantsof the pest. Seven species of parasitoids, one nematode, and four pathogens were recorded on the larvae and pupae of the pest at the study sites.

8. The life table and key-factor analysis revealed that at both sites pathogens, especially Nosema sp. and Bacillus contributed significantly to the overall mortalities of M. testulalis.

Parasitoids contributed minimal towards the overall mortality. Mortality due to unknown factors termed here as 'disappearance' was also high especially in the egg and the early instar larval stage. The exact role of predators was not determined. Disappearance at the egg stage at MPFS (k_0) and disease at the third instar larval stage in Lambwe (k_3) were identified as key-factors causing population change at these sites.

9. The apparent lack of a significant density dependent factor is indicative of the fact that the dominant factors effecting M. testulalis population change at both sites are density-independent. The increase in population during the season are probably related more to density independent weather and climatic factors such as temperature, rainfall and R.H., as well as food availability, while low food value and quantity of the cowpea plants as the crop matures could be the explanation for the population crash that occurred after the peaks. These observations were supported by results from the laboratory and field studies on the effect of climatic (rainfall and temperature) and host plant phenological factors on survival and development of M. testulalis.

10. Wild host plants especially, S. sesban, V. vexillata and V. luteola play a major role in survivorship, and maintaining

populations of M. testulalis, as well as their natural enemies under natural conditions, particularly during the dry periods of the year. This is particularly important since no diapause has been recorded in this pest in the tropics. Also during the dry periods there is no other plant to survive on except the wild hosts at both study sites.

11. Preliminary studies on biology of a selected parasitoid (T. sesamiae) and a protozoan pathogen (Nosema sp.) of M. testulalis provided some important information of their biocontrol potential against this pest. More detailed studies, not only on these natural enemies but also on the others, are necessary to determine their role in population regulation and potential in biological control of M. testulalis.

In general, the present studies have yielded important information on the bionomics and population ecology of M. testulalis in cowpea agroecosystem. The role of the different mortality factors have clearly been elucidated. The discovery of these natural enemies have contributed a significant addition to the list of natural enemies known on the pest. Similar observations are true in the case of wild host plants. These studies further confirmed that M. testulalis still remains the key pest of cowpea which justified the development of a sound IPM system for its control.

R E F E R E N C E

AGYEN-SAMPONG, M. (1978). Pests of cowpea and their Control in Ghana. In "Pests of Grain Legumes; Ecology and Control" S.R. Singh Eds, T.A. and H.F. van Emden, London Academic Press 85-92.

AKENFENWA, S. (1975). Bioecological study of Maruca testulalis Geyer (Lepidoptera, Pyralidae) in the Zaria area of northern Nigeria. M. Sc. thesis, Ahmado Bello University, Zaria, Nigeria.

ALLEN, G.E. and C.M. IGNOFFO, (1969). Nuclear Polyhedrosis Virus of Heliothis: Quantitative in vivo estimates of virulence. Jour Invert. Pathol. 13: 378-381.

AL SALTI, M.N. and G.F. GILICHET, (1968) Seasonal variations in the resproductive ability of Sesamia nonogrioides Lefebr (Lep. Noct.) Acta Oecologia 7 (2): 115-122.

ALTIERI, M.A. (1983). Vegetational designs for insect-habitat management. Environmental Management 7 (1): 3-7.

ANDREADIS, T.G. (1979). Use of Bacillus thuringiensis for control of lepidopterous pest on sweet corn. Insecticides and Acaricide Tests 6: 70 (iii).

ANDREADIS, T.G. (1982). Current status of imported and native parasites of the European corn borer (Lepidoptera, Pyralidae). Jour. Econ. Entomol 75 (4): 620-629.

ANDREADIS, T. G. (1984). Epizootology of Nosema pyrausta in field populations of the European corn borer (Lepidoptera, Pyralidae). Environ. Entomol. 13 (3): 882-887.

ANDREWARTHA, H. G. and L.C BIRCH. (1954). The distribution and abundance of animals. University of Chicago Press, 2-57.

ANON, (1981). Pests of Legumes. Queenland Agric. Jour. 107 (1): V-VI.

ANON, (1985). Report of Primary Industries; Vegetables, Parliamentary paper, Fiji No. 62: 61-62.

ARAUJO, J.R. De; P.S.M. BOTELHO, H. De CAMPOS, L.C. De ALMEIDA, N. De GASTPARI, (1984). Influence of the number of Apanteles flavipes released on effectivenss of control of sugar cane borer, Diatrea saccharalis Cadarnos PLANAL SUGAR, 3 (3): 12-21.

AT SATT, P.R. and D.J. O'DOWD, (1976). Plant defence guilds. Science 193: 24-29.

AVER, C. (1968). Erste ergebnisse einfecher stochastischar modelluntersuchungen uber die ursanchen der populations - bewegung des grauen Larchenwicklers. Zeiraphare diniana Gn. (Z. griseana Hb.) in Oberengadin 1949/1966. Zeitschrift fuer Agewandte Entomologies 62: 202-235.

BAKER,C. R.B; and G.W. MILLER, (1974). Some effects of temperature and larval food on the development of Spodoptera littoralis (Boisd) Lep, Noctuidae). Bull. Entomol. Res. 63: 495-511.

BARBOSA, P. and J.L. CAPINERA, (1977). The influence of food types in the development structure of laboratory populations of the gypsy moth, Porthetra dispar (L). Can. Jour. Zool. 55:1424-1429

BARBOSA, P. and J. GREENBLATT, (1979). Susceptibility, digestibility and assimilation of various hosts plants of gypsy moth, Lymantria dispar (L). Oecologia (Berl.) 43: 111-119.

BARROGA, S.F. (1969). Control of lepidopterous pests attacking bush beans, Phaseolus vulgaris L. blossoms and pods. Philipp. Jour. Plant In. 34: 159-62.

BEDDINGTON, R.J.; C.A. FREE, and J.H. LAWTON, (1978). Characteristics of successful natural enemies in models of biological control of insect pest. Nature 273: 513-519.

BERNEJEE, T.C. and N. HAQUE, (1985). Influence of host plants on development, fecundity and egg hatchability on the articiid moth, Diacrisia casignetum, Entomological Experimentalis et Applicata (1985) 37 (2): 193-198.

BEROZA, M, L.J. STEVENS, B.A. BEIRL, F.M. PHILIPS and J.G.R. TARDIF (1978). Pre and post seasonal field tests with disparlure, the sex pheromone of the gypsy moth, to prevent mating. Environ. Entomol . 2 (6); 1051-1057.

BESS, H. A. (1961). Population ecology of the gypsy moth, Porthetria dispar L. (Lepidoptera, Lymantridae) Comm, Agr. Exp. Sta. Bul. 646: 43 pp.

BIEVER, K.D. and D.L. HOSTETTER, (1971). Activity of the nuclear-polyhedrosis virus of the cabbage looper evaluated at programmed temperature regimes (Trichoplusia ni Lep.,Noctuidae). Jour. Invert. Pathol. 18: 81-84.

BILAPATE, G.G. (1985). Studies on overlapping generations of Earias vittella (Fab) in pesticide free cotton field. Jour. Maharastra Agric. Univ. 10 (2): 147-150.

BIRLEY, M. (1977). The estimation of insect density and instar survivorship functions from census data. Jour. Anim. Ecol. 46: 497-510.

BOHLEN, E. (19730. On pests of pulses and their control. In "Crop pests of Tanzania and their control" (Publ. Fed. Agency Econ. Colop.): 91.97.

BONZI, S.M. and Y.O DOUMBIA, (1985). Sorghum midge as a limiting factor in the sorghum production in Burkina Faso and Mali. In proceedings of the Internatinal Sorghum Entomology Workshop, 15-21 July 1984, Texas U.S.A. Pantecheru, I.C.R.I.S.A.T.: 157-264.

BOOKER, R.H. (1963). "Notes on pests complex of cowpeas in northern Nigeria". Proc. Grain Legume Conf., (1963): pp. 9-12.

BOOKER, R.H. (1965). Pests of cowpeas and their control in northern Nigeria. Bull Entomol. Res. 55: 663-672.

BRENIERA, J.; D. BORDAT, B. VERCABRE, H. HAMZA and M. RENAND. (1985). Biological control of the maize stalk borer, Chilo partellus (Lepidoptera) in Ngazidha (Comoro Islands), Agron. Trop. Riz. Tizic. Cult. Vivrieres Trop. 40(2): 157.166.

BUES, R. and S. Poitout, (1983). Development cycle of five species of lepidopterous articiid in France. Annales Soc. Entomol. France 19 (3): 251-260.

CAMPELL, R.W. (1963). some ichneumonid - sarcophagid interactions in the gypsy moth, Porthetria dispar (L). Entomologist, 95: 337-345.

CAMPION, D.G., B.W. BETTANY, J.B. MCGINNEGIE and L.R. TAYLOR, (1977). The distribution and migration of Spodoptera littoralis (Boisd.) (Lepidoptera, Noctuidae) in relation to meteorology on cyprus interprated from maps of pheromone trap samples. Bull. Ent. Res. 67: 501-522.

CANERDAY, T.D. (1968). On cross infection of the cabbage lopper nuclear polyhedrosis virus to some related plusiinae (Noctuidae, Lepidoptera) Jour. Inver. Pathol. 10: 76-78.

CARL, K. P. (1982). Biological control of native pests by introduced natural enemies. Biocontrol News and Information 3: 191-200.

CHAMBERLAIN, F.S. and S.R. DATKY, (1958). Tests of pathogens for the control of tobacco insects. Jour. Econ. Entomol. 51: 560.

CHUBACHI, (1979). An analysis of the generation mean life table of the Mosquito, Culex tritaeniorhynchus Summonrosus, with particular reference to population regulation. Jour. Animal Ecol. 48: 681-702.

CLERK, L.R.; P.W. GEIER; R.D. HUGHES; R.F. MORRIS, (1972). The ecology of insect populations in theory and practise. London): pp. 232.

COAKER, J.H. (1958). Experiments with a virus disease of the cotton boll worm, Heliothis armigera (Hbn) Ann. Appl. Biol. 46: 536-541.

COCHRAN, W.G. (1963). Stratified random sampling. In "Sampling Technique. Publ. John Wiley and Sons Inc. New York. 85-153.

COCK, M. J. W. (1985). The use of parasitoids for augmentative biological control of pests in the Peoples' Republic of China. Biocontrol News and Information. 6(3): 213-223.

COCK, M. J.W. (1986). Requirements for biological control; an ecological perspective. Biocontrol News and Information. 7 (1): 7-21.

CROOK, N.E. (1981). A comparison of the granulosis viruses from Pieris brassicae and Pieris rapae. Virology. 115: 173-181.

DANTHANARAYANA, W. (1976a). Diel and lunar flight periodicities in the light brown apple moth Ephiphyas postvittana (Wlk) Totritricidae) and their possible adoptive significance. Australian Jour. Zool. 24: 65-73.

DANTHANARAYANA, W. (1976b). Flight threshold and seasonal variation i flight activity of the light brown apple moth, Ephiphyas postvittana (Wlk) Totricidae. Oecologia (Bert.) 23: 171-182.

DANATHANARAYANA, W. (1980). Parasitism of the light brown apple moth, Epiphyas postvittana (Wlk) (Totricidae) by its larval ectoparasite Goniozus jacintae Furragia (Hymenoptera, Bethylidae) in natural populations in Victoria. Australian Jour. zool. 28: 685-692.

DANATHANARAYANA, W. (1983). Population ecology of the light brown appl moth, Epiphyas postvittana (Lepidoptera; Totricidae). Jour. Anim. Eco. 52:1-33.

DAVID, W.A.L. (1978). The granulosis virus of Pieris brassicae and its relationship to its host. Advan. Virus. Res. 22: 111-161.

De-BACH, P. (1974). "Biological control of insect pest and weeds" Publ. Chapman and Hall Ltd. London: pp 844.

DEEVEY, E.S.Jr. (1947). Life table for natural populations of animals. Quart. Rev. Biol. 22: 283-314.

DEMPSTERS, J.P. (1956). The estimation of number of individuals entering each stage during the development of one generation of an insect population. Jour. Animal. Ecol. 25: 1-5 (1956).

DEMPSTER, J.P. (1961). The analysis of data obtained by regular sampling of an insect population. Jour. Anim. Ecol. 30: 429-432.

DINA, S. O. (1978). Maruca testulalis a pest of soybean in Nigeria Trop. Grain Legum. Bull. Nos. 11 and 12: 28-34.

DINA, S. O. and J.A. MEDAIYEDU, (1976). Field tests with insecticides to control Maruca testulalis and other pod boring insects of cowpea in southern Nigeria. Jour. Econ. Entomol. 69 (2): 173-177.

DON-PEDRO, K.N. (1983). Level of parasitism of Maruca testulalis Geyre (Lepidoptera, Pyralidae) larvae in early and late cowpea (Vigna unguiculata) cultivar (Prima) in Nigeria. Rue de Zoologie Africaine 97 3: 677-683.

DRIESCHE VAN, R.G. (1983). Meaning of "Percent parasitism" in studies of insect parasitoids. Environ. Entomol. 12: 1611-1622.

EVANS, H.F. (1981). Quantitative assessment of the relationships between dosage and response of the nuclear polyhedrosis virus of Mamestra brassicae. Jour. Invert. Pathol. 37: 101-109/

EVANS, H.F.; C.J. LOMER, D.C. KELLY, (1981). Growth of nuclear polyhedrosis virus in larvae of the cabbage moth, Mamestra brassicae L. Archives of Virology 70: 207-214.

EZUEH, M.I. (1982). Effect of planting dates on pest infestation, yield and harvest quality of cowpea (Vigna unguiculata). Experimental Agric. 18 (3): 311-318.

EZUEH, M.I. and T.A. TAYLOR, (1984). Effect of time of intercropping with maize on cowpea susceptibility to three major pests. Trop. Agric. (Trinidad), 61: 82-86

FARRAH, R.R. Jr. and J.R. Jr. BRADLEY, (1985). Effects of within plant distribution of Heliothis zea (Boddie) (Lep; Noc.) eggs and larval development and survival on cotton. Jour. Econ. Entomol. 78. (b): 1233-1238

FELLOWES, R.W. and J. AMARASENA, (1977). Natural enemies of some grain legume pests in the dry zone. Trop. Agriculturalist 133 (2) 83-89.

FERRO, D.N.; R.R. SLUSS and T.P. BOGYO, (1975). Factors contributing to the biotic potential of the codling moth, Lespeyresia pomonella (L) in Washington. Environ. Entomol. 4: 385-391.

FUJIYOSHI, N.; M. YAMANAKA, and T. TAKASAKI, (1984). Effect of temperature on the development of the pink borer, Sesamia inferens walker, reared on artificial diet. Proc. Assoc. Plant Prot. Kyushu 30: 82-85.

HALL, I. M. (1957). Use of polyhedrosis virus to control the cabbage looper on lettuce in California. Jour. Econ. Entomol. 50: 551-553.

HALL, I. M. (1963). Microbial control. In E.A. Steinhous (Ed.). Insect Pathology, an advanced treatise 2: 477-517. Academic Press. New York.

HARCOURT, D.G. (1960). Distribution of the immature stages of the diamond - back moth, Plutella maculipennis (Curt.) on Cabbage. Can Entomol. 92: 517-521 (1960).

HARCOURT, D.G. (1961a). Design and sampling plan for studies on the population dynamics of the diamond - back moth, Plutella maculeppenis (Curt.) Can. Entomologist. 93: 820-831.

HARCOURT, D.G. (1961, 1961b). Spatial pattern of the imported cabbage worm, Pieris rapae (L) on cultivated cruciferae. Can. Entomologist. 93: 945-952 (1961).

HARCOURT, D.G. (1962). Design of a sampling plan for studies of the population dynamics of the imported cabbage worm Pieris rapea (L) Can. Entomologist. 94: 849-859. (1962).

HARCOURT, D.G. (1963). Major mortality factors in the population dynamics of the diamond - back moth (Curt), Can. Entomol. Soc. Mem. 32: 55-66 .

HARCOURT, D.G. (1964). Population dynamics of Leptinotarsa decemlineata (Day) in eastern ontario II. Population and mortality estimation during six age intervals. Can Entomolgist. 94: 314-336 .

HARCOURT, D.G. (1966). Major factors in survival of the immature stages of Pieris rapae (L) Can. Entomologist 98: 653-662.

HARCOURT, D.G. (1969). The development and use of life tables in the study of natural insect populations. Ann. Rev. Entomol. 14: 175-196.

HARCOURT, D.G. (1971). Population dynamics of Leptinotarsa decemlineata (Say) in eastern Ontaria III. Major population processes. Can. Entomol. 103: 1049-1061.

HARGREAVES, E. (1937). Some insects and their food plants in Sierra Leone. Bull. Entomol. Res. 28: 505-520.

HARTSTACK, A.W. Jr., J.P. HOLLING-SWORTH; R.L. RIDGWAY; AND J.R. COPPEDGE. (1973). A population dynamics study of the boll-worm and tobacco bud-worm with light traps. Environ. Entomol. 2 (2): 244-253.

HUSSELL, M.P. (1978). "The dynamics of Arthropod predator-prey system", Princeton University Press. Princeton. pp. 237. Jour. Anim. Ecol. 54: 323-334.

HASSELL, M.P. and C.B. Huffacker, (1969). The appraisal of delayed and direct density dependence. Can. Entomol. 101: 353-361.

HASSELL, M.P , J.H. LOWTON and R.M. MAY. (1976). Patterns of dynamic behaviour in single-species population. Jour. Anim. Ecol. 45: 471-486.

HILL, D. (1975). "Agricultural insect pests of the tropics and their control". Cambridge Univ. Press, Cambridge. 294.295.

HILL, R. E.; D.P. CARPINO and Z.B. MAYO, (1978). Insect parasites of the European corn-borer Ostrinia nubilalis in Nebraska from 1948-1976. Environ. Entomol. 7 (2): 249-253.

HOFMASTER, R.N. (1961). Seasonal abundance of the cabbage looper as related to light trap collection, precipitation, temperature and the incidence of a nuclear polyhedrosis virus. Jour. Econ. Entomol. 54 (4): 796-798.

HOKKANEN, H. and D. PIMENTEL, (1984). New approach for selecting biological control agents. Can. Entomol. 116: 1109-1121.

HOSTETTER,D.L. R.E. PINNEL, P.A. GREÉR, and C.M. IGNOFFO. (1973).A granulosis virus of Pieris rapae, as a microbial control agent on cabbage in Missouri. Jour. Environ. Entomol. 2: 1109-1112.

HOUGH, J.A. and D. PIMENTEL, (1978). Influence of host foliage on development, survival and fecundity of gypsy moth. Environ. Entomol. 7: (1), 97-102.

HSIAO, T.H. AND G. FRAENKEL, (19680). Host selection and growth response of Leptinotarsa decemlineata. Ann. Entomol. Soc. Am. 61: 493.

HUDON, M. (1960). some aspects of seasonal development of the European corn borer, Ostrinia nubilalis (Hubn.) (Lepidoptera, Pyralidae) in southern Quebec. Rep. Que. Soc. Prot. Pl 121-128.

HUDON, M. and E.J. LE ROUX, (1961). Variation between samples of immature stages and of mortalities from some factors of the European corn-borer, Ostrinia nubilalis (Hubner), on sweet corn in Quebec. Can Entomologist 93: 867-888.

HUFFACKER, C.B. and C.E. KENNETT, (1966). Studies of two parasites of olive scale, Parlatoria oleae IV. Biological control of Parlatoria oleae through compensatory action of two introduced parasites. Hilgrade 37: 283-335.

HUGHES, K.M. (1957). An annotated list and bibliography of insect reported to have virus diseases. Hilgrade, 26: 597-629.

HUGHES, R.D. (1962). A method of estimating the effect of mortality o aphid populations. Jour. Animal Ecol. 31: 389-396.

HUGHES R.D. (1963). Population dynamics of the cabbage aphids Brevicoryne brassicae. Jour. Anim. Ecol. 32: 393-424.

IGA, M. (1985). The seasonal incidence and life tables of the diamond back moth, Plutella xylostella (L) (Lep., Ypononeutidae) Japanese Jour. Appl. Entomol. and Zool. 29 (2): 119-125.

IGNOFFO, C.M. (1964). Production and virulence of nuclear - polyhedrosis virus from larvae of Trichoplisia ni (Hub) reared on semi-synthetic diet. Jour. Insect pathol. 6: 318-326.

IGNOFFO, C.M.; D.L. HOSTETTER; R.L. PINNELL, and C.GARCIA, (1977). Relative susceptibility of six soybean caterpillars on standar preparation of Bacillus thuringiensis var. kurstaki Jour. Econ. Entomol. 70 (1): 60-63.

JACKAI, L.E.N. (1981a). Use of an oil soluble dye to determine the oviposition sites of the legume pod borer, Maruca testulalis. Insect Sci. Appl. 2 (4): 205-207.

JACKAI, L.E.N. (1981b). Relationship between crop phenology and field infestation by the legum podborer, Maruca testulalis. Ann. Entomol. Soc. America. 74 (4): 402-408.

JACKAI, L.E.N. (1981). Studies on some behavioural aspects of Maruca testulalis on selected species of crotolaria and Vigna unguiculata. Trop. Grain Legum Bull. 22: 1-3.

JACKAI, L.E.N. and S.R. SINGH (1982). A field screening technique for resistance of cowpea, Vigna unguiculata, to the pod borer Maruca testulalis (Geyer (Lepidoptera, Pyralidae). Bull. Entolom. Res. 72 (1): 145-156.

JACKAI, L.E.N. (19830. Effect of insecticide application at different times of the day against the legume pod borer Maruca testulalis Geyer (Lepidoptera, Pyralidae) on cowpea in Nigeria. Protection Eco. 5 (3): 245-251.

JACQUES, R.P. (1970a). Application of viruses to soil and foliage for control fo cabbage looper and imported cabbage worm. Jour. Invert. Pathol. 15: 328-340

JACQUES, R.P. (1970b). Natural occurrence of viruses of the cabbage looper in field plots. Can. Entomol. 102: 36-41.

JACQUES, R.P. (1972). Control of the cabbage looper and the imported cabbage worm by viruses and bacteria. Jour. Econ. Entomol. 65: 757-760.

JACQUES, R.P. (1974). Occurrence and accumulation of viruses of Trichoplusia ni in treated field plots. Jour. Invert. Pathol. 23: 140-152.

JACQUES, R.P. (1983). The potential of pathogens for pest control. Agric. Ecosystems and Environ. 10 (2): 101-126.

JEPSON, W.F. (1948). An annotated list of insects associated with groundnuts in East Africa. Bull. Entomol. Res. 39: 231-236.

JERATH, M.L. (1968). Insecticide control of Maruca testulalis on cowpea in Nigeria. Jour. Econ. Entomol. 61: 413-416.

JOHNSON, S.J. (1978). The population dynamics of the lesser corn stalk borer, Elasmopalpus lignosellus, in the peanut agroecosystem and the biology of selected primary parasites. A Ph. D. Dessertation. Texas A & M. University

KALODE, M.B. and N.C. PANT, (1967). Effect of host plants on the survival, development and behaviour of Chilo zonellus (Swinhoe) under laboratory conditions. Indian Jour. Entomol. 29: 48-57.

KE, LE-DAO; FANG JUE-LIAN and LI ZHI-JIANG, (1985). Bionomics and control of the legume pod borer, Maruca testulalis Geyer. Acta Entomological sinica 28 (1): 51-59.

KLEIN, M. and H. PODOLER, (1978). Studies on the application of nuclear polyhedrosis virus to control populations of the Egyptian cotton worm, Spodoptera littoralis. Jour. Invert. Pathol. 32: 244-248.

KLOMP, H. (1962). The influence of climate and weather on mean density level, the fluctuations and regulations of animal populations: Intraspecific competition and the regulation of insect numbers. Annual Rev. Entomol. 9: 17-40.

KLOMP, H. (1966). The analysis of density dependence in studies of insect populations. Proc. FAO Symp. Integ. Control. Vol. 2: 25-31.

KOEHLER, C.S. and P.N. MEHTA, (1972). Relationships of insect control attempts by chemicals to components of yield of cowpeas in Uganda. Jour. Econ. Entomol. 65 (5): 1421-1427.

KRAMER, J.P. (1959). Some relationships between Peresia pyrausta Paillot (Sporozoa, Nosematidae) and Pyrausta nubilalis (Huner) (Lepidotera, Pyralidae). Jour. Insect Pathol. 1: 25-33.

LASTER, M.L.; D.F. MARTIN, and S.D. PAIR, (1978). The attraction of wild Heliothis virescens males to sex pheromone traps baited with Heliothis virescens and backcross females. Ann. Entomol. Soc. am. 7 (1): 19-20.

LE-ROUX, E.J. (1959). Importance of second generation larvae of the codling moth, Carpocapsa pomonella (L) (Lepidoptera, Totricidae). Ann. Entomol Soc. Queb. 3: 75-80.

LEVER, R.J.A.W. (1944). Insect pest of some economic importance in Fiji I. Bull. Entomol. Res. 35: 367-377.

LEVER, R.J.A.W. (1947). Insect pests of some economic importance in Fiji II. Bull. Entomol. Res. 38: 137-143.

LEWIS, L.C. (1978). Migration of larvae of Ostrinia nubilalis (Lepidoptera, Pyralidae) infected with Nosema pyrausta (Microsporidia, Nosematidae) and subsequent dissemination of this microsporidia. Can. Entomol. 110 (9): 897-900.

LEWIS, L.C. (1982). Persistance of Nosema pyrausta and Vairimorpha nectrix measured by microsporidiosis in European corn borer. Jour. Econ. Entomol. 75 (4): 670-674.

LEWIS, L.C. and R.E. LYNCH, (1976). Influence on the European corn borer by Nosema pyrausta and resistance in maize to leaf feeding. Environ. Entomol. 5 (1): 139-142.

LEWIS, L.C. and R.E. LYNCH (1978). Foliar application of Nosema pyrausta for suppression on European corn-borer . Entomophaga. 23 (1): 83-88.

LI, L.C. (1985). Sugarcane insect pests with special reference to the moth borer in Markham Valley, Papua New Guenea. Mushi. 50 (2): 13-18.

LIMA, L. M. and VAN A. HARTEN, (1985). Biological control of crop pests in Cape Verde. Current situation and future programmes. Revista Investigaticao Agraria, Centro de Estudos Agrarios. A (1): 3-12.

LUBLINKOF, J.; L.C. LEWIS AND E.C. BERRY, (1979). Effectivenss of integrating insecticides with Nosema pyrausta for suppression of the European corn borer when using a combination with insecticide. Environ. Entomol. 9: 69-70.

LUCK, R. F. (1971). An appraisal of two methods of analysing insect life tables. Can. Entomol. 103: 1261-1271.

LUNA, J. M. LINKER, J.L. STIMATIC, AND S.L. RUTHERFORD, (1982). Estimatation of absolute larval density and calibration of relative methods for velvet caterpillar, Anticorsia gemmatilis (Hubn) in soybean. Environ. Entomol. 11 (2): 497-502.

LYNCH, R E. and L.C. LEWIS (1976). Influence on the European corn borer of Nosema pyrausta and resistance in maize to shieth collar feeding. Environ. Entomol. 5: 254-258.

MACEDO, N.; P.S. BOTELHO; N. De GASPARI; L.C. De ALMEIDA; J.R. De ARAUJO and E.A. MAGRINI. (1985). (Biological control of the sugarcane borer) Controle biologico de broca da cana-de-acucar. Priacidaba, Brazil Instituto do Acucar e do cana-de-acucar. p. 22.

MACFOY, C.A.; Z.T. DABROWSKI and S.H. OKECH, (1983). Studies on legume podborer, Maruca testulalis Geyer VI. Cowpea resistance to oviposition and larval feeding. Insect Sci. Appl. 4 (1/2) 147-152.

MAY, R.M. and M.P. HASSELL, (1981). The dynamics of multi-parasitoid host interaction. America Naturalist. 117: 234-261.

MANLY, B.F.J. (1974a). Estimation of stage specific survival rates and other parameters for insect populations developing through several stages. Oecologia 15: 277-285.

MANLY, B.F.J. (1974b). A comparison of the methods for analysis of insect stages frequency data. Oecologia 17: 335-348.

MILNE, A. (1957). Theories of natural control of insect populations. Cold spring Harbor. Symp. Quart. Biol. 22: 253-271.

MILNE, A. (1961). A defination of competition among animals. Symp. Soc. Exp. Biol. 15: 4071.

MILNE, A. 1962). On a theory of natural control of insect population. Jour. Theoret. Biol. 3: 19-50.

MORRIS, R.F. (1957). The interpration mortality data in studies on population dynamics. Can Entomologist. 89: 49-69.

MORRIS, R.F. (1959). single factor analysis in population dynamics. Ecology. 40: 580-588.

MORRIS, R.F. and FULTON (1970). Models for the development and survival of Hyphantria canae in relation to temperature and humidity. Men. Entomol. Soc. Can. No. 70: p. 60.

MORRIS, R.F. and C.A. MILLER, (1954). The development of life tables for the spruce budworm. Can. Jour. Zool. 32: 283-301.

MURDOCH, W.A. J. CHESSON, and P.L. CHESSON, (1985). Biological control in theory and practice. American Naturalist. 125: 344-366.

MURULI, B.I.; R.S. PATHAK; D.M. MUKUNYA; A.K. KAREL; S.O. KEYA and SSALI (1979). Cowpea research in Kenya. Top. Grain Legum. Bull. 19: 13-16.

NASR A. EL. SAYED; A.A.S. KATTAB; and SAOUD M. EL-SHARER, (1978). A comparison of light and pheromone trap catches of Spodoptera littoralis in Egypt. PANS 24 (3): 290-293.

NICHOLSON, A.J. (1957). Self adjustment of populations to change. Cold Spring Harbor Symp. Quart. Biol. 22: 153-173.

OCHIENG', R.S. and D.M.O. BUNGU, (1983). Studies on the legume podborer, Maruca testulalis Geyer - IV. A model for mass rearing; Rearing on artificial diet. Insect Sci. Appl. 4 (1/2): 83-88.

OCHIENG' R.S.; J.B. OKEYO-OWUOR, and Z. T. DABROWSKI, (1981). Studies on the legume podborer Maruca testulalis Geyer. II. Mass rearing on natural food. Insect Sci. Appl. 1 (3): 369-272.

ODEBIYI, J.A. (1981). Studies on the legume pod borer, Maruca testulalis Geyer. Insect Sci. Appl. 1 (4); 339-341.

ODINDO, M.O. (1981). Dosage - Mortality and time mortality responses of the army-worm, Spodoptera exempta, to a nuclear polyhedrosis virus. Jour. Invert. Pathol 38: 251-255.

OKEYO-OWUOR,J.B. and P.O. AGWARO (1982) Studies on the legume podborer, Maruca testulalis Geyer III. Use of pheromone trap in population studies. Insect Sci. Appl. 3(2/3):233-235.

OKEYO-OWUOR, J.B. and R.S. OCHIENG' (1981). Studies on the legume podborer, Maruca testulalis (Geyer)-I Life cycle and behaviour. Insect Sci. Appl. 1 (3): 263-268.

OKEYO-OWUOR, J.B.; P.O. AGWARO AND C.O.J. SIMBI (1983). Studies on the legume podborer Maruca testulalis Geyer- V. Larval population. Insect Sci. Appl. 4 (1/2):75-81.

OTIENO W.A.; ODINDO M.O, J.B. OKEYO-OWUOR, and D. SABWA, (1983) . Studies on the legume podborer, Maruca testulalis (Geyer) - VII. Field Surveys on pathogenic microorganisms. Insect Sci. Appl. 4 (1/2): 211-215.

PAYNE, C.C.; G.M. TATCHELL and C.F. WILLIAMS, 1981). The comparative susceptibility of Pieris brassicae and P rapae to granulosis virus from P. brassicae. Jour. Invert. Pathol. 38: 273-280.

PICKETT, A.D. (1959). Utilization of native parasites and predators. Jour. Econ. Entomol. 52: 1103-1105.

PODOLER, H. and D. ROGERS, (1975). A new method for identification of key-factor from life tables data. Jour. Animal. ecol. 44: 85-114.

POINER, G.O. Jr. and G.M. THOMAS, (1984). Laboratory guide to insect pathogens and parasites. Plenum press. new York. London. pp. 392.

PRICE, W.P. (1975). "Insect Ecology". Wiley-Interscience Publ. New York, Brisbane, Toronto. pp. 514.

RAHEJA, A.K. (1976). Assessment of losses caused by insect pests to cowpea in northern Nigeria. PANS 22 (2): 229-223.

REYNOLDS, S.E. and S.F. NOTTINGHAM, (1985). Effect of temperature on growth and efficiency of food utilization in fifth instar caterpillar of the tobacco corn worm, Manduca Sexta. Jour. Insect. Physiol. 31 (2): 122-139.

RICHARDS, O.W. and N. WALOFF, (1954). Studies on the biology and population dynamics of British grasshopper. Antilocust. Bull. No. 17; p. 182.

RICHARDS, O.W.; N. WALOFF AND J.P. SPRAYBERG, (1960). The measurement of mortality in an insect population in which recruitment and mortality widely overlap. Oikos 11: 306-310.

ROGERS, D.J., R.E. TEAKLE and H.B. BRIER, (1983). Evaluation of Heliothis nuclear polyhedrosis virus for control of Heliothis armigera on navy beans in Queensland, Australia. Jour. Appl. Entomol. 15: 31-34.

ROHLFS, W.M., III and T.P. MACK, (1985). Seasonal parasitism rate host size, and adult emergence pattern of parasitoids of the fall army worm, Spodoptera frugiperda (J.E. Smith) with emphasis on Ophion flavipes Brulle (Hymenoptera, Ichneumonidae). Ann. Entomol. Soc. American 78 (2): 217-220.

SALES, F.J.M. (1985). Manipulation of the fall army worm with homeostatic strips. Fitossanidade. 6/9: 11-25.

SALICK, J. (1983). Natural history of crop-related wild species; uses in pest habitat management. Environ. Management. 7 (1): 85-89.

SILVERSTEIN, R.M. (1981). Pheromones: Background and potential use for insect pest control. Science 2131: 1326-1333.

SINGH, S.R. and H.F. VAN EMDEN, (1979). Insect pests of grain legumes. Ann. Rev. Entomol. 24: 255-278.

SNEDECOR, G.W. and W.G. COCHRAN (1967). Statistical Methods 6th ed. Amer. Iowa State Univ. Press. pp 593.

SOLOMON, M.E. (1949). The natural Control of animal populations. Jour. Animal. Ecol. 18: 1-35.

SOLOMON, M.E. (1964). Analysis of processes involved in the natural control of insects. Adv, Ecol. Res. 2: 1-58.

SOLOMON, M.E. (1970). Population dynamics. St. Martin's Press, New York. p. 60. Re-printed 1973.

SOUTHWOOD, T.R.E. (1969). Population studies of insects attacking sugarcane. In Williams J.R., Metcalf, J.R. Mungomery, R.W., and Mathes, R. (Eds) Pests of Sugarcane. Amsterdam; Elseviet Publ. Co. 427-459.

SOUTHWOOD, T.R.E. (1978). Ecological methods with particular reference to the study of insect populations. Mathuen, London. Chapman and Hall. p. 524.

SOUTHWOOD, T.R.E. and W.F. JEPSON, (1962). Studies on the population of Oscinella frit L. in the oat crop. Jour. Anim. Ecol. 31, 481-495.

SOUTHWOOD, T.R.E. and P.M. READER, (1975). Population census data and key-factor analysis for the Viburnum white fly Aleurotracholus Jelinekii (Frauenf) on three bushes. Jour. Anim. Ecol. 45: 313-325.

STACEY, A.L.; S.Y. YOUNG III and W.C. YEARIAN, (1977). Effect of larval age and mortality level on damage to cotton by Heliothis zea infected by Baculovirus heliothis. Jour Econ. Entomol. 70. (3): 383-386.

STARLING, W.L. and P.L. ADKISSON, (1978). Population dynamics of the ball weevil inhibiting the high and rolling plains of Texas. Eviron. Entomol. 7 (3): 439-444.

STEINHAUS, E.A. (1954). The effect of disease on insect populations. Hilgradia. 23: 197-261.

SUBASINGHE, S.M.C. and R.W. FELLOWES, (1978). Recent trends in grain legume pest research in Sri-Lanka. "Insect of Grain Legumes and their control". (ed. Singh S.R., T.A. Taylor and H.F. van Emden, Academic Press. London and New York). 37-41.

TANADA, Y. and C. REINER, (1962). The use of pathogens in control of corn ear worm, Heliothis zea (Boddie). Jour. Insect Pathol. 4: 139-154.

TANADA, Y. (1963). Epizootiology of infectious diseases. In insect pathology. An advanced treatise (E.A. Steinhous) 2: 423-475.

TANADA, Y. (1966). Field observations on the biotic factors regulating the population of army worm, Pseudaletia unipuncta (Haworth). Proc. Hawaiian Entomol. Soc. 19: 302-308.

TAYLOR, T.A. (1967). Bionomics of Maruca testulalis Geyer. (Lepidoptera, Pyralidae), a major pest of cowpeas in Nigeria. Jour. West African Sci. Assoc. 12: 111-129.

TAYLOR, T.A. (1968). Effect of insecticide applications on insect damage and the performance of cowpea in southern Nigeria. Niger. Agric. Jour. 5: 29-37.

TAYLAOR, T.A. (1978). Maruca testulalis an important pest of tropical grain legumes, in "Pests of Grain legumes. Ecology and control" (Ed. Singh, S.R., T.A. Taylor and H.F. van Emden Academic press, London, New York): 193-200.

TAYLOR, T.A. and F.O.C. EZEDINMA, (1964). Preliminary investigations on field pests of cowpeas and methods of control. Nig. Agric. Jour. 1: 8-11.

THORVISON, H.G., L.P. PEDIGO and L.C. LEVIS (1985). Plathypena Scabra (F) (Lepidoptera, Noctuidae), population and incidence of natural enemies on four soybean tillage systems. Jour. Econ. Entomol. 78 (1): 213-218.

USUA, J.E. (1975). Studies in relation to Maruca testulalis. In Lusa, R.A.; K.O. Rachie. Eds. Proc. IITA collab. meeting on Grain legume improvement, Ibadan Nigeria. (9-13 June 1975): 52-54.

USUA, J.E. (1976). Description of the larvae and pupae of Maruca testulalis (Geyer) (Lep., Pyralidae) Nigerian Jour. Sci. 10 (1/2): 179-196.

USUA, J.E. and S.R. Singh, (1977). Parasites and predators of the cowpea pod borer Maruca testulalis (Lep., Pyralidae). Nigerian Jour. Entomol. 3 (1): 100-102.

VARLEY, G.E. and G.R. GRADWELL, (1960). Key-factor in population studies. Jour Animal. Ecology, 29: 399-401.

VARLEY, G.C. and G.R. GRADWELL, (1963). The interpretation of insect population changes. Proc. Ceylon. Assoc. Adv. Sci. 18 (D): 145-156.

VARLEY, G.C. and G.R. GRADWELL, (1968). Population models for the winter moth. Insect abundance (Ed. by T.R.E. Southwood). Black-well Scientific Publications, Oxford. pp. 132-142.

VARLEY, G.C. and G.R. GRADWELL, (1970). Recent advances in insect population dynamics. Annual. Rev. Entomol. 15: 1-24.

VARLEY, G.C. and G.R. GRADWELL, (1971). The use of models and life tables in assessing the role of natural enemies. In. C.B. Huffacker (ed.) Biological Control. Plenum, New York: 93-112.

VARLEY, G.C.; G.R. GRADWELL and M.P. HASSELL, (1973). Insect population Ecology: an analytical approach. Blackwell Scientific Publ. Oxford. pp. 212.

VISHAKANTAIAH, M. and C.J.J. BABU, (1980). Bionomics of the tur webworm, Maruca testulalis (Lepidoptera, Pyralidae). Mysore Jour. Agric Sci. 14: 529-532.

WALKER, J.K. and G.A. NILES, (1971). Population dynamics of the boll-weevil and modified cotton types. Tex. Agric. Exp. Stn. Bull. 1109: p. 14.

WINDELS, M.B., H.C. CHIANG and B. FURGALA, (1976). Effect of Nosema pyrausta on pupa and adult stages of the European corn borer Ostrinia nubilalis. Jour. Invert. Pathol. 27 (2): 239-242.

WOLCOTT, G.N. (1933). The lima bean pod borer caterpillars and predators attacking diamond back moth, Plutella xylostella (L). Japanese Jour. Appl. Entomol. Zool. 29 (2): 170-173.

YAMADA,H.and T. YAMAGUCHI (1985) Notes on parasites and predators attacking diamond back moth, Plutella xylostella (L). Japanese Journ.Appl. Entomol. 29 (2):170-173.

YOUNG, S.Y., L.A. MAC-CAUL and W.C. YEARIAN, (1980). Effect of Bacillus thuringiensis - Trichoplusia nuclear polyhedrosis virus mixtures on the cabbage looper, Trichoplusia ni. Jour. Georgia Entomol. Soc. 15 (1): 1-8.

ZIMMACK, H.L. and T.A. BRINDLEY, (1957). The effect of the protozoan parasite, Perezia pyrausta Paillot, on the European corn borer. Jour. Econ. Entomol. 50: 637-640.