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FEEDING BY LARVAE OF THE AMERICAN BOLLWORM,  
HELIOTHIS ARMIGERA (HÜBNER) (LEPIDOPTERA: NOCTUIDAE)  
ON COTTON PLANTS

by

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Dissertation submitted to Rhodes University  
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South Africa

January 1988



Heliothis armigera

reduces

cotton yields

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## ACKNOWLEDGEMENTS

Sincere thanks are due to my employer, the Plant Protection Research Institute, Department of Agriculture and Water Supply, for the opportunity to study. The study depended upon the support of my Directors, Dr I.H. Wiese and Dr D.P. Keetch, and their permission to use the results for thesis purposes. I also wish to thank Professor B.R. Allanson, Head of the Department of Zoology and Entomology at Rhodes University, for sanctioning the project.

My supervisors (Dr P.E. Hulley, Rhodes University and Professor V.C. Moran, University of Cape Town) and co-supervisor (Dr H. van Hamburg, PPRI) provided guidance and constructive comments on the thesis draft. The study was initiated under the guidance of Professor Moran and his continued interest after moving to Cape Town is greatly appreciated. I am indebted to Dr J.D. Möhr, PPRI, who unselfishly undertook the day-to-day supervision of the research and preparation of the thesis. Dr H. van Ark, Directorate of Biometric and Datametric Services of the Department, supervised the statistical analyses and volunteered much appreciated comments on the final draft.

Rewarding research meetings were held with Mr N.C.J. Basson (PPRI), Dr J.H. Botha (Fruit and Fruit Technology Research Institute, Department of Agriculture and Water Supply), Dr S.W. Broodryk (South African Development Trust Corporation), Dr C.J. Cilliers (PPRI), Dr R.L. Kluge (PPRI), Dr J.D. Mumford (Imperial College, Silwood Park) and Dr S. Nesor (PPRI).

The work was made possible through the experimental sites prepared by the Tobacco and Cotton Research Institute of the Department; in particular, I wish to record the enthusiastic co-operation of Mr J. Steyn of the Hartebeespoort Experimental Farm near Brits. Sites for preliminary trials were provided by Mr N.C.J. Basson in the Brits district.

The companionship and assistance of colleagues in the American Bollworm Unit of the Institute is gratefully acknowledged. The remarkable ability of Miss M.J. van Jaarsveld to conduct field work and collate results was indispensable. Mrs M.C.T. Botha, Mrs R.I. Botes, Miss E. Engelke (of the Forest Entomology Section), Mr J.M. Erasmus, Miss C.S. Kolver, and Mrs C.E. Weidemann helped in innumerable ways in the field and in the laboratory. The insect cultures were ably maintained by Mr D. Kewane, Mr S. Madisha, Mrs L. Kewane and Mrs E. Ringane.

Without the contributions of Mrs S. Thompson, National Collection of Insects, PPRI (drawings), Miss S.G. Claassens (photographs) and Mr M. Scheepers (binding), completion of the thesis would have been delayed.

I am grateful to the people who share my home for their encouragement and understanding during sometimes trying times.

My parents, who believed in me and assisted financially, have my sincere love and appreciation.

## RÉSUMÉ

H. armigera larvae are a key stage for pest management in commercial irrigated cotton crops in South Africa. Effective survey methods for detecting larval populations in the field require an understanding of the biology of the larvae, particularly their feeding habits. Their feeding is central to the development of pest threshold levels for the implementation of integrated control programmes. This applies to routine surveys for the larvae as well as to the damage they cause.

Biological characteristics of the larvae are described with the emphasis on the identification of the larval instars, which were consistently five in number in both field and laboratory populations.

The distribution of H. armigera larvae on cotton plants in the field was examined, but was found to more or less random; had there been a clear preference for any height zones or compass direction this would have been an obvious avenue for improving the survey methods currently in use. Details of field and laboratory investigations of the selection of feeding sites by the larvae are given. The study confirmed a clear preference by the larvae for cotton buds, flowers and bolls (in the thesis collectively called "fruiting forms"), over leaves. There were indications that the larvae selected flowers more readily than buds or bolls. This "preference", however, is shown to be of no

practical value for refining survey methods.

Damage levels to cotton due to H. armigera are discussed. Both direct losses and indirect losses due to the abortion of fruiting forms are considered. These criteria are inadequate since they do not take into account the ability of cotton plants to compensate for these losses. It is concluded that this compensation by cotton plants should be taken into account in further studies of the pest status of H. armigera.

## 1. INTRODUCTION

Heliothis armigera (Hübner) is a typical noctuid whose larvae feed on a wide range of plants and has been identified as probably the most polyphagous and injurious pest in South Africa (Annecke & Moran 1982; Moran 1983). In many parts of the world H. armigera is a key pest of cotton and is no less so in South Africa. Consequently, it has been the subject of considerable study and significant progress has been made in the development of integrated pest management strategies for cotton in South Africa (Mumford & Van Hamburg 1985). Thus, this study is a component of a much wider research project on cotton pests and H. armigera in particular.

Until recently spray thresholds for H. armigera were based on surveys of the eggs in the field, but egg counts were found to be an unreliable criterion, due to high mortality rates of egg populations, and larval counts were shown to be more reliable indicators of the pest (Broodryk 1980; Van Hamburg 1981; Van Hamburg & Kfir 1982; Kfir & Van Hamburg 1983). Currently the spray threshold is set at 5 larvae per 24 plants, with larvae from about the third instar counted as two (Basson 1986; Bot et al. 1986). Consequently, the emphasis in this thesis is on the second to final-instar larvae. It will be seen in the Discussion that the first larval instar deserves further study.

The shift to H. armigera larvae as the key stage for the implementation of control programmes dictated a need for a better

understanding of the biology of the larvae, particularly a description of the feeding habits of the larvae and the damage they cause to cotton under field conditions, the subject of this thesis. Most of the investigation was carried out in the field and supplemented with laboratory trials, using both field populations of larvae and laboratory-reared larvae. Despite its obviously high pest status, H. armigera occurs in relatively low numbers and searching for them is extremely time consuming, hence the use of laboratory-reared larvae. Furthermore, the ages of larvae from a culture can be determined more precisely than those from the field. These larvae were easily transferred from the artificial diet to cotton plants and commenced feeding almost immediately. No obvious differences between the natural and laboratory populations were evident and, as will be seen in context, the results were generally pooled.

Larvae which attack the buds, flowers and bolls of cotton plants are collectively called bollworms (Proctor 1974). H. armigera is distinctive and cannot conceivably be confused with Diparopsis castanea Hampson, the "red bollworm" or Earias spp., the "spiny bollworms"; as their common names imply, these species are respectively conspicuously red and spiny. The vernacular name "American bollworm" for H. armigera is an unfortunate misnomer which became entrenched because it was initially misidentified as a conspecific of the North American Heliothis zea Boddie; H. armigera occurs in the Old World, especially in Africa, Australia and India, but not in the New World, while the reverse is true for H. zea and the other important North American species

Heliothis virescens (Fabricius) (Pearson & Maxwell Darling 1958; Annecke & Moran 1982).

Cotton originated in the tropics and subtropics (Theron 1977). The genus Gossypium belongs to the family Malvaceae, order Malvales (Prentice 1972). Most of the world's cotton is produced outside the tropics and only four of the 30 or more known varieties are grown commercially (Reynolds et al. 1975). Two species from the New World are commercially important, namely, Gossypium barbadense Linn., a long staple, high-quality type from the West Indies and the Nile Valley and Gossypium hirsutum Linn., which includes the "Upland" or "American" varieties grown in most parts of the World (Proctor 1974). The bulk of the World's cotton, including that which is grown in South Africa, includes various cultivars of G. hirsutum (Prentice 1972; Reynolds et al. 1975). It is this species which is referred to as "cotton" in this study.

Both dry-land and irrigated cotton is grown in South Africa for the commercial and industrial textile industries (Bakkes & Clarke 1977), but this study relates to irrigated cotton only. Neither do the conclusions apply to ratoon cotton. Ratooning of cotton is a contentious issue and was ignored for the purpose of this study. A key characteristic of cotton plants, particularly when irrigated, is that they produce buds, flowers and bolls (collectively called "fruiting forms"), during a large part of the season and in varying proportions. These fruiting forms are the food of H. armigera on cotton and central to this study.

## CONTENT AND SEQUENCE OF THE THESIS

In Chapter 2 the general materials and methods are described; details are given in context in individual chapters. The method of rearing *H. armigera* was a simple procedure using a meridic diet and provided a constant source of accurately-aged larvae. The use of small and large organdie sleeves, to contain the larvae on individual fruiting forms or parts of plants, is explained and the experiments are described. Choice experiments to examine the feeding preferences of the larvae for cotton fruiting forms in the laboratory are described.

The salient characteristics of cotton plants which are relevant to the study are described in Chapter 3. These include the growth form of cotton plants and the more-or-less even distribution of the fruiting forms in height zones of the plants. Details of the structure of the fruiting forms are given, their sizes conveniently arranged into 12 size classes. The relationship between the diameter and mass of the fruiting forms proved to be approximately linear for the size classes before and after flowering. This, together with the diameter:mass ratios for representative classes of buds and bolls are detailed.

The biology of *H. armigera* (Chapter 4) is discussed to provide further background information. The emphasis is on the development of the larvae and the identification of the larval instars. Reliable identifications could be made on the basis of head-capsule widths, a crucial issue for the studies which followed because the results are presented separately for the

larval instars. In both the field and laboratory populations five larval instars were consistently found.

Because of the importance of surveying for H. armigera larvae for experimental as well as pest management purposes, the distribution of the larvae on plants is examined in Chapter 5: obviously, had it been found that the larvae occurred preferentially on certain parts of the plants, this would have been useful for improving sampling procedures. It transpired that, for practical purposes, the larvae occurred in all compass directions. Even though the larvae were found mainly in the upper two-thirds of the plants, this depended on the distribution of fruiting forms and the lower third cannot be ignored. The investigations of the distribution of the larvae inevitably required some understanding of the movement of the larvae within plants. However, this is not to imply that the dispersal of the larvae was studied. A separate study of dispersal is suggested in the Discussion.

The simultaneous presence of various fruiting forms on cotton plants begs the question whether H. armigera larvae showed any preferences in the selection of feeding sites (Chapter 6). The only clear preference found in the field was for fruiting forms over leaves. The symptoms of damage to the fruiting forms are described, but are useful only to differentiate between extremes in larval size. Both the field and laboratory trials suggested a slight preference by the larvae for flowers, but this does not have any practical significance and it is concluded that the larvae tend to feed on the fruiting forms they encounter.

In Chapter 7 an assessment of the damage caused by H. armigera to cotton is provided in terms of the number of fruiting forms destroyed irrespective of the amount of feeding on them, and the relative amount of food consumed by the larval instars. These aspects are pursued in the Discussion. It is concluded that reliable estimates of the pest status of H. armigera cannot be realised pending further research which takes into account the ability of cotton plants to compensate for loss of fruiting forms. This is identified as a vital research priority in terms of refining the pest control strategy.

## 2. GENERAL MATERIALS AND METHODS

Only the general procedures are presented here; specific details are given in context. Statistical analyses used were those of Snedecor & Cochran (1969) and appropriate programs of the Directorate of Biometric and Datametric Services, Department of Agriculture and Water Supply.

### REARING OF H. ARMIGERA

Laboratory-reared H. armigera larvae were obtained from a culture which had been maintained for about 12 years on a modified Shorey & Hale (1965) meridic larval diet in which dry, powdered kidney beans were substituted for soaked pinto beans (Table 1).

The rearing laboratory was kept under natural photoperiods, with temperature and humidity controlled at 25 - 26 °C and 50 - 60 % RH. The EGGS were deposited by the females on cloth netting. The netting with eggs was soaked for 10 minutes in 2 % formaldehyde, washed in running tap water for 10 - 20 minutes, drip-dried and placed in lidded glass jars for the eggs to hatch. First-instar LARVAE were transferred (singly or in groups of two or three) to the larval diet (Table 1). About 10 g of the diet was forced into 100 x 25 mm glass tubes with a domestic cake syringe (nozzle diameter 13 mm) and the tubes were stoppered with cotton wool. The larvae completed their feeding and pupated without further attention (Fig. 1).

Table 1. A modified Shorey & Hale (1965) diet for rearing Heliothis armigera larvae in the laboratory.

INGREDIENTS	QUANTITY
White kidney beans (powdered)*	360 g
Brewer's Yeast**	48 g
Methyl-4-hydroxybenzoate	3 g
Agar, Commercial Gel***	20 g
Ascorbic Acid	4,8 g
Sorbic Acid	2,1 g
Formaldehyde	1,1 ml
Distilled water	1 000 ml

The water was boiled with the ingredients stirred in and left to cool for 30 minutes. After cooling, the gelled medium was used as explained in the text.

\* Phaseolus vulgaris L.

\*\* Manufactured by Gold Star Yeast (Pty) Ltd, 86 Maraisburg Avenue, Industria, Johannesburg 2092.

\*\*\* Since completing the experiments for this study, it has become apparent that the agar is superfluous and can be omitted from the diet.

The PUPAE were disinfected with 0,2 % sodium hypochlorite. About 15 male and 15 female pupae (the sexes separated using the criteria of Butt & Cantu 1962; Paul et al. 1979) or the same numbers of MOTHS (in which the greenish males are distinct from the brownish females) were placed in oviposition cages. The cages were 5 litre Perspex jars containing a layer of vermiculite and a Petri dish with some cotton wool soaked with 7 % sucrose to feed



Fig. 1. *Heliothis armigera* larvae reared in glass tubes stoppered with cotton wool and kept in the laboratory until pupation.

the moths. The females deposited their eggs on the cloth-netting lids of the cages and these could be collected on a daily basis.

More moths, fertile eggs and first-instar larvae than were needed to maintain the culture were usually available. Because the larvae are cannibalistic, only one larva per tube normally survived to pupate causing limited production and raised costs. The use of large containers to rear groups of larvae (Singh & Surrey 1980) would improve the method considerably.

#### FIELD TRIALS

Field trials were carried out on commercially-grown cotton of the cultivar Acala 1517/70 on the Hartebeespoort Experimental

Farm of the Tobacco and Cotton Research Institute, Department of Agriculture and Water Supply, in the Brits, Transvaal district. Experimental plots of 1/4 - 1/2 ha within larger stands of about 2 ha were used. These plots were routinely irrigated (approximately once a week, depending on rain) by a conventional overhead irrigation system. Planting dates were staggered, to provide a range of plant sizes for experiments, as follows:

1983/84 SEASON	1984/85 SEASON	1985/86 SEASON
24/10/1983	22/10/1984	17/10/1985
16/11/1983	5/12/1984	
14/12/1983	9/01/1985	

Individual plants for experiments were selected without bias within the plots. Two experimental procedures were followed: H. armigera larvae from the natural population were identified, or, alternatively, the plants or parts of the plants were infested with larvae from the laboratory culture. In both procedures the plants were cleared of other larvae (including H. armigera and other bollworm species) and damaged plant parts. For some of the experiments the plants were covered with organdie sleeves (Fig. 2), or in the case of large plants, parts of the plants were covered, or for some of the experiments, individual plant parts were covered with smaller sleeves (Fig. 3). The organdie sleeves served to contain the larvae, protect them from predation and, importantly, prevented infestations from natural



Fig. 2. A cotton plant covered with an organdie sleeve.



Fig. 3. A cotton fruiting form covered with a small organdie sleeve.

populations whose feeding damage would have been inseparable from that caused by the larvae used in the experiments.

#### LABORATORY TRIALS

Pairs of fruiting forms namely buds and flowers, buds and bolls and flowers and bolls were held in soaked florist's plastic foam (Oasis\*) and arranged to touch each other. Larvae of each of the second to fifth larval instars were released in equal numbers on each structure comprising the pairs of fruiting forms. Observations were made to see if the larvae fed on the structure they were released on or if they moved to an adjacent structure.

\* Distributed by Elro J. Braak c.c., P. O. Box 6, Pretoria 0001.

### 3. CHARACTERISTICS OF COTTON PLANTS.

This section deals with the characteristics of cotton which are central to the study. Emphasis is on a description of the morphology and anatomy of the fruiting forms. As explained in the Introduction, "fruiting forms" is used throughout the study as the collective term for any stage of development of buds, flowers or fruits of the cotton plant.

#### DISTRIBUTION AND GROWTH FORM

Cotton produces fairly good yields under dryland conditions with a rainfall of 600 mm or more (Theron 1977), but irrigated cotton generally produces a better quality fibre. This study is restricted to irrigated cotton, specifically the cultivar Acala 1517/70 (Frontispiece), the most common variety grown in South Africa. It is known that this cultivar produces far more fruiting forms than they are capable of retaining to maturity, even under ideal growing conditions (Smith & Falcon 1973). According to Reynolds *et al.* (1975) and Theron (1977), the maximum yield (i.e. ripened bolls) is genetically fixed but yield is strongly influenced by environmental conditions. Even under optimal growing conditions, but especially when the plants are stressed, they shed large numbers of fruiting forms; up to 60 % of the flowers do not produce bolls, thus avoiding the production of excess bolls unable to develop seeds. Without this protective mechanism of boll shedding, the cotton plant would undoubtedly

produce too many fruits, leading to smaller fruit and poor quality fibres (Eaton 1955; Smith & Falcon 1973).

Cotton is a herbacious plant which grows to about 1,4 m with a characteristic arrangement of dimorphic branches (Eaton 1955; Van Heerden 1978). Growth of the monopodial main stem and sympodial vegetative branches is indeterminate (Gillham 1972). The sympodia or fruiting branches grow outwards and produce several nodes, each node producing a flower (Fig. 4).

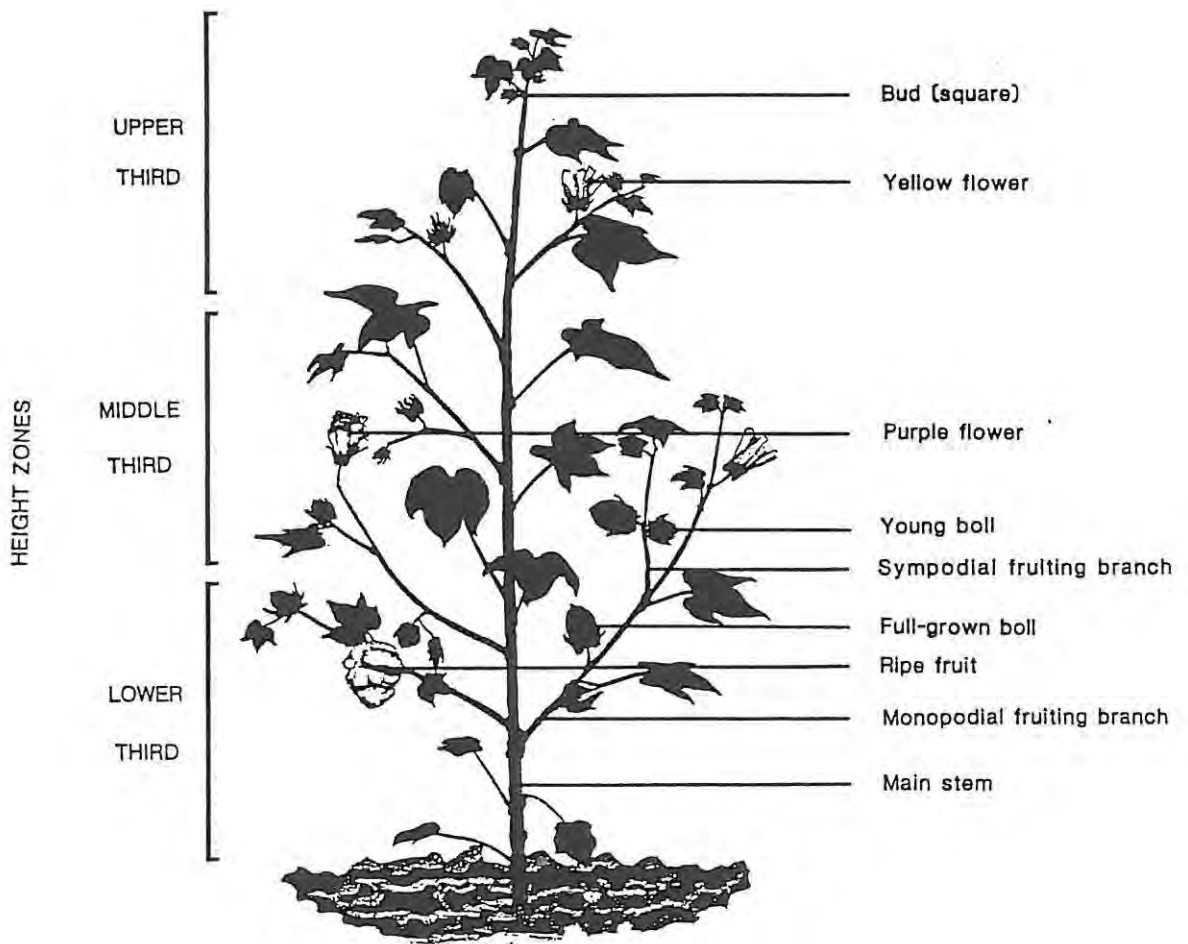


Fig. 4. Diagram of a cotton plant showing the different fruiting forms, fruiting branches and height zones used in this study. Partly after Botha (1986).

The succession of fruiting branches, arising from the nodes of the main stem, follows a set spiral course of three-eighths of the circumference of the main stem (Fig. 5). Leaves are formed on the sympodial branches with two buds at the base of each leaf. The axillary bud produces a vegetative branch and if the extra-axillary bud develops, it produces a further fruiting branch. The bolls first ripen near the bases of the branches (Eaton 1955; Prentice 1972; Van Heerden 1978).

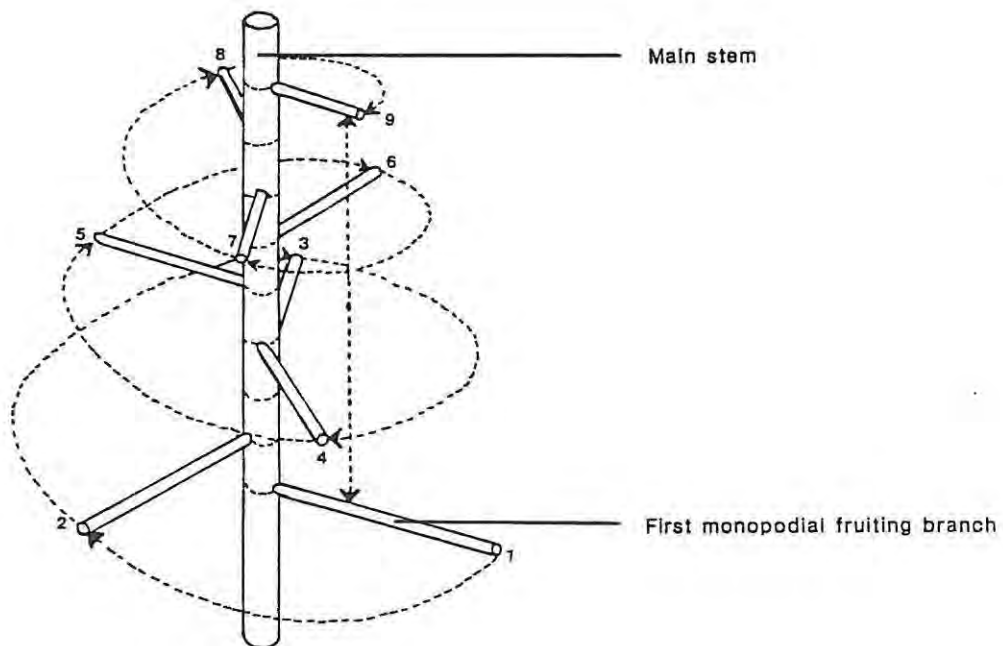


Fig. 5. Diagram of the three-eighths spiral course that the fruiting branches follow around the circumference of the main stem. After Prentice (1972).

Growth is irregular, depending largely on the availability of soil moisture, so that fruiting forms are formed for the greater part of the season, with a peak flowering period occurring about 90 - 100 days after plant emergence (Fig. 6).

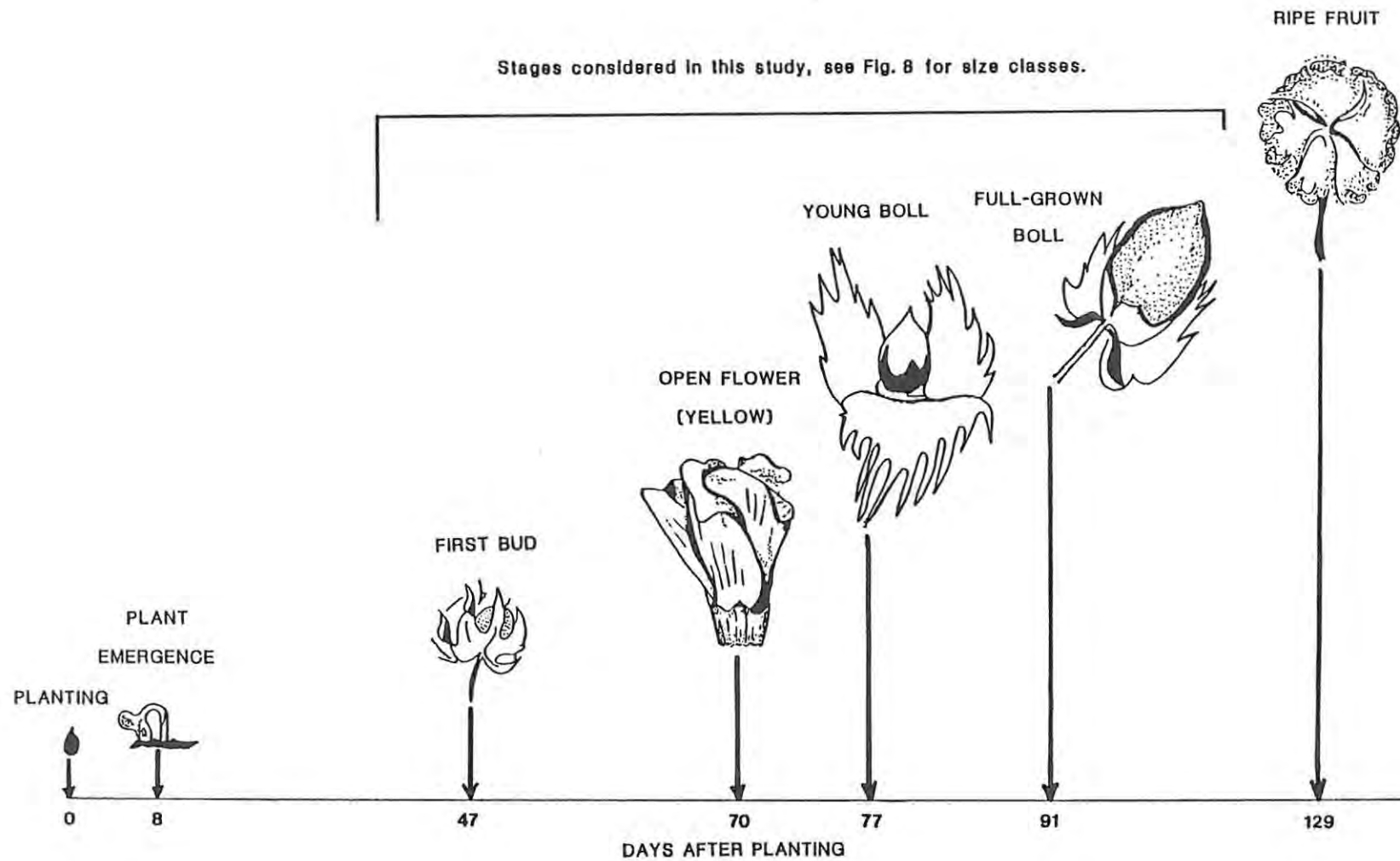


Fig. 6. Development of the fruiting forms of cotton plants. Partly after Botha (1981).

Predictably, at the beginning of the seasons, buds were the most abundant on the plants, but as the season progressed, flowers and bolls became relatively more abundant and towards the end of the season the bolls were the most abundant fruiting form (Fig. 7). As shown in Fig. 7, the distribution of the various fruiting forms was similar in the height zones defined in Fig. 4. Therefore, all stages of fruiting forms are present from about the 4th week after planting, but in varying proportions. Cotton is a perennial plant and can be ratooned. However, this is a contentious issue (see Introduction) and only annual plantings were considered in this study.

#### DEVELOPMENT OF FRUITING FORMS

For the purpose of this study, the fruiting forms of cotton plants were divided into twelve size classes or categories which are defined in Fig. 8. The mass and diameter of the categories are given in Fig. 9. The high correlation coefficient between mass and diameter ( $r = 0,96$ ), compares favourably with the results of Wilson & Gutierrez (1980b). Increments in both the mass and diameter were lower for Categories 7 (purple flower) and 8 (first boll stage). This was probably due to the desiccation and subsequent loss of the corolla in Categories 7 and 8. From Category 8, the first boll stage, there was a marked and clearly correlated increase in mass and diameter as the bolls developed to maturity. The growth increments of the developing bolls were much greater than that of the buds. For convenience, the

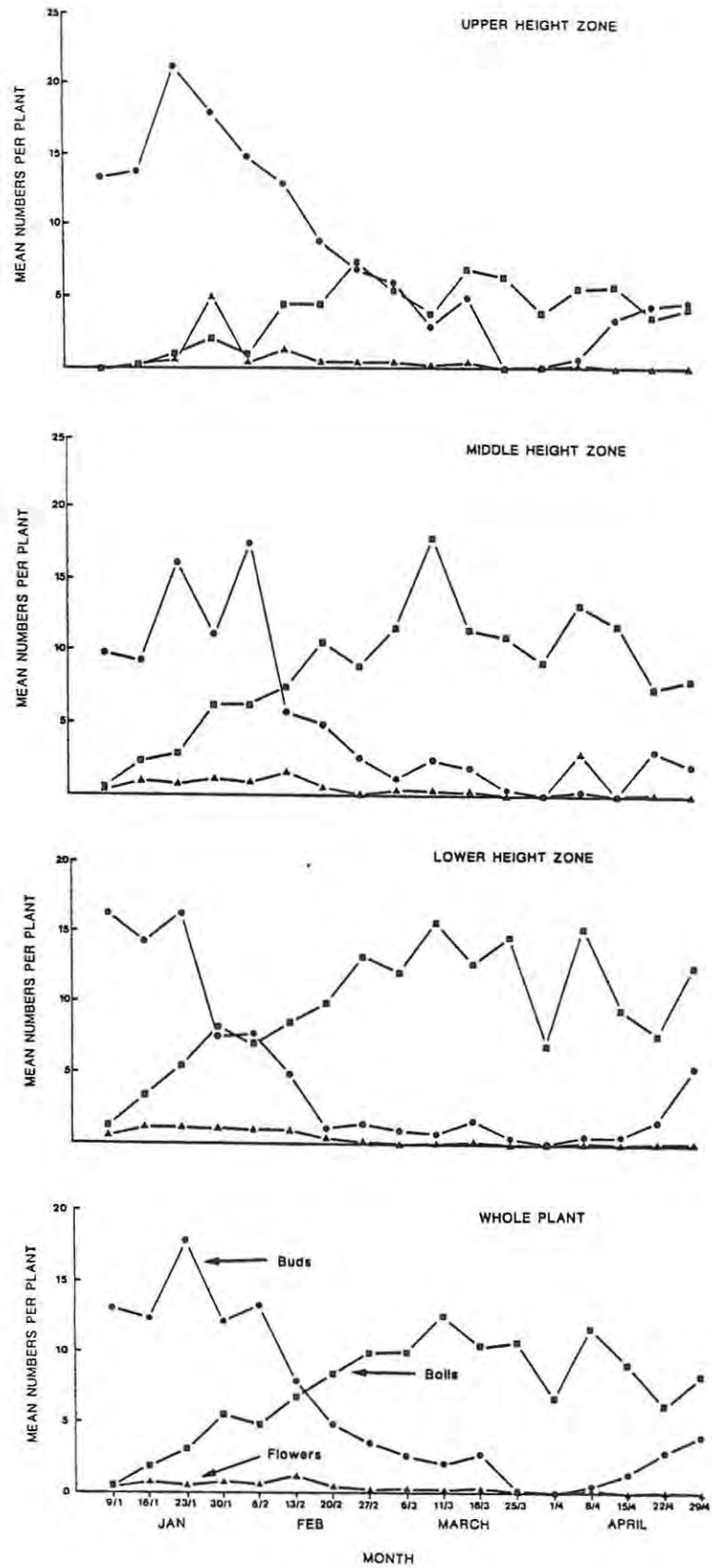


Fig. 7. Distribution of buds (circles), flowers (triangles) and bolls (squares) on the upper, middle and lower regions of cotton plants and the totals for whole plants during the 1985/86 season. Calculated from the totals for 30 plants per sampling date.

development of the size classes for the pre-flowering and post-flowering stages were considered as separate linear progressions and further measurements of Category 4 buds and Category 10 bolls were taken to obtain average values for these size classes, again showing a clear correlation (Figs 10 and 11).

The buds are surrounded by three green bracts (epicalyx) which are joined at their bases (Fig. 12). These bracts form a pointed canopy over the buds (hence the often-used term "square" in the literature), presumably to protect them as well as the later stages. The bracts respond to any damage to the buds resulting in a characteristic "flaring" of the bracts, leaving the fruiting form exposed (Fig. 13). The calyx, or inner bract, covers the bud in the early stages of development and later covers the bases of the bolls. The arrangement of the stamens is in a column with anthers. Still a bud, a conical yellow corolla protrudes from the inner calyx for about one day before the flower opens, which in turn, remains yellow (Figs 8 and 12) for about a day before darkening to purple and dropping off two days later (Prentice 1972). The boll passes through four more size classes before reaching its maximum size, with the mature "boll stage" (Figs 6 and 12) after a further 20 - 22 days. This maximum boll size, which contains the unripe seeds and fibres originating from the seed coats, was effectively the last category studied in terms of the feeding of *H. armigera* larvae. The contents of the boll are covered with a thick layer of tissue that hardens during the last few categories before ripening and hinders, but does not entirely prevent, feeding by the smaller larvae (Fig. 12). The

CATEGORY 1 - growth tip

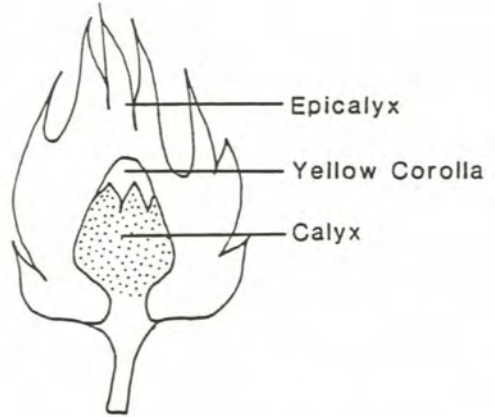
CATEGORY 2 BUD - bud barely visible



CATEGORY 3 BUD - calyx closed, epicalyx fully formed



CATEGORY 5 BUD - corolla prominent, unopened, longer than the calyx



CATEGORY 4 BUD - yellow corolla protruding from the calyx, shorter or equal to the calyx



↑  
← CATEGORIES 6 & 7 - yellow and red-purple flowers

Fig. 8. Definitions of the 12 size classes of cotton fruiting forms used in this study. Terms are also defined in Fig. 12. (Continued overleaf.)



CATEGORY 8 BOLL - corolla lost, boll smaller than calyx



CATEGORY 9 BOLL - boll fills calyx



CATEGORY 10 BOLL - boll larger than calyx, calyx split, boll shorter than epicalyx (structure can be suspended by holding tips of epicalyx together)



CATEGORY 11 BOLL - boll as long as epicalyx (structure cannot be held by tips of epicalyx)



CATEGORY 12 BOLL - boll longer than epicalyx, last category before boll burst (Frontispiece)

Fig. 8 (continued). Definitions of the 12 size classes of cotton fruiting forms used in this study. Terms are also defined in Fig. 12.

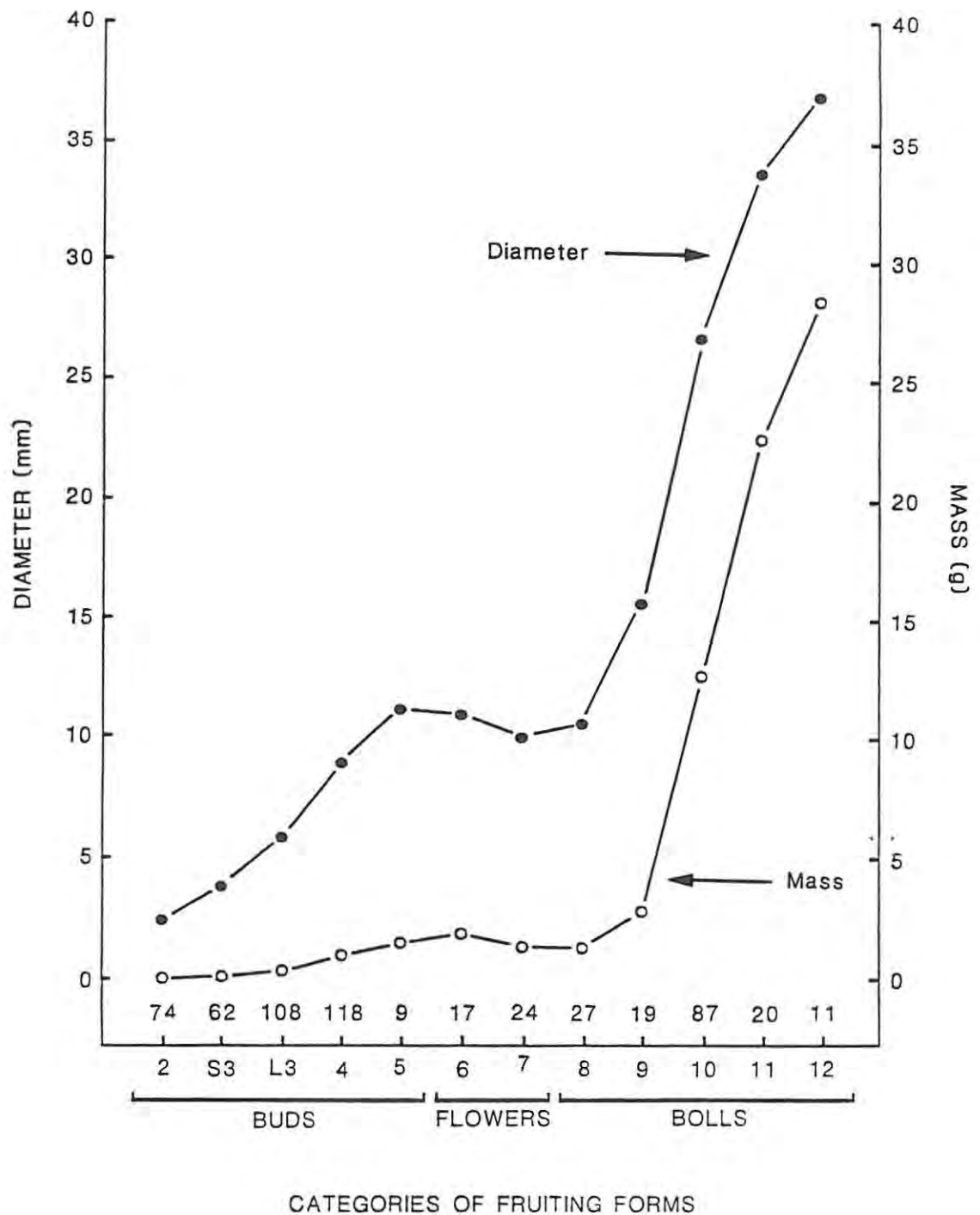


Fig. 9. The mean mass (open circles) and diameter (closed circles) of the categories of fruiting forms of cotton plants. The young buds (Category 3) were subdivided into small and large Category 3 buds for some purposes. The numbers of fruiting forms measured are shown above the horizontal axis.

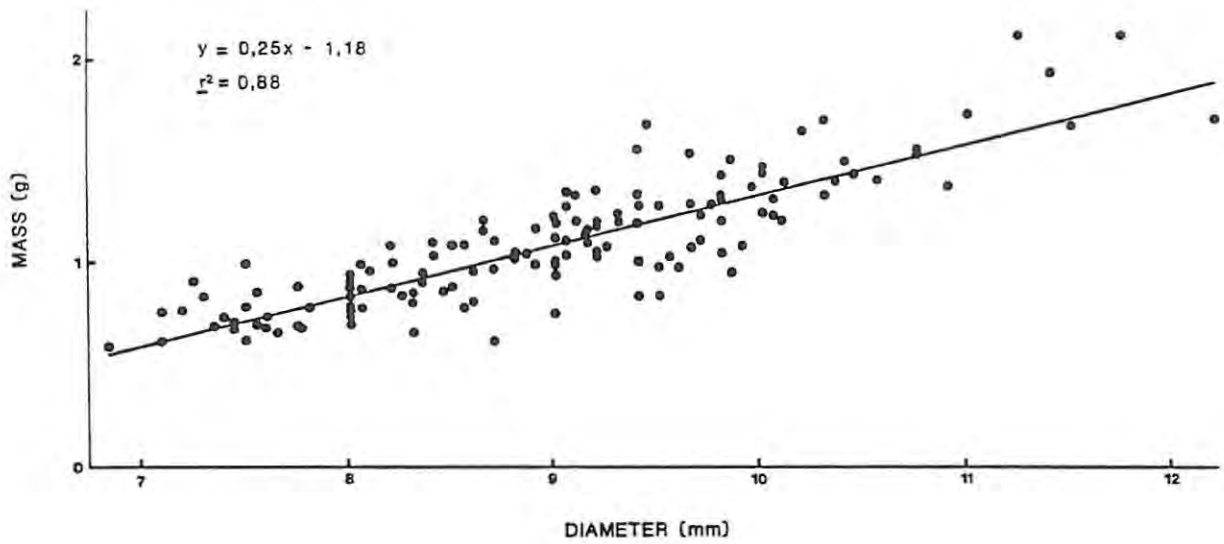


Fig. 10. Relationship between the diameter and mass of Category 4 buds of cotton plants.

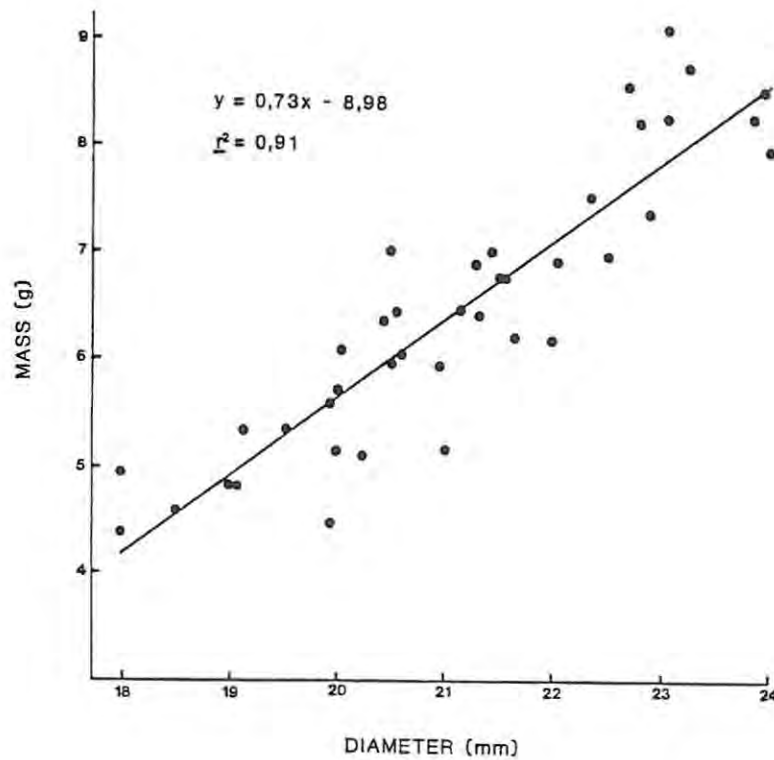


Fig. 11. Relationship between the diameter and mass of Category 10 bolls of cotton plants.

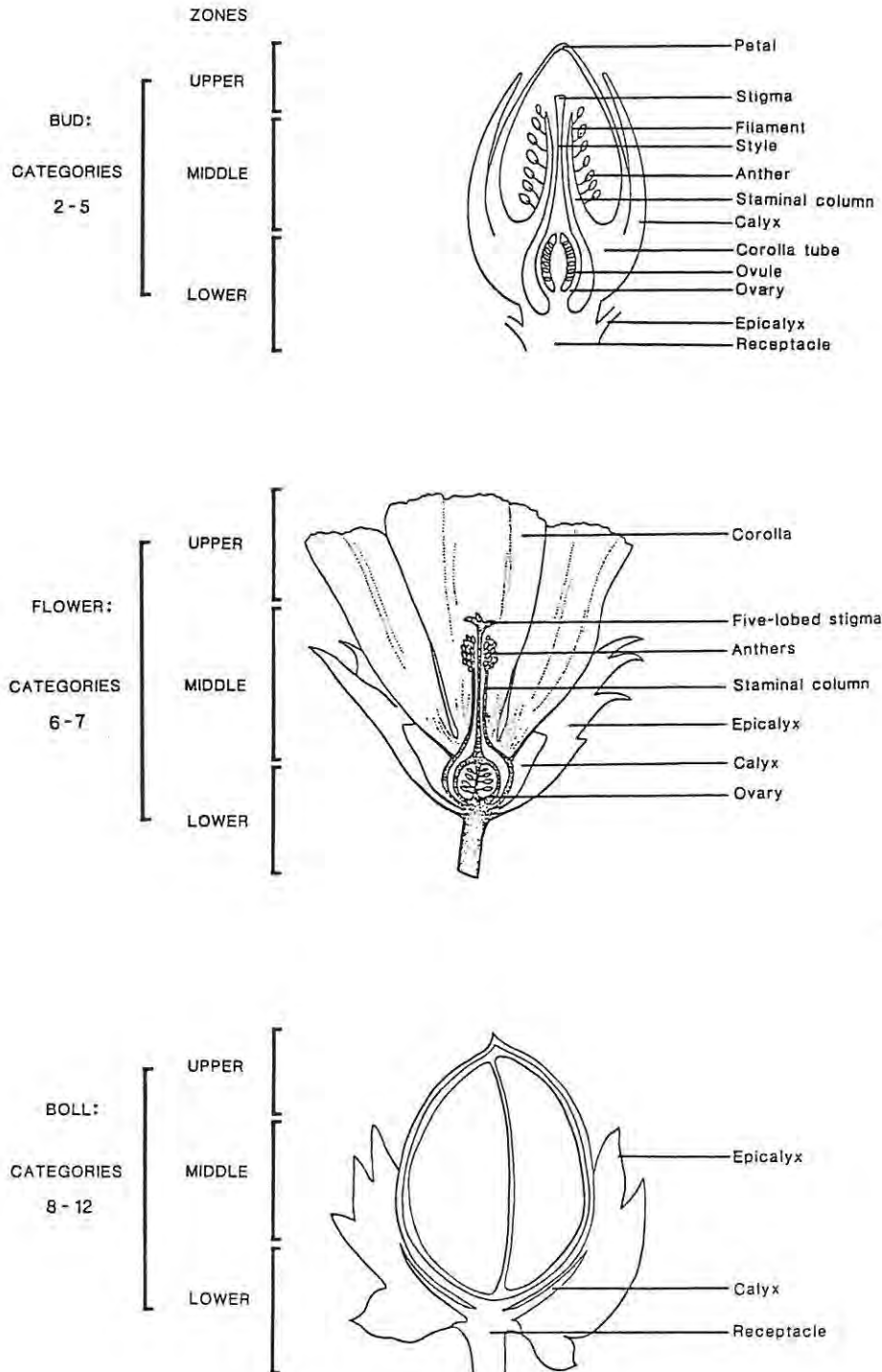


Fig. 12. Diagrams of a bud, flower and boll of the cotton plant. The categories are defined in Fig. 8. Partly after Reese *et al.* (1981) and Van Heerden (1978).



Fig. 13. "Flaring" of the epicalyx of a cotton bud following damage by an Heliothis armigera larva.

ripe fruit (referred to as "boll burst" (Frontispiece)) is a dry dehiscent schizocarp of three to five loculi, each containing eight to nine lint-bearing seeds (Prentice 1972; Van Heerden 1978) and is not fed on by H. armigera larvae. The lint-bearing seeds eventually ripen and are harvested, mainly for the textile industry.

#### 4. BIOLOGY OF H. ARMIGERA.

This chapter describes the salient characteristics of the biology of H. armigera. Emphasis is on the development and recognition of the larval instars, a central issue in the study.

##### LIFE HISTORY

A brief description of the life cycle of H. armigera will suffice. The adults are typical noctuid moths with nocturnal habits of flight, mating and oviposition. The female moth is stout bodied, a reddish-brown colour and somewhat bigger than the more greenish males (Pinhey 1975; Jayaraj 1982). The number of eggs laid per female in the laboratory culture averaged about 1400 (Botes, unpublished data). In the field, eggs are laid singly on plants, mainly during the early evening (Taylor 1982). On cotton, eggs are laid mainly on leaves, with a preference for young leaves when the plants are still young, but favouring the fruiting forms in older plants (Beeden 1974; Stoeva 1979; Mabbett 1983; Mabbett & Nachapong 1984). Most eggs are laid on the top third of the plants (Beeden 1974; Pitre 1983; Basson 1987). The oviposition sites bear no obvious relationship to the plant parts which are fed on by the first instar larvae, an aspect which is dealt with in the Discussion. The larvae are full-grown after about 14 - 18 days and burrow into the soil where they overwinter or pupate, the pupal stage lasting about 11 - 14 days.

## IDENTIFICATION OF LARVAL INSTARS

Mature H. armigera larvae vary widely in colour from shades of yellow-green, pink to brown to almost black (Taylor 1982). They are recognised by a fine white mid-dorsal line, edged with black, as well as lateral markings, including a creamy white stigmatal line (Frontispiece). Importantly, as explained in the Introduction, they cannot conceivably be confused with any other lepidopterous larvae which occur on cotton in South Africa.

Details of the duration of larval instars of H. armigera were required in order to quantify the damage caused by each larval instar and to study their feeding patterns which is the purpose of this study. The durations of the larval instars of H. armigera in the laboratory culture, under both laboratory and field conditions, as well as the development of the larval instars in the natural population in the field, are given in Table 2. Some differences in the relative durations of the larval instars of H. armigera were found between those reared in the laboratory, laboratory-reared larvae placed on cotton in the field and natural populations of larvae, but these differences were not sufficiently marked to confound the field experiments described later. The duration of the larval instars were well within the limits reported by other authors (Table 3).

The length and mass of the individual larval instars in the laboratory culture were recorded. The larval instars could be roughly distinguished using these criteria, but were somewhat

Table 2. Duration of the larval instars of Heliiothis armigera larvae from the laboratory culture, the laboratory culture under field conditions and of a natural population. Means and ranges (in parentheses) are shown.

LARVAL INSTAR	NUMBERS OF OBSERVATIONS	LABORATORY CULTURE	DURATION IN DAYS	
			LABORATORY CULTURE UNDER FIELD CONDITIONS	NATURAL POPULATION
I	149	3,5 (3 - 5)	*	2,6 (2 - 3)
II	135	2,5 (2 - 4)	2,55 (2 - 4)	3,2 (3 - 4)
III	150	2,1 (1 - 3)	2,81 (2 - 4)	3,3 (2 - 4)
IV	124	2,7 (1 - 6)	3,24 (2 - 4)	3,7 (3 - 4)
V	313	2,5 (2 - 3)	6,22 (4 - 7)	5,2 (4 - 7)
TOTAL	871	13,3	14,82	18,0

\* It was not possible to recover first-instar larvae with the survey method used in the field.

unreliable due to the overlap in the ranges between instars (Table 4). More reliable measurements of the widths of the head capsules of Lepidoptera larvae to separate the larval instars are widely used. The measurements of head capsules and clypei of H. armigera larvae are given in Fig. 14. The head capsules were measured at their widest point when viewed in silhouette from above, usually immediately behind the ocelli. The clypeal widths refer to the extremities across the base of the clypeus. The clypeal widths are especially useful because, unlike the head capsule, the clypeus remains intact after the final larval moult and can often be used to

Table 3. Duration of the larval stages of Heliothis armigera under different temperature regimes on cotton, artificial diets and various other food plants. Means and standard errors, where available, or ranges (in parentheses) are given.

COTTON					
AUTHOR	COUNTRY	DIET	TEMPERATURE RANGE (°C)	RH (%)	DURATION (DAYS)
Coaker (1960)	Uganda	Cotton FF*	?	?	25,6
Reed (1965a)	W. Tanganyika	Cotton FF	21 - 27	80 +	21,1 ± 0,32
Pretorius (1976)	South Africa	Cotton FF	23 - 27	60	18,2 (16 - 32)
Dhandapani & Ballasubramanian (1980b)	India	Cotton FF	24 - 28	?	18,3 (16 - 20)
Singh & Sidhu (1980)	Punjab	Cotton leaves	?	?	13,35 ± 0,53 to 27,21 ± 3,27
Iss-Hak <i>et al.</i> (1981)	Egypt	Cotton FF	27,35	51,1	16,03
Mansour <i>et al.</i> (1981)	Egypt	Cotton leaves	27	60	16,08 ± 1,32
Ramos & Morallo-Rejesus (1981)	Philippines	Cotton	24 - 26	75	30,61
ARTIFICIAL DIETS					
Bot (1966)	South Africa	Artificial diet	25	75	12 - 15
Pretorius (1976)	South Africa	Artificial diet	23 - 27	60	17,4 (13 - 26)
Ayad (1977)	Fayoum	Artificial diet	23 - 27	65 ± 5	21,42
Twine (1978)	Queensland	Artificial diet	18,5	?	35,3 ± 2,0
Twine (1978)	Queensland	Artificial diet	21,3	?	24,0 ± 2,2
Twine (1978)	Queensland	Artificial diet	24,6	?	18,5 ± 1,3
Twine (1978)	Queensland	Artificial diet	27,1	?	14,5 ± 1,0
Twine (1978)	Queensland	Artificial diet	33,9	?	11,7 ± 0,9
Ramos & Morallo-Rejesus (1981)	Philippines	Artificial diet	24 - 26	75	32,29
Odindo (1981)	Philippines	Artificial diet	24 - 26	75	31,6
	Kenia	Artificial diet	22 - 24	75 - 85	17
VARIOUS OTHER FOOD PLANTS					
Pearson & Maxwell Darling (1958)	South Africa	?	?	?	15 - 32
Pearson & Maxwell Darling (1958)	U.S.A.	?	?	?	14 - 70
Pearson & Maxwell Darling (1958)	Nyassaland	?	?	?	18 - 35
Pearson & Maxwell Darling (1958)	S. Rhodesia	?	22,5	?	18
Pearson & Maxwell Darling (1958)	S. Rhodesia	?	17,5	?	51 (17 - 61)
Coaker (1960)	Uganda	Sorghum grain	15 - 26	?	24,025
Coaker (1960)	Uganda	Maize	?	?	23,16
Coaker (1960)	Uganda	Beans	?	?	24,5
Coaker (1960)	Uganda	Sunflower	?	?	33,6
Ismail & Swailem (1975)	Egypt	?	29	53,4	13,7 (12 - 16)
Pretorius (1976)	South Africa	Ground nuts	23 - 27	60	24,9 (18 - 32)
Pretorius (1976)	South Africa	Green beans	23 - 27	60	19 (14 - 27)
Pretorius (1976)	South Africa	Sunflower	23 - 27	60	18,7 (14 - 30)
Pretorius (1976)	South Africa	Potato leaves	23 - 27	60	21,6 (17 - 27)
Ayad (1977)	Fayoum	Castor leaves	23 - 27	65 ± 5	22,95

Table 3. (Continued)

AUTHOR	COUNTRY	DIET	TEMPERATURE RANGE (°C)	RH (%)	DURATION (DAYS)
Dhandapani & Ballasubramanian (1980b)	India	Bengal gram	24 - 28	?	19,2 (18 - 20)
Dhandapani & Ballasubramanian (1980b)	India	Red gram	24 - 28	?	17 (15 - 18)
Dhandapani & Ballasubramanian (1980b)	India	Lab-Lab	24 - 28	?	19 (17 - 20)
Dhandapani & Ballasubramanian (1980b)	India	Tomato	24 - 28	?	20 (17 - 22)
Dhandapani & Ballasubramanian (1980b)	India	Sorghum	24 - 28	?	19,8 (17 - 24)
Dhandapani & Ballasubramanian (1980b)	India	Maize	24 - 28	?	18 (15 - 20)
Dhandapani & Ballasubramanian (1980b)	India	Sunflower	24 - 28	?	19,5 (14 - 23)
Bilapate <i>et al.</i> (1978)	India	Lima bean pods	?	?	18
Abdel-Fattah <i>et al.</i> (1978)	Egypt	Castor bean leaves	24 - 26	65 ± 3	20,08 ± 0,19
Stoeva (1979)	Sandansu	Lucerne leaves	25	?	12,95 ± 0,07
Stoeva (1979)	Sandansu	Green pepper leaves	25	?	23,35 ± 0,24
Stoeva (1979)	Sandansu	Green pepper	25	?	15,7 ± 0,14
Stoeva (1979)	Sandansu	Tomato	25	?	18,7 ± 0,12
Stoeva (1979)	Sandansu	Tomato	22	?	27,1
Stoeva (1979)	Sandansu	Tomato	30	?	14,3
Poitout & Bues (1979)	France	Tomato	?	?	± 20
Singh & Sidhu (1980)	Punjab	Tomato	?	?	8 - 12
Singh & Sidhu (1980)	Punjab	Gram	?	?	21,28
Dubey <i>et al.</i> (1981)	India	Chickpea	33,2	16,5 - 72,5	18,0
Dubey <i>et al.</i> (1981)	India	Berseem	?	?	17,8
Dubey <i>et al.</i> (1981)	India	Pigeon pea	?	?	19,6
Dubey <i>et al.</i> (1981)	India	Sweet pea	?	?	19,8
Iss-Hak <i>et al.</i> (1981)	Egypt	Castor oil leaves	22,5	58,45	29,55
Iss-Hak <i>et al.</i> (1981)	Egypt	Chine rose petals	24,75	57,28	29,58
Ramos & Morallo-Rejesus (1981)	Philippines	Maize	24 - 26	75	28,32
Ramos & Morallo-Rejesus (1981)	Philippines	Tomato	24 - 26	75	39,3
Ramos & Morallo-Rejesus (1981)	Philippines	Tobacco	24 - 26	75	33,42
Odindo (1981)	Kenia	Grass based	22 - 24	75 - 85	22
Bilapate <i>et al.</i> (1981)	Marathwada	Chickpea	25 - 27	?	12,94
Bilapate <i>et al.</i> (1981)	Marathwada	Chickpea	25 - 27	?	14,55
Mansour <i>et al.</i> (1981)	Egypt	Lettuce	27	60	12,78 ± 0,68
Mansour <i>et al.</i> (1981)	Egypt	Kidney bean pods	27	60	14,19 ± 0,93
Mansour <i>et al.</i> (1981)	Egypt	Dwarf melon	27	60	19,2 ± 0,89
Mansour <i>et al.</i> (1981)	Egypt	Musk mellow	27	60	23,32 ± 1,2
Mansour <i>et al.</i> (1981)	Egypt	Castor oil leaves	27	60	21,68 ± 0,96

Table 3. (Continued)

AUTHOR	COUNTRY	DIET	TEMPERATURE RANGE (°C)	RH (%)	DURATION (DAYS)
Chaudhary & Sharma (1981)	Hissar	Gram	27 - 29	?	15,52 ± 0,52
Chaudhary & Sharma (1981)	Hissar	Gram	26 - 28,4	?	15,5 (14 - 17)
Chaudhary & Sharma (1981)	Hissar	Gram	19 - 21,4	?	29,9, (26 - 32)
Chaudhary & Sharma (1981)	Hissar	Gram	25,7 - 28,1	?	15,8 (14 - 20)
Chaudhary & Sharma (1981)	Uttar Pradesh	Gram	?	?	21 - 28
Chaudhary & Sharma (1981)	Punjab	Gram	?	?	8 - 12
Chaudhary & Sharma (1981)	California	Gram	?	?	21 - 44
Chaudhary & Sharma (1981)	Ohio	Gram	?	?	18 - 51
Tripathi & Sharma (1984)	Uttar Pradesh	Gram	?	?	22,5 - 30,0

FF<sup>a</sup> Fruiting Forms.

determine the instar when head capsules are damaged. The occurrence of five larval instars in the laboratory culture of *H. armigera* was confirmed by arranging the head-capsule widths into frequency classes as was done for other Lepidoptera by Allen & Grimble (1970); Broodryk (1970); Atkinson (1980), and by following the daily development of 20 larvae to record the number of moults as advocated by Kishi (1971). Borderline cases between the instars, indicated by the ranges in Fig. 14, were highly exceptional. The mean head-capsule and clypeal widths for each larval instar are plotted on a logarithmic scale in Fig. 14. The resultant straight lines show that the larvae conformed to Brooks' Rule (Crosby 1973) of geometric growth of sclerotised structures and that no instars were overlooked (e.g. Crosby 1973; Surgeoner & Wallner 1975; Bilapate *et al.* 1981; Fredeen 1981). Further, if the fitted

Table 4. Length and mass of the larval instars of Heliothis armigera larvae in the laboratory culture. Means and ranges (in parentheses) are shown. These values correspond to the measurements of head-capsule and clypeal widths given in Fig. 14.

LARVAL INSTAR	NUMBERS OF OBSERVATIONS	LENGTH (mm)	MASS (g)
I	149	2,6 (1,3 - 4,4)	0,00017*
II	135	6,3 (3,1 - 13,2)	0,0025*
III	150	15,7 (7,8 - 22,4)	0,02 (0,0023 - 0,06)
IV	124	19,6 (11,4 - 34,0)	0,09 (0,01 - 0,28)
V	313	30,7 (17,0 - 41,0)	0,44 (0,11 - 0,77)

\* The mass of first and second-instar larvae was obtained from groups of larvae so that no ranges were obtained.

regression lines in Fig. 14 are extended to include a sixth larval instar, the extrapolated values are unrealistically high. Irrespective of the number of larval instars of H. armigera reported by various authors (Table 5), the head-capsule widths of the final larval instars are similar. Consequently those of the intermediate instars are smaller when more instars occur. Similarly, as would be expected, the growth ratios between the head-capsule widths of successive larval instars (see references to geometric growth cited above) are also lower in H. armigera when more larval instars occur (Bilapate et al. 1981). The mean growth ratios for the data in Fig. 14 were 1,78 for the head capsule and 1,82 for the clypeus. Significant departures from these values would provide a useful indication that a different number of larval instars occurred. The five larval instars found

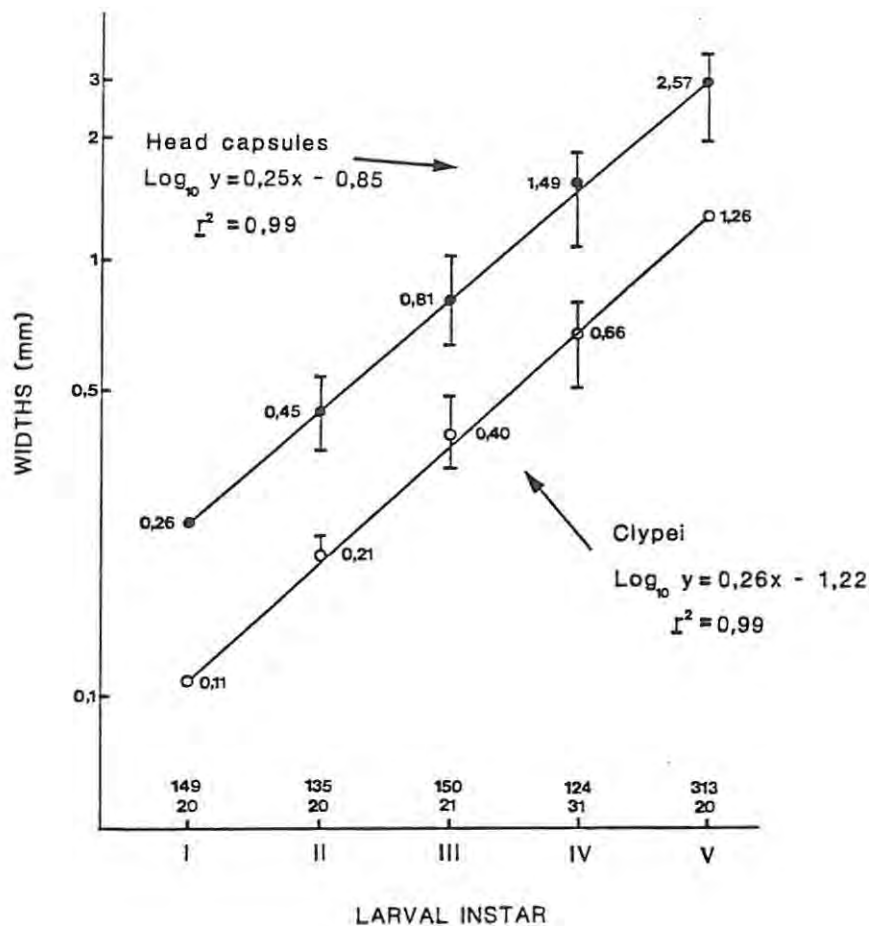


Fig. 14. Width, on a logarithmic scale, of head capsules (closed circles) and clypei (open circles) for each larval instar of *Heliothis armigera*. Means and ranges (where they extend beyond the circles) are shown. Actual means are shown alongside the plotted points. Numbers of observations are above the horizontal axis for head capsules (upper line) and clypei (lower line).

in this study (Fig. 14), lasted 3,5 2,5 2,1 2,7 and 2,5 days successively. Similar and contrasting results from a variety of authors are listed in Table 6. It is, however, not possible from the information given in Table 5 to decide why the larval instar numbers varied. Furthermore, five larval instars were found in a

Table 5. Numbers of larval instars of Heliothis armigera larvae on various food plants according to several authors. Rearing conditions used by some of the authors are listed in Table 3.

AUTHOR	DIET	NUMBER OF LARVAL INSTARS
Pearson & Maxwell Darling (1958)	?	6-7
Reed (1965a)	Cotton FF*	6
Ismail & Swailem (1975)	?	6
Ayad (1977)	Artificial diet	6
Abdel-Fattah <u>et al.</u> (1978)	Artificial diet	6
Twine (1978)	Artificial diet	6
Poitout & Bues (1979)	Tomato	5 or 6
Mabbett <u>et al.</u> (1980)	Cotton FF	5
Bilapate <u>et al.</u> (1981)	Chickpea	5 or 6
Chaudhary & Sharma (1981)	Gram	5
Dubey <u>et al.</u> (1981)	Green Chickpea pods	6
Iss-Hak <u>et al.</u> (1981)	Cotton FF	6
Iss-Hak <u>et al.</u> (1981)	Castor oil leaves	6
Iss-Hak <u>et al.</u> (1981)	Chine rose petals	6
Ramos & Morallo-Rejesus (1981)	Artificial diet	6
Ramos & Morallo-Rejesus (1981)	Maize	6
Ramos & Morallo-Rejesus (1981)	Cotton	6
Ramos & Morallo-Rejesus (1981)	Tomato	7-8
Ramos & Morallo-Rejesus (1981)	Tobacco	7
Toquebaye & Couilloud (1982)	?	5 or 6
Wilson & Waite (1982)	Cotton	6
Tripathi & Sharma (1984)	Gram	6

FF\* Fruiting Forms.

Table 6. Widths of the head capsules and duration of the larval instars of *Heliothis armigera* on different food sources and temperature regimes according to various authors. Means and standard errors, where available, are given.

AUTHOR	DIET	TEMPERATURE (°C)	DURATION (DAYS)	LARVAL INSTAR				
				I	II		III	
				HEAD CAPSULE WIDTH (mm)	DURATION (DAYS)	HEAD CAPSULE WIDTH (mm)	DURATION (DAYS)	HEAD CAPSULE WIDTH (mm)
Reed (1965a)	Cotton FF*	21 - 27	2,83	0,25	2,23	0,4	2,46	0,6
Ismail & Swailem (1975)	?	29	2	0,21	2	0,42	2	0,62
Ayad (1977)	Castor oil leaves	23 - 27	3,83 ± 0,13	0,22 (0,2 - 0,25)	3,0 ± 0,1	0,37 (0,3 - 0,4)	3,39 ± 0,09	0,58 (0,51 - 0,7)
Ayad (1977)	Artificial diet	23 - 27	3,5 ± 0,11	0,22 (0,22 - 0,25)	2,7 ± 0,08	0,38 (0,38 - 0,44)	2,82 ± 0,07	0,62 (0,59 - 0,7)
Twine (1978)	Artificial diet	18,5	3,0 ± 0,0		2,9 ± 0,5		4,0 ± 0,5	
		21,3	2,0 ± 0,2		2,1 ± 0,4		3,1 ± 0,5	
		24,6	1,5 ± 0,5		1,5 ± 0,5		3,0 ± 0,1	
		27,1	1,0 ± 0,0		1,0 ± 0,0		1,8 ± 0,5	
		33,9	1,0 ± 0,0		1,0 ± 0,0		1,1 ± 0,4	
Chaudhary & Sharma (1981)	Gram	27 - 29	1,48 ± 0,5		2,56 ± 0,49		2,76 ± 0,2	
Bilapate et al. (1981)	Chick pea	25 - 27	2,06 ± 0,36	0,28 ± 0,0	1,62 ± 0,49	0,5 ± 0,02	2,14 ± 0,36	0,83 ± 0,04
Toquebaye & Couilloud (1982)	Chick pea	25 - 27	2,13 ± 0,34	0,28 ± 0,0	1,7 ± 0,52	0,5 ± 0,01	2,06 ± 0,25	0,31 ± 0,04
	?	?	?	0,27 ± 0,02		0,47 ± 0,03		0,79 ± 0,08
	?	?	?	0,27 ± 0,02		0,47 ± 0,03		0,79 ± 0,08

AUTHOR	DIET	TEMPERATURE (°C)	DURATION (DAYS)	LARVAL INSTAR				
				IV	V		VI	
				HEAD CAPSULE WIDTH (mm)	DURATION (DAYS)	HEAD CAPSULE WIDTH (mm)	DURATION (DAYS)	HEAD CAPSULE WIDTH (mm)
Reed (1965a)	Cotton FF*	21 - 27	2,4	1,0	3,11	1,6	5,37	2,4
Ismail & Swailem (1975)	?	29	2	0,94	3	1,71	7	3,5
Ayad (1977)	Castor oil leaves	23 - 27	3,85 ± 0,1	0,88 (0,74 - 1,7)	4,2 ± 0,33	1,61 (1,48 - 1,77)	4,68 ± 1,47	2,13 (1,92 - 2,29)
Ayad (1977)	Artificial diet	23 - 27	3,25 ± 0,58	0,99 (0,92 - 1,07)	4,3 ± 0,24	1,59 (1,55 - 1,7)	4,85 ± 0,17	2,22 (2,07 - 2,4)
Twine (1978)	Artificial diet	18,5	5,1 ± 0,7		6,2 ± 1,6		8,3 ± 1,2	
		21,3	3,1 ± 0,4		4,0 ± 1,0		6,1 ± 1,3	
		24,6	2,6 ± 0,5		2,0 ± 0,6		5,5 ± 0,8	
		27,1	1,9 ± 0,3		2,0 ± 0,5		4,3 ± 0,8	
		33,9	1,7 ± 0,5		1,4 ± 0,6		3,5 ± 0,6	
Chaudhary & Sharma (1981)	Gram	27 - 29	2,76 ± 0,58		6,0 ± 0,4			
Bilapate et al. (1981)	Chick pea	25 - 27	2,44 ± 0,65	1,58 ± 0,08	4,68 ± 0,55	2,59 ± 0,03		
Toquebaye & Couilloud (1982)	Chick pea	25 - 27	2,1 ± 0,66	1,2 ± 0,02	2,4 ± 0,49	1,71 ± 0,02	4,16 ± 0,46	2,6 ± 0,09
	?	?	?	1,39 ± 0,03		1,79 ± 0,01		
	?	?	?	1,18 ± 0,03		1,79 ± 0,01		2,59 ± 0,8

FF\* Fruiting Forms.

separate study on a field population of H. armigera larvae by P.J. Guest (unpublished data). These experiments were conducted at the same locality and during the same period as this study.

To summarise, the identification of H. armigera larvae for the field trials was easy and the larval instars could be reliably separated at a glance. With these criteria available it was possible to examine the feeding habits of the larvae in the field, the subject of the next chapter.

5. DISTRIBUTION OF H. ARMIGERA LARVAE ON COTTON PLANTS

Three criteria, namely compass direction, plant height zones and the distances moved within the plants by H. armigera larvae were examined in relation to the distribution of the larvae on cotton plants. The positions of H. armigera larvae from the laboratory culture and the natural population were recorded on half grown to full grown cotton plants. These preliminary studies were necessary to examine the selection of feeding sites by the larvae and also, have important implications in the planning of surveys for H. armigera larvae in cotton fields.

## DISTRIBUTION IN RELATION TO COMPASS DIRECTION

From Fig. 15 it appears as if more H. armigera larvae occurred in an east-west distribution than along a north-south position. However, when the numbers of larvae found in the different compass directions on individual plants were statistically tested against the average by a Chi-squared test, significant differences were evident. An important factor influencing these results could be that the rows in the field were planted in a north-south direction, but because of irrigation requirements, the experiment was not repeated with rows planted in an east-west direction. Within the rows the plants overlapped on the northern and southern sides, resulting in more space and sunlight on the eastern and western sides of the plants. It may be that the larvae preferred these conditions

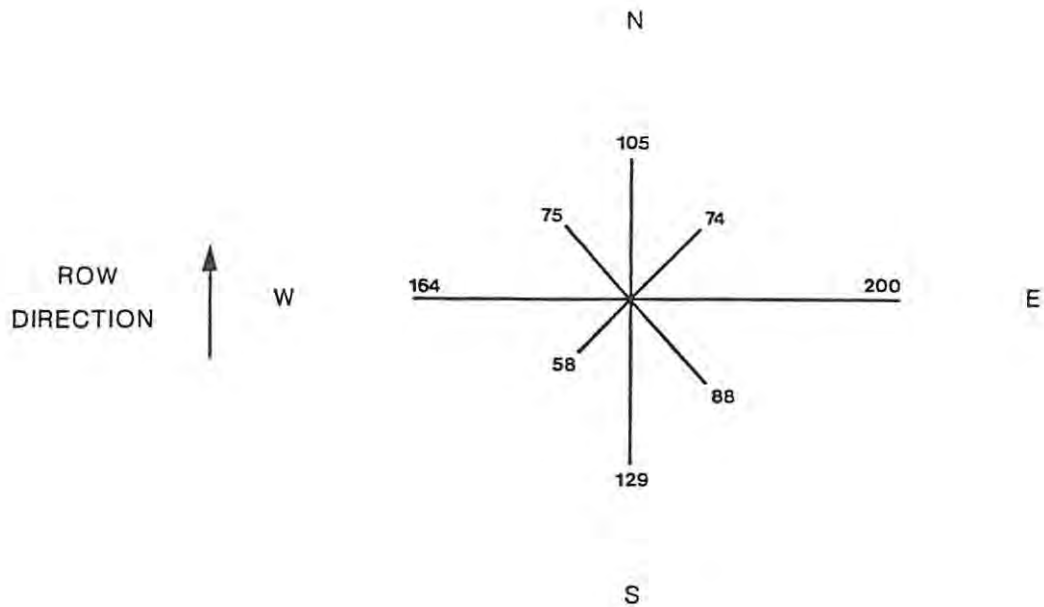


Fig. 15. Numbers of Heliothis armigera larvae feeding on field-grown cotton plants in relation to compass direction. The lengths of the compass directions are illustrated in proportion to the numbers of larvae.

to the denser foliage in the row direction. Be that as it may, no clearly dominant compass direction could be identified and the matter was not pursued.

#### DISTRIBUTION IN PLANT HEIGHT ZONES

The distribution of the larvae in the plants is influenced by the distribution of fruiting forms and the distances moved by the larvae.

Fruiting forms and H. armigera larvae are more likely to occur in some strata of cotton plants than in others. Presumably all the fruiting forms on a branch are equally exposed to the larvae on a branch (Wilson & Gutierrez 1980a). According to

Wilson et al. (1982), plant density and the time of the season are two key factors which not only determine the state of plant growth, but also influence the feeding pattern and within-plant distribution of H. zea. Fye & Bonham (1971) state that the temperature of buds were similar throughout the plant during the early stages of plant development, but much cooler in the lower parts of the plants later in the season due to shading, although only a few buds and older bolls are available in these lower zones, these structures provided shelter for insects in extremely hot weather. Wilson et al. (1983) found that initially H. armigera occurred in the upper third of a plant but that the first three instars moved downwards from the plant terminal. Smaller larvae of H. zea and H. virescens were found in the upper third of the cotton plants and although the larger larvae were equally distributed at all levels of the plants there were equal percentages of larvae in the middle and upper zones of the plant (Farrar & Bradley 1985a; Ramalho et al. 1984a).

There is no clear-cut pattern in the movement of the larvae of Heliothis spp.; some of the reported results are actually somewhat contradictory. The tendency for H. zea and H. virescens is for small larvae to occur in the upper third of cotton plants, specifically the branch tips and young buds around the periphery, but later moving downwards and away from the terminal to feed on mature fruiting forms before entering the soil to pupate (Kincade et al. 1967; Wilson & Gutierrez 1980a, 1980b; Snodderly & Lambdin 1982). These results suggest that the larvae "migrate" to the lower parts of the plants during their development. Fye (1972)

reported that 88 - 100 % of H. zea and H. virescens larvae occurred in the upper two feet of the cotton plant and that at the end of the season, the larvae moved to the lower parts of the plants due to the lower temperatures in the lower zones of the plant, providing ideal temperatures for development of the larvae later in the season.

For this study plants were divided into three approximately equal height zones namely upper, middle and lower zones (Fig. 4, Chapter 3), a practice adopted by many authors namely Kincade et al. (1967); Mabbett et al. (1979); Wilson et al. (1983); Ramalho et al. (1984a). The distribution of feeding of H. armigera larvae is shown in Fig. 16. The larvae occurred mainly in the upper third or at least in the upper two-thirds of the cotton plants. It was found that the smaller larvae, that is until the third instar, fed mainly in the upper third of the plant and the older larvae, namely the fourth and fifth instars, moved to and fro between the upper two thirds of the cotton plants. Only a very small proportion of larvae fed in the lower third: for most of the season the larvae remained in the upper two-thirds of the plants (Fig. 16). This is more or less in agreement with the findings of Mabbett et al. (1979, 1980) for H. armigera and of Wilson et al. (1980) for H. zea and does not support the hypothesis that larvae migrate to the lower parts of the plants. The distribution of the fruiting forms in the height zones were recorded (Fig. 7, Chapter 3), but with a view to examine the selection of feeding sites, not the dispersal of the larvae.

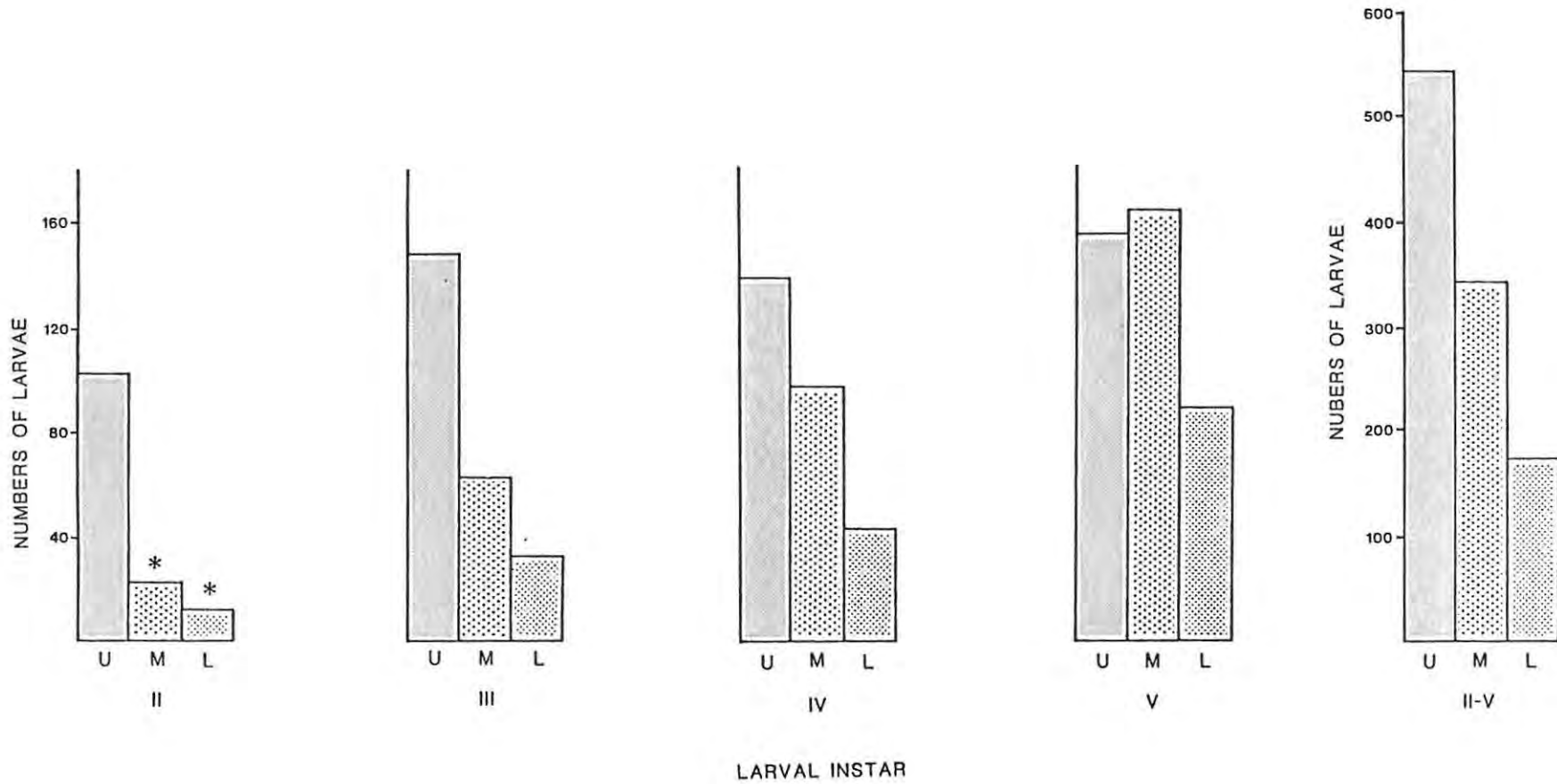


Fig. 16. Numbers of *Heliothis armigera* larvae of instars II - V and the total for all larval instars, feeding on the upper (U), middle (M) and lower (L) height zones of cotton plants in the field. The asterisks above the histogram bars for larval instar II indicate the only non-significant Chi-squared value at the 5 % level.

## MOVEMENT WITHIN PLANTS

This too, was studied in order to interpret the selection of feeding sites by H. armigera larvae and further, because the degree of movement relates to the number of fruiting structures damaged by the larvae.

Linear distances between feeding sites of individual larvae caged in large sleeves (Fig. 2, Chapter 2), were recorded along with the instars of the larvae (Fig. 17). The movement of a few larvae was followed for the duration of the larval instars. These distances corresponded almost exactly with the data shown in Fig. 17 and are incorporated in the figure. The linear distances between feeding sites can, of course, only be an underestimate of

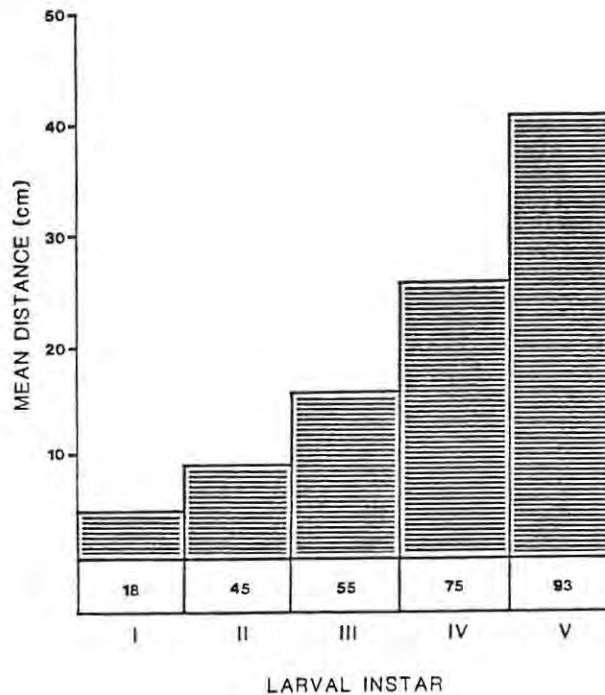


Fig. 17. Mean linear distances (cm) between feeding sites of Heliothis armigera larval instars on cotton plants. The numbers of observations are shown above the horizontal axis.

the actual distances moved by dispersing larvae and the data in Fig. 17 permit no more than a comparison of the relative distances moved by the larval instars.

Due to the fact that most of the eggs are laid in the upper third of cotton plants (Fye 1972; Hillhouse & Pitre 1976) and up to 90 % on the younger leaves (Basson 1987) it appears as if the majority of newly-hatched larvae move to the stem terminal bud, thereby increasing their chances of finding suitable food. However, no detailed study of the movement of newly-hatched larvae was undertaken.

The first and second-instar larvae moved an average of 6,5 cm. Apart from the obvious fact that it would take a small larva much longer to move a given distance than it would take a larger one, the limited movement clearly indicates that the smaller larvae tended to stay on the fruiting forms which they encountered initially. Small larvae are less likely to deplete the food supply in a fruiting form, eliminating the need to search for fresh food. The third to fifth-instar larvae moved considerably longer distances (Fig. 17). Whereas the first two larval instars moved between closely grouped feeding sites at the branch tips, the later instars also fed on fruiting forms more widely separated on the branches, even moving between branches. This supports the findings that the time the larvae spent moving between feeding sites tended to increase with larval age (Mabbett *et al.* 1979, 1980; Snodderly & Lambdin 1982). The thesis was not intended to examine the dispersal of *H. armigera* larvae, a topic about which little is known and deserves separate study (see Discussion). Movement of *H. armigera* larvae between

adjacent plants is known to occur (Mabbett et al. 1980) and was noted, but not measured because the plants were covered with organdie sleeves.

H. armigera larvae showed no clear preference for any compass direction on cotton plants. The larvae did, however, occur in greater numbers in the upper zones of the plants and moved about considerably. It remains to describe the selection of feeding sites by the larvae, the subject of the next chapter.

## 6. SELECTION OF FEEDING SITES

This chapter describes the tendency of H. armigera larvae to feed on cotton fruiting forms rather than leaves, the selection of feeding sites on individual fruiting forms and the selection between fruiting forms. The term "preference" is largely avoided because the data presented indicates that what the larvae eat is dictated by the availability of fruiting forms rather than the actual preferences of the larvae.

### SELECTION OF LEAVES AND FRUITING FORMS

Annecke & Moran (1982) stated that H. armigera larvae has a "... catholic taste in food plants, preferring flower buds, flowers and developing fruits ..." which effectively summarises the feeding habits of Heliothis spp. Mabbett et al. (1979) found that although H. armigera larvae exhibited leaf feeding, only the larger larvae caused notable damage. H. zea and H. virescens feed on young soybean leaves, causing minor perforations (Mueller & Engroff 1980; McWilliams 1984). Chamberlin & Tenhet (1926) found that on tobacco H. virescens larvae also preferred the seed heads, with only limited feeding on the foliage. In studies on larval nutrition, Parsons (1940) indicated that a diet of flower and fruit parts are essential for optimum development. In complementary laboratory and field studies, it was found by Farrar & Bradley (1985b) that H. armigera larvae are adapted to feed preferentially on certain plant parts which are nutritionally more suitable. Belcher et al. (1984) found that

even though larvae of H. virescens were not attracted by nectar, the nectar appeared to be a feeding arrestant.

It is obvious from the record of feeding sites encountered in field surveys (Table 7) that all the H. armigera larval instars preferred fruiting forms over leaves. The number of leaves fed on was negligible and seldom amounted to more than "nibbling". Apparently the larvae used the leaves mainly to move between fruiting forms.

Table 7. Relationship between the numbers of fruiting forms and leaves on cotton plants fed upon by Heliothis armigera larvae during the 1984/1985 season.

LARVAL INSTAR	NUMBERS OF LARVAE	NUMBERS OF FRUITING FORMS FED UPON	NUMBERS OF LEAVES FED UPON	PERCENTAGE OF FRUITING FORMS FED UPON
I	18	23	2	92
II	75	100	4	96
III	130	205	13	94
IV	150	239	10	96
V	209	572	15	97
TOTALS	582	1139	44	96

#### SELECTION OF FEEDING SITES ON FRUITING FORMS

Characteristically, H. armigera larvae eat holes in the

fruiting forms and continue feeding on the contents, sometimes until most, or all of the body of the larva is inside the fruiting form. The size of these holes, the "entry holes" so to speak, is highly variable and cannot be used to distinguish between the larval instars, except in very broad terms between large and small larvae (Fig. 18). Alternatively, the larvae merely nibble the outside of the fruiting form without destroying the structure or they feed on the inner or outer calyxes (McWilliams 1983).

The external feeding sites of Heliothis larvae on cotton fruiting forms have been described by several authors. It was

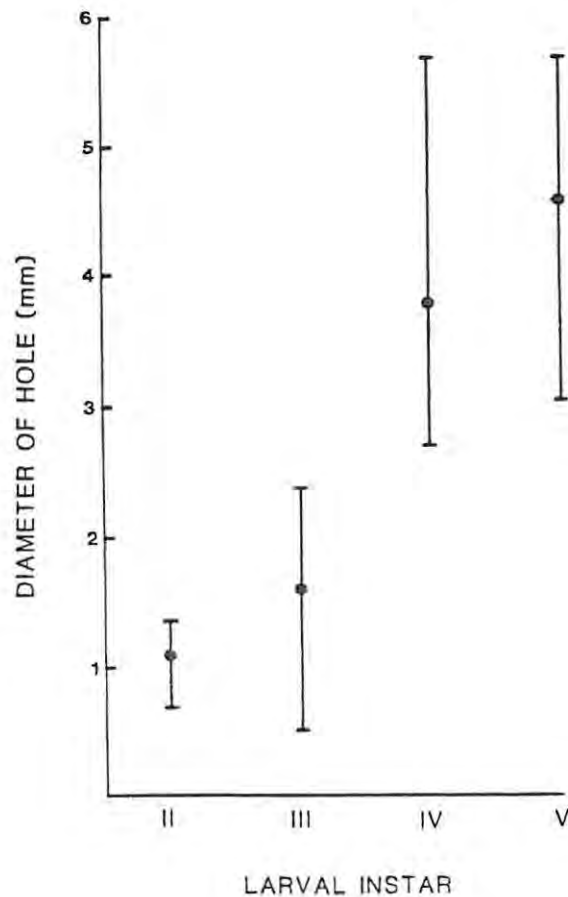


Fig. 18. Diameter (mm) of holes made by instars II - V of Heliothis armigera larvae when feeding on cotton fruiting forms. Means and ranges are given.

found by Mabbett et al. (1980) that H. armigera larvae usually fed from a position on the buds inside the epicalyx which means that they fed either at the middle or at the lower parts of a bud. A similar feeding behaviour was found for H. virescens by Shaver et al. (1977); Belcher et al. (1984) and Ramalho et al. (1984a). According to Shaver et al. (1977), using bouquets of buds in laboratory trials, most H. virescens larvae entered through the middle parts and to a lesser extent at the upper and lower parts. When these larvae entered the bud at the base it was usually at the base of the receptacle.

In order to determine whether there was any tendency for the larvae to feed more on some parts of the fruiting forms than others in the field, the division described in Fig. 12, Chapter 3, (that is an upper, middle and lower region) was employed. Although several statistically significant differences between the numbers of larvae found in the different regions (Table 8), Fig. 19 shows no marked difference of feeding by H. armigera larvae in the different height regions except a slight tendency for the later larval instars to feed more on the lower regions of the fruiting forms. Certainly there were no preferences indicated. It may be that when the larger larvae entered the fruiting forms from above, their heads were situated at the bases of the fruiting forms and that they started to feed at the bases simply due to their positions. There was also a tendency to start feeding on the bolls at the edges of the calyx (inner bracts). On cotton buds and bolls, even small larvae are able to cling to the sides of the structures in order to feed, contrary to, for

Table 8. Numbers of feeding sites of *Heliothis armigera* larvae found in the upper, middle and lower regions of cotton fruiting forms.

LARVAL INSTAR	UPPER : MIDDLE	MIDDLE : LOWER	UPPER : LOWER
I	14 : 16	16 : 25	14 : 25
II	41 : 72*	72 : 72	41 : 72*
III	94 : 118	118 : 139	94 : 139*
IV	114 : 143	143 : 222*	114 : 222*
V	175 : 288*	288 : 502*	175 : 502*

\* Chi-squared values significant at the 5 % level. Expected values were mean frequencies.

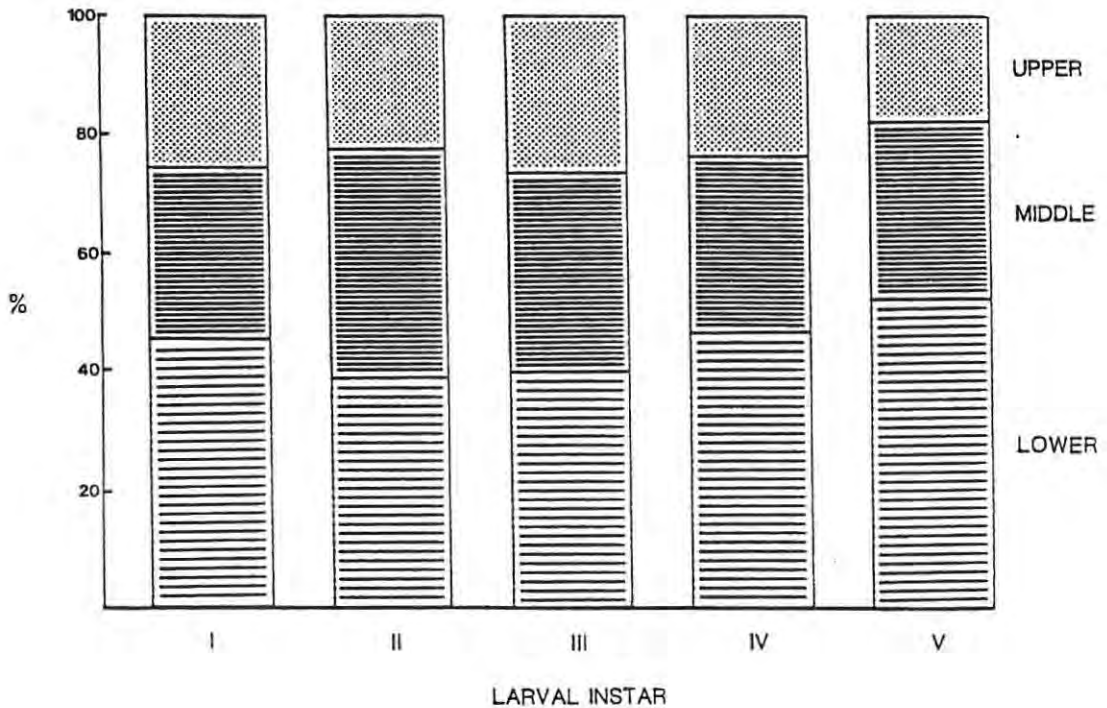


Fig. 19. Percentages of *Heliothis armigera* larvae feeding on the upper, middle and lower regions of cotton fruiting forms. The regions on the fruiting forms are defined in Fig. 12, Chapter 3.

example, tomatoes (Snodderly & Lambdin 1982).

According to Mabbett et al. (1980) and Jayaraj (1982), full-grown H. armigera larvae habitually feed with only the front of the body inside the holes chewed into the bolls. This was found to be only partly true in this study. The larvae, particularly the later instars, tended to "hollow out" fruiting forms by eating the contents. Many larvae were encountered which had hollowed out the fruiting forms completely, and, depending upon the size of the larvae relative to the size of the fruiting forms, they sometimes disappeared inside the structures. When feeding larvae protruded from the fruiting forms (Frontispiece), they had either not hollowed out enough space or the fruiting forms were too small.

#### SELECTION OF FRUITING FORMS

The experiments described here were designed to determine whether H. armigera larvae preferred any of the cotton fruiting forms and were carried out during the 1983/84 and 1984/85 seasons. The selection of fruiting forms is discussed in relation to their availability on whole plants (or parts of plants covered with organdie sleeves), the plant height zones defined in Chapter 3 and choice experiments in which different fruiting forms were offered to the larvae in both the field and in laboratory trials. During surveys for larvae of the natural population, their instar, as well as the category of fruiting forms they were feeding on, were recorded and similar data were collected for

larvae from the laboratory culture released on cotton plants in the field. It is important to note that these data do not reflect the total number of feeding sites during the lifespan of a larval instar, but are merely a record of the fruiting forms which larvae were found on. Again no differences between the natural population and those of the laboratory population were apparent and the results were pooled.

#### Selection of fruiting forms on whole plants

Many researchers have examined the feeding preferences of Heliothis spp. for the different fruiting forms on cotton plants, but there does not seem to be a clear-cut pattern. Several of the reports suggested that the young larvae fed on small to medium-sized buds and that when the larvae became older, they fed on larger buds, flowers and young bolls (Table 9). Others have found that the larger larvae of H. zea and H. virescens also fed on cotton flowers and mature bolls, but preferred buds to the other fruiting forms (e.g. Baldwin et al. 1974; Gutierrez et al. 1981; Wilson & Waite 1982). Nadgauda & Pitre (1983) also found that the ability to feed on plant tissue improved with an increase in larval size. Tanskiy (1969) stated that H. armigera larvae showed a clear preference for buds and flowers.

The incidence of damage to cotton fruiting forms by H. armigera larvae (Fig. 20) suggests that the damage is correlated to the relative abundance of the buds, flowers and bolls. The graphs shown in Fig. 20 masks a possible existence of preferences

Table 9. Reports that young larvae of Heliothis spp. tended to feed on younger fruiting forms and that the older larvae tended to feed on more mature fruiting forms.

<u>HELIOTHIS SPECIES</u>			
AUTHOR	<u>H. ARMIGERA</u>	<u>H. ZEA</u>	<u>H. VIRESCENS</u>
Reed (1965a)	x		
Reed (1965b)	x		
Kincade <u>et al.</u> (1967)			x
Roome (1975)	x		
Blood & Wilson (1978)		x	x
Slosser <u>et al.</u> (1978)		x	
Mabbett <u>et al.</u> (1979)	x		
Mabbett <u>et al.</u> (1980)	x		
Wilson & Gutierrez (1980b)		x	x
Jayaraj (1982)	x		
Wilson & Waite (1982)		x	x
Farrar & Bradley (1985a)		x	x

by the larvae and was investigated further.

During the course of the field surveys two aspects of the distribution of H. armigera larvae were recorded: the larvae which were merely present on the fruiting forms (Fig. 21) at the time of the surveys and the larvae which were actually feeding (Fig. 22). The positive correlation between fruiting forms visited and damaged is obvious and means that the larvae tended

to feed on the fruiting forms which they encountered. This was also apparent in direct observations of larvae released on fruiting forms during the choice experiments presented below.

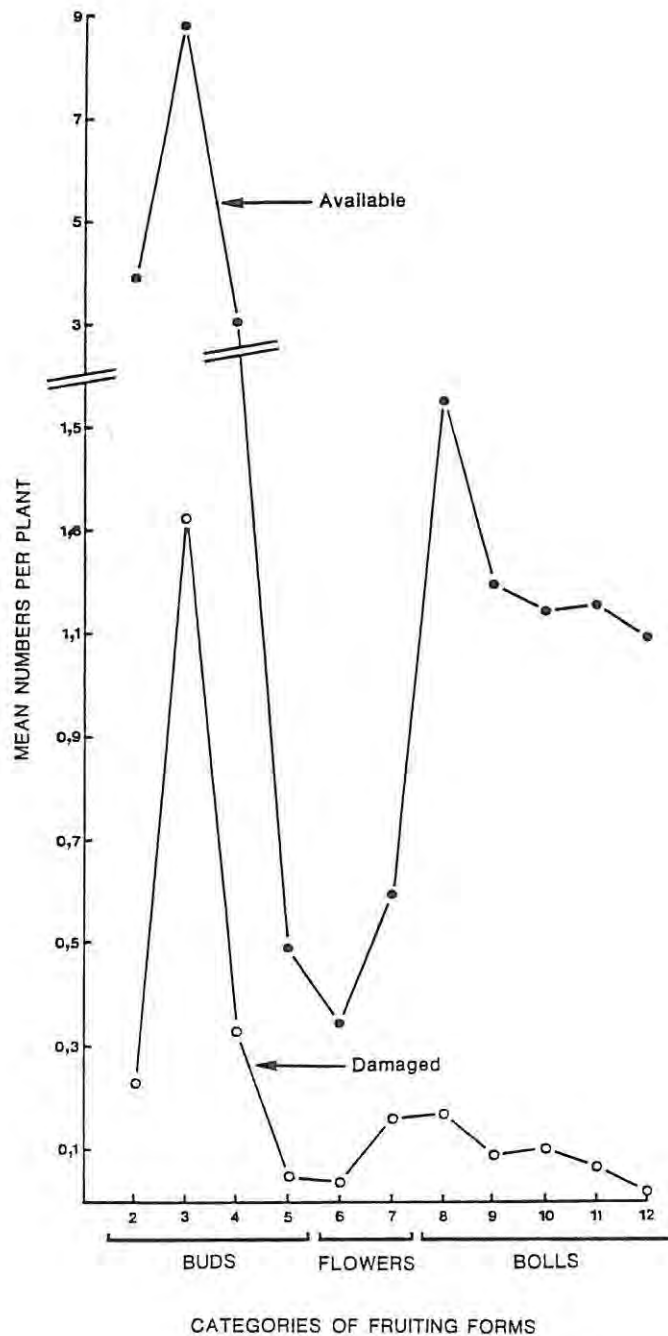


Fig. 20. Mean numbers per plant of the available fruiting forms (closed circles) and damaged (open circles) by *Heliothis armigera* larvae. The individual means were derived from 258 available and 235 damaged fruiting forms.

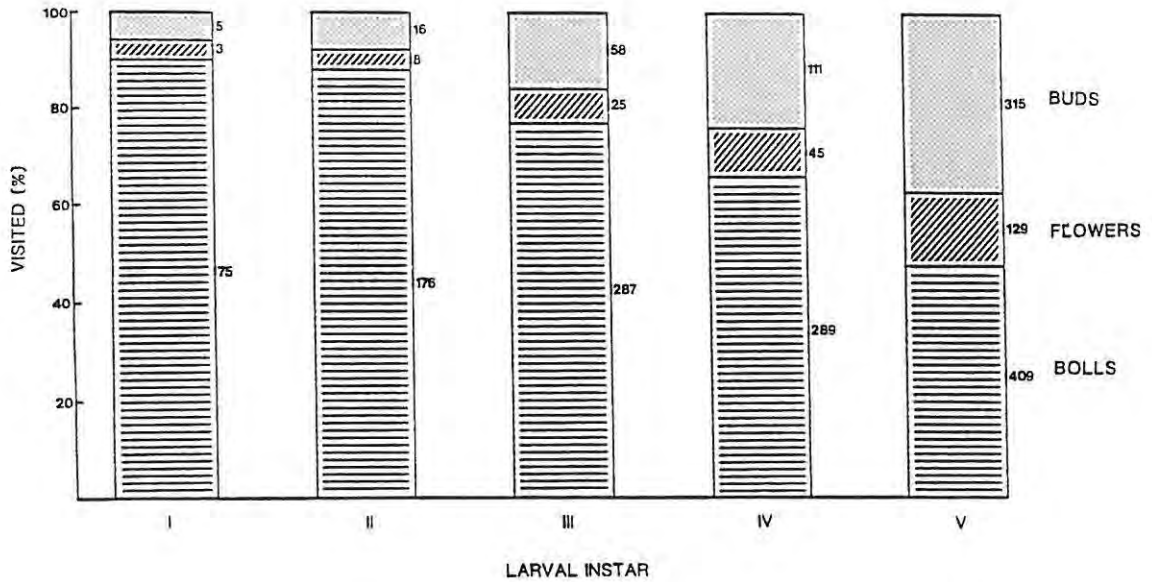


Fig. 21. Percentages of fruiting forms visited by Heliothis armigera larval instars on cotton plants. Actual numbers of larvae are shown alongside the histogram bars.

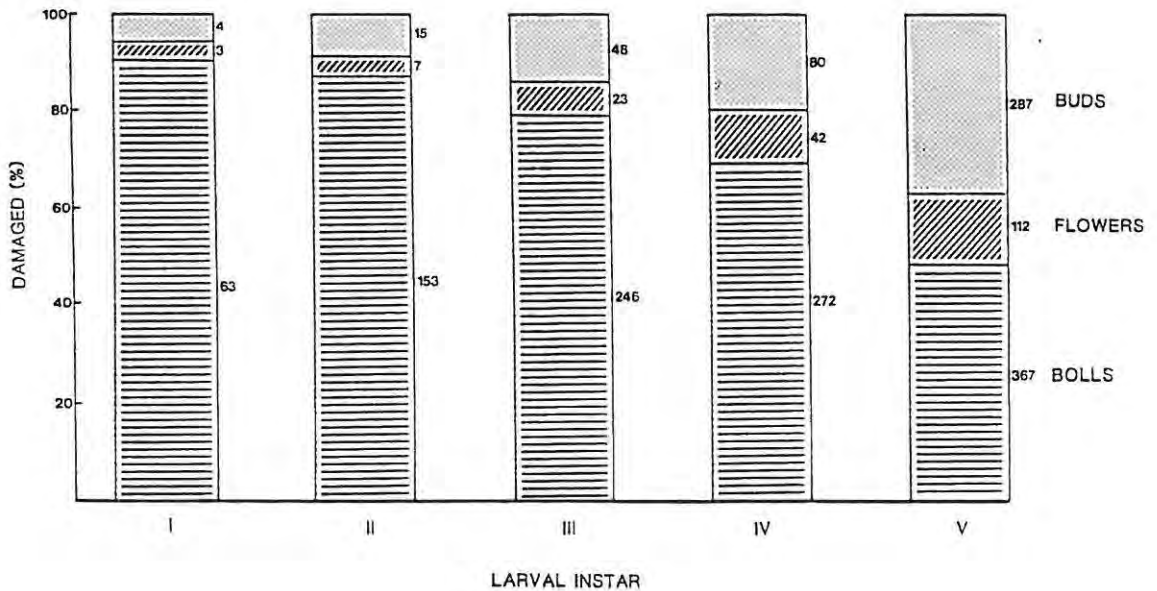


Fig. 22. Percentages of fruiting forms damaged by Heliothis armigera larval instars on cotton plants. Actual numbers of larvae are shown alongside the histogram bars.

The data in Fig. 22 show that H. armigera larvae fed mostly on buds and that they tended to feed progressively less on buds and more on flowers and bolls as they became older. But, this does not imply a preference: statements about the preference of the larvae are not valid without taking into account which fruiting forms, and in what proportions, were available on the plants. This is particularly true for cotton where buds, flowers and bolls are all present, albeit in differing proportions, during much of the season (see similar arguments followed by Blood & Wilson (1978); Wilson & Gutierrez (1980b); Wilson & Waite (1982); Farrar & Bradley (1985a)). A further analysis of the data in Fig. 22, to accommodate the availability of the fruiting forms, is presented in Fig. 23. The numbers of fruiting forms fed on were expressed as proportions of the buds, flowers and bolls available. These values were then calculated as a percentage of the proportion of all the fruiting forms fed upon, the data shown in Fig. 23.

Three conclusions can be drawn from Figs 22 and 23. Firstly, the tendency for the larvae as they became older, to feed progressively less on buds and more on flowers and bolls is confirmed. Secondly, the pattern of feeding responses shown in Fig. 22 was due to the relative abundance of the fruiting forms rather than the preferences of the larvae and is in agreement with the findings of Slosser, et al. (1978). Thirdly, a relatively large proportion of the flowers were fed upon (Fig. 23), even though they were comparatively few in number, and suggests a preference by the larvae for flowers. Also, it was observed that

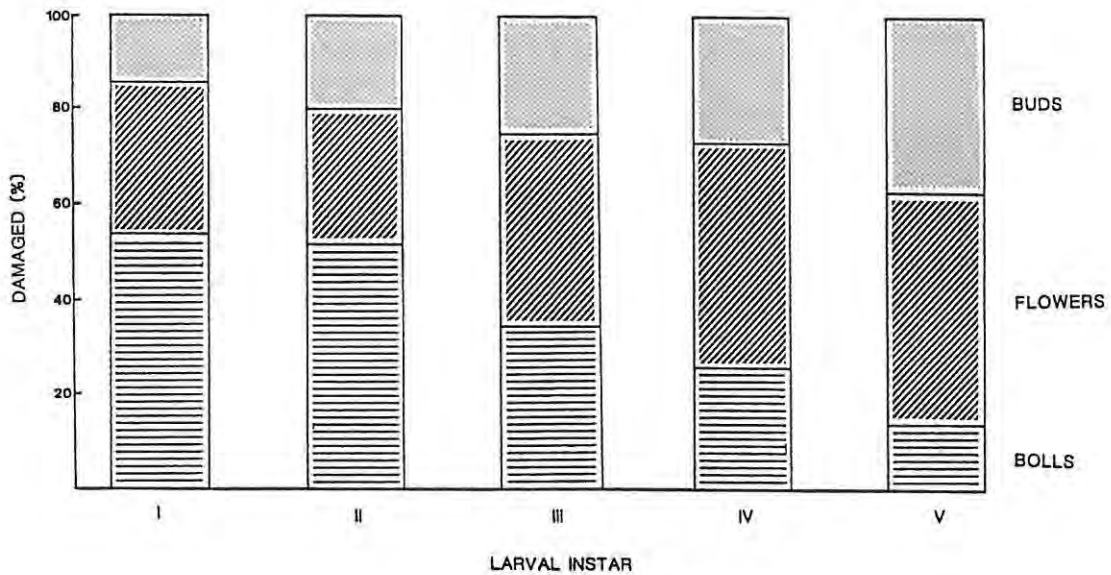


Fig. 23. Percentages of fruiting forms damaged by *Heliothis armigera* larval instars on cotton plants in relation to the numbers of fruiting forms available.

damage to small bolls with bloomtags (that is drying flower corollas still adhering to the small bolls) occurred frequently, typically on the tip of the boll covered by the bloomtags, similar to the findings of Farrar & Bradley (1984) for *H. zea* larvae. There was a sharp decline in the availability of older bolls, with corresponding decline in the numbers damaged. This may explain why comparatively more young bolls were damaged and not necessarily, as Tanskiy (1969) suggested, because the outer sheaths of the bolls obstructed the larvae. A similar preference by *Heliothis* spp. for flowers of other crops has also been reported (Mueller & Engroff 1980; Jackson & Mitchell 1984).

As mentioned in Chapter 5, *H. armigera* larvae occurred mainly in the upper and middle thirds of the cotton plants. To determine whether this was due to the distribution of the fruiting forms or perhaps a preference for any categories of the fruiting forms, a survey was made of the available fruiting structures in the three height zones (Fig. 24) and the numbers

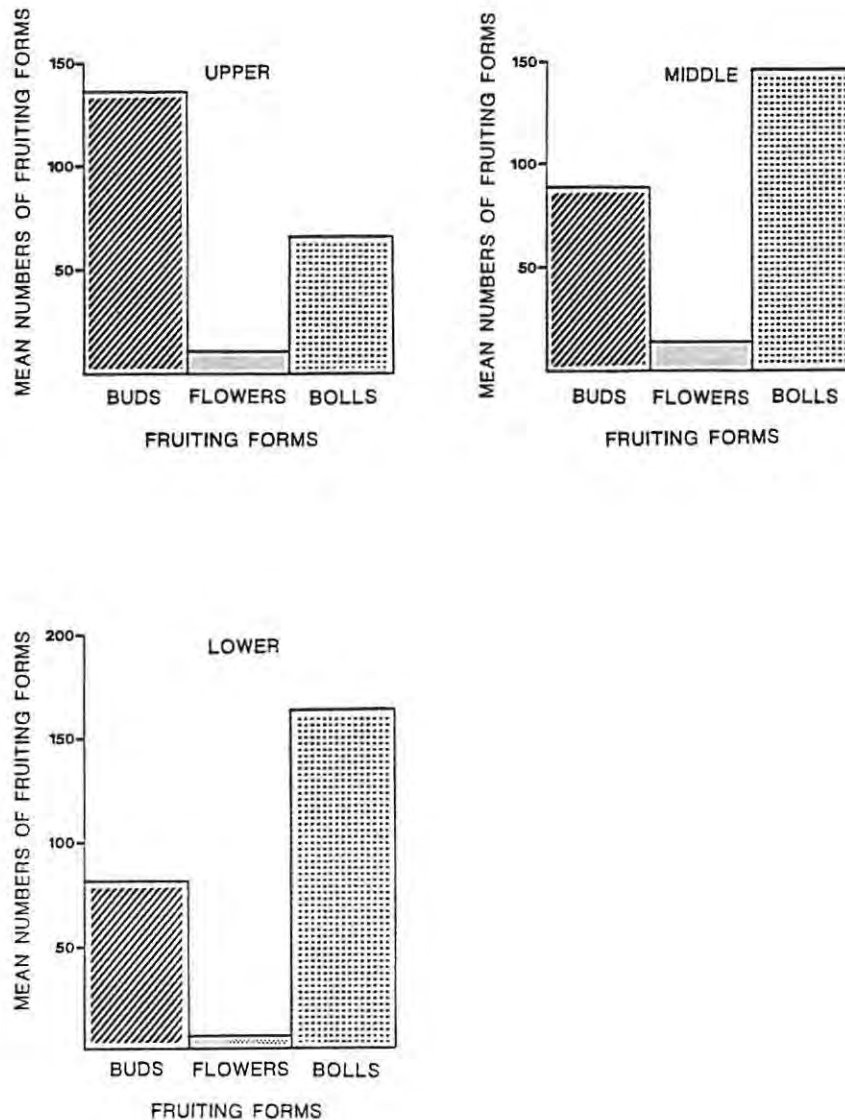


Fig. 24. Mean numbers of fruiting forms in the upper, middle and lower height zones of cotton plants. The numbers of *Heliothis armigera* larvae which fed in these zones are shown in Fig. 16.

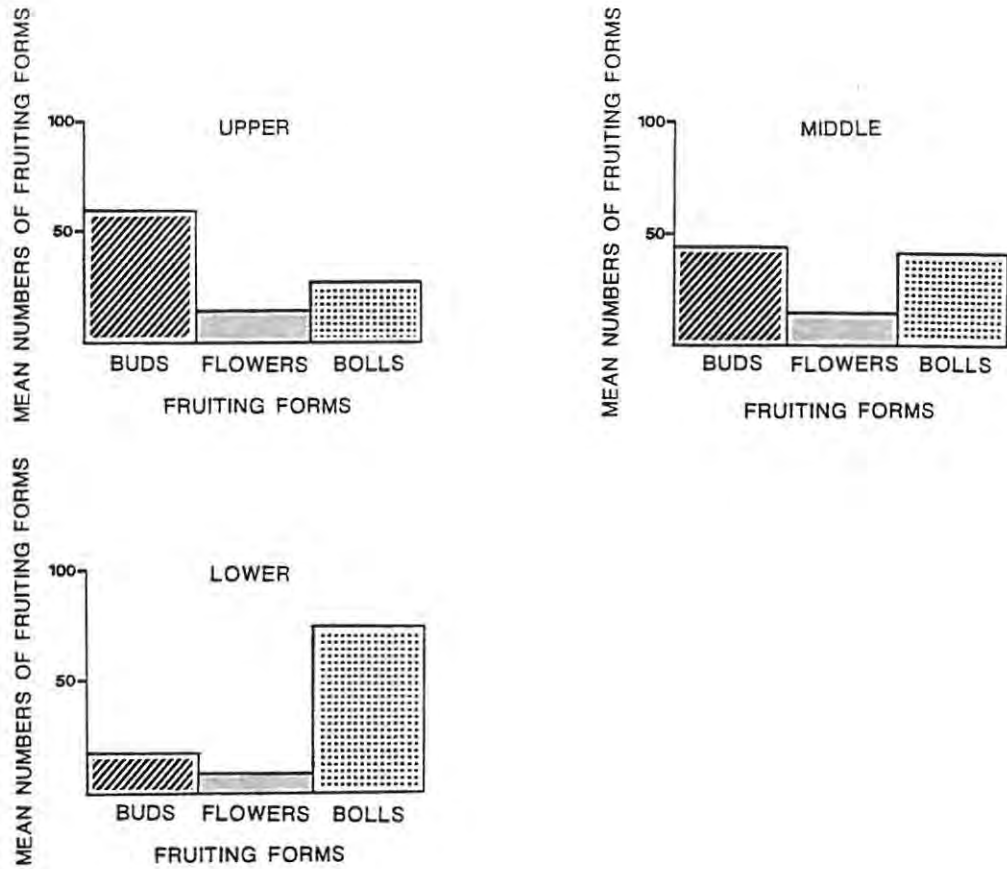


Fig. 25. Mean numbers of buds, flowers and bolls on cotton plants damaged by *Heliothis armigera* larvae, in the upper, middle and lower height zones of cotton plants.

damaged by *H. armigera* (Fig. 25). The data in Figs 24 and 25 suggest that the selection of fruiting forms by the larvae depended largely upon the relative abundance of the buds, flowers and bolls, as in the case of the fruiting forms on whole plants.

#### Choice experiments

A series of choice experiments were carried out to determine

if H. armigera larvae settled and fed on the fruiting forms on which they were released or whether they moved to alternative fruiting forms. The experiments were conducted in the field and the laboratory using only laboratory-reared larvae. Individual larvae were released in all replications.

Larvae of instars two to five were released on buds, flowers and bolls in the field. The numbers released and those which settled on the fruiting forms were recorded (Table 11). The ratios of larvae which settled were compared by 2 x 3 Chi-squared tests but no significant preference at the 5 % level was detectable, although the larvae appeared to settle more readily on flowers.

Complementary choice experiments were carried out in the laboratory (Table 12). Pairs of fruiting forms were arranged in bouquets comprising flowers and buds, flowers and bolls, and buds and bolls. Larvae were released on one of the two fruiting forms of a pair and the choice made was noted. The procedure was repeated by releasing larvae on the alternative fruiting forms. The percentages of larvae which settled on the fruiting forms on which they were released (Table 13), substantiates the previous indications that the larvae settled more readily on flowers. Furthermore, if the numbers of larvae which settled on the alternative fruiting forms are expressed as a percentage of all the larvae which left the release sites (Table 14), the evidence of a preference for flowers is strengthened.

In a further choice experiment conducted in the field, the larvae were released on stems between pairs of buds and flowers,

Table 11. Numbers of Heliothis armigera larvae released on cotton buds, flowers and bolls in the field, and the numbers and percentages which settled.

LARVAL INSTAR		FRUITING FORMS		
		FLOWER	BUD	BOLL
II	Released	35	22	11
	Settled	31	15	8
	% settled	89	68	73
III	Released	35	23	30
	Settled	32	11	18
	% settled	91	48	60
IV	Released	35	19	30
	Settled	27	11	16
	% settled	77	58	53
V	Released	36	24	30
	Settled	35	23	18
	% settled	97	96	60
TOTAL	Released	141	88	101
	Settled	125	60	60
	% settled	89	68	59

Table 12. Numbers of Heliothis armigera larvae which settled on bouquets of pairs of cotton fruiting forms and the numbers lost. The fruiting forms on which the larvae were released are listed first (upper case) followed by the alternative fruiting forms (lower case). Lost larvae are shown in parentheses.

LARVAL INSTAR	PAIRS OF FRUITING FORMS											
	FLOWER : bud		BUD : flower		FLOWER : boll		BOLL : flower		BOLL : bud		BUD : boll	
II	23	0	12	5	23	0	6	13	14	3	12	0
	(1)		(7)		(1)		(5)		(7)		(12)	
III	19	2	3	17	22	2	3	17	8	8	11	5
	(3)		(4)		(0)		(4)		(8)		(8)	
IV	15	3	8	13	20	2	4	17	12	7	14	7
	(6)		(3)		(2)		(3)		(5)		(3)	
V	24	0	12	12	22	0	4	19	13	9	18	3
	(0)		(0)		(2)		(1)		(2)		(3)	
TOTAL	81	5	35	47	87	4	17	66	47	27	55	15
	(10)		(14)		(5)		(13)		(22)		(26)	

bolls and flowers and buds and bolls. Other plant structures in the immediate vicinity of the release sites were removed and the fruiting forms to which the larvae moved and settled were recorded (Table 15). Again there was a tendency for larvae to move more readily to flowers than to the other fruiting forms.

Table 13. Percentages of Heliothis armigera larvae that settled on the cotton fruiting forms they were released on. Underlining shows non-significant Chi-squared values at the 5 % levels. The data are derived from Table 12.

LARVAL INSTAR	FRUITING FORMS		
	FLOWER	BUD	BOLL
II	<u>96</u>	<u>50</u>	<u>42</u>
III	85	<u>29</u>	<u>23</u>
IV	<u>73</u>	<u>46</u>	<u>33</u>
V	<u>96</u>	<u>63</u>	<u>35</u>
AVERAGE	88	<u>47</u>	<u>33</u>

The results of the choice experiments (which indicate a preference on cotton for flowers over buds and bolls, but not between buds and bolls) are in agreement with the reported preferences of Heliothis spp. on various crop plants (Coaker 1960; Slosser et al. 1978; Mabbett et al. 1980; Mueller & Engroff 1980; Wilson & Waite 1982; Burkett et al. 1983; Farrar & Bradley 1984, 1985a, 1985b).

In conclusion, H. armigera larvae preferred fruiting forms over leaves and tended to feed more readily on flowers than on buds or bolls. The preference for flowers is mainly of academic interest and the choice experiments in which the larvae were offered alternative feeding sites were contrived, artificially

Table 14. Numbers of Heliothis armigera larvae which settled on alternative fruiting forms as a percentage of larvae which left the fruiting forms on which they were released. The data are derived from the totals given in Table 12. Chi-squared significance tests apply to the two treatments for each pair of fruiting forms.

RELEASE SITE	ALTERNATIVE FRUITING FORM	NUMBERS LOST	NUMBERS SETTLED ON ALTERNATIVE FRUITING FORM	PERCENTAGE SETTLED ON ALTERNATIVE FRUITING FORM
Flower	Bud	10	5	33*
Bud	Flower	14	47	77*
Flower	Boll	5	4	44*
Boll	Flower	13	66	84*
Boll	Bud	22	27	55
Bud	Boll	26	15	37

\* Chi-squared values significant at the 5% level.

offering disproportionately large numbers of flowers to the larvae. In the field the selection of feeding sites was dictated by the relative abundance or availability of the fruiting forms; the implications for pest management are reviewed in the Discussion. For the purposes of the next chapter, in which estimates of damage levels by H. armigera are presented, the fruiting forms were regarded as equally acceptable to the larvae.

Table 15. Numbers of Heliothis armigera larvae released between pairs of cotton fruiting forms in the field, and the numbers which settled on the fruiting forms.

LARVAL INSTAR	PAIRS OF FRUITING FORMS			
	FLOWER : BUD	FLOWER : BOLL	BUD : BOLL	
II	Released	23	23	23
	Settled	16 : 9	16 : 5	11 : 11
	Chi-squared significance		*	
III	Released	23	18	18
	Settled	14 : 6	11 : 8	5 : 7
	Chi-squared significance			
IV	Released	23	23	18
	Settled	17 : 2	11 : 11	5 : 13
	Chi-squared significance	*		
V	Released	23	23	18
	Settled	16 : 3	13 : 3	3 : 10
	Chi-squared significance	*	*	

\* Chi-squared values significant at the 5 % level.

7. DAMAGE LEVELS AND FOOD CONSUMPTION BY H. ARMIGERA LARVAE

In examining the impact of H. armigera larvae on cotton plants, there were two issues at stake, namely, the actual amount of material consumed and the damage to cotton plants. The wasteful nature of the feeding habits of the H. armigera larvae dictates that more material will always be destroyed than consumed by the larvae. To what extent this influences yield is outside the scope of this study (but see Discussion).

To estimate the quantity of cotton fruiting forms consumed by H. armigera larvae, the mass of damaged fruiting forms was subtracted from the expected mass of undamaged structures, based on the known diameter:mass relationships (Figs 10 and 11, Chapter 3), a method also used by Tewari & Krishna Moorthy (1984). Second to fifth-larval instars, were released singly on Category 4 buds and Category 10 bolls of known diameter and caged with small organdie sleeves as before. When the larvae consumed the fruiting forms which they were released on, they were transferred to fresh ones of similar size. The larvae were left to feed until they changed their instar. From the results (Fig. 26) it is evident that the larvae consumed about equal amounts of squares or bolls.

In a second procedure larvae were released on plants or parts of plants and covered with large sleeves and the larvae were allowed to complete their instars. The material consumed was computed from the expected mass of fruiting forms fed on (Fig. 9, Chapter 3), from which was subtracted estimates of the amount of material consumed by the larvae in the following classes

(numerical values are given in parentheses as actual values of mid-points of ranges): 1 - 25 % (0,13), 25 % (0,25), 26 - 50 % (0,38), 50 % (0,5), 51 - 75 % (0,63), 75 % (0,75), 76 - 100 % (0,88) and completely hollowed out (1,00). These values were

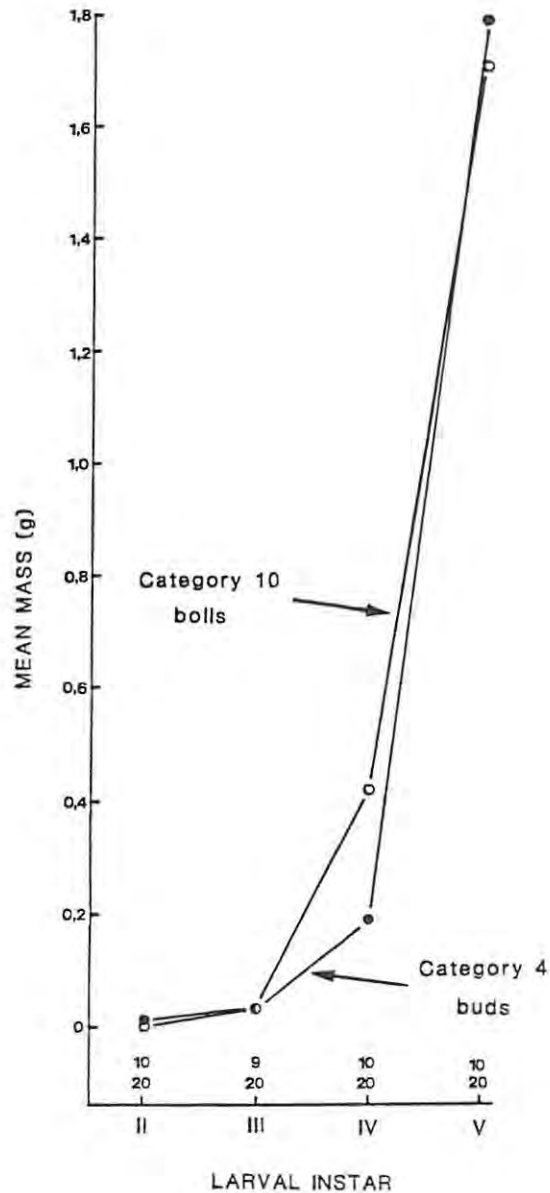


Fig. 26. Mean mass (g) of Category 4 buds and Category 10 bolls in the field consumed by the separate instars of *Heliothis armigera* larvae. The numbers of larvae released are shown above the horizontal axis for buds (upper row) and bolls (lower row).

summed to provide an estimate of the material consumed (Fig. 27).

The results in Figs 26 and 27 permit two further conclusions.

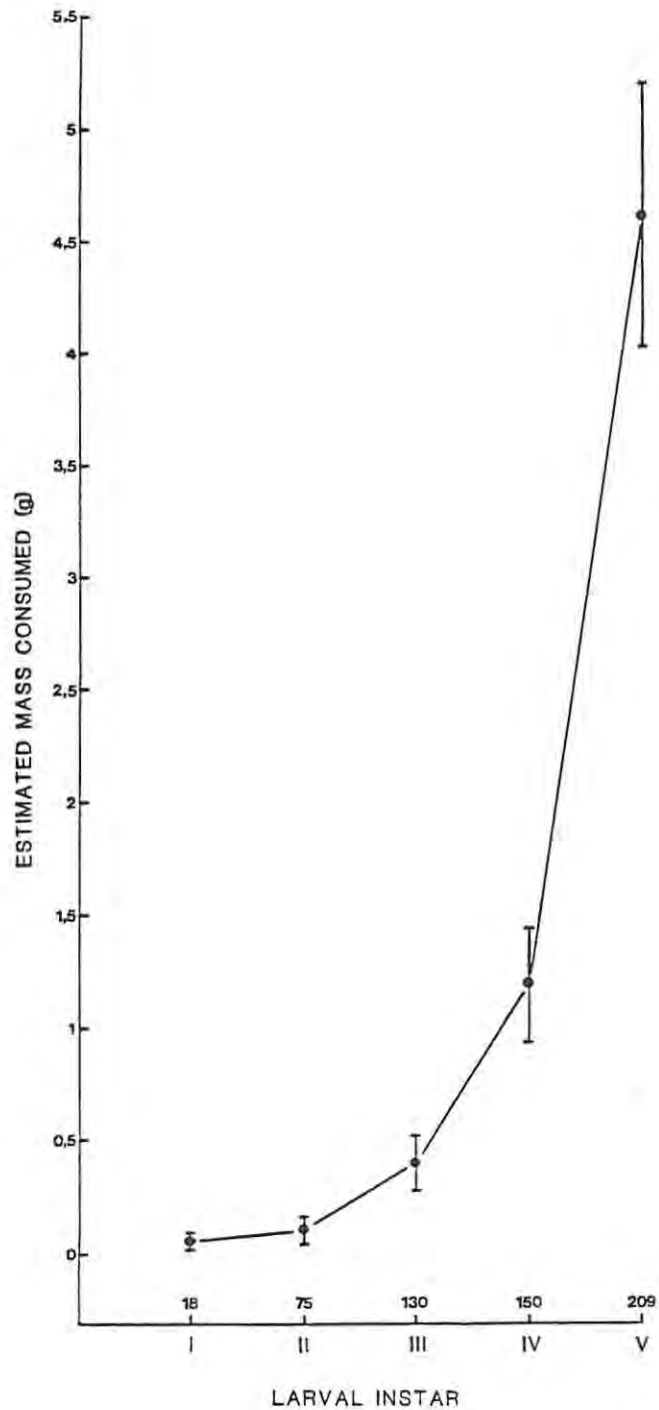


Fig. 27. Estimates of mean mass of cotton fruiting forms consumed by *Heliothis armigera* larval instars and the 95 % confidence limits. The numbers of larvae are shown above the horizontal axis.

Firstly, the fifth-instar larvae consumed three times as much material as the first four instars together and four times more than the fourth-instar larvae alone. This is within the limits of the conclusions of Reed (1965a); Koehler & Pimentel (1973); Boldt et al. (1975) and McWilliams (1983) which stated that the final larval instar accounted for 50 - 95 % of the total food consumption by the larvae. Secondly, the intake by the first two larval instars was negligible, which agrees with the findings of Reed (1965a) and Baldwin et al. (1974). It was only from the third-larval instar that the intake was of any consequence.

The data in Figs 26 and 27 should not be regarded as absolute criteria of food consumed by the larvae. The cumulative totals suggest that during their development the larvae consumed 2,14 g to 6,33 g of material, which is within the limits reported by Dhandapani & Balasubramanian (1980a) of 4,854 g. Still, the data can be interpreted to provide an indication of the intake of food in terms of fruiting forms consumed (Table 16).

Information on the mass of material required by H. armigera larvae to complete their development is of limited value. From observations made during the course of this study and the reported findings of other authors for Heliothis spp. (e.g. Adkisson et al. 1964a, 1964b; Boldt et al. 1975; Singh & Singh 1975; Hopper & King 1984) the larvae of H. armigera are known to feed on, and sometimes destroy, several fruiting forms. In pilot trials it was found that individual H. armigera larvae damaged up to 17 fruiting forms, depending on what they encountered, and is

Table 16. Proportions of fruiting forms consumed by Heliothis armigera larvae expressed as percentages of the expected mass of undamaged Category 4 buds and Category 10 bolls (Figs 10 and 11, Chapter 3). The numbers of larvae released are as in Fig. 26.

LARVAL INSTAR	% CONSUMED	
	CATEGORY 4 BUDS	CATEGORY 10 BOLLS
II	0,83	0,16
III	3,3	0,32
IV	35,8	1,6
V	142,5	14,4

within the limits reported by others (Adkisson et al. 1964a, 1964b; Kincade et al. 1967, 1970; Mabbett et al. 1980). The loss of fruiting forms by cotton plants cannot be unconditionally ascribed to feeding by H. armigera larvae - or any other insects for that matter - for the plants tend to abort large numbers of fruiting forms, even under ideal growing conditions, depending largely on the location, cotton variety and the time of the year (Mauney 1984). Therefore, a series of experiments were designed to evaluate what degree of feeding by H. armigera larvae was required to cause the plant to abort the fruiting forms. Separate data were collected for each of the instars tested to determine which were the most destructive.

Second to fifth-instar larvae were placed singly on buds (Category 3) and medium-sized bolls (Category 10) and caged with

small organdie sleeves (Fig. 3, Chapter 2) to restrict feeding by the larvae to the fruiting forms on which they were released and to protect the larvae against predators and parasitoids. The second and third larval instars were kept on the fruiting forms until they moulted, whereas the fourth and fifth larval instars were left to feed on the fruiting forms for only two hours and then removed; if fourth and fifth-instar larvae were left on buds for longer periods they would have consumed the entire structures and defeated the purpose of the experiment. After exposure of the buds and bolls to the larvae, the development of the fruiting forms was followed until they either aborted or ripened. Undamaged ripe bolls were harvested.

From the results (Figs 28 and 29) several trends in the damage caused by *H. armigera* larvae emerged. It is clear that the damage to fruiting forms due to feeding by the second-instar larvae, was of little or no consequence and is in keeping with conclusions of Reese et al. (1981), but, predictably, increased with the size of the larvae. Note that the damage caused by the fourth and fifth-instar larvae is a gross underestimate since feeding was restricted to two hours; the results nevertheless demonstrate that higher rates of abortion resulted from feeding by fifth than fourth-instar larvae. As would be expected, considerably more damage resulted from feeding on buds than on bolls.

The buds and bolls which aborted naturally are shown in Fig. 28 as controls. However, the shedding of both damaged and

undamaged buds and bolls is highly variable (Tanskiy 1969; Hopper & King 1984) and is likely to be affected by a plethora of factors. These results must not be interpreted as being generally applicable, but are crucial to the development of pest management strategies (see Discussion).

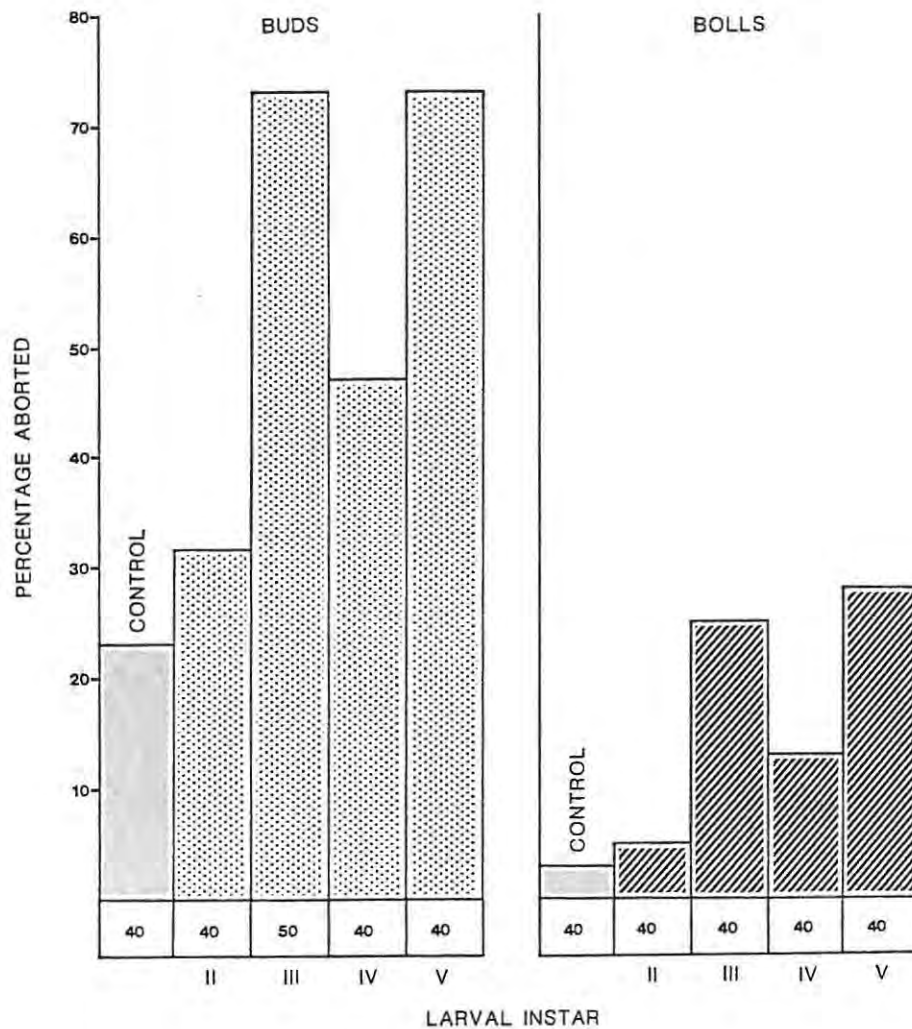


Fig. 28. Percentages of cotton buds and bolls that aborted naturally (controls) or as a result of feeding by *Heliothis armigera* larvae in the field. Fourth and fifth-instar larvae were removed after feeding for two hours (see text). The numbers of larvae released are shown above the horizontal axes.

The numbers of aborted fruiting forms are an underestimate of the actual damage done by *H. armigera* larvae. The proportions of buds and bolls which were undamaged and could be harvested following feeding by the larvae (Fig. 29) are markedly less than the "non-aborted" component of the histograms in Fig. 28. This difference was due to secondary diseases and partial damage

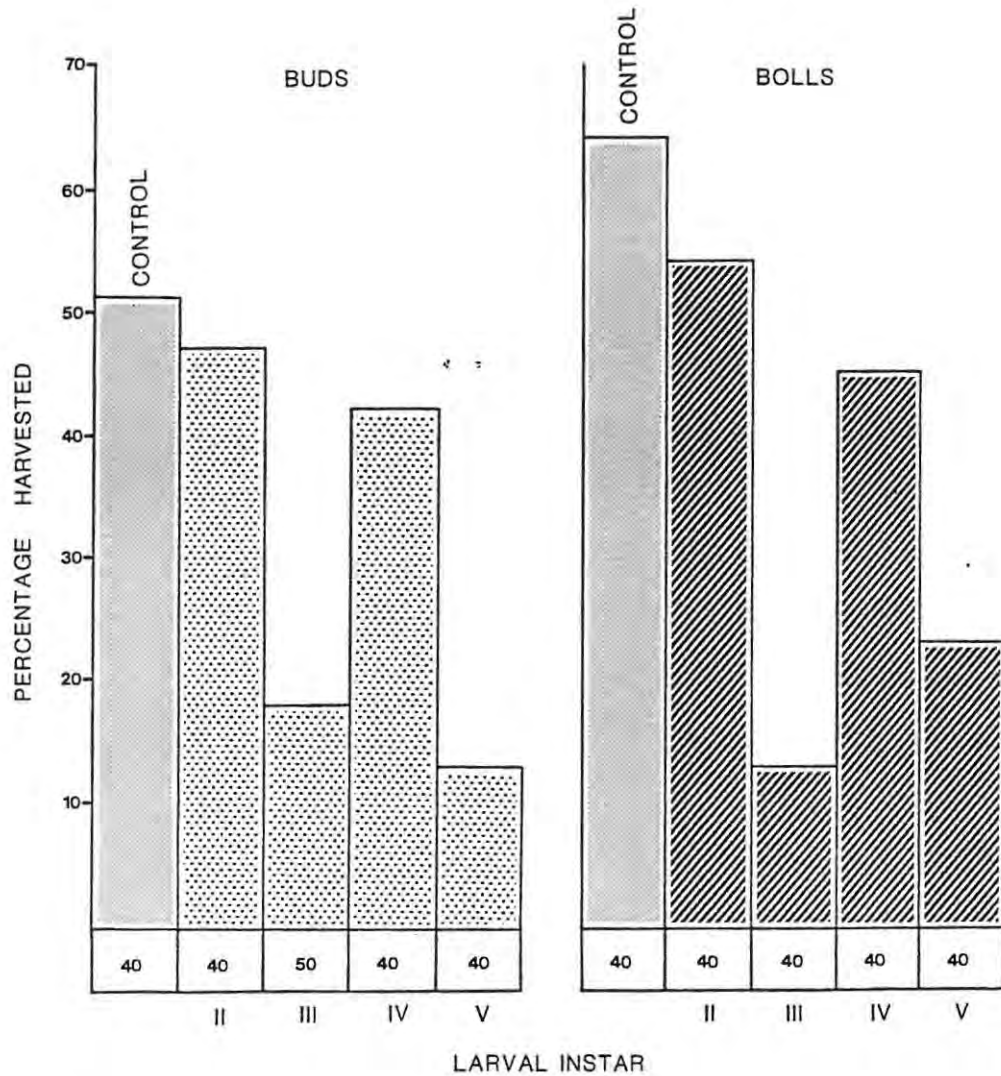


Fig. 29. Percentages of undamaged cotton buds and bolls harvested after an *Heliiothis armigera* larval infestation in the field. Fourth and fifth-instar larvae were removed after feeding for two hours. The numbers of larvae released are shown above the horizontal axes.

caused to some of the fruiting forms. Granted, some of the partial damage was such that the bolls still yielded fibres, but this holds disadvantages for the picking and spinning processes and were not included in Fig. 29.

Young bolls are often naturally deformed and if they are not shed by the plants, remain so until boll-burst. A survey of 72 deformed cotton bolls revealed that they did not abort more (or less) readily than normally-shaped bolls and superficial examination indicated that minor deformities did not obviously affect yield. Therefore, feeding by H. armigera larvae on deformed bolls constitutes real damage.

In conclusion, it is clear that the damage caused by H. armigera cannot be expressed in terms of the intake of cotton fruiting forms, but that the actual damage is far greater. In the Discussion it will be shown that there is yet a further dimension which should be taken into account when evaluating the pest status of H. armigera on cotton, that is, the habit of cotton plants to abort excess fruiting forms and their ability to compensate for many kinds of damage, of which feeding by the larvae is but one.

## 8. DISCUSSION

The biology of H. armigera, with emphasis on the feeding habits of the larvae, is related to survey methods for detecting the pest and to threshold levels of the pest which are crucial for the implementation of insecticidal and biological control measures in the production of irrigated cotton.

Only five larval instars were found in both the laboratory and field populations of H. armigera, which is not in keeping with the variation within and between populations in the number of larval instars reported by other workers, as explained in Chapter 4. It is not possible to determine from the reported results of these other workers why there appears to be a variable number of larval instars in H. armigera. The larval instars were easy to recognise on the basis of head-capsule widths, greatly simplifying the experimental procedures. H. armigera larvae typically chew holes in cotton buds, flowers and bolls, collectively called "fruiting forms" for the purpose of this study. However, the damage caused by the complex of bollworms is superficially similar and reliable identifications of the H. armigera larval instars required that the larvae were located.

The well-known characteristic that cotton plants produce buds, flowers and bolls during a large part of the growing season has important implications for the development of survey methods for H. armigera larvae, raising the questions of whether they occur more frequently on any specific parts of the plants and

whether they prefer any of the fruiting forms. The selection of oviposition sites is dealt with below. Although the larvae tended to occur more in the upper zones of the plants - tempting one to suggest that only these zones need to be surveyed - this depended largely on the distribution of the fruiting forms in the height zones of the plants and was not due to a preference by the larvae. Similarly, the larvae were found in all compass directions. Consequently, larval surveys based on parts of plants only are likely to be misleading at times. This is not in agreement with Fye (1972) and Wilson *et al.* (1980), who recommended that only the upper two-thirds of the plants need to be surveyed.

H. armigera larvae were seldom found on the leaves of cotton plants, showing a clear preference for buds, flowers and bolls. Obviously there is no need to search the leaves during larval surveys. While this would seem axiomatic to field entomologists familiar with the the control of H. armigera on cotton, this principle is often unstated and easily overlooked. Eliminating the need to examine leaves - that is for H. armigera larvae, not all cotton pests - during surveys constitutes a meaningful saving in time for researchers and farmers alike. Still, the fruiting forms need to be carefully searched for larvae. Even though the larvae fed more readily near the bases of fruiting forms, especially buds and bolls, the larvae are by no means conspicuous since they penetrated fruiting forms and sometimes even disappeared inside the structures. Moreover, the larvae are usually hidden by the epicalyxes which cover the

usually hidden by the epicalyxes which cover the fruiting forms.

There was a tendency for larvae of H. armigera, especially the older ones, to prefer flowers over buds and bolls (Fig. 23, Chapter 6). However, this "preference" did not restrict the larvae to flowers and in all the situations examined they invariably also occurred on the other fruiting forms. Importantly, the incidence of flowers - like the buds and bolls - is erratic and not in a fixed ratio to the other fruiting forms. During most of the season there are actually relatively few flowers (see Fig. 7, Chapter 3). Counts of larvae on any one type of the fruiting forms are therefore likely to be unreliable measurements of the population. For conducting larval surveys, it is expedient and more practical to accept that the larvae mainly feed on what they encounter, which in turn, depends on what is available on the plants.

Conducting surveys for H. armigera larvae and other cotton pests is a well-developed and crucial aspect of pest control decision making (Van Hamburg 1981; Van Hamburg & Kfir 1982; Kfir & Van Hamburg 1983; Basson 1986). It is, nevertheless, a time-consuming procedure and research to improve the techniques deserve attention. H. armigera causes significant damage at low densities, with the current spray threshold set at 5 larvae per 24 plants (Bot et al. 1986), leaving little room for error in the sampling. This study has not identified any major preferences by H. armigera larvae for feeding sites which can be used to refine the sampling procedures other than confirming that leaves need not be searched for the larvae. It may be feasible to base the

surveys on random samples of either plant parts (given the conclusion that the larvae occur in all height zones and compass directions), or the collective fruiting forms. In this way it may be feasible to examine fewer fruiting forms per plant from more plants, rather than following the current procedure of simply selecting 24 plants in a field of about 1 - 15 ha as is currently recommended (Bot et al. 1986). This, and the development of sequential sampling techniques (Southwood 1978) is likely to be a fruitful area of research.

The distances moved by the larvae varied with their size, the larger larvae moving more frequently and over greater distances between feeding sites. There are a number of logical explanations for this: the pubescence of the cotton plants restricts the earlier instars more than the later instars (Ramalho et al. (1984b) and larger larvae deplete their food supply more readily, compelling them to move to new feeding sites.

H. armigera moths oviposit on cotton fruiting forms, leaves and stems. Many of the oviposition sites do not correspond to the feeding sites of the larvae, not even the first-instar larvae. The first-instar larvae were frequently observed hanging from silken threads from where they were blown to other plants or plant parts. The discrepancy between oviposition sites and the initial feeding sites of H. armigera larvae suggests a need for a study of larval dispersal, particularly the first-instar larvae. With the wisdom of hindsight, it has become apparent that many aspects of the biology and survival of the first-instar larvae

have been neglected. This also applies to the damage by the smaller larvae to cotton growth tips, an aspect overlooked in this study because the first two larval instars did not cause a significant abortion of the fruiting forms and, further, consumed little material (Chapter 7).

The usefulness of the techniques used to measure the amount of material consumed by the larvae (Chapter 7) is restricted to a comparison of the relative amounts eaten by the larval instars. While this work highlighted the obvious significance of the later larval instars, it provides little information on the actual damage caused. Apart from the fruiting forms consumed by the larvae, their feeding results in the abortion of a considerable number of fruiting forms (Fig. 28). Efforts to measure the damage by a count of the fruiting forms destroyed (including those lost due to abortion and secondary rotting), on the other hand, is frustrated by the natural abortion of fruiting forms and the ability of cotton plants to compensate for these losses by producing additional fruiting forms to replace the aborted ones. Alternatively, it may be that when the plants lose fruiting forms due to feeding by H. armigera larvae, this actually reduces the normal abortion of undamaged fruiting forms. Until the impact of H. armigera and other cotton pests is studied in relation to the ability of the plants to compensate for losses, estimates of damage in terms of the numbers of fruiting forms lost will continue to be of limited value. It may well be that some insecticidal treatments, particularly those applied early in the season, serve only to protect fruiting forms which will be lost

for other reasons, or which will be replaced by the plants without a reduction in yield. Several authors (such as Dunnam et al. 1943; Eaton 1955; Tanskiy 1969; Kincade et al. 1970; Graham et al. 1972; Koehler & Pimentel 1973; Baldwin et al. 1974; Cothran & Summers 1974; Blood & Wilson 1978; Hartstack et al. 1978; Broodryk 1980; Liapis et al. 1984) stated that damage, especially to buds early in the season, may have no effect on yield and may even increase the yield. With our current knowledge about the impact of H. armigera on cotton, speculation about the compensation of cotton plants in terms of pest status would be premature. Cotton yields are determined by a multitude of agronomic and climatic factors which, together with pest attacks, affect compensation. The influence of compensation by cotton plants on the pest status of H. armigera must be accepted as a high research priority if the threshold levels on which integrated control strategies are based are to be refined.

## 9. SUMMARY

Five larval instars for H. armigera were found in both field and laboratory populations. The larvae were easily identified on the basis of their head-capsule widths and, further, are easily separated from the other bollworms which occur on cotton in South Africa.

The H. armigera larvae were found to occur in all compass directions and in all height zones of the plants. Although the larvae occurred mostly in the upper two-thirds of the plants, this was due to the distribution and availability of cotton buds, flowers and bolls (the "fruiting forms" used in the thesis) and not due to a preference by the larvae. The larvae showed a clear preference for fruiting forms over leaves and there were indications of a preference for flowers over the other fruiting forms. This "preference" for flowers has little influence on the feeding habits of the larvae; feeding occurred on the most abundant fruiting forms and besides, there are generally few flowers compared to buds and bolls in cotton fields. Therefore, the feeding habits of the larvae cannot be used to improve survey methods on which pest control strategies are based and while there is no need to examine cotton leaves, there is no alternative but to search all the fruiting forms on the plants. Improvements in the survey methods should be sought in developing sequential sampling procedures based on the collection of randomly-selected fruiting forms rather than searching a fixed number of plants.

The study of feeding by the first two larval instars of H. armigera is incomplete insofar their selection of feeding sites, which do not correspond to the oviposition sites of the moths, was overlooked. A study of their dispersal remains an important research priority. Neither was their feeding on the growth tips of cotton plants examined. Detection of these small larvae is impractical in the field and moreover, their damage was insignificant in terms of the quantity of food consumed and the numbers of fruiting forms that aborted due to their feeding. In these respects the last three larval instars obviously caused most damage. Clearly, this is because the larger larvae are able to move greater distances and consume several of the smaller fruiting forms.

Measurements of the damage caused by H. armigera and other cotton pests are worthless without taking into account the ability of cotton plants to compensate for losses of fruiting forms. These plants characteristically produce more fruiting forms than can eventually ripen and abort the excess buds and bolls. Therefore, assessments of damage as a count of fruiting forms destroyed, provides little information on the actual yield losses and with our current spray programmes we may be protecting fruiting forms which will be lost for other reasons. A study of the pest status of H. armigera in relation to compensation by the plants should be undertaken.

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