SOME ASPECTS OF THE NATURAL

CONTROL OF LARVAL <u>HELIOTHIS</u> <u>ARMIGERA</u> (Hubn.)

IN MAIZE

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C O N T E N T S

SUMMARY

Heliothis armigera (Hübner) is the most common pest attacking maize on the Darling Downs and in some seasons can be present in economic numbers, particularly on the newly emerged silks of the maize cob. In spite of the size of the population on infested cobs, the damage caused by its presence seems to be consistent from season to season. During the study it was established that, irrespective of the initial egg density recorded on the silks, the population of final instar larvae per infested cob rarely exceeded unity. The mortality factors associated with an infestation on maize were monitored and the extent of egg and larval parasites and diseases was established as being insignificant in causing this decline. These results would be expected in view of the protection afforded by the tight husks around the cob. The decline in population within the cob has therefore been associated with the activity of intraspecific competition (namely cannibalism) with the major proportion of the total population decline taking place during the first and second instars. This time period coincides with the stage of larval feeding when larvae begin to enter the cob by feeding along the silks. For most lines of maize, this area represents a restricted "arena" where larval density increases towards the cob and, as such, provides a greater opportunity for conflict between larvae.

Laboratory studies of the nature of larval growth were undertaken in order to prepare a suitable method of sampling and identifying field populations of _H. armigera_.

The relationship of development time to temperature was examined using the Thermal Summation method. From the analysis of these data the Threshold of Development was estimated to be 10.7° and the development time 260 day degrees (in excess of 10.7°) for development from hatching to final instar.

In order to identify the stage of development of the larvae, head capsule measurements were made of laboratory bred larvae. However, it was established that the use of head capsule widths did not give a consistent indication of the stage of larval development due to variation recorded in the number of larval moults. The cause of this variation was outside the scope of this study but was considered to be due to the nutritional qualities of the larval food. This nutritional deficiency increased development time and resulted in more moults.

For field collected material the recording of head capsule widths indicated that there were commonly six larval instars but these were not precisely defined. There was a large degree of overlap in the head widths of third, fourth and fifth instar larvae.

A method of rearing Heliothis sp. on an artificial diet is discussed but its usefulness is considered as limited to four consecutive generations, after which larval and pupal development times become more variable, the incidence of malformed adults increases and the pupal weight decreases.

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I. REVIEW OF LITERATURE

Heliothis armigera (Hübner) (Noctuidae;
Lepidoptera) belongs to a particularly complex genus of moths
known throughout the world as major agricultural pests since
first described by Fabricius in 1794. Although it is difficult
to estimate the monetary value of damage associated with this
group, the vast quantity of literature is an indication of its
importance.

Unfortunately, earlier studies on
H. armigera are now confounded by the problem of conspecificity.
Common (1953) described four Australian species, all previously
recognised as H. armigera and Hardwick (1965) in a study of
world species has described seventeen species. As a result, the
identity of the species referred to in previous papers is in
doubt.

The name Heliothis was first used by Hübner
in his Tentamen Lepidopterorum (1806) although it wasn't until
1816 that the genus Heliothis was described by Ochsenheimer. The
validity of this description was discussed by Hampson (1903) who
reasoned that Ochsenheimer's description was invalid and hence
attributed the genus to Treitschke although Tams (1935) disputed
this criticism on the grounds that Ochsenheimer's description of
the genus and the species involved was quite definite and indicated
that the genus should be ascribed to Ochsenheimer.

Prior to the turn of the century most species
now recognised as belonging to the Heliothis group were considered
as one species although Hampson (1893) and Piepers and Snellen
(1906) recognised Heliothis assulta Guenee as a distinct species.

Aurivillius (1897) and Hampson (1903) indicated
a change of name from <u>armigera</u> to <u>obsoleta</u> with Hampson (1903) placing
several species including <u>Noctua</u> <u>armigera</u> in the genus <u>Chloridea</u>.
However, Tams (1935) disputed the use of <u>obsoleta</u> on the grounds that
it was a homonym of <u>Bombyx</u> <u>obsoleta</u>, a species included in the
Lymantriidae. Since then the name <u>Heliothis</u> <u>armigera</u> has come into
more general use.

Common (1953) recognised and described four
Australian species belonging to the <u>Heliothis</u> group and discussed
their relationship to the North American species <u>Heliothis</u> <u>umbrosus</u>
Grote, which has since been shown to be <u>Heliothis</u> <u>zea</u> Boddie by
Todd (1955). There were then six species recognised as belonging to
the genus.

Hardwick (1965), in describing the genus <u>Heliothis</u>,
described eleven new species and two sub species distinguishable
on the structure on the penis and proposed that all these species
constituted a morphological homogeneous group. Since they all
differed significantly from <u>dipsacea</u> (Linneus), the type species
of <u>Heliothis</u>, Hardwick suggested that they be excluded from this
genus and the name <u>Helicoverpa</u> was proposed. Hardwick (1965)
failed to recognise <u>Heliothis</u> <u>rubrescens</u> (Walker) as described by
Common (1953) but regarded it as belonging to the genus <u>Thalpophila</u>
in which it was originally described by Walker in 1858. This genus,
Hardwick said "represents a morphological condition in some respects
intermediate between that of <u>Helicoverpa</u> and <u>Heliothis</u>". By that he
presumably meant that morphologically <u>Thalpophila</u> was intermediate
between <u>Heliothis</u> and <u>Helicoverpa</u>, an observation that immediately
weakens his conclusion that the last two groups are generically
distinct.

The proposed name _Helicoverpa_ has failed to gain recognition by Noctuid specialists although it may be used as a sub-genus.

(i) Distribution and Host Records

In the light of this confusion it is still possible to examine critically the current host records and distribution data.

Unlike some of their relatives in the family, many of the species of the corn earworm group will feed on an extensive array of food plants. _H. armigera_ has been shown to be widely distributed and common throughout Australia. Common (1953) recognised this species as largely confined to the coastal and sub coastal areas of Queensland and New South Wales. Kirkpatrick (1961) substantiated this claim in Queensland by showing that only _Heliothis punctigera_ Wallengren was found further than 100 miles inland. However, with the recent introductions of a range of host material to the drier inland of Australia, both major species of _Heliothis_ have been recorded beyond this limit. Records of Common (1953) indicate that _H. armigera_ was most prevalent in the warmer half of the continent. Cullen (1969) recognised _H. punctigera_ as the only economically important species in South Australia, the only records of _H. armigera_ in this area being three specimens in the South Australian Museum collected more than 60 years ago. Few reports of _H. armigera_ have been recorded from Tasmania, Victoria and southern Western Australia.

Sloan (1940) gave a rather extensive review of hosts of _Heliothis_ species in Central Queensland although the actual identification of the species involved is doubtful.

The distribution of <u>Heliothis</u> in Queensland is still rather confused. Kirkpatrick (1961) gave an extensive review of host records of the four recognised Australian species. Recent host records and distribution data taken from the Darling Downs 1970-1972 confirm many host records in this list. <u>H</u>. <u>armigera</u> has been found attacking barley, french beans, celery, cotton, Tonga beans, lettuce, maize, navy beans, potatoes, sorghum, tobacco, tomatoes, wheat and millet. <u>H</u>. <u>punctigera</u>, on the other hand, has been recorded attaching apples, cotton, geraniums, linseed, lucerne, peanuts, peas, rape, thistle, sunflower and tobacco.

(ii) Pattern of attack on Maize

Patterns of <u>Heliothis</u> attack on maize are generally restricted to three stages of plant growth, namely the late vegetative stage, tasseling and silking. The principal site attacked is the silks although Twine (1971 a) reported that with heavy infestations of moths early in plant development, infestations in the throat of the plant are not uncommon. Such infestations often retard growth.

Eggs are laid singly over the newly emerged silks and larvae hatching from these immediately seek the husk-enclosed portions of the silks and begin to feed. As feeding continues the larvae eventually reach the grain which serve as the final larval food. McMillian <u>et</u> <u>al</u>. (1970) established a relationship between larval development of <u>H</u>. <u>zea</u> and plant development to explain why early instars of the corn earworm feed on the silks and then penetrate to various depths of the kernel according to larval age. The chemical nature of these phago-stimulative substances was not determined.

Upon completing larval development on the kernels the larvae tunnel through the husk and move down the plant to form an earthen cell beneath ground level where they pupate.

(iii) Life Cycle

The life cycle of this pest has been fairly well documented by many workers (Anon. 1951, Hardwick 1965), but it is only in recent years that the effect of temperature on development of the life cycle has been studied in any detail.

Kirkpatrick (1962) attempted to relate development time to temperature for the four Australian species of Heliothis by following larval development under insectary conditions throughout the year. Popava (1969) was able to relate development times of eggs, larvae and pupae to field temperatures in different areas of Bulgaria.

Mangat and Apple (1966) reported on development time studied under controlled temperature conditions and, using the principle of Thermal Summations as outlined by Wigglesworth (1965), were able to establish a threshold of development at 12.6^{o} and a temperature summation for development from egg to adult as 383.4 day degrees for H. zea. More recently, Fye and Surber (1971) reported on laboratory studies of egg mortalities associated with exposure to high temperatures and concluded that, under arid conditions when leaf temperatures exceed 40° for four hours, the survival of H. zea eggs may be adversely affected.

With the development of artificial diets for mass rearing of large numbers of insects, the interest of the effect of heat on development has shifted to the effect of short term exposure of eggs to high temperatures ($> 50^{o}$) incurred in the continuous process of media dispensing and container infesting. Hare et al. (1973) considered that temperatures of 45° to 50° for 3-12 minutes were sufficient to seriously affect egg hatch.

Massey et al. (1973) investigated the use of heat as a nonchemical control agent for use against Lepidopterous pests of cotton. Their results however indicated that the heat required for significant larval mortality was also injurious to crop growth.

(iv) Larval Instars

The larval life of H. armigera is classically defined by five larval moults with the final sixth larval instar terminated by a prepupal stage which is completed once the pupal cell has been constructed.

Kirkpatrick (1961) in detailing the morphological characters of the four Australian species gave an outline of the head capsule measurement for each instar of each species. His work suggested the presence of six definite instars for H. armigera. However, for many years the number of instars has been shown to be variable and several workers have associated causal agents with these conditions. Quaintance and Brues (1905) ascribed all variation in the number of larval instars to nutritional factors. The authors noted that larvae fed on maize and cotton, completed development in six instars whereas a few larvae, reared on cowpeas, completed development in only five instars.

Work by Gaines and Campbell (1935), while not entirely consistent with the work of Quaintance and Brues (1905) did support the role of nutrition in instar determination. Larvae of H. obsoleta fed on maize completed development in six instars whereas those fed on cotton developed through seven instars.

On the other hand, Jones (1936) suggested that temperature was a determinant for the nature of instar development. Larvae of H. armigera observed in South Africa usually go through seven instars during the winter months but take only six instars to develop during the warmer months.

In the light of these data, Hardwick (1965) bred larvae of H. armigera on shelled peas in the laboratory under constant temperature (24°) and still found variability in the number of instars. He found that for H. armigera, 69% completed development in six instars, 1% in seven and 30% in five instars. Hardwick in this same paper showed that under the same conditions these proportions varied for different species of the Heliothis genus.

(v) Control

The control of populations of Heliothis may be broadly divided into two categories: those aimed at an overall reduction of a population and secondly those aimed at the protection of a specific crop. Controls of the first category include the use of parasites and predators and, in general, have not proved successful. In the second category such techniques as the use of resistant varieties, repellents, insecticides or cultural methods have met with a more general success.

Walker and Anderson (1938), Phillips and Barber (1940), Douglas (1954) and Farrier and Reid (1961) have reported on the importance of planting date for Heliothis control. Ditman and Cory (1936) and Ditman (1937) reported on the use of baits to reduce oviposition but no measurable reduction was realised. Similarly, the use of light traps (Carruth and Kerr (1937)), repellents (Chamberlain 1954) and trap crops (Quaintance and Brues 1905) have proved useless.

Attempts to decrease larval infestations by destroying eggs have been both chemical and biological. Gouck and Blanchard (1951) tested a number of ovicides but concluded that the oils used in the preparations were more active than the chemicals tested. A number of attempts with the egg parasite Trichogramma minutum Riley have been detailed (Fletcher 1933)(Larrimer 1935) but no reduction in larval populations was recorded.

The use of resistant lines of maize has received extensive study. Collins and Kempton (1917) associated resistance with the length and thickness of the husks. More recently, Guthrie and Walter (1961) and Widstorm et al. (1970) have described the factors associated with Heliothis spp. resistance in maize lines.

The direct destruction of larvae has involved a range of methods from hand picking (Boddie 1850) and pinching Skerman (1909) to the more popular method of insecticides, for example, DDT, endosulfan, carbaryl, (Quaintance and Bishopp 1905, Rolfs 1907, Fletcher 1929, Arant 1951).

More recently, with the use of chemicals gaining unfavourable reports, Oatman et al. (1970) have examined the use of a nuclear polyhedrose virus and the bacterium (Bacillus thuringiensis) for larval control.

Despite the use of various forms of control applied against Heliothis, one important factor to be considered in discussions on control is the nature of the larvae to attack and devour larvae of their own kind. Phillips (1931) reported that cannibalism of Heliothis was the most important factor limiting populations in maize. Subsequently, Barber (1936) reported that, as a result of the concentration of larvae of Heliothis obsoleta at the neck of the cob, it was most common to find only one larva completing development in the ears. He established cannibalism as characteristic of all instars.

Conflicting reports have since been published on this subject, largely based on observations associated with the development of artificial diets and mass rearing techniques. Bot (1966) considered that only the final instar of H. armigera had cannibalistic tendencies. Patel et al. (1965) reared larvae of H. armigera on potted gram plants until third instar and then isolated them in separate specimen tubes since they considered that larvae "developed cannibalistic tendencies in their later instars". Kinzer and Henderson (1968), studying losses in grain sorghum attributed to various density levels of H. zea larvae, concluded that cannibalism did not reduce the size of artificial infestations and reported up to thirteen larvae per head completing development.

Twine (1971 b) described the decline of artificial populations of
H. armigera under laboratory conditions and concluded that
cannibalism operated on all instars and is a major regulatory
factor for high density populations and of less importance at
lower densities.

(vi) The area of study

The Darling Downs comprises a vast area of
8×10^6 ha extending north and south from Dalby with the Great
Dividing Range forming the eastern and northern boundaries. The
general elevation of the Downs is in the vicinity of 150 m to
300 m with the central drainage line to the southwest through the
Condamine River and its tributaries.

The centre part of the Downs is an extensive
open plain, merging into the adjoining lands in a fashion which
enables the whole area to be sub-divided into distinct regions,
each somewhat comparable in area.

Eastern Downs

This is a stretch of undulating country
connecting the south east half of the open plain to the Great
Dividing Range and is the most populous and intensively farmed
sector. The dominant soils of the area are brown black, self
mulching clays and, except for the steepest slopes and stony
ridges, the whole of the region is cultivated. Closer settlement
and consequent cultivation of these soils have introduced an
erosion problem of some magnitude. Exposed weathered parent
material on unprotected slopes, shallow gullies, transversing
cultivations and deep sided gullies in the alluviums are
already obvious.
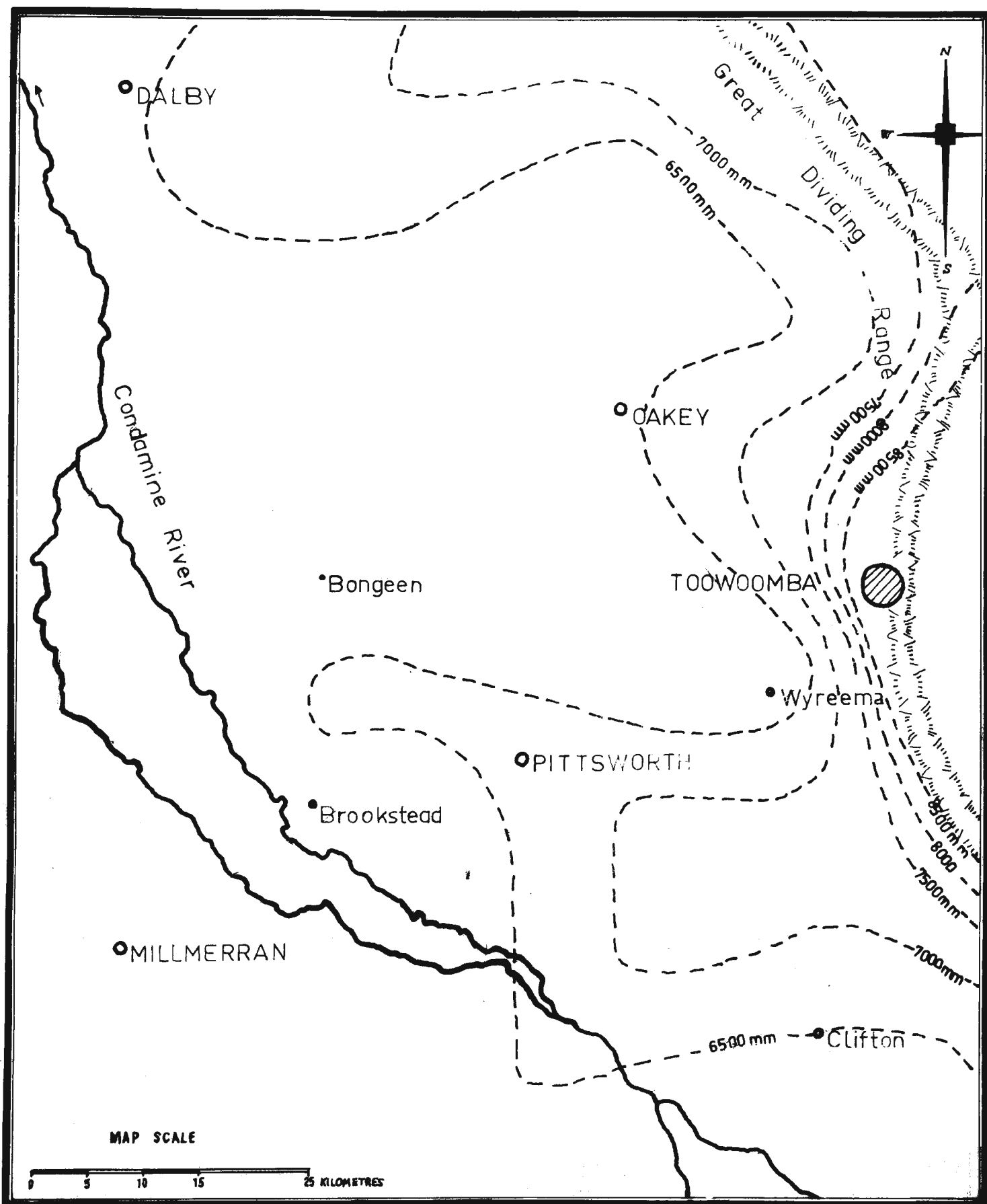
AREA OF STUDY Showing isohyets (in mm. annual rainfall)

North Eastern Downs

The area runs from the north eastern edge of the open plain through to the main range. Topographically, the region is not unlike the south eastern sector but, because the soils and their inter-types are more stable and since smaller areas are arable, soil erosion is less obvious but nevertheless equally important.

Western Downs

This term is used to describe those lands generally regarded as belonging to the Darling Downs but lying west and south of the open plain. The Condamine River is regarded as the border between these two regions.

Open Downs

Broken only at its centre around Dalby, the open downs is an otherwise continuous stretch of flat, featureless, treeless, black soil plain. This deep black soil was formed under grassland vegetation subjected to conditions of summer rainfall and winter drought. The high clay content gives the soil its renowned moisture holding capacity.

After the introduction of dwarf grain sorghum, maize has become a summer crop of secondary importance with future production to be confined to the more favoured sections of the Eastern Downs. Realisation locally that the newer maize hybrids have a hardiness not found in the open pollinated varieties and the development of irrigation areas has caused somewhat renewed interest in maize.

The Darling Downs is now regarded as the main maize growing area of the State, with some 26 323 ha planted to maize in 1969-1970 (see footnote). This represents approximately 45% of the State's total acreage. An average farm yield is approximately 820 kg per ha with yields up to 4 300 kg per ha being obtained in the south eastern region. Local disease and insect activity has been of little commercial consequence to date, although, in more recent years, the tendency for growers to apply chemical controls to combat pest presence is increasing. The present study was undertaken to establish the extent of natural mortalities operating against larval populations.

Footnote: This figure was obtained by summing data presented in the relevant Shire Handbooks published by the Queensland Department of Primary Industries.

II. DEVELOPMENT AT CONSTANT TEMPERATURES

i) INTRODUCTION:

A prerequisite to the formulation of sampling techniques for larvae from field populations is a knowledge of the duration of each larval instar so as to determine a suitable frequency of sampling. Insufficient sampling would result in failure to record all instars and give a biased estimate of population trends.

Although an estimate of the duration of the life cycle is roughly documented (Anon. 1951), no accurate assessment of the effect of temperature on the rate of larval development has been made.

ii) MATERIALS AND METHODS:

A colony of H. armigera was started using larvae found attacking maize at Wyreema. In the laboratory, these larvae were fed on an artificial diet and this fact must be considered when assessing the results obtained, since continuous rearing on the artificial diet leads to a general decline in vigour of the colony after three or four generations (Appendix A). The eggs used in the study were laid by moths developing from field collected larvae, i.e., first generation.

Eggs less than 12 hours old were collected from the laboratory colony of H. armigera and placed individually in 55 g glass jars containing 10 ml of an artificial diet (see Appendix A). Fifty larvae were used at each temperature and these were examined every 24 hours to record the stage of development.

The study was carried out under continuous darkness using a ten chamber multitemperature incubator giving a range of temperatures from 10° to 38° of which only seven temperatures (13, 18, 21, 24, 27, 34 and 38) were used. The accuracy of chamber temperature decreased towards the extremities of the range.

iii) RESULTS:

The duration of each age interval for each temperature treatment is set out in Table II (a). The durations of larval life at 13°, 18°, 21°, 24°, 27° and 34° were 120, 35, 24, 18, 14 and 12 days respectively. These data were converted, for ease of calculation from a hyperbolic to a linear form by relating the rate of development (reciprocal of development time) to temperature. This relationship is illustrated in Fig. 2 (a), to which the following linear regressions have been fitted.

Larvae $\qquad$ $Y = 0.00385 \ X - 0.041$ $\qquad$ (1)

Pupa $\qquad$ $Y = 0.00473 \ X - 0.054$ $\qquad$ (2)

Total Life $\qquad$ $Y = 0.00209 \ X - 0.023$ $\qquad$ (3)

where Y = reciprocal of development time

in days

X = temperature (°C)

Extrapolation of this graph indicated a threshold of development at 10.65° (i.e., Theoretical temperature below which development does not occur) and a Thermal Summation Constant for larvae from egg hatch to final instar at 259.74 day degrees.

Although complete larval mortality was recorded at 38° the duration of the few larvae which did survive early instars indicate that at 38° larval instar development was retarded and the fastest development time for larvae would be 34°.

TABLE II(a) MEAN AND STANDARD DEVIATION OF DEVELOPMENT TIME (days) FOR IMMATURE STAGES OF Heliothis armigera.

AGE INTERVAL	TEMPERATURE (°C)						
	13·1	18·5	21·3	24·6	27·1	33·9	38·4
1st instar	7·5 ± 0·8	3·0 ± 0·0	2·0 ± 0·2	1·5 ± 0·5	1·0	1·0	1·0
2nd "	7·1 ± 1·2	2·9 ± 0·5	2·1 ± 0·4	1·5 ± 0·5	1·0	1·0	2·0
3rd "	12·8 ± 1·	4·0 ± 0·5	3·1 ± 0·5	3·0 ± 0·1	1·8 ± 0·5	1·1 ± 0·4	1·3 ± 0·2
4th "	19·0 ± 8·9	5·1 ± 0·7	3·1 ± 0·4	2·6 ± 0·5	1·9 ± 0·3	1·7 ± 0·5	5·0
5th "	24·7 ± 5·5	6·2 ± 1·6	4·9 ± 1·0	2·0 ± 0·6	2·0 ± 0·5	1·4 ± 0·6	—
6th "	28·0 ± 5·9	8·3 ± 1·2	6·1 ± 1·3	5·5 ± 0·8	4·3 ± 0·8	3·5 ± 0·6	—
Pre Pupa	20·8 ± 3·9	6·0 ± 0·7	3·0 ± 0·7	2·5 ± 0·5	2·4 ± 0·5	2·0 ± 0·2	—
Larval Life	119·9 ± 9·6	35·3 ± 2·0	24·0 ± 2·2	18·5 ± 1·3	14·5 ± 1·0	11·7 ± 0·9	—
Number of Larvae	12	45	47	49	44	41	0
Pupal Life	—	33·9 ± 3·6	22·6 ± 2·0	15·7 ± 2·2	11·5 ± 1·6	10·0 ± 0·7	—
Number of Pupae	·0	16	40	44	42	36	0
Total Life	—	69·0 ± 4·1	46·6 ± 2·2	34·2 ± 3·1	26·1 ± 1·8	21·6 ± 0·9	—

However, the larval mortality associated with development at 34° (8.9%) is higher than that at 27° (4.3%). At 38° it is probable that heat stress has been responsible for prolonged development and for temperatures in excess of this value thermal mortality would occur earlier.

The duration of pupal development associated with temperature described in equation (2) and illustrated in Figure 2 (a) gives a threshold temperature of 11.42° and a Thermal Summation Constant of 211.4 day degrees. It is apparent that heat stress conditions do not operate on pupae up to 34°, since pupal development time is not prolonged at this temperature. However, over the range of temperatures used, pupal mortality decreased as temperature increased up to an optimum of 27°, above which mortality begins to increase. This compares with an optimum temperature for larval survival at 24°.

Egg mortality as outlined in Table 2 (b) appears to be unaffected by low temperatures in excess of the threshold temperatures whereas, in excess of 34° the viability of eggs is greatly reduced. The mortality associated with development at the various temperatures indicates that for optimum survival, temperatures should be maintained within the range 24° - 27°.

The effect of temperature on total development from newly hatched larvae to adult emergence is illustrated in Figure 2 (a). From results of individuals completing development at each temperature (Table II (c)) it is significant that, at lower temperatures, development is faster for females than males (P=0.015).
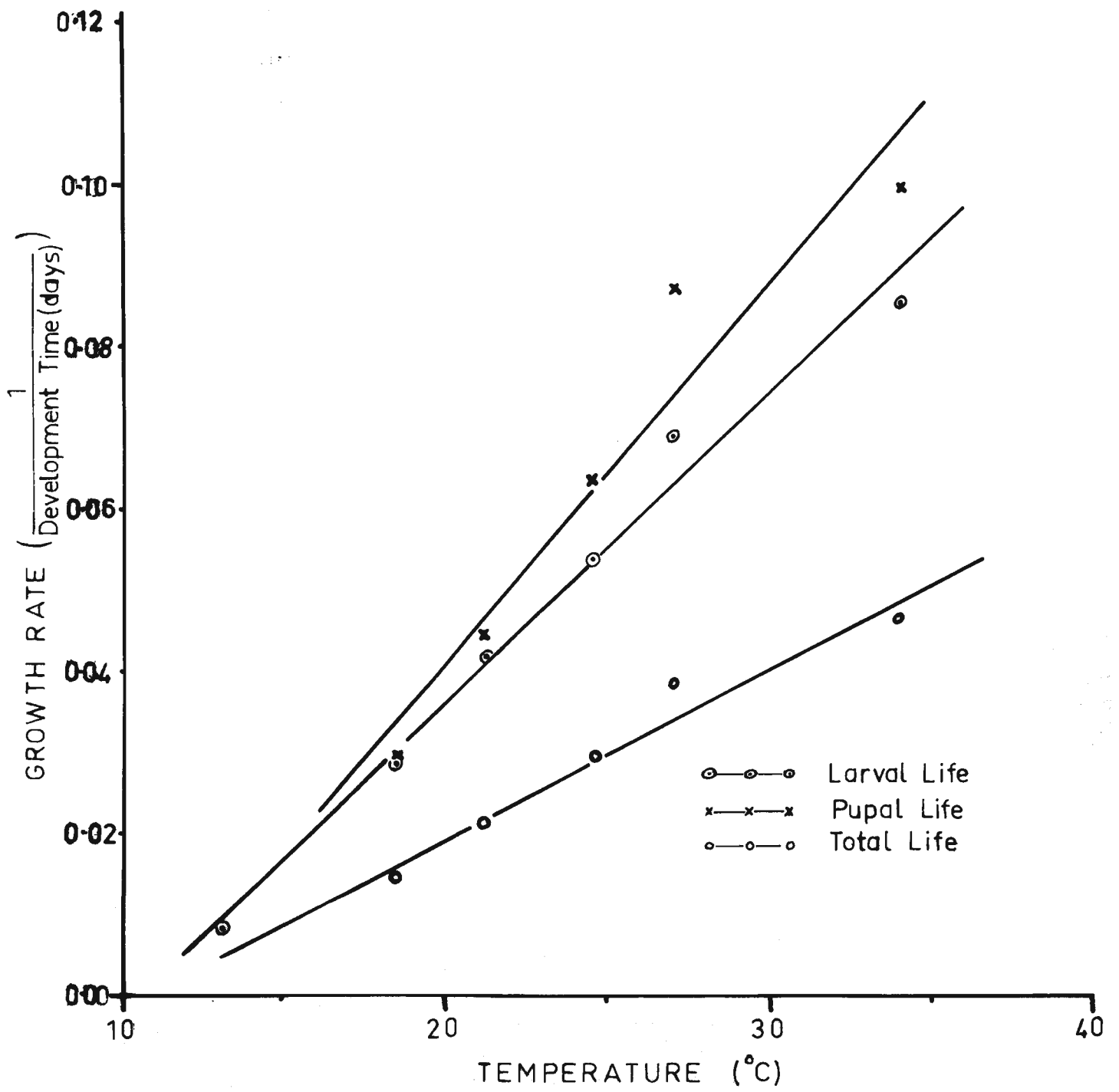
FIGURE 2 (a)   RELATIONSHIP OF GROWTH RATE OF Heliothis armigera
WITH TEMPERATURE.

TABLE II(b)   MORTALITY (%) FOR IMMATURE STAGES OF Heliothis armigera
EACH OBSERVATION BASED ON 50 EGGS.

	TEMPERATURE (°C)						
	13·1	18·5	21·3	24·6	27·1	33·9	38·4
Egg Mortality	2·0	0·0	2·0	0·0	8·0	10·0	92·0
Larval Mortality	75·5	10·0	4·1	2·0	4·3	8·9	100·0
Pupal Mortality	(a)	64·4	14·9	10·2	4·5	12·2	—
Total Mortality		68·0	20·0	12·0	16·0	28·0	100·0

(a) Pupae in diapause

TABLE II(c)   DEVELOPMENT TIME (in days)

AT EACH TEMPERATURE

	Temperature (°C)			
	21·3	24·6	27·1	33·9
Males	47·5 ±2·3	34·4± 2·3	26·1± 1·7	21·5 ±0·9
Females	45·6 ±2·0	33·0± 3·0	25·9± 1·8	21·8±1·0
t value	2·551	1·631	0·354	0·996
Probability of difference	15%	11%	50%	33%

Above 27°, however, this difference does not persist (P=0.33).
There is no significant difference between the sex ratio (see
Table II (d)) at any of the temperatures employed (P=0.50)
(see page 67).

During larval development no measurements were
made of the head capsule or of cast head capsules so as to actually
establish each moult. Instead, overall morphological characters
were considered to gauge instars. Because of the variations in
larval development (see Section III) results could not be analysed
on the basis of individual instars.

The distributions of development times for all
temperatures have been transformed to a common mean (o) and unit
variance. The transformed distribution of larval life is
illustrated in Figure 2 (b) and differed from the expected normal
distribution (P < 0.005) (see page 64), thereby indicating the
possibility of a bimodal distribution and thus supporting the
hypothesis of a proportion of the larvae having a longer develop-
ment time, probably as a result of including an extra larval instar.
The distribution for pupal life (see Figure II (c)) also differs
significantly from normality (P < 0.005) (see page 65) although the
bimodal relationship is not so apparent. The larval life and pupal
life distributions are not significantly different from each other
(P=0.005) (see page 66).

iv) DISCUSSION:

Wigglesworth (1965) when discussing the mathematical
descriptions of temperature effects on insect development, considers
that the velocity of development is proportional to temperature
within the "normal range" of temperatures for many Lepidoptera and
Diptera.

TABLE II(d) SEX RATIO OF MOTHS
DEVELOPING AT EACH
TEMPERATURE

	Temperature (°C)			
	21·3	24·6	27·1	33·9
No. males	17	22	21	21
No. females	19	15	21	13
% males	47·2	59·5	50·0	61·8
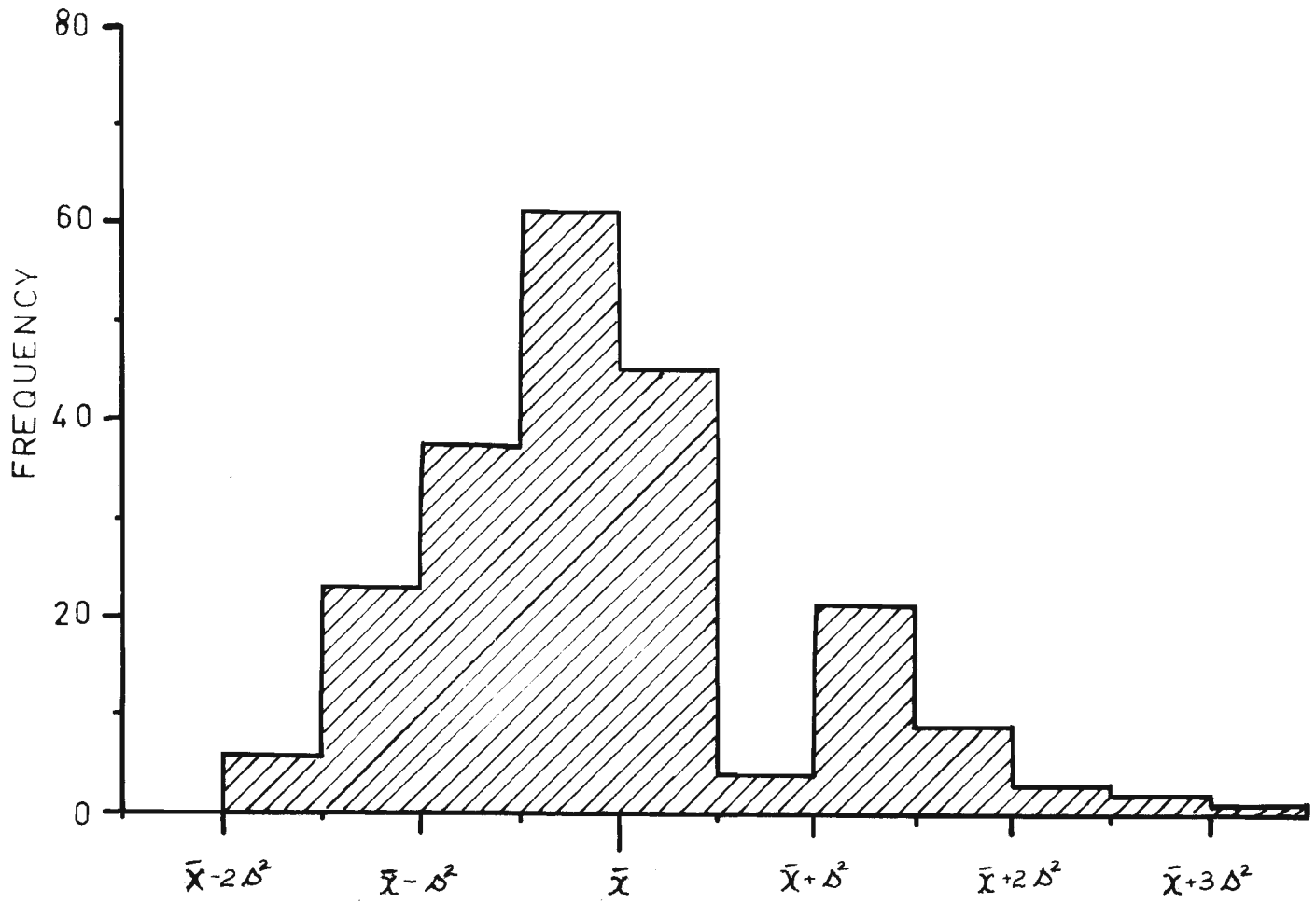
FIGURE 2 (b)   STANDARDISED DISTRIBUTION OF LARVAL LIFE
                AT ALL TEMPERATURES
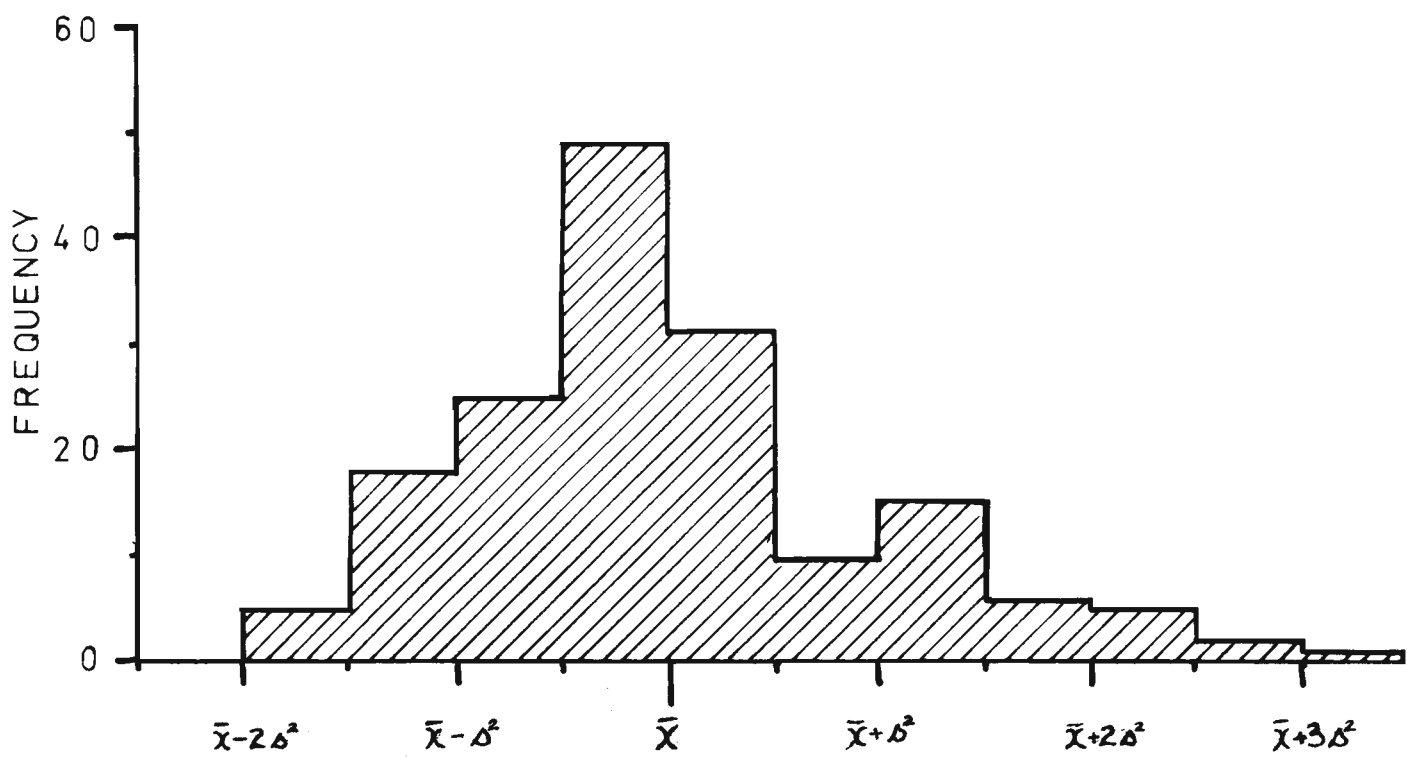
FIGURE 2 (c)   STANDARDISED DISTRIBUTION OF PUPAL LIFE

AT ALL TEMPERATURES.

Howe (1967) in his review of the effect of temperature on embryonic development partly rejects this relationship for the assessment of embryonic development since the concept assumes that the changes from fertilisation to hatching always take. the same course of events and that environmental changes will affect it equally at all stages. This situation is not true however for many eggs going through a facultative diapause stage. Howe (1967) adopted the asymmetric caternary relationship on the grounds that it attempts to cover the curve for the entire temperature range. Cullen (1969) working with H. punctigera adopted a method similar to that of Pradham (1946) and fitted all his curves by eye.

From a practical viewpoint the use of the Thermal Summation and Development Zero is acceptable. Since the tempe atures considered in this present study fall within Wigglesworth's "normal range" a linear relationship of development velocity and temperature was adopted. Mangat and Apple (1966) applied this principle to development of Heliothis zea and established a threshold temperature of 12.6° and a Thermal Summation Constant for development from egg to adult at 383.4 day degrees. This would indicate that the sample population of Heliothis zea used by these authors was less adapted to cooler conditions than those from this present study. This difference might also be attributable to the different artificial diets used. The Thermal Summation Formula $(Y = (t - c) T)$ where Y = Thermal Summation constant, t = temperature, c = Threshold Temperature, T = Development Time at temperature t) necessitates two sets of data for temperature and development time for a solution of the two unknown values.

The r sults of Mangat and Apple (1966) may be criticised in that only the minimum of two temperatures were used to compute their results, thereby making no allowance for error in observation at either temperature. The use of more than two temperatures allows for regression analyses of the results to obtain a best fit relationship for the data as well as to obtain an estimate of error.

Howe (1967) **considers that a minimum of ten temperatures** spaged at intervals no greater than 2.5° as well as further experiments spaced at 1° to 0.5° intervals for about 3° on either side of tne optimum and limits of development are needed to determine the relationship of temperature and development time. He regards this minimum necessary to fit a line by eye without bias. It was considered unnecessary to require such fine discrimination in the present study. However, regression analysis defines the best line of fit for the data as well as an estimate of the accuracy of this line (correlation coefficient).

Kirkpatrick (1962) reported development times for larvae taken from a range of host material and bred under insectary conditions without temperature control but did not relate these to a Thermal Summation situation. Using his data one can calculate a Threshold temperature of 5.2° and Thermal Summation Constant of 475 day degrees, from egg to adult emergence, These results suggest the material used by Kirkpatrick to be more adapted to a milder climate than that of the present material, although the Thermal Summation Constant for both materials are identical. Unfortunately, the lack of accurate recordings of temperatures would jeopardise a critical comparison of the threshold temperature calculated to that of the present work.

The optimum temperature range of 24° - 27° calculated in this study compares favourably with temperatures commonly quoted for use in mass rearing techniques of Heliothis under laboratory conditions (Callahan 1961, Vanderzant et al. 1961, Burton and Perkins 1972).

The bimodal nature of larval emergence histograms has been reported on a number of occasions. From work on Tribolium (species unstated), Stanley (1946) reported a bimodal distribution of development time at 35°. Howe (1961), working with Tribolium castaneum (Herbst) observed a heterogeneity factor amongst a laboratory **population of the species. He recognised two strains, each** with a log. normal emergence curve but differing in that the second strain, constituting 20% of the population, had a heavier pupal weight. Howe (1957) working with Lasioderma serricorne (Fabricius) also reported a bimodal distribution of development time for this species.

In the present study it is suggested that the bimodal condition is associated with a proportion of the larval population undergoing more moults than normal.

v) CONCLUSION:

Although the problem of identifying the various instars has limited this study, the data confirmed that under field conditions equivalent to continuous temperature of 21°, samples will be required every two days to maximise the likelihood of detecting peak numbers of each larval instar in a field population of H. armigera.

It is apparent from the study that to assess accurately the relationship between temperature and development it will be necessary to use a wider range of temperatures and to study in more detail development at the extreme of the "normal temperature" range.

III. INSTAR DEVELOPMENT

i) INTRODUCTION:

Before any detailed study of the dynamics of larval populations of H. armigera can be undertaken it is necessary that the nature of larval growth be sufficiently well documented. Hence, a definition of each of the larval growth phases should be constructed in order to accurately identify each of these. Owing to variation in colour, shape and size within each larval instar the head capsule width of each larva has to be measured to gauge larval size. Kirkpatrick (1961) measured the head capsules of four Australian species of Heliothis and described each instar giving the range of values of head capsule widths associated with each instar for each species. These results indicated a regular growth pattern with no overlap of measurements from one instar to another. He did, however, record that H. armigera and H. punctigera completed development in six instars, and that H. assulta and H. rubrescens completed development in only five instars. Later reports (Hardwick 1965) indicate that larval growth is not as regular as originally thought. Hardwick studied twenty two species and sub-species of his genus Helicoverpa (Heliothis) and for each species he recorded variation in the number of instars, with the first and ultimate instar the same, irrespective of the number of instars as varying from five to seven.

The present study was set up to follow the development of groups of larvae under uniform conditions so as to assess the details of larval growth and to note any irregularities. Two such evaluations were carried out in the laboratory, Series A during September 1972 and Series B during 1973.

ii) MATERIALS AND METHODS:

Early in 1972, larvae attacking maize at Wyreema were collected and bred through in the laboratory on the artificial diet (see Appendix A). After four complete generations on this food, eggs were taken for Series A of the present study. Material for Series B was taken from larvae also collected at Wyreema but these were bred for only one generation in the laboratory.

Eggs less than 24 hours old were collected and placed singly into 55 g glass bottles containing 10 ml of artificial food. Fifty such eggs were set out at 24° and bred under total darkness except during observations.

Each larva was examined daily and the head capsule width recorded using a stereo binocular microscope (x31) fitted with a calibrated micrometer eyepiece. The larvae were not anaesthetised or handled at any stage of their development and were left to pupate in the media. Pupae were checked daily for the emergence of adults.

Further data were obtained from field collections of larvae attacking maize to establish the occurrence of the various instars in the field. During both the 1972 and 1973 maize seasons larvae were preserved in 70% alcohol solution and transferred to the laboratory where the head capsule widths were measured within four hours of collection.

iii) RESULTS:

The head capsule widths of larvae in Series A and Series B are listed in Table III (a). They show considerable variation in the number of larval moults.

TABLE III(a) HEAD CAPSULE SIZE(mm), DEVELOPMENT TIME (days) AND SURVIVAL OF Helicothis armigera AT 24°C

DEVELOPMENT STAGE	SERIES A				SERIES B			
	Six Instars		Seven Instars		Five Instars		Six Instars	
	WIDTH	DURATION	WIDTH	DURATION	WIDTH	DURATION	WIDTH	DURATION
1st instar	0·25	5·3	0·25	7·0	0·23	3·0	0·25	4·0
2nd "	0·42	3·8	0·41	4·1	0·47	2·1	0·44	3·0
3rd "	0·66	3·3	0·60	3·8	0·89	2·3	0·73	2·5
4th "	1·07	3·5	0·91	4·3	1·67	3·2	1·19	2·5
5th "	1·72	4·6	1·27	4·8	2·65	4·3	1·82	3·0
6th "	2·63	8·5	1·78	6·0			2·72	5·0
7th "			2·57	8·9				
Pre-Pupa		3·9		4·0		3·5		4·0
Pupa		19·7		19·0		15·5		16·7
Larval Life	29·6 $\pm$ 7·5		39·8 $\pm$ 10·2		18·8 $\pm$ 2·8		24·0 $\pm$ 3·6	
No. of Pre-Pupa	22		7		29		3	
No. of Pupa	18		5		29		3	
Adults ♂	9		1		15		2	
♀	6		—		14		1	

In Series A, of the 29 larvae completing development to pre-pupa, 22 (75.9%) required six instars, the remainder seven, whereas in Series B, 90.6% completed development in five instars and the remainder in six instars.

The development times associated with each instar are also included in Table III (a). In both Series, the larval development time differs according to the number of instars, the longer development times are largely accounted for by the time taken in the extra instar although the development time for particular instars with each Series (i.e., first, ultimate instar) is generally longer for those undergoing an extra moult. It would seem therefore that conditions causing a lengthening of larval development time favour the occurrence of extra moults.

Within each series, the durations of the pre-pupal or pupal stage are similar and therefore unaffected by the speed of larval growth. The difference in pupal development time for Series A and B is better attributed to the "vigour" of the material used (see Appendix A).

Because a proportion of the larval populations has fewer instars and a shorter development time, it would be expected that the distribution of larval development times for the total population would be bimodal. The distance between the maxima would largely represent the time taken in the extra instar and the difference in their size would indicate the relative proportions of the variation in the population (see Section II).

For larvae developing in six instars there was a difference in development time for both Series A (29.6 days) and B (24.0 days).

Also the standard deviations of the development times (7.5 and 3.6) are much greater for Series A than B. The Coefficient of Variation for these data (25.3% for Series A and 15.0% for Series B) further exemplify the difference between the Series which are attributed to the origin of the material used. With continuous breeding on an artificial diet the vigour of the colony declines, and, after four generations is marked by increasing larval development times and a decline in fertility (see Appendix A). In support of this suggestion is the higher mortality recorded for the "older" Series A (Table III (a)), which had mortalities of 18% and 17% associated with its pre-pupal and pupal stages respectively whereas there was no mortality in Series B.

Besides the bimodal distribution proposed for total larval population development times there is an indication that there is a "long tail" associated with the development time distribution for the six instar situation in Fig. 3 (a) and the five instar situation in Fig. 3 (b). Although not measured these distributions are definitely skewed to the right.

Despite the variable nature of the number of larval moults within each series there is a definite growth pattern discernible. Regression analysis of the various instars and associated head capsule width (log scale) indicate that there is a constant regular growth increase associated with each moult. This relationship may be quantified by the following equations:

Series A — $Y = 0.204 X + 0.205$ (six instars)

$Y = 0.166 X + 0.268$ (seven instars)

where $Y = Log_{10}$ Head Capsule Width (mm)
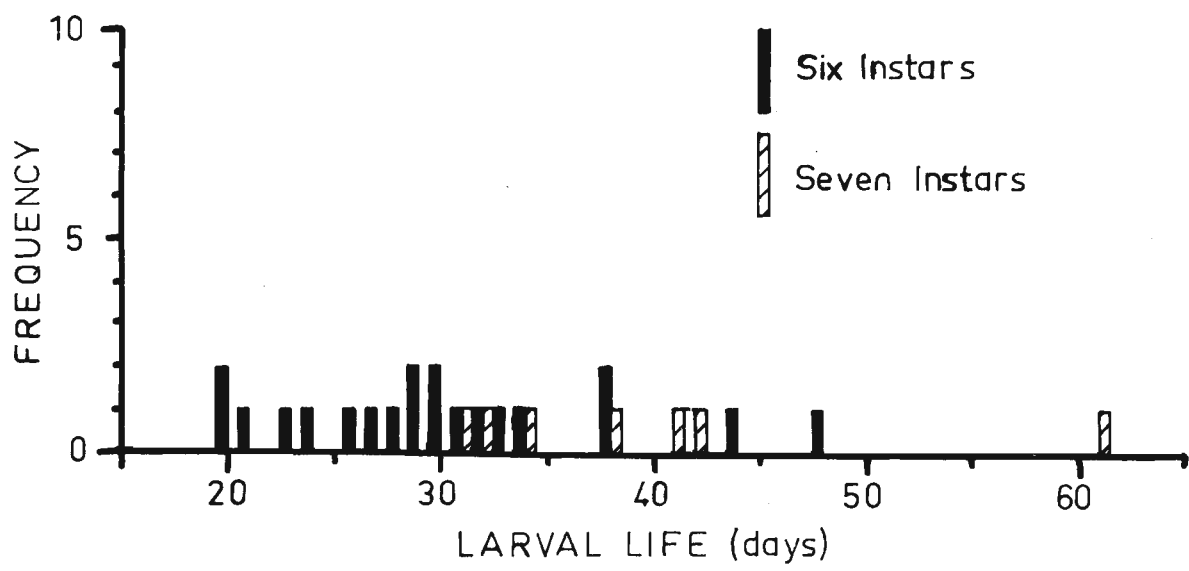
$X =$ Instar

FIGURE 3(a)   HISTOGRAM OF LARVAL DEVELOPMENT TIME
FOR SERIES A
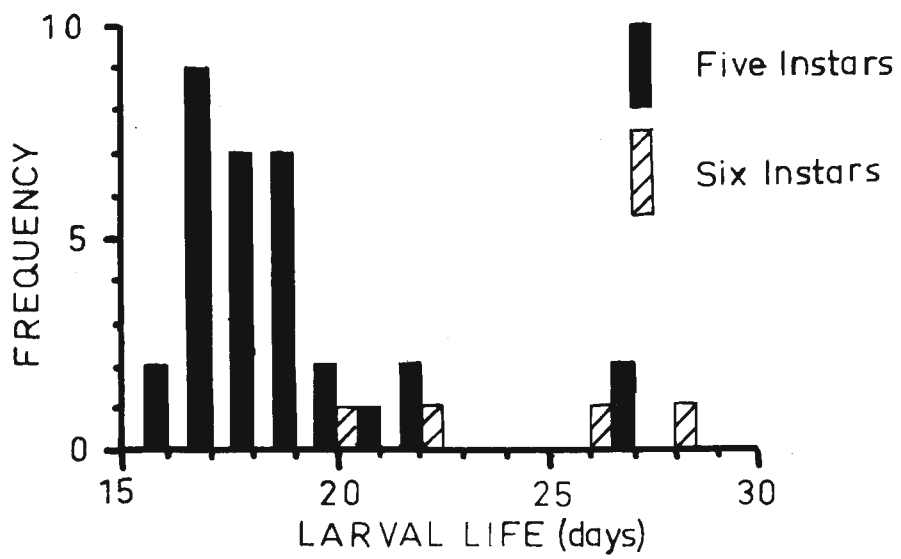
FIGURE 3(b) HISTOGRAM OF LARVAL DEVELOPMENT
TIME FOR SERIES B

Series B — $Y = 0.267 X + 0.125$ (five instars)

$Y = 0.207 X + 0.221$ (six instars)

where $Y = \text{Log}_{10}$ Head Capsule Width (mm)

$X = \text{Instar}$

For each regression the correlation coefficient (r) is greater than 0.997. The way in which each situation closely follows a regular growth pattern would seem to infer that the nature of larval development has been predetermined or established either before or early in larval life. The variation in number of moults observed does not result from omitted or additional larval instars.

The relationship of head capsule width and instar has indicated a very regular increase in larval size associated with each moult. This condition is predictable from empirical laws and was shown by Dyar (1890) to hold true for many Lepidoptera larvae. In the present study the incremental growth factor was 1.6 for the six instar situation (1.85 for those developing in five instars and 1.48 for those taking seven).

There is no significant difference between head capsule widths for the first and ultimate larval instar of any of the observed variations. Neither is there any suggestion of these variations being attributable to the sex of the resulting moths.

The frequency distribution of head capsules of larvae collected in the field (Fig. 3 (d)) indicates that there are six regular larval instars occurring within natural populations with an overlap of the individual instar distributions probably resulting from the proportion, in this case small, of the total population which undergo five or seven moults.
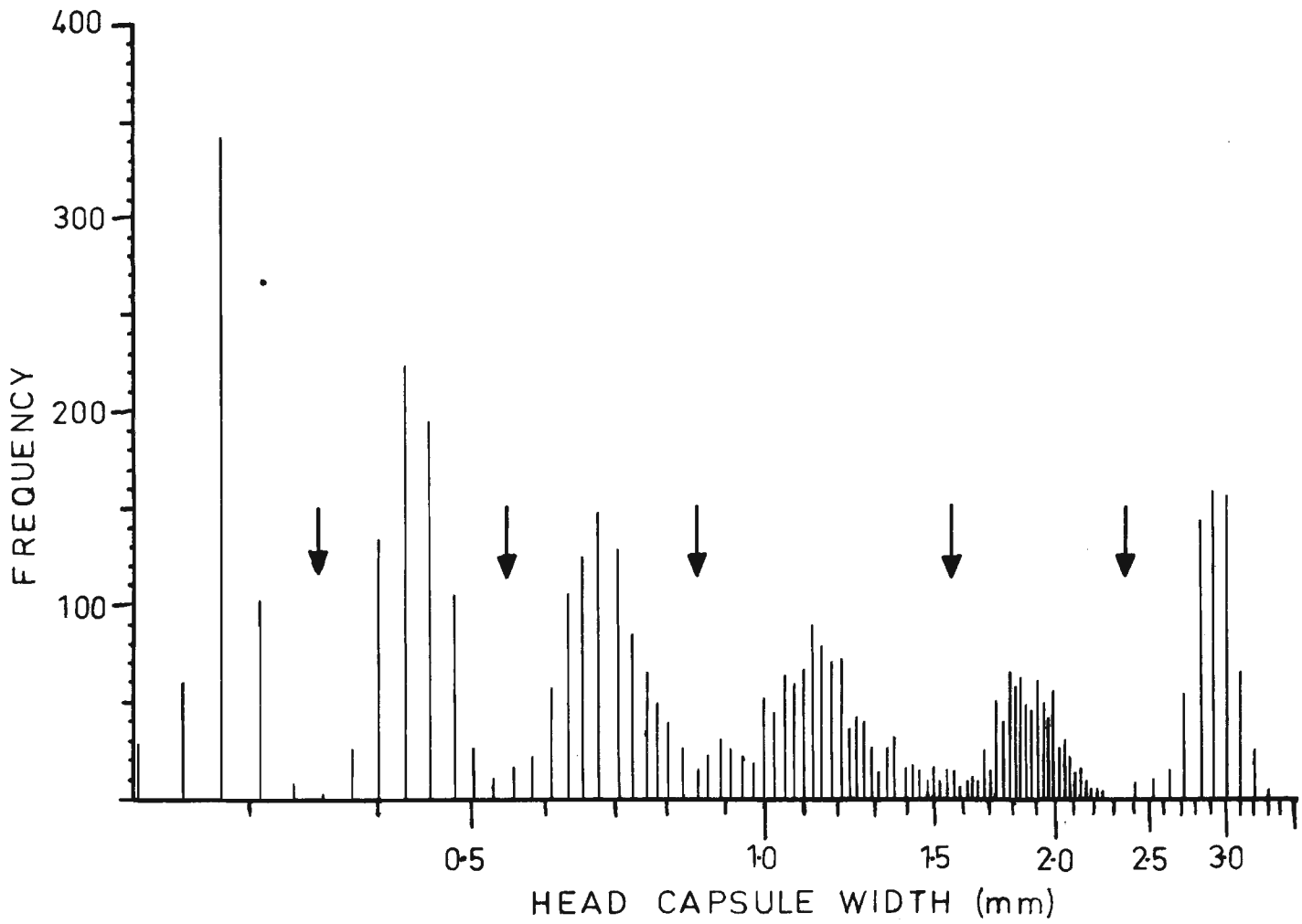
FIGURE 3 (d)   FREQUENCY DISTRIBUTION OF HEAD CAPSULE
WIDTH OF FIELD COLLECTED LARVAE OF
Heliothis armigera
(arrows indicate limit of each instar)

The field collected material originated from a range of sites and the same peaks and overlaps were recorded at each site.

Since the degree of overlap of the distributions between particular instars was small it was decided to neglect these and classify field collected material generally as having six instars with the following ranges associated with each:

1st — less than 0.35 mm

2nd — 0.36 mm to 0.55 mm

3rd — 0.56 mm to 0.85 mm

4th — 0.86 mm to 1.55 mm

5th — 1.56 mm to 2.35 mm

6th — greater than 2.36 mm

Results for the second, third and fifth instar values show a regularity of these ranges in that the upper limit of the range for a particular instar is equal to 1.5 times the lower limit. For the fourth instar however, this ratio is much greater and it is within this range that the presence of the "irregular" instars is detected.

iv) DISCUSSION:

The variation in numbers of larval instars from five to seven observed in Series A and B is consistent with that quoted by Hardwick (1965) although he noted this same variation for one series of larvae bred on shelled peas at a constant 25°. However, he gave no indication of the parentage of his material. For similar conditions Hardwick was able to record a wide range of variability for each of the known species of Heliothis although he regularly observed the five, six and seven instar situations existing for each species under the same conditions.

Kiski (1971), in a consideration of the measurements of the head capsule width of <u>Pissoides</u> <u>nitidus</u> Roelofs decided that the method of recording head capsule width was unacceptable and that the only true indication of larval instar came from a count of the moulted head capsules in the larval gallery and pupal cell. For <u>Heliothis</u> species this method would prove impractical due to the mobility of the larvae. Also, where larvae do remain within restricted areas (e.g., maize cobs), the likelihood of finding the cast head capsule amongst partly devoured food and faeces is low.

Early work on <u>H</u>. <u>zea</u> by Quaintance and Brues (1905) and on <u>H</u>. <u>obsoleta</u> by Gaines and Campbell (1935) suggested that such variability in the number of larval instars was related to nutritional factors. Larvae of <u>H</u>. <u>zea</u> developed through six instars when fed on maize and cotton whereas larvae fed on cowpeas required only five instars.

On the other hand, Jones (1936) considered temperature as a **causal** factor to this condition. In support of his theory he quotes <u>H</u>. <u>obsoleta</u> as having seven instars in winter yet only six instars when developing during the warmer summer months.

Wigglesworth (1965) carried further the ideas of Quaintance and Brues (1905) and Gaines and Campbell (1935) and suggested that inadequate nutrition, resulting in a prolonged larval life, may increase the number of insect moults and in fact, moults may occur without growth under conditions of poor nutrition.

This present study indicates that temperature is not as important as thought by Jones (1936) and suggests that the nutritional factors of the host material as well as the vigour of the insect under study are more important factors determining larval growth.

Hence, although different larval development patterns have been shown to be related to food and temperature, it has also been established that the variations in larval growth have been observed under constant conditions of food and temperature.

A laboratory study carried out on a wide range of Heliothis species as in the case of Hardwick (1965) using the one host material (which probably is not a natural food for many species concerned), would therefore be more likely to give an abnormal picture of larval growth than would a study carried out using natural plant host.

The mean head capsule widths cited for the larvae completing development in six instars of both Series A and B compare favourably with those of Hardwick (1965) and Kirkpatrick (1961) (See Table 3 (b)) – although the range of head capsule widths quoted by Kirkpatrick (1961) infer that,contrary to present study,there was no overlap of measurements.

The "long tail" distributions for development time observed in Fig. 3 (a) and Fig. 3 (b) is a situation which has been described by several workers for similar measurements with other insects (Laughlin, 1960; Messenger and Flitters, 1958). Such a distribution confounds calculations of the average development time for each situation but may be partially overcome by a logarithmic transformation of the time scale. Such transformations however, would not remove the bimodal nature of distributions as described in Section II.

TABLE III(b)   HEAD CAPSULE MEASUREMENT(mm) OF
                H.armigera   QUOTED BY VARIOUS AUTHORS

	A	B	C	D	E
Instar 1	0·27	0·27	0·25	0·23	0·25
„ 2	0·42	0·45	0·43	0·47	0·41
„ 3	0·69	0·73	0·70	0·89	0·60
„ 4	1·14	1·13	1·13	1·67	0·91
„ 5	1·88	1·80	1·77	2·65	1·27
„ 6	2·79	2·72	2·68		1·78
„ 7					2·57

A) Hardwick(1965)   B) Kirkpatrick(1961)

C),D),E) Present work

v) <u>CONCLUSION</u>:

       Although there is great variation in the number of larval instars between larvae of different parentage it is possible to approximately define limits for each of six larval instars which appear to be meaningful in the classification of field material. The explanation of this variability of larval growth lies outside the bounds of these studies and would necessitate far more detailed and critical work to establish the causal factor.

IV. MORTALITY IN MAIZE

i) INTRODUCTION:

Many workers (Barber, 1935; Sloan, 1940) have reported high mortalities during larval development in maize and have attributed this population decline to parasite and disease activity and to Heliothis larvae being cannibalistic. The "tight husk" varieties of maize which have been grown in areas of Southeast Queensland in recent years afford protection to the larvae from the action of parasites, predators and disease, leaving cannibalism as the most likely cause of this population decline.

The present study was undertaken to quantify the population decline for field conditions, using as a basic unit, H. armigera population per cob. Associated with the monitoring of this decline a study was made of the activity of the various causal agents.

ii) MATERIALS AND METHODS:

Seven plantings of maize (three in 1971/72, and four during 1972/73) were studied and, as concluded on page 25 samples of fifty infested cobs were taken on three occasions each week from the beginning of silking to the completion of larval development. On all occasions it was necessary to examine more than fifty cobs, with the number of cobs examined being determined by the density of the infestation in the sampling area. Partly devoured or diseased larvae were not included. The head capsule width of the larvae in each cob was recorded and used to identify the larval instars, based on results in Section III (page 31).

Plantings at each site were of maize variety XL306 except site II which was variety 805 A. Both these lines are considered to be "tight husk" varieties and do not differ significantly in cob characteristics.

When eggs were present a sample of fifty eggs was taken with individual eggs isolated in cells, following a technique described by Hoffman et al. (1970) for determination of egg parasite activity. Samples of twenty larvae were taken on each occasion and bred through singly in the laboratory on an artificial diet (see Appendix A) to record the incidence of parasites attacking larvae as well as the presence of larval pathogens. All causal agents recorded were preserved for subsequent identifications.

iii) RESULTS:

The data obtained from each of the seven sites are detailed in Appendix B.

(a) Population Decline

Since oviposition by H. armigera on maize is restricted usually to the shortlived silking stage of plant growth, eggs and larvae within each site have been considered as belonging to one cohort. Within limits therefore, there was a preponderance of one stage of development present at any particular time. Hence all analyses, discussions and computations have been developed using the instars as definite age intervals.

Because of the normal variation in the time taken to complete a particular development stage, it is usual to find a situation where more than one development stage might be present within one cob at any sampling time.

Since all larvae had an opportunity to interact and were subjected to the same conditions the stages found in each cob were all regarded as being that of the largest instar present.

The population declines, calculated on a per cob basis, are presented in Figures 4 (a) to 4 (g) inclusive, for observations made at Sites I to VII respectively.

In general, population decline for each site follows an exponential curve with the initial rate of decline increasing with increasing initial egg population. In the case of site I (Fig. 4 (a)), where the egg density was comparatively low, the overall reduction in population was extremely low. For all sites however, irrespective of the initial egg density, the population of sixth (final) instar was consistently reduced to unity. Since only those cobs containing larvae were used as samples it would be impossible to reduce the population beyond this point.

The collection data for all seven sites have been summed and presented in Table IV (a). They demonstrated the general decline in larval density per cob as the size of the larvae increase It is significant that in only 4% of cobs were there more than one final instar larva.

Using the data in Figures 4 (a) to 4 (g) the density of each development stage at each site has been converted to logarithms and the differences between the log. values for two successive development stages have been designated as "k" which represents the mortality associated with these two stages. "k" is the mortality operating between eggs and first instar larvae whereas "k_6" signifies the difference between fifth and final instar larval populations.
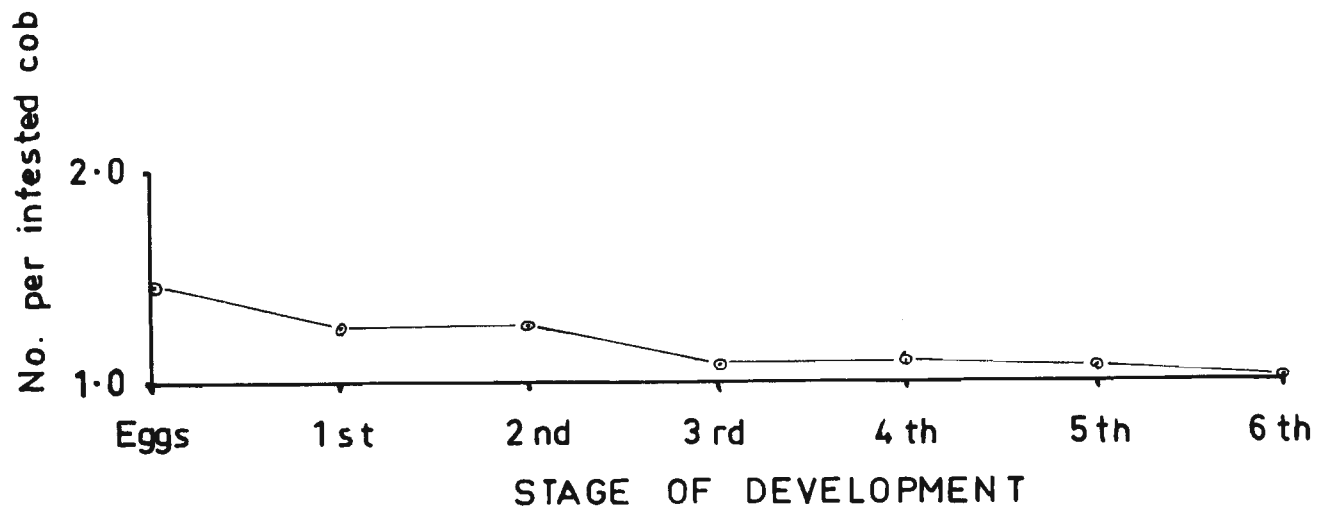
Figure 4(a)   Population Decline per Cob - Site 1
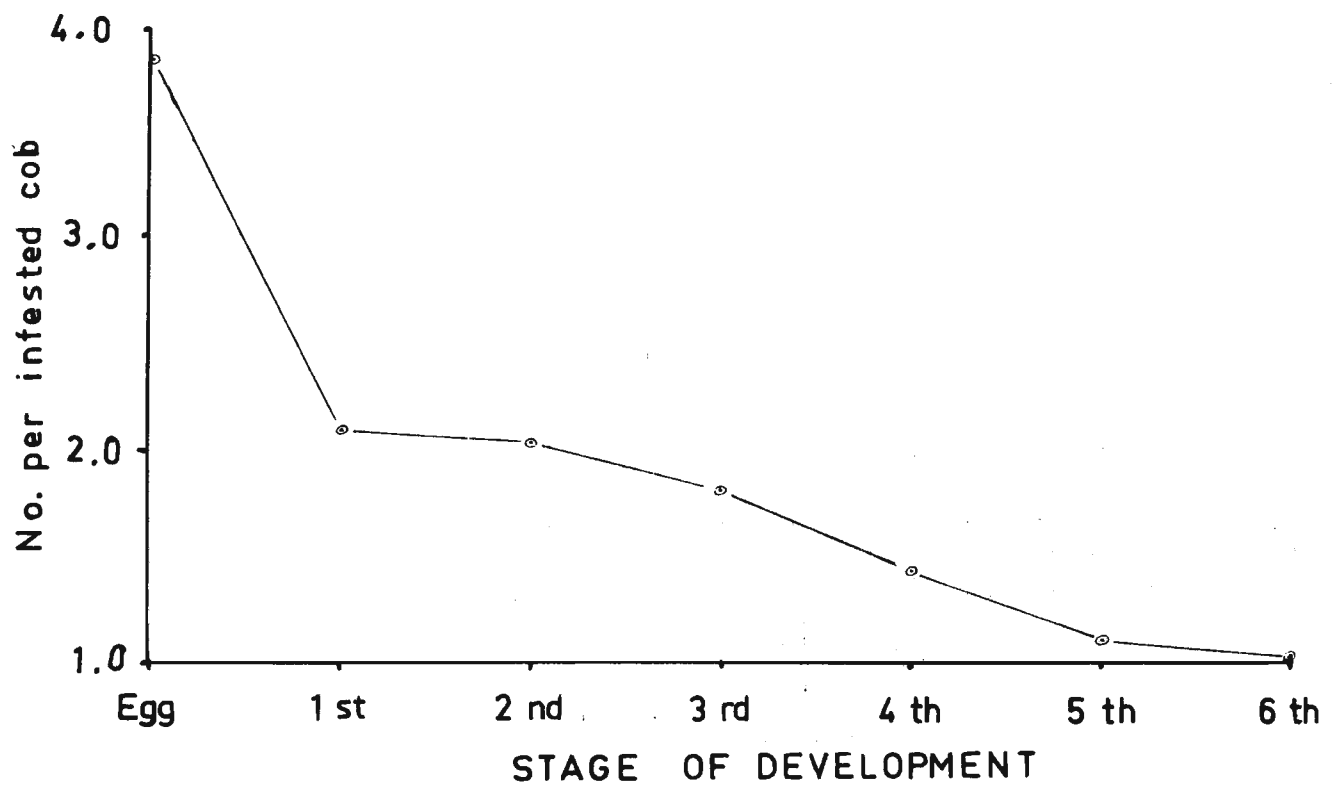
Figure 4 (b)   Population Decline per Cob - Site 11
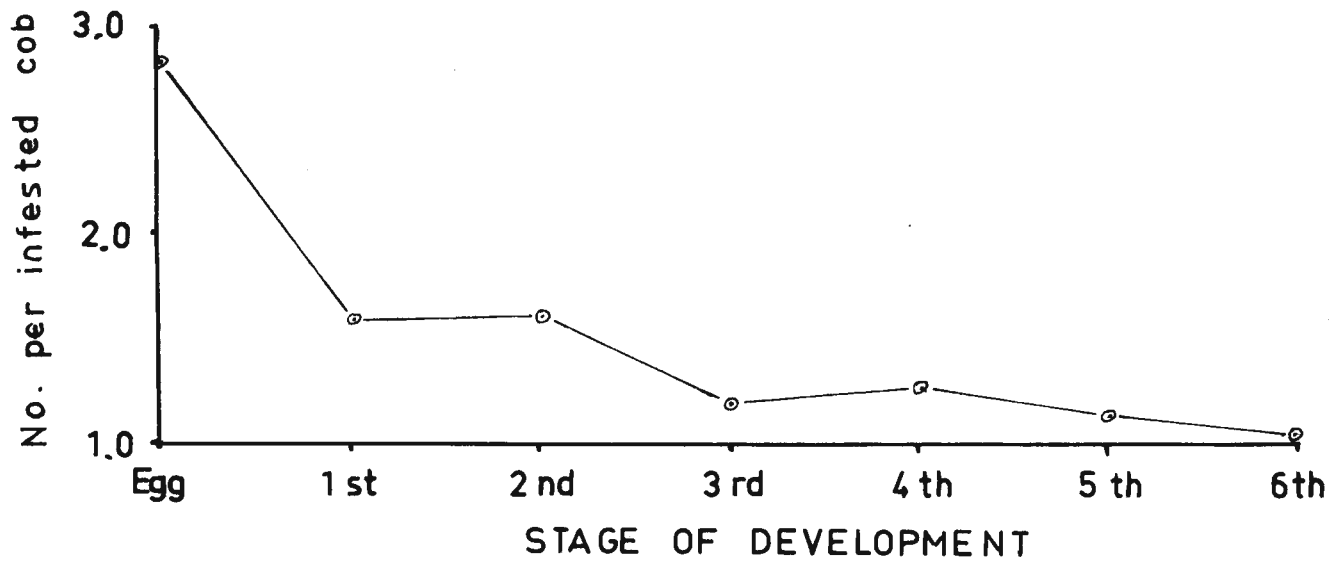
Figure 4(c)   Population Decline per Cob   Site III
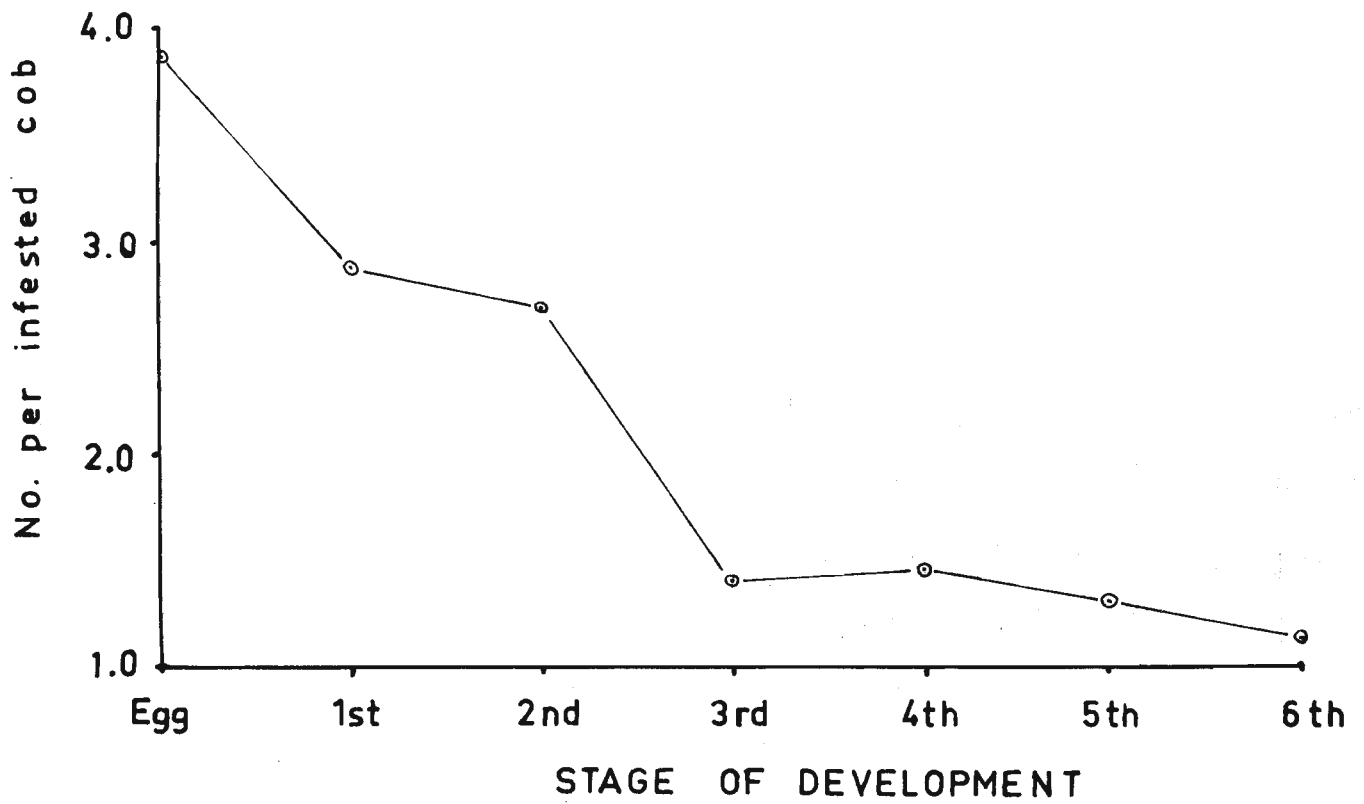
Figure 4(d) Population Decline per Cob   Site IV
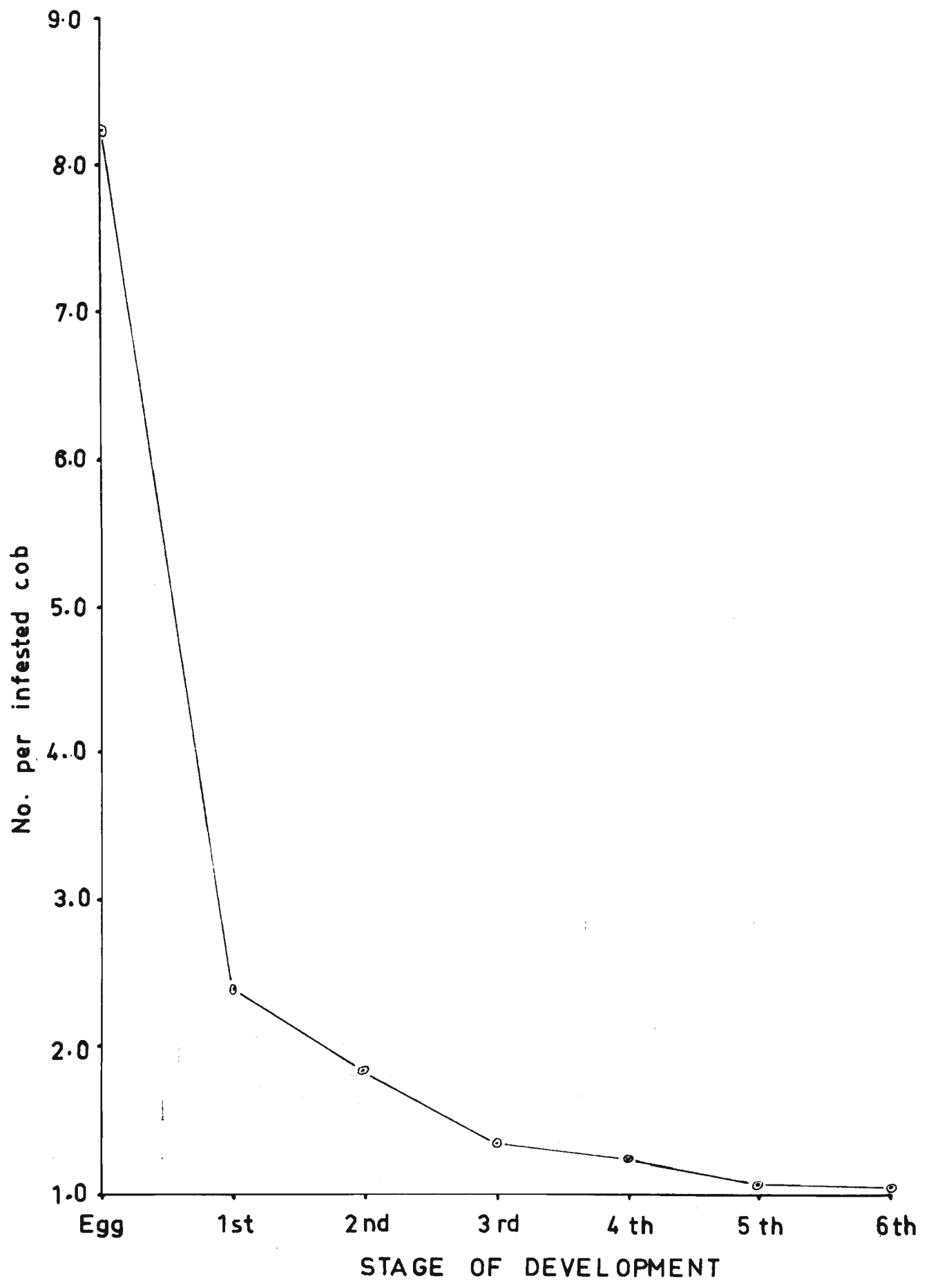
Figure 4 (e)   Population Decline   per Cob - Site V
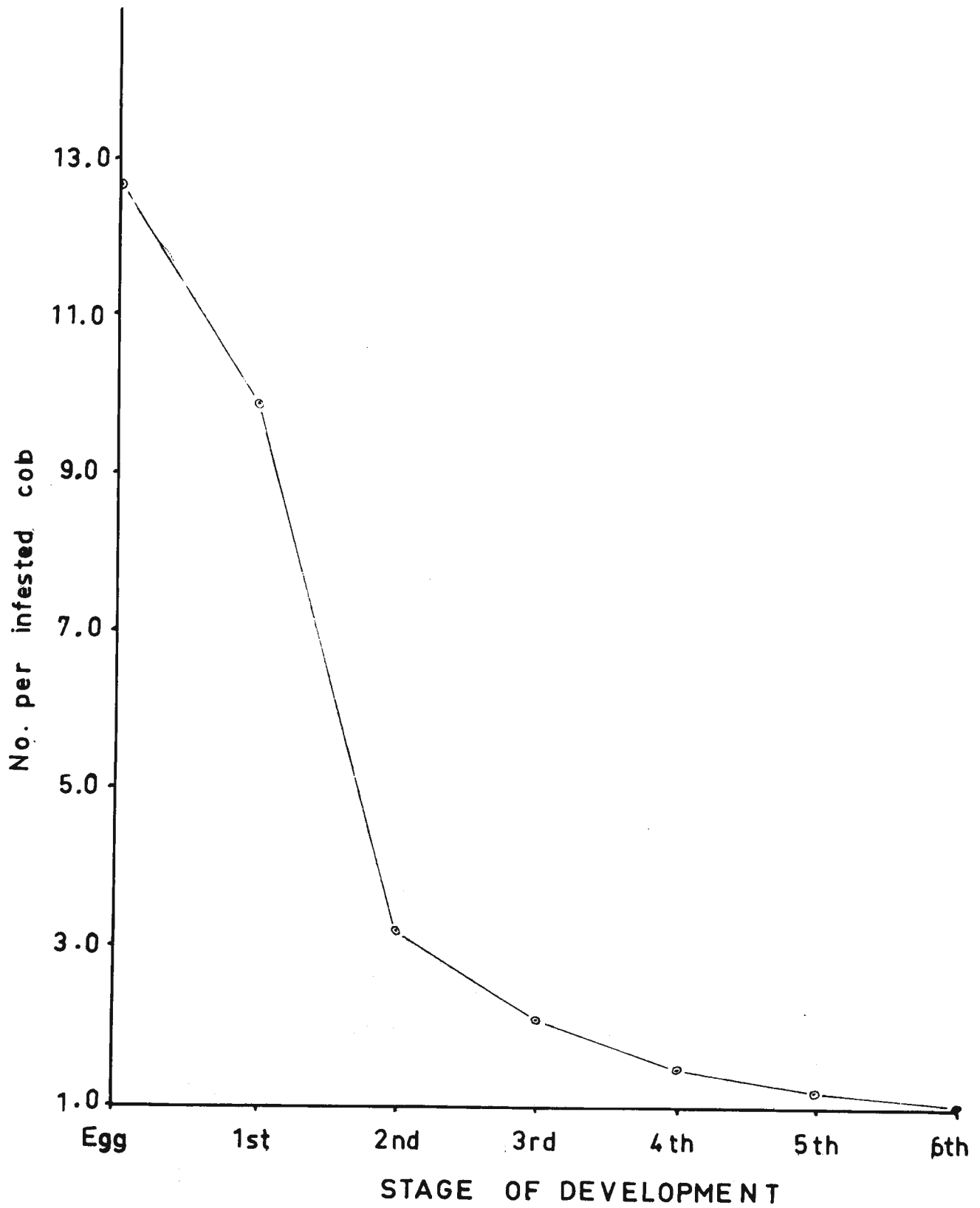
Figure 4(f)   Population Decline per cob — Site VI
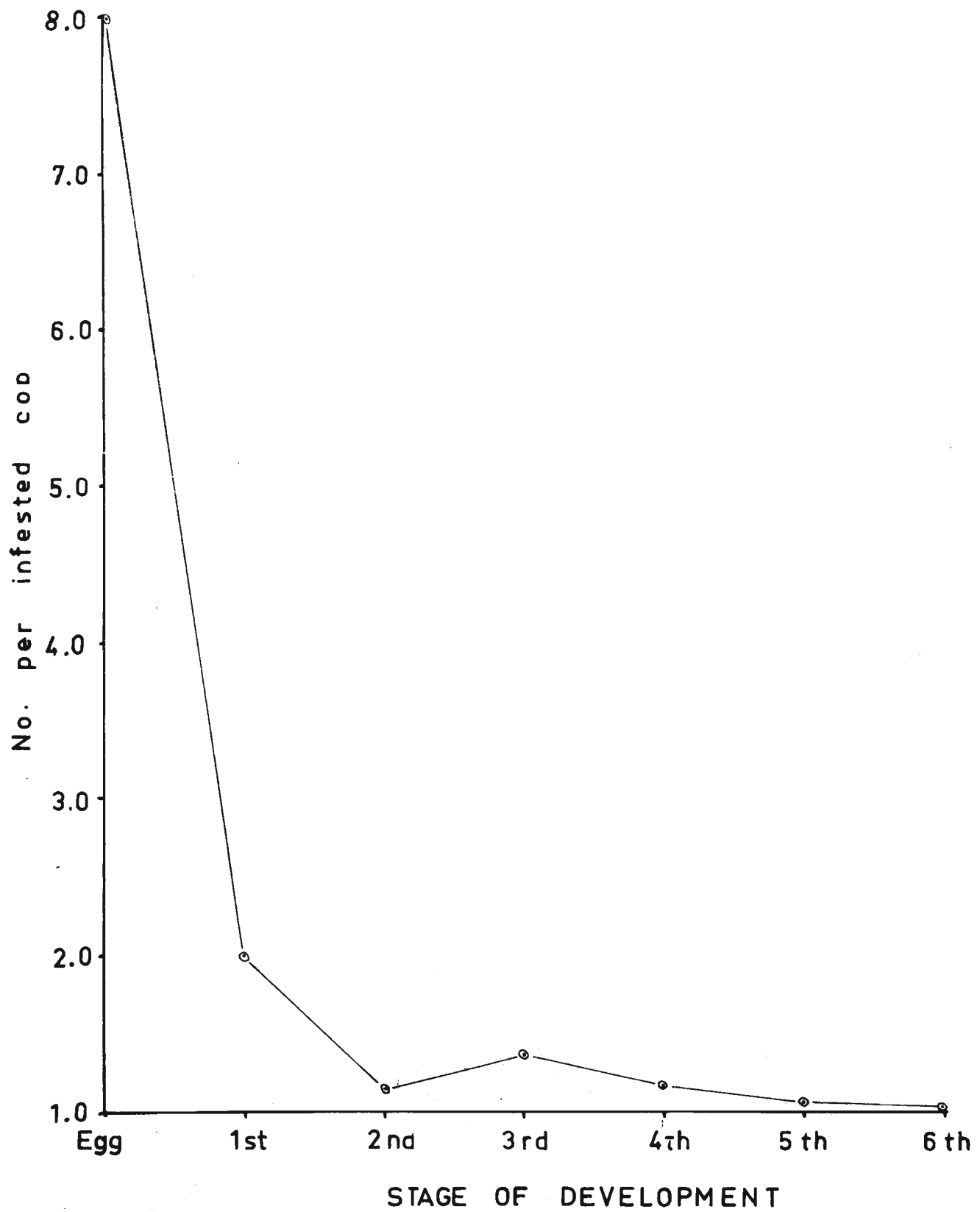
Figure 4 (g)   Population Decline per cob — Site VII

TABLE IV(a)

TABLE IV(a)   SUMMARY OF DISTRIBUTION OF LARVAL DENSITY AT ALL SITES

No. per Cob	No. cobs in which largest stage was that indicated						
	Eggs	1st	2nd	3rd	4th	5th	6th
1	285	144	258	459	616	681	682
2	151	48	62	90	108	75	27
3	117	13	28	38	33	17	2
4	93	8	15	20	12	2	
5	55	10	6	8	3	1	
6	46	7	7	8	2		
7	51	6	1	2			
8	41	2	2	1			
9	31	1	2	—			
10	31	—	2	-			
11	16	3	1	—			
12	27	3	1	1			
13	16	—	2				
14	16	3	-				
15	10	1	1				
16	7	—	—				
17	10	1	—				
18	7	2	—				
19	7	1	—				
20	10	2	—				
21	6	2	—				
22	9	—	1				
23	2	—					
24	2	—					
25	8	—					
26	2	1					
27	6						
28	1						
29	1						
30	7						
31	—						
32	1						
33	1						
34	—						
35	5						
36	—						
37	2						
38	—						
39	1						
40	1						
41	—						
42	—						
43	—						
44	—						
45	2						
46	—						
47	1						
TOTAL NO. COBS	1085	258	389	627	774	776	711

Tht total mortality "K" operating between egg and final instar larvae is equivalent to the sum of these individual "k"s.

$$i.e., \quad K = \sum_{i=1}^{i=6} k_i$$

The relationship between egg density and the subsequent total mortality "K" is illustrated in Figure 4 (h) and may be represented by the following equation:

$$K = 0.984E - 0.007 \quad (r^2 \quad .9979)$$

where K = Total Mortality

$E = \log_{10}$ Egg Density

The unity slope of this line (0.984) emphasises the closely balanced relationship between total mortality and egg density. The action of K operating as a result of the initial egg density is a truly density dependent relationship, operating to control the <u>Heliothis</u> population in maize.

(b) <u>Key Factors</u>

Although the observations at each site do not cover a complete life cycle and hence fail to recognise any relation between subsequent generations, an attempt has been made to define the developmental stages at which mortality factors operate most effectively. This has been done by establishing which "k" value is most closely related to Total Mortality "K". Results for these analyses are presented in Table IV (b). From these analyses, k_1, k_2 and k_4 are considered the more important mortality factors contributing to K.
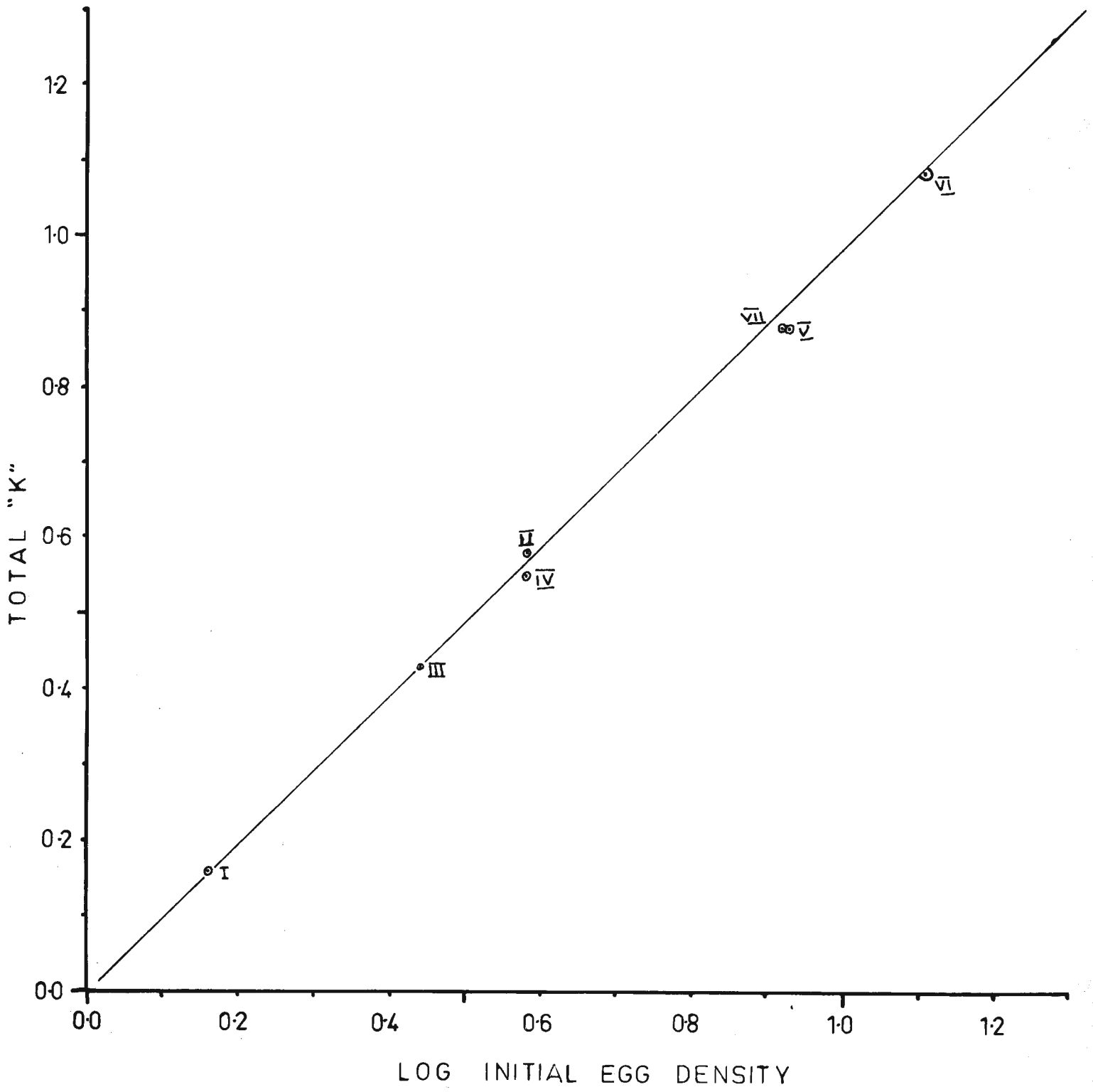
FIGURE 4(h) RELATIONSHIP OF TOTAL MORTALITY TO INITIAL EGG DENSITY

TABLE IV(b) CORRELATION DATA FOR INDIVIDUAL "k" VALUES AND TOTAL MORTALITY "K"

	"k" Values					
	k_1	k_2	k_3	k_4	k_5	k_6
r^2	0·2323	0·6043	0·0115	0·5543	0·2358	0·0003
b	0·3210	0·4414	0·0279	0·1595	0·0488	0·0012
a	0·0680	0·1345	0·0650	0·0600	0·0227	0·0389

r = Correlation Coefficient   b = Regression Coefficient (Slope)
a = Y intercept of regression line when   k = 0

It is significant that the values of the regression coefficients for k_1 and k_2 together amount to approximately three quarters of Total Mortality K. Although not evident from these calculations, it was expected that, in view of the exponential nature of the population graphs, the significance of k_1, would have been greater.

The density dependence of the key factors has been analysed by relating them to the log. of the population density before they acted (i.e., log. P_1 and k_1). These results are set out in Table IV (c). However, since there is no independence between these two values $(k_1 = \log. P_2 - \log. P_1)$, these analyses may be biased.

For this reason the relationship between successive populations $(P_{N-1}$ and $P_N)$ were calculated and results tabulated in Table IV (d). Any significant difference between the Regression Coefficient for each factor and unity was taken as an indication of density dependence. This follows the method as set out by Southwood (1968). From these analyses, the role of k_2 and k_4 as the key factors is shown to operate as undercompensating direct density dependent factors.

The time interval for each stage of development is set out in Table V (a) and for the purpose of these discussions is regarded as being similar for all stages. In the event of one stage having a longer duration than others the values of k associated with these stages would have to be compared with respect to the time over which they operated. Since it is assumed that the duration of each development stage is constant, no such considerations have been made.

TABLE IV(c) CORRELATION DATA FOR INDIVIDUAL
`k` VALUES AND LOG_{10} POPULATION DENSITY AT
START OF EACH AGE INTERVAL.

		k Values				
		k_1	k_2	k_3	k_4	k_5	k_6
r^2		0·2310	0·8290	0·5572	0·8465	0·5570	0·1990
b		0·3153	0·5694	0·4273	0·8285	0·5229	0·4104
a		0·0602	-0·0701	-0·0171	-0·0540	0·0040	0·0290

r = Correlation Coefficient   b = Regression Coefficient

a = Y intercept of regression line when k = 0

TABLE IV (d) REGRESSION DATA FOR ANALYSES OF POPULATIONS OF TWO SUCCESSIVE STAGES.

For the regression log N (X) against log N+1 (Y)

	2-1	3.-2	4-3	5-4	6-5	7-6
r^2	0·5464	0·7349	0·6933	0·6585	0·5114	0·4396
b	0·8123	1·7068	1·2106	1·7725	1·0720	1·2983
a	0·3413	-0·0154	0·0503	-0·0423	0·0505	0·0344

For the regression log N+1 (X) against log N (Y)

	1-2	2-3	3-4	4-5	5-6	6-7
b	0·6727	0·4305	0·5727	0·3715	0·4771	0·3392
a	-0·0454	0·0701	0·0191	0·0540	0·0040	-0·0018

r = Coefficient of Determination , b = Regression Coefficient

a = Y intercept when X = 0

TABLE V(a) FIELD OBSERVATIONS OF DEVELOPMENT
TIME(days) FOR Heliothis armigera

	Site No.			
	I	II	III	VI
Eggs	5·9	4·8	4·9	3·4
1 st	4·4	4·0	3·2	4·8
2 nd	3·5	1·5	6·6	5·0
3 rd	2·9	4·5	2·0	5·0
4 th	2·7	4·8	3·9	2·6
5 th	5·2	4·9	3·3	2·0
Total	24·6	24·5	23·9	22·8
Temperature	18·3°C	19·4°C	18·7°C	20·6°C

(c) Mortality Agents

Samples of eggs and larvae, taken on each sampling
date, failed to establish the activity of either parasites or
diseases operating against any stage of development during either
the 1971-72 or 1972-73 seasons. During 1971-72 however, at sites I
and II, 4.3% and 4.1% respectively of eggs sampled failed to hatch.
Examination of the unhatched material showed that these eggs were
fertile but they were damaged when collected. The majority of larval
parasites which have been observed from the south-eastern Queensland
area have been noted by Sloan (1940) as emerging from the host during
the prepupal and pupal stage and as such would not be regarded as a
causal factor in relation to the decline in the larval population
per cob.

Since no significant decrease in populations may be
attributed to either parasites (against egg and larva) or diseases,
it remains that the observed decline in population is a result of
climatic factors, predators or cannibalism between larvae and of eggs
by larvae. Of these three possibilities neither climate nor predators
were monitored. Apart from the occasional Arachnid, no recognised
predators of Lepidopterous larvae were collected or observed in the
sample areas.

It is considered that, in view of the cannibalistic
habits of H. armigera cited elsewhere, (see page 15) the
population decline as monitored is a result of cannibalism between
larvae and of larvae devouring unhatched eggs.

The mortality factor "k_2", regarded in this present study as being one of the major key factors associated with population decline, is that operating between first and second instar populations, a condition which operates most frequently at the throat of the cob. This area is a relatively constricted one and represents the point through which all newly emerged larvae pass to enter the cob and begin feeding on the developing grain. The opportunity for larvae to come in contact with each other and thereby encourage conflict between individuals is greater at this point than at any other point within the cob.

(d) <u>Prediction of Density Levels Per Cob</u>

Since the total mortality K from egg to final instar is equivalent to the sum of the individual mortalities associated with each stage of development, the sum of regression coefficients in Table IV (b) approximates to unity.

Table IV (b) sets out the relationship between the value of total mortality (in this case the logarithmic value of the number of eggs per cob since the density of final instars is unity) and the individual mortalities operating between successive development stages.

The slope of these regression lines then indicates the proportion of the egg population which is removed after that mortality factor has operated. Hence of 10 eggs found on a cob (10−(0.32x10)) = 6.8 will survive to first instar and, of these (6.8−(0.44x10)) = 3.4 will survive to second instar and continue to reduce through remaining instars. Density of the final instar is unity.

From these regression coefficients it is therefore possible to construct an equation to describe the decline in density of instars per cob:-

$$\log. Y_i = \log. E (1-X_i)$$

where Y_i = number of stage i per cob

         E = number of eggs per cob

$$X_i = \sum_{a=i}^{a=1} b_i$$

where b_1 = 0.3210

         b_2 = 0.4414

         b_3 = 0.0279

         b_4 = 0.1595

         b_5 = 0.0488

         b_6 = 0.0012

From these equations the population decline associated with initial egg density has been calculated and presented on page 68. A Chi Squared analysis to test the suitability of this equation is set out in Appendix C (see page 68). This test shows a good fit of the data to this equation. However, such a situation was to be expected since the observed population decline data was used to calculate the regression coefficients used in the equation being tested.

A predictive equation as is discussed above must be regarded as a function of a particular variety of maize. Although breeding of hybrid maize varieties now tends to favour the "tight husked" varieties and all such varieties would be relatively well covered by the above equation, any variation in cob characteristics from those of the variety used here would tend to alter the value of the regression coefficients calculated from analyses of results for each k value and total mortality K.

iv) DISCUSSION:

(a) Methods

The study of insect populations and the quantification of results in terms of life tables and subsequent mortality analyses has been used in ecological studies since the 1940's when Richards (1940) and Deevey (1947) focused attention on these methods. Southwood (1968) has reviewed the methods of quantifying population dynamics and then recognises three main methods of relating population trends to mortality agents. They all relate variation in population numbers to the activity of mortality factors. Southwood (1968) emphasises that the methods in no way prove a causal relationship and illustrates this point by citing work by Varley (1963).

The first method was proposed by Watt (1961) in which he expresses graphically, and then mathematically, the magnitude of the various factors with the population survival in particular stages of development. Watt (1961) set out to describe the survival of each development stage as a function of factors most likely to have caused mortality at these stages. The appropriate function was calculated and its suitability tested by comparing calculated and observed results. Further variables were added to the function in order to explain as much of the observed results as possible. Morris' (1959) approach is a little less mathematical and involves sampling a particular stage of development for successive generations and at the same time monitoring the likely limiting factors. Morris regards populations as being regulated by several key factors and his approach is designed to formulate predictive equations describing population trends.

The last method, developed by Varley and Gradwell (1960) is the easiest to use but relies heavily on mathematical correlations as well as sampling each age interval within the life cycle over a number of successive generations. From these results the age interval at which key factors operate is easily distinguished and natality between successive generations is measured. It is then possible to assess the way in which the key factors operate in controlling populations. Southwood (1968) presents further extensions to the method of Varley and Gradwell (1960) which covers situations where only incomplete life tables may be produced for successive generations.

My results have been analysed using a system similar to that of Varley and Gradwell (1960) since the purpose of the study was to follow population decline from egg to final instar and relate this decline to the activity of "key factors". Since the agronomics of the crop do not allow for successive generations on the one plant, assessments of population trends from generation to generation were not needed. The value referred to in the present calculations as Total Mortality (K) does not then represent mortality within one complete life cycle but rather the mortality operating from egg to final instar.

From analysis of the data along these lines it is obvious that mortality due to cannibalism operating within the larval stages represents a major regulating factor in the development of populations of H. armigera within maize crops under a monoculture regime. The present analyses also indicate that the expression of this factor is related to initial egg density and hence is a density dependent factor.

The role of density dependent factors has been disputed by several workers such as Andrewartha and Birch (1954, 1960) and Andrewartha (1961) who regard the control of populations to be a result of the activity of physical factors such as inaccessibility to material resources. The work by Andrewartha (1939) on _Austroicetes cruciata_ (Saussure) and by Andrewartha and Birch (1954) on _Thrips imaginis_ Bagnall confirm their theories. However, Smith (1961) concluded that from correlation methods of data for _T_. _imaginis_ there was a strong "inverse correlation between population change and population size" hence signifying that density dependence could also be inferred from the data.

Nicholson (1957) has rejected the theory of Andrewartha and Birch (1954) and developed further the ideas of Howard and Fiske (1911) and recognised a number of environmental elements as being necessary for population growth and control. He considers these elements to operate as density governing (i.e., density dependent) or non-reactive (density independent) and as such accepts a population as being a self regulating system within the ecosystem.

Further to these two theories Milne (1957, 1962) synthesised yet another theory incorporating the value of both these previous two theories and suggested that control of a population is due to a "combined action of density independent and imperfectly density dependent" factors and in cases where the combined action of these two factors fails, any population increase is prevented by competition between individuals, a situation which has been experienced by the present study.

When considering all these theories Clark et al. (1967) regarded them as different ways of regarding and evaluating the same things, conditioned by personal experience and preference, but overall they favour that of Nicholson (1957) as the most "comprehensive and penetrating".

(b) Cannibalism

The importance of cannibalism as a population governing factor has been documented by many workers (Barber, 1936, Sloan, 1940, Hardwick, 1965). However, none of them report a population decline as low as one final instar per cob. Wiseman et al. (1969) reported that when three species of maize pest (H. zea, H. virescens, and Spodoptera frugiperda (Smith) are placed together in a maize cob, only one larva of H. zea survived per cob and concluded that the corn earworm was obviously the "most cannibalistic" of the three species. Further, Blanchard and Douglas (1953) also reported cannibalistic habits as an important factor in helping to reduce damage to corn, and report that when large numbers of Heliothis are present in cobs, less damage is done since more time is spent by the larvae in conflict with each other and hence devouring each other. Barber (1936), although only recording population decline to 2.2 larvae per cob from sampling in the field, did recognise that, for populations of larvae in salve boxes fed on dough stage corn kernels (a condition he recognised as providing conditions as close as possible to those in the field) in no case was there more than one larva completing development in each box, even with initial populations as high as fifty first instar larvae. Barber (1936) also recognised the need to breed plant types with a well developed husk to promote the activity of cannibalism amongst larvae.

Widstrom et al. (1970) further confirmed this by showing that, after an extensive study of 36 inbred lines, the mechanical protection of tight husks reduced damage considerably.

(c) Other Mortality Factors

The incidence of parasites of both the egg and larval stage appears to vary from area to area and season to season. Work by Twine (1973) establishing the incidence of parasites of Heliothis spp. in South-east Queensland at the time these present studies were carried out, failed to find any evidence of egg parasites operating in samples of eggs from maize silks, and reported an overall parasitism rate of 8.0% Sloan (1940), on the other hand, reported a higher degree of parasitism in Central Queensland but also concluded that the incidence of these parasites varies a great deal.

Overseas data by Oatman (1966) also confirm this variability although, for their samples from maize silks in Southern California, the parasitism rate was as high as 38% over a three year period.

From the temperature data recorded at some sites (I, II, III and VI) and the results established in Section II it has been assumed that the mortality associated with temperature was negligible. Although very little work has been carried out on the influence of climatic factors, the results of Bertels (1970) indicate that humidity at least plays a very minor part in population control.

v) CONCLUSION:

The dynamics of a larval population of H. armigera has been quantified in terms of the decline in larval numbers per cob, associated with larval growth.

Although a wide range of initial egg densities on the cobs was examined, it was significant that the density of final instar larvae per infested cob was consistently reduced to unity, thereby emphasising the density dependent nature of the larval mortality factors operating. The activity of parasites and diseases was monitored but this failed to adequately explain the observed decline in population density. Predators and climatic factors, although not accurately monitored and assessed, were considered insufficient to have caused the larval population decline.

The mortality associated with intraspecific competition of developing larvae was considered to be the main causal factor operating and, in particular, the mortality observed between the first and second instar. The cannibalism amongst developing larvae was considered as operating at all instars as well as by first instar larvae on eggs.

As a result of these conclusions it would seem there is a need for further field assessments of the extent of cannibalism amongst H. armigera larvae in other susceptible economically important crops where recognition of this natural controlling condition may be sufficient to exclude the need for use of any of the artificial control agents.

This would be particularly true of sorghum where the demand for a "closed head" line is increasing. These plants provide a restricted area in which intraspecific competition would be pronounced with high egg numbers laid on the head.

Also of importance in some crop situations would be an assessment of Heliothis spp. populations in conjunction with other pest species in order to describe the possible existence of interspecific competition by Heliothis spp. larvae.

V. DEVELOPMENT UNDER FIELD CONDITIONS

i) INTRODUCTION:

An account of the relationship between rate of development of the larval stage of H. armigera and temperature was developed in Section II. The calculations involved in this work were based on development under controlled conditions of constant temperature.

From the data collected in Section IV and from measurements of temperature at the Sites examined it was possible to evaluate the development of successive instars, the time taken for their development and hence the relationship between this rate of development and observed temperature.

Temperatures were recorded at four sites only (Sites I, II, III and VI) with a Casella Thermohydrograph in a meteorological screen box one metre above ground level in the vicinity of the sampling area. For each day, 24 hourly temperatures were averaged to calculate the mean daily temperature.

ii) RESULTS:

Since the population being sampled on each occasion could be regarded as a single cohort it was possible to estimate the time taken for each development stage. The dynamics of the development of population of the various stages of development are presented in Figure 5 (i) to 5 (iv) inclusive for Sites I, II, III and VI respectively with the populations illustrated being determined from examinations of fifty infested cobs. When fewer than fifty infested cobs were examined the populations were adjusted accordingly.
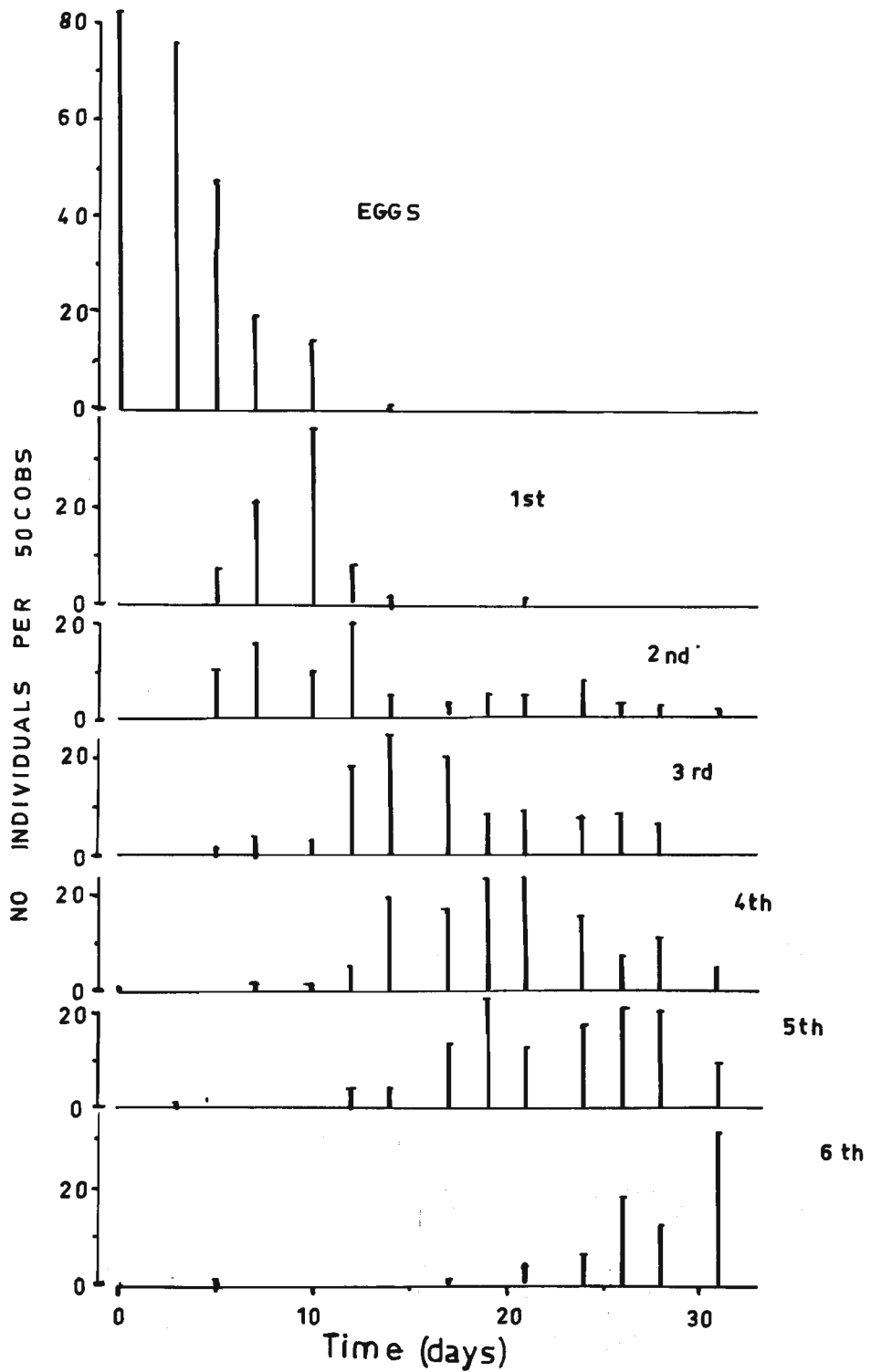
FIGURE 5(i)   POPULATION DEVELOPMENT FOR EACH
STAGE OF GROWTH — SITE I
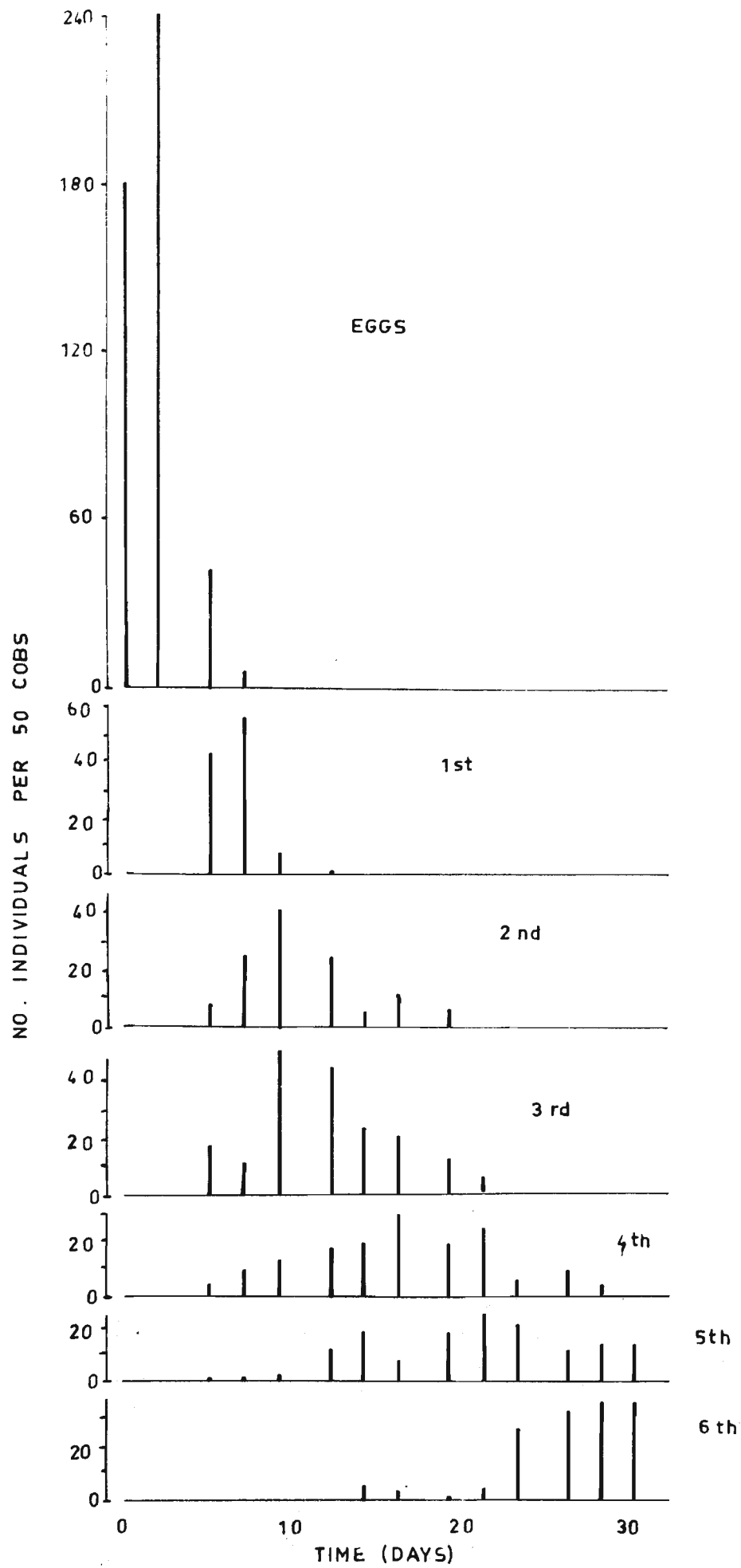
FIGURE 5(ii) POPULATION DEVELOPMENT FOR EACH
STAGE OE GROWTH — SITE II

FIGURE 5(iii) POPULATION DEVELOPMENT FOR EACH
STAGE OF GROWTH—SITE III
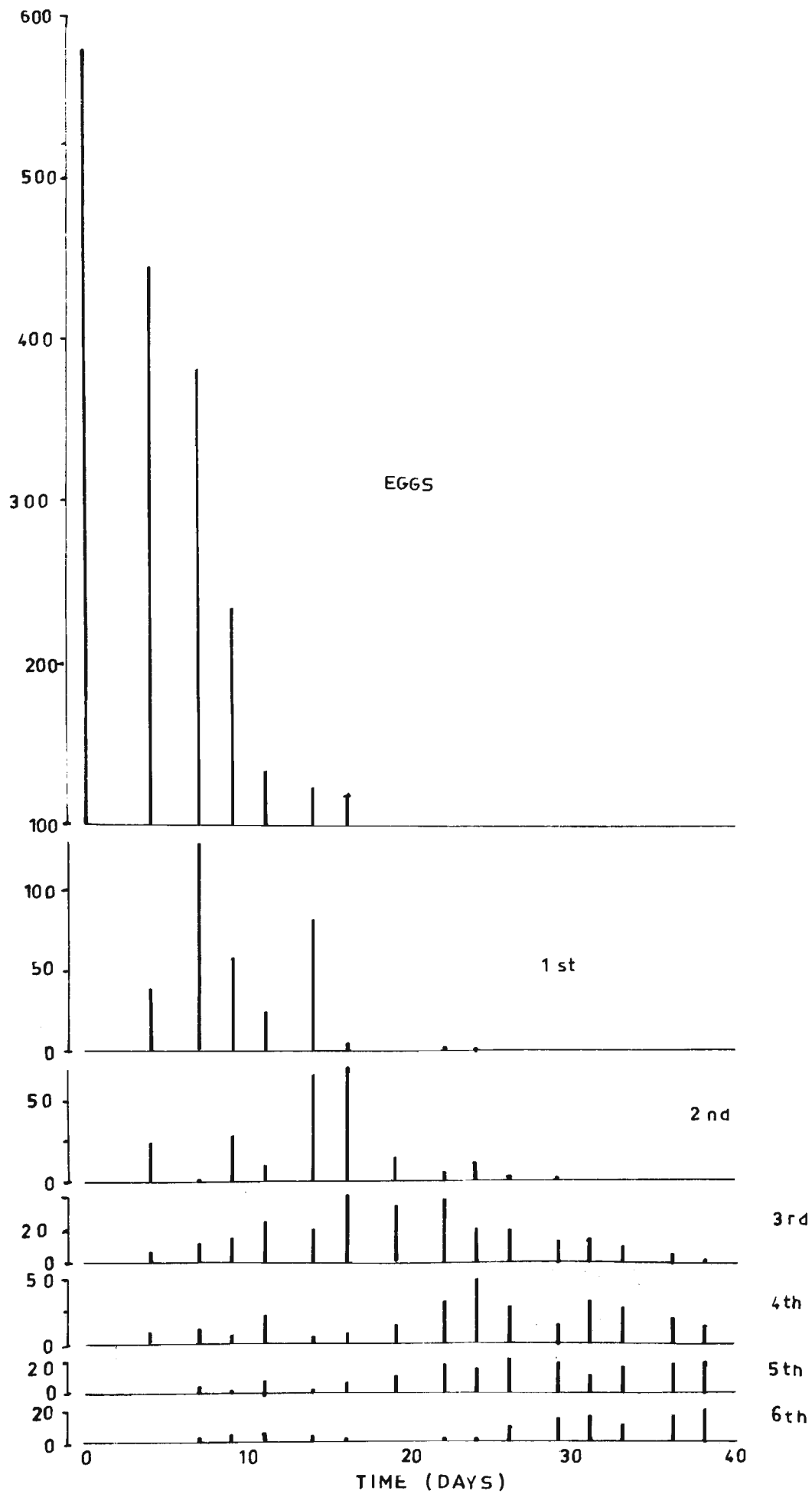
FIGURE 5(iv)   POPULATION DEVELOPMENT FOR EACH
STAGE OF GROWTH-SITE VI

For each development stage the mean time taken for the appearance of all individuals was calculated with the difference between this value for two successive stages representing the development time of the earlier stage. The results of calculations have been listed in Tables V (a).

Summation of development times of particular stages over all four sites indicate that, while varying greatly from site to site, the duration of each of the first five instars is comparable to one another and that the egg stage is slightly in excess of that of the larval instars. Recording of the prepupal or pupal stage of development was not made and hence no evaluation of the duration of the final (sixth) instar was possible.

The calculated average for the duration of the egg stage could be slightly lower than expected since in most cases the sampling of cobs was not commenced until almost peak of oviposition activity and the calculated mean time taken for the appearance of eggs would be higher than if the eggs laid prior to the commencement of sampling were included.

By applying the principle of the Thermal Summation Constant as outlined in Section II for results of development time from egg to fifth instar in relation to the screen box temperatures, the relationship may be expressed by the following equation

$$Y = 0.00124 \; X + 0.0179 \quad (r = .8593)$$

where Y = Reciprocal of Development time in days

T = Temperature (^{o}C)

r = Regression Coefficient

Such an equation, based on results at four temperatures only, evaluates the Threshold Temperature at 14.4^o and a Thermal Summation Constant of 806.4 day degrees from egg to fifth instar. These results are inconsistent with data presented in Section II and indicate general inconformity with the Thermal Summation Principle under the conditions of the study.

iii) DISCUSSION:

Examination of the temperatures recorded at each of the four sites indicates that screen box temperatures regularly approached the Threshold temperature of approximately 10°, as calculated on page 20, each evening. In view of the fact that the principle of Thermal Summation, as described by Wigglesworth (1965) holds only over the "normal" range of temperatures, a discrepancy of this nature would be anticipated.

The principle assumes that the effect of temperature on growth is the same at all stages of the developmental process and where this is not the case, particularly at the extremes of the temperature range, it is only possible to apply the thermal summation procedure when the effect of temperature has been evaluated over the entire temperature range.

The slope of the regression line relating temperature to the speed of development was expected by Wigglesworth (1965) to become less steep as it approaches the lower temperatures so that the calculated threshold temperature is not in fact the true threshold of development.

Another factor to be considered in the comparison of laboratory and field collected results is the effect of alternating temperatures on growth rate.

Parker (1930) whilst observing temperature effects on <u>Melanoplus</u> <u>atlanis</u> concluded that the alternation of temperature seemed to stimulate development when compared to development times under continuously hot conditions.

Howe (1967) criticised the study of the effect of temperatures on growth rate where fewer than ten temperatures were involved. While the practicality of this suggestion for field observations is questionable, the variability of results of the present study indicates that further data **are** required for an accurate assessment of temperature effects in the field.

VI. GENERAL DISCUSSION

The use of life tables to describe the dynamics of
an insect population is an extension of a technique used by
actuaries in following the life expectancy of human beings
(Southwood 1968). Basically they are intended to define the number
of individuals entering particular age classes within the
population and from an analysis of these data, to establish the
stage of growth at which mortality factors are most likely to cause
reduction in the population, and finally to describe the nature of
the mortality factor involved.

Pest control research is now centering around these
ecological studies whereby the dynamics of the natural insect
population is defined in terms of a life table and the nature of
the natural mortality factors operating is studied to ascertain
their usefulness in terms of a practical method of pest control.

Life tables are highly desirable for important
economic pests, where resources are available to permit the
construction of an adequate series of them. The age specific data
accrued in this way include the effects of both the key variables and
other variables and are ideal for use in pest population management.

The present study was set up with this goal in view.
However, before such a life table could be formulated to provide the
detail required, several unknown aspects of the pest species had to
be ascertained.

The first of these was the study of the larval growth
patterns of H. armigera. This was necessary to define the various
instars so that the role of mortality factors could be calculated in
terms of the population decline between successive instars.

Histograms drawn from the field collected material (Fig. 3 (d)) indicated that the distinction of instars on the basis of head capsule width measurements was not reliable since there was an overlap of distributions of head capsule width measurements for successive instars.

Two series of examinations of individual larvae throughout larval life were made using laboratory bred larvae. These studies confirmed that the number of larval instars was not consistent, even under similar conditions of food and temperature, and varied between five and seven. This variability confirmed that documented by Hardwick (1965) although the proportions of the population studied by Hardwick which developed through the various number of instars, differed from those of the present work. This was attributed to the different food sources used in the two studies. It was also suggested that the viability of the material used in terms of the breeding of the parent stock was different for the two cases and, as such, may be responsible for these discrepancies. For the purpose of identification of field collected larvae, larval growth was considered to be defined by six larval instars only and no allowance made for the discrepancies observed.

The causal nature of the observed variability of the the number of instars was not investigated although, as previously discussed, the variation existed even under controlled conditions of food and temperature.

The second study undertaken was to investigate the reaction of larval growth to field temperatures. This was necessary to evaluate the life expectancy of the various instars so that a sampling programme could be planned which adequately detected the various instars as they developed.

The Principle of Thermal Summation (Wigglesworth 1965) was applied to larval development times observed at four temperatures within the "normal range". Because of the variability of the number of instars previously noted, no assessment of the development times for particular instars was made, but rather it was assumed that it was equal for all instars. This assumption was later shown to be valid, based on results of development times noted under field conditions.

The Threshold Temperature calculated for the larval stage was 10.7°. Examination of the temperatures recorded in meteorological screen boxes at Sites I, II, III and VI showed that the evening temperatures at each of these Sites regularly approached the Threshold Temperature. Since the Thermal Summation Principle only holds within the "normal range" of temperatures, as temperatures approached the threshold temperature it was expected that development times would be longer than those predicted by the Summation formula. Analysis of data collected from field observations confirmed this difference.

Due to the variability of success of breeding of larvae of Heliothis spp. under laboratory conditions, a technique of breeding using an artificial diet and requiring a minimum of handling was developed. The artificial diet proved sufficient for short term use but had obvious deficiencies when used on a long term basis.

On the basis of results obtained with the various laboratory studies, a sampling programme was set up whereby fifty infested cobs were examined on each of three occasions each week and the head capsule measurements of larvae found within each cob was used to define its instar. From these data the decline in population density per cob was detailed.

Although the larvae present within one planting were considered as belonging to a single cohort, it was common for a number of larval instars to be present within one cob. To overcome this situation, the stage of development of the whole population within a cob was regarded as belonging to that of the largest instar present.

The results of population decline were analysed along similar lines to those of Varley and Gradwell (1960) although the Total Mortality (K) referred to by these authors as the mortality between two successive generations has been taken as the mortality operating between the egg and the sixth instar of one generation, and k values representing the mortality operating between two successive instars.

The regression analyses carried out on the data collected from seven sampling sites indicate the importance of k_1, k_2 and k_4 as the main factors contributing to the overall mortality measured, and of these three factors, k_1, and k_2 account for 76% of the Total Mortality (K).

The most significant result from the study was the role of total larval mortality in terms of the initial egg density. At each of the seven sites, irrespective of the initial egg density, the population of final instar larvae in infested cobs was consistently reduced to unity.

The significance of the density dependence of larval mortality as a controlling influence on population dynamics was exemplified by the regression coefficient (b=0.9839) and correlation coefficient (r=0.9989) from regression analyses between total larval mortality (K) and egg density (log. scale).

During the course of sampling at each site, eggs and larval samples were returned to the laboratory for assessment of the incidence of egg and larval parasites and disease. Such samplings failed to explain the observed population decline and it was proposed that the causal factor related to k_1 and k_2 was cannibalism, particularly of newly hatched larvae on eggs and between the early larval instars as they move from the silks into the developing cob.

Cannibalism has frequently been observed in insect species, especially at time of overcrowding or when food is in short supply. Cannibalism also commonly occurs when individuals suffer accidental injury or when they are temporarily incapacitated during moulting. Barber (1936) observed and described the method of attack and subsequent consumption associated with cannibalism of H. zea larvae. Two other of the best known insects in which cannibalism occurs are the flour beetle Tribolium confusum (Chapman 1928) and the Codling moth (Geier 1963).

From results detailed in Table IV (b), the regression coefficient for a regression of individual k and total K represents the proportion of K attributable to each k. It was therefore possible to quantitatively define the decline in population within a cob from egg to final instar in the form of an equation in terms of the initial egg density and the calculated values of the regression coefficient. Such an equation then allows the prediction of the densities of the various instars, and, in conjunction with food intake studies would allow for assessment of theoretical food intake calculations prior to pupation and the likelihood of a population posing an economic threat.

It has become apparent during the study that the role of larval mortality of H. armigera in maize represents the major population controlling factor operating, with the incidence of disease and parasites insufficient to significantly reduce a population of larvae. Although the size of moth populations may vary from season to season, it does not necessarily follow that larval populations in excess of one larva per infested cob will result. The cannibalistic habit of the developing larvae and the confined ecological niche where development occurs favour a natural controlling factor to operate and act as a regulatory agent of an otherwise intense larval population.

Although the extent of population decline possibly attributable to H. armigera is expected to be greater in maize than in many other crops, it must be assumed that its magnitude may still be significant in situations where high larval numbers can be expected within relatively restricted areas of plant. One crop in which this would be assumed to exist is in sorghum where, once again, relatively high numbers of early instar larvae can be observed but, particularly with the "tight head" characteristic observed with many hybrid varieties, the final instar population is often economically insignificant. In lucerne and similar crops which afford a large leaf area per larva ratio, the likelihood of conflict between two larvae is reduced as would be the possible decline in larval population attributable to this cause.

Like all attempts to explain the abundance of insect species, the present study is far from complete and some of the conclusions drawn will doubtlessly require modification in the light of further investigation.

APPENDIX A

THE METHOD OF REARING H. ARMIGERA IN THE LABORATORY

As has been the experience of a number of workers
(Wate s, 1943; Callahan, 1962; and Cullen 1969) attempts to rear
large numbers of Heliothis sp. under laboratory conditions have
resulted in varying degrees of success. For the present work,
early attempts at rearing presented considerable difficulty and a
number of techniques were tested in an attempt to devise a method
to provide the required number of individuals for the minimum of
effort.

The feeding of larvae on natural foods, while
simulating natural conditions, is a laborious task necessitating
the provision of fresh food (usually French Beans) on a daily
routine and in doing this the likelihood of inflicting damage or
contamination is increased. For small numbers of larvae however,
this method proved satisfactory.

To overcome the requirement of periodic handling of
larvae and food the use of artificial diets was attempted. Although
some methods are time consuming in preparation, the time saved by
handling larvae only once more than compensated. The artificial
diet used for the present work was one based on Navy Beans, the
contents of which are listed in Appendix Table A (i). Navy Beans
were soaked overnight, drained and weighed prior to use.

Using a commercial Waring blender all A ingredients
were thoroughly blended into a smooth thin paste. The agar is
dissolved in boiling water and then both A and B ingredients
thoroughly mixed and allowed to s and at 60° until required for
dispensing.

APPENDIX TABLE A(i)   CONTENTS OF ARTIFICIAL DIET

A. INGREDIENTS

Soaked Navy Beans	234 gms.
Dried Yeast	35 gms.
Wheat Germ	50 gms.
l-Ascorbic Acid	3·5 gms.
Nipagin	2·2 gms.
Sorbic Acid	1·1 gms.
Formaldehyde (10%)	8·8 mls.
Corn Oil	2 mls.
Water	400 mls

B. INGREDIENTS

Agar	14 gms.
Water	400 mls.

<u>APPENDIX TABLE A (ii)</u>   PHYSICAL PROPERTIES OF DIET

% Protein (Dry Wt Basis)	24·3 %
% Dry Matter	16·8 %
pH	5·3
Melting Point	93°C
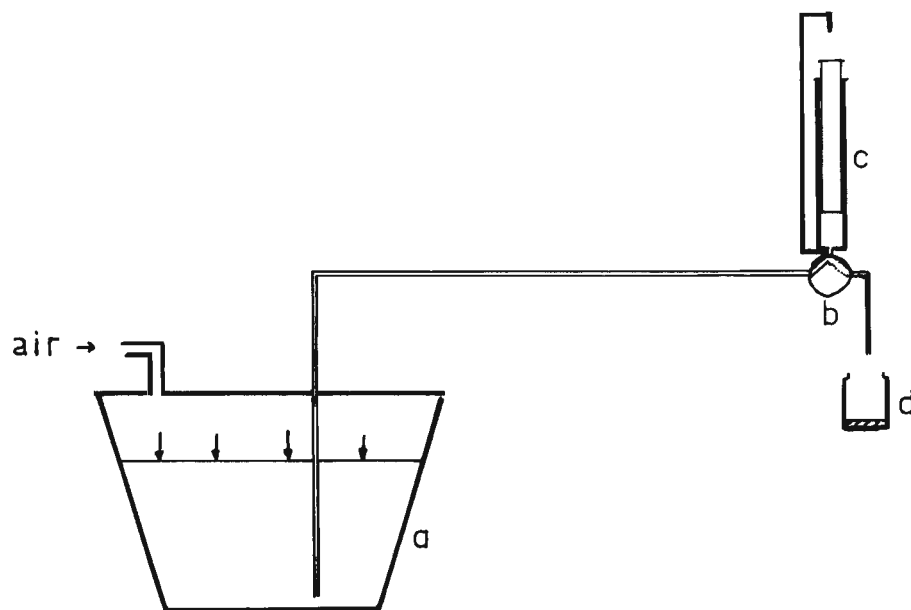
APPENDIX FIGURE A(i)   DIAGRAM OF DISPENSING
APPARATUS

a).pressure vessel   b).two-way valve
c).graduated syringe d).vial

The thermal instability of several vitamins in the mixture prevents the storage of this hot mixture and does not allow it to solidify and be subsequently melted (94°) when required. Some physical properties of the diet are listed in Appendix Table A (ii).

The liquid is held in a modified pressure cooker similar to that used by Burton et al. (1966) immersed in a water bath and dispensed under pressure through an automatic media dispenser as illustrated in Appendix Figure A (i). Dispensed media was stored under refrigeration (5°).

For most work glass vials were used to contain the larvae and media and when required for breeding the bottles were not handled until after moth emergence.

An important phase in the entire process is cleanliness. The use of antibiotics should be avoided and any source of contamination (particularly of wilt virus) should be traced and eliminated by exclusion, disinfestation or sterilisation. For the work described here only the rearing containers were autoclaved (100k Pa. for 20 minutes). However, when field collected material was returned to the laboratory for further study, a high degree of hygiene was required to eliminate the introduction of diseases.

Eggs may be surface sterilized by washing them in a 0.2% Sodium hypochlorite solution for 5-7 minutes (or 0.05 M Potassium hydroxide - McMillian and Wiseman 1972) and then thoroughly washed with distilled water and dried. Timing is critical. A marked reduction in egg fertility is produced by excessive exposure to the sterilising solution.
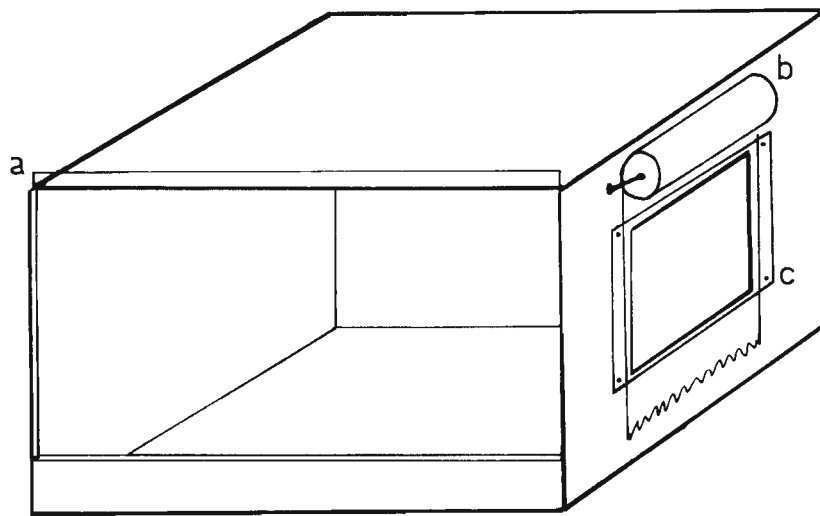
APPENDIX FIGURE A (ii)   OVIPOSITION CAGE
a) glass sheet b) paper roll
c) perspex cover

Cannibalism (Barber 1936a; Patel 1965; Bot 1966)
can be overcome by breeding larvae in individual containers
although adequate numbers can be bred by rearing larvae together
until the third instar stage.

For the present study first instar larvae were placed
into each vial although McMillian and Wiseman (1972) have described
a technique of infestation involving the preparation of egg
suspensions in 0.1% agar solutions.

Moths emerging from the rearing containers were
released into wooden boxes (see Appendix Figure A (ii)) and
provided with a 10% honey solution and an oviposition site of paper
towel. The boxes were entirely light proof except for the paper
towel area which was given a low illumination to simulate dusk
conditions inside the box. When the box was subjected to daylight,
oviposition was noticeably reduced. To avoid decreased egg
production with increasing moth density (Guerra et al. 1972) no more
than 15 pairs of moths were used in each cage.

The usefulness of the diet and technique may be
gauged by results listed in Appendix Table A (iii) based on
colonies of both H. armigera and H. punctigera bred for consecutive
generations on this diet. The results indicate that successful
rearing can only be obtained over four generations with the final
generation being characterised by abnormally long larval and pupal
life as well as decreased pupal weight. The problem of malformed
wings of emerging adults is considered as being related to a
Vitamin E deficiency as described by Cunningham (1972).

APPENDIX TABLE A (iii)   VIGOUR OF COLONY OF HELIOTHIS SPP. BRED ON ARTIFICIAL DIET

GENERATION NO.	EGGS		LARVAE		PUPAE			ADULTS	
	NO. EGGS PER FEMALE	% HATCH	LARVAL LIFE (Days)	% MORTALITY	PUPAL WT. (gms)	PUPAL LIFE (days)	% MORTALITY	% MALE	% MALFORMED
Heliothis punctigera									
1					·3601	10·1	11·0	57·6	2·0
2	1256	84·6	14·0	8·0	·3349	15·8	15·9	66·7	8·3
3	1144	89·0	13·9	12·0	·2546	19·2	36·3	70·0	4·5
4	634	97·7	26·5	34·0	·2663	23·7	69·6	50·0	4·8
Heliothis armigera									
1				14·8	·4072	14·8	13·9	48·8	17·3
2	1263	93·0	13·4	2·2	·3986	15·8	10·8	48·0	34·7
3	713	100·0	19·7	19·2	·3752	17·6	23·7	53·2	7·8
4	1709	81·9	34·6	51·0	·3572	26·4	34·7	50·0	31·2

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Burton (1970) further modified a previous technique (1969) incorporating C.S.M. (for Corn, Soy flour and Milk solids) by the addition of yeast and wheat germ, two inexpensive supplements that allowed continuous breeding for more than 12 generations as compared to 4 generations prior to the modification.

Vanderzant (1969) however, considers that in many cases, the failure of a diet to support continuing generations of insects is not always due to the nutritional qualities of the media but rather to some deficiencies in the physical aspects of the diet. The detrimental effect of too much water in the media has been shown by Raulston and Shaver (1970) and further confirmed by Hare et al. (1973a). These latter authors consider that the best results are obtained by having most of the moisture of the diet removed by the time of pupation.

Patel et al. (1965) recognised the need to alter the constituents of diets to suit various species in different areas. By using powdered lucerne for H. armigera in India, they were able to successfully rear at least 22 consecutive generations.

It is obvious therefore that, although the present diet can support a few generations, it is lacking in quality to enable long term breeding without loss of vigour.

APPENDIX B

FIELD DATA

Data collected during the field assessment of
population decline per cob are presented in Tables B (1) to B(7).
At each of the seven plantings of maize examined, samples of fifty
infested cobs were taken on three occasions each week during which
immature stages of H. armigera were present in the field. On a
number of occasions bad weather conditions made the sampling sites
inaccessible and, to overcome this, one hundred samples were taken
at the next sampling date.

In order to assess the density of individuals within
fifty infested cobs it was necessary to examine more than this
number of cobs owing to the low infestation levels. The number of
uninfested cobs is also presented in the Tables.

Although the cohort examined on each occasion was
regarded as being uniform, it was common that more than one stage
of development be present within the cob. Rather than assessing
the density in these cobs in relation to each of the stages it was
decided that all the individuals present be regarded as belonging
to the largest development stage present. Hence a cob containing two
third instars and one fourth instar was classified in this present
data as having three fourth instar larvae present.

TABLE B(1) THE NUMBERS OF VARIOUS STAGES OF DEVELOPMENT OF <u>Heliothis armigera</u> PRESENT ON EACH SAMPLING DATE — SITE I

Date	eggs no.	eggs cob	1st no.	1st cob	2nd no.	2nd cob	3rd no.	3rd cob	4th no.	4th cob	5th no.	5th cob	6th no.	6th cob	Total no.	Total cob	No. of uninfested cobs
4.ii.1972	82	49							1	1					83	50	134
7.ii.1972	76	49									1	1			77	50	76
9.ii.1972	47	37	7	5	10	6	1	1					1	1	66	50	157
11.ii.1972	19	17	21	18	15	9	4	4	2	2					61	50	170
14.ii.1972	14	13	36	27	10	6	3	3	1	1					64	50	191
16.ii.1972			7	6	20	19	18	16	5	5	4	4			54	50	140
18.ii.1972	1	1	1	1	5	5	25	23	19	17	4	3			55	50	107
21.ii.1972					3	3	20	18	17	16	13	12	1	1	54	50	107
23.ii.1972					5	5	8	8	23	19	22	18			58	50	115
25.ii.1972			1	1	5	4	9	9	23	21	12	11	4	4	54	50	138
28.ii.1972					8	7	7	6	15	14	17	17	6	6	53	50	210
1.iii.1972					3	2	8	8	7	6	20	16	18	18	56	50	126
3.iii.1972					2	2	6	6	11	11	19	19	12	12	50	50	342
6.iii.1972					1	1			5	5	9	9	35	35	50	50	271
8.iii.1972							1	1	1	1	3	3	1	1	6	6	109
Total	239	166	73	58	87	69	110	103	130	119	122	113	78	78	839	706	2393
No. per cob	1·440		1·259		1·261		1·068		1·092		1·080		1·000				

Date	eggs no.	eggs cob	1st no.	1st cob	2nd no.	2nd cob	3rd no.	3rd cob	4th no.	4th cob	5th no.	5th cob	6th no.	6th cob	Total no.	Total cob	No. of uninfested cobs
16.ii.72	181		2												183		44
		49		1												50	
18.ii.72	240														240		8
		50														50	
21.ii.72	42		43		8		17		4		1				115		34
		17		15		3		10		4		1				50	
23.ii.72	6		56		25		11		8		1				107		21
		6		30		6		4		3		1				50	
25.ii.72			7		40		51		13		2				113		17
				5		16		21		7		1				50	
28.ii.72			1		24		45		16		8				94		18
				1		16		18		9		6				50	
1.iii.72					4		24		19		17		5		69		27
						4		16		13		12		5		50	
3.iii.72					11		21		28		7		3		70		20
						9		16		15		7		3		50	
6.iii.72					5		13		19		17		2		56		88
						3		13		16		16		2		50	
8.iii.72							6		23		23		4		56		81
								6		20		20		4		50	
10.iii.72					1				5		20		26		52		50
						1				4		20		25		50	
13.iii.72									9		10		32		51		203
										8		10		32		50	
15.iii.72									3		14		34		51		182
										3		13		34		50	
17.iii.72									1		10		23		34		202
										1		10		23		34	
Total	469		109		118		188		148		130		129		1291		995
		122		52		58		104		103		117		128		684	
No. per cob	3.844		2.096		2.035		1.808		1.437		1.111		1.008				

TABLE B(3)   THE NUMBERS OF VARIOUS STAGES OF DEVELOPMENT OF <u>Heliothis armigera</u> PRESENT ON EACH SAMPLING DATE — SITE III

Date	eggs no.	eggs cob	1st no.	1st cob	2nd no.	2nd cob	3rd no.	3rd cob	4th no.	4th cob	5th no.	5th cob	6th no.	6th cob	Total no.	Total cob	No. of uninfested cobs
6.iii.1972	191														191		40
		50														50	
10.iii.72	114		21		1										136		21
		43		6		1										50	
13.iii.72	80		12		10		1								103		48
		34		9		6		1								50	
15.iii.72	27		36		2		3		3						71		51
		17		27		2		2		2						50	
17.iii.72	10		21		44		9		3						87		60
		7		15		21		5		2						50	
24.iii.72			2		14		29		61		21		4		131		162
				1		12		24		43		16		4		100	
27.iii.72					6		18		50		28		9		111		240
						6		17		41		23		9		96	
29.iii.72							16		43		39		15		113		298
								15		37		35		13		100	
6.iv.72							6		6		36		51		99		566
								5		6		35		50		96	
11.iv.72									1				3		4		327
										1				3		4	
Totals	422		92		77		82		167		124		82		1046		1813
		151		58		48		69		132		109		79		646	
No. per Cob	2·795		1·586		1·604		1·188		1·265		1·138		1·038				

TABLE B(4) THE NUMBERS OF VARIOUS STAGES OF DEVELOPMENT OF <u>Heliothis armigera</u> PRESENT ON EACH SAMPLING DATE – SITE <u>IV</u>

Date	eggs no.	eggs cob	1st no.	1st cob	2nd no.	2nd cob	3rd no.	3rd cob	4th no.	4th cob	5th no.	5th cob	6th no.	6th cob	Total no.	Total cob	No. of uninfested cobs
8.i.73	322														322		3
		50														50	
10.i.73	134		34		1		4								173		4
		40		7		1		2								50	
12.i.73	94		32		15		2								143		16
		37		9		2		2								50	
16.i.73	63		20		40		12		12		10		20		177		47
		32		10		17		8		6		9		18		100	
19.i.73					7		4		3		6		30		50		7
						7		4		3		6		30		50	
23.i.73			5		12		39		63		51		8		178		23
				4		10		22		32		29		7		104	
26.i.73			1		2		10		14		18		8		53		32
				1		2		12		9		16		8		48	
30.i.73			8		37		27		29		17		12		130		88
				4		26		21		25		15		9		100	
2.ii.73					3		14		14		15		11		57		37
						3		12		12		12		11		50	
6.ii.73					12		42		20		34		15		123		44
						9		31		19		30		11		100	
Total	613		100		129		154		155		151		104		1406		301
		159		35		77		111		109		117		94		702	
No. per Cob	3·855		2·857		1·675		1·387		1·422		1·291		1·106				

TABLE B(5)   THE NUMBERS OF VARIOUS STAGES OF DEVELOPMENT OF _Heliothis armigera_ PRESENT ON EACH SAMPLING DATE – SITE $\underline{V}$

Date	Stage of Development														Total		No. of uninfested cobs
	eggs		1st		2nd		3rd		4th		5th		6th				
	no.	cob	no.	cob	no.	cob	no.	cob	no.	cob	no.	cob	no.	cob	no.	cob	
9.ii.73	740														740		0
		70														70	
12.ii.73	310		3		14										327		2
		48		1		1										50	
14.ii.73	116		9		12		15		10		2				164		24
		24		4		8		11		7		2				56	
16.ii.73					5		16		27		17		4		69		17
						5		11		18		12		3		49	
20.ii.73							6		25		48		35		114		61
								5		24		43		28		100	
23.ii.73					1		4		3		22		25		55		45
						1		3		3		22		24		53	
27.ii.73					7		8		4		20		61		100		168
						6		6		3		20		61		96	
Total	1170		12		39		49		69		109		125		1573		317
		142		5		21		36		55		99		116		474	
No. per Cob	8·239		2·400		1·857		1·361		1·255		1·101		1·078				

TABLE B(6) THE NUMBERS OF VARIOUS STAGES OF DEVELOPMENT OF Heliothis armigera PRESENT ON EACH SAMPLING DATE — SITE VI

Date	eggs no.	eggs cob	1st no.	1st cob	2nd no.	2nd cob	3rd no.	3rd cob	4th no.	4th cob	5th no.	5th cob	6th no.	6th cob	Total no.	Total cob	No. of uninfested cobs
12 ii 1973	615														615		2
		53														53	
16.ii.73	983		86		52		18		15		2				1156		7
		73		7		9		8		11		12				110	
19.ii.73	433		147		1		15		10		4		3		613		4
		29		10		1		3		7		4		3		57	
21.ii.73	271		68		32		18		6		2		4		401		9
		25		7		9		8		3		2		4		58	
23.ii.73	147		25		11		24		18		7		7		239		5
		13		3		6		8		13		5		7		55	
26.ii.73	139		90		73		22		4		2		3		333		4
		10		12		18		8		2		2		3		55	
28.ii.73	139		6		70		41		7		6		1		270		2
		11		1		16		15		3		5		1		52	
2.iii.73					14		33		11		10				68		9
						12		21		6		9				48	
5.iii.73			2		5		37		26		17		3		90		5
				1		5		16		14		11		3		50	
7.iii.73			2		11		20		40		15		1		89		18
				2		6		13		20		10		1		52	
9.iii.73					3		19		22		21		10		75		7
						2		8		16		16		8		50	
12.iii.73					2		12		11		18		14		57		25
						1		8		10		17		14		50	
14.iii.73							14		26		10		15		65		25
								7		22		8		13		50	
16.iii.73							10		22		14		10		56		8
								10		19		11		10		50	
19.iii.73					1		4		14		18		16		53		46
						1		4		13		16		16		50	
21.iii.73							2		12		19		20		53		80
								2		11		17		20		50	
Total	2727		426		275		289		244		165		107		4233		256
		214		43		86		139		170		135		103		890	
No. per Cob	12·743		9·907		3·198		2·079		1·435		1·222		1·039				

TABLE B(7)   THE NUMBERS OF VARIOUS STAGES OF DEVELOPMENT OF Heliothis armigera PRESENT ON EACH SAMPLING DATE - SITE VII

Date	eggs No.	eggs cob	1st no.	1st cob	2nd no.	2nd cob	3rd no.	3rd cob	4th no.	4th cob	5th no.	5th cob	6th no.	6th cob	Total No.	Total cob	No. of uninfested cobs
16.ii.73	906	100													906	100	1
19.ii.73	71	19	8	4	3	2	9	7	15	12	11	8			117	52	14
21.ii.73	23	3			5	5	18	9	27	20	16	14	2	2	91	53	18
23.ii.73	16	5					7	7	12	12	19	18	13	12	67	54	18
26.ii.73							7	6	5	5	19	18	21	21	52	50	46
28.ii.73					1	1	5	4	5	5	10	10	24	22	45	42	58
2.iii.73					5	4	12	7	14	10	14	14	16	16	61	51	68
5.iii.73					16	14	20	14	8	7	7	7	8	8	59	50	125
7.iii.73					3	2	8	7	5	5	13	13	21	21	50	48	196
9.iii.73					3	3	5	5	6	5	6	6	5	5	25	24	200
Total	1016	127	8	4	36	31	91	66	97	81	115	108	110	107	1473	524	744
No. per Cob	8·000		2·000		1·161		1·379		1·198		1·065		1·028				

APPENDIX C

STATISTICAL ANALYSES

I. COMPARISON OF DISTRIBUTION OF LARVAL LIFE TO A

NORMAL DISTRIBUTION

All larval development times have been transformed to
a common mean (5.0) and variance (1.0). These transformed values have
been grouped as listed below. From a consideration of the
probabilities associated with the Normal Distribution, the expected
frequencies associated with each group has been calculated.

Group	Observed Distribution	p. of Normal Distribution	Expected Distribution
<3.5))	6	0.0668	14.4
3.5)) 4.0)	23	0.0919	19.8
4.5	37	0.1498	32.4
5.0	61	0.1915	41.4
5.5	45	0.1915	41.4
6.0	8	0.1498	32.4
6.5	21	0.0919	19.8
7.0	9	0.0440	9.5
7.5	3	0.0166	3.6
8.0	2	0.0049	1.0
>8.0	1	0.0013	0.3
	N = 216		N = 216

A Chi Squared test using expected cell values greater
than 5.0 was carried out.

$$\chi^2 = 34.15 \text{ for } 7 \text{ degrees of freedom}$$

$$P \ll 0.005$$

II. COMPARISON OF DISTRIBUTION OF PUPAL DEVELOPMENT

TIME TO A NORMAL DISTRIBUTION

All pupal development times have been transformed to a common mean (5.0) and variance (1.0). These transformed values have been grouped as listed below. From a consideration of the probabilities associated with the Normal Distribution, the expected frequencies associated with each group has been calculated.

Group	Observed Distribution	p. of Normal Distribution	Expected Distribution
<3.5)) 3.5)	5	0.0668	11.1
) 4.0)	18	0.0919	15.4
) 4.5)	25	0.1498	25.0
5.0	49	0.1915	32.0
5.5	31	0.1915	32.0
6.0	10	0.1498	25.0
6.5	15	0.0919	15.4
7.0	6	0.0440	7.3
7.5	5	0.0166	2.8
8.0	2	0.0049	0.8
>8.0	1	0.0013	0.2
	N = 167		N = 167

A Chi Squared test using expected cell values greater than 5.0 was carried out.

$$\chi^2 = 22.69 \text{ for } 7 \text{ degrees of freedom}$$
$$P < 0.005$$

III. <u>COMPARISON OF THE DISTRIBUTION OF LARVAL AND</u>

<u>PUPAL DEVELOPMENT TIMES</u>

        All larval and pupal development times have been transformed to a common mean (5.0) and variance (1.0). These transformed values have been grouped as listed below. Owing to the differing sizes of the total frequency of the two distributions, each value in the distributions have been altered in proportion, each resulting distribution having a similar total frequency, e.g., the value "6" in the pupal development time distribution will be altered thus: $\frac{6 \times (167 + 216)}{167} = 13.76$.

Group	Observed Distributions Larvae	Pupae	Transformed Distributions Larvae	Pupae
3.0				
3.5	6	5	10.64	11.47
4.0	23	18	40.78	41.28
4.5	37	25	65.61	57.34
5.0	61	49	108.16	42.39
5.5	45	31	79.79	71.10
6.0	8	10	14.18	22.94
6.5	21	15	37.24	34.40
7.0	9	6	15.96	13.76
7.5	3	5	5.32	11.47
8.0	2	2	3.55	4.59
8.5	1	1	1.77	2.29
	N = 216	N = 167	383	383

t Test Calculations

$d = 44.03 \quad \frac{d}{N} = 4.0027 \quad \frac{(d)^2}{N} = 176.2401 \quad d^2 = 291.5585$

$s = 1.0238$

$t = 3.91$

$p = 0.005$

IV. <u>COMPARISON OF SEX RATIO OF ADULTS EMERGING AT</u>

<u>VARIOUS TEMPERATURES TO A RATIO 1:1</u>

Data presented in Table **II** (d)

Using a χ^2 test:-

$$\chi^2 = \frac{(\text{No. Observed } - \text{ No. Expected})}{\text{No. Expected}} \quad \text{for both males and females}$$

$$\chi^2 = \frac{(17-18)^2}{18} + \frac{(19-18)^2}{18} + \frac{(22-18.5)^2}{18.5} + \frac{(15-18.5)^2}{18.5} + \frac{(21-21)^2}{21} +$$

$$\frac{(21-21)^2}{21} + \frac{(21-17)^2}{17} + \frac{(13-17)^2}{17}$$

$\chi^2 = 3.318$ for 4 degrees of freedom (p 0.50)

V. COMPARISON OF OBSERVED AND PREDICTED DENSITY

LEVELS OF INDIVIDUALS PER COB

Predicted values of the density of particular instars are calculated from the equation:-

$$\log. Y_i = \log. E. \; (1.0 - X_i)$$

where Y_i = number of stage i per cob

E = number of eggs per cob

$$X_i = \sum_{a=i}^{a=1} b_i$$

where b_1 = 0.3210

b_2 = 0.4414

b_3 = 0.0279

b_4 = 0.1595

b_5 = 0.0488

b_6 = 0.0012

	SITE NO.							
	I		II		III		IV	
Stage	O	P	O	P	O	P	O	P
E	1.44		3.84		2.79		3.86	
1	1.26	1.28	2.09	2.50	1.59	2.01	2.86	2.50
2	1.26	1.09	2.03	1.38	1.60	1.28	1.68	1.38
3	1.07	1.08	1.81	1.33	1.19	1.24	1.39	1.33
4	1.09	1.02	1.44	1.07	1.27	1.05	1.42	1.07
5	1.08	1.00	1.11	1.00	1.14	1.00	1.29	1.00
6	1.00	1.00	1.01	1.00	1.04	1.00	1.11	1.00

Stage	SITE NO					
	V		VI		VII	
	O	P	O	P	O	P
E	8.24		12.74		8.00	
1	2.40	4.17	9.91	5.63	2.00	4.10
2	1.86	1.65	3.20	1.83	1.16	1.64
3	1.36	1.56	2.08	1.71	1.38	1.55
4	1.25	1.11	1.44	1.14	1.20	1.11
5	1.10	1.00	1.22	1.00	1.06	1.00
6	1.08	1.00	1.04	1.00	1.03	1.00

Chi squared test using cell comparisons of values greater than 5

$$\chi^2 = 5.40 \text{ for 7 degrees of freedom}$$

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