THE GROWTH, DEVELOPMENT AND SURVIVAL OF *SPODOPTERA EXEMPTA* (WALK.) (LEPIDOPTERA, NOCTUIDAE) ON SOME SELECTED GRASS SPECIES

By

JACOB GHADWE YARRO

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ABSTRACT

Growth, development and survival of the African armyworm Spodoptera exempta were studied in the laboratory at 25°C and 70% R.H. on maize, Zea mais L., star grass, Cynodon dactylon (L.) Pers.; Kikuyu grass, Pennisetum clandestinum Chiov.; Guinea grass, Panicum maximum Jacq. and Setaria plicatilis (Hochst) Hack. The results obtained from fecundity, percent egg hatch, larval and pupal survival and adult longevity were used in estimating the net reproductive rates and the capacity for increase in order to evaluate the contribution of each host plant to the build up of the population of the insect to pest status. The suitability of the host plants was also estimated by estimating growth indices.

The number of instars through which larvae on each host plant pass was determined using the head capsule widths and the distances between the frontal setae on the clypeus of the head capsule. These studies were carried out at 18°C and 80% R.H., 25°C and 70% R.H. and 30°C and 60% R.H.

Since grass species are usually found in mixed stands or communities in the field and outbreak larvae feed on the less preferred grass species on

depletion of the preferred ones, it was found necessary to evaluate how the less preferred grass species and the older leaves contribute to the population dynamics of S. exempta.. Larvae were reared on C. dactylon and transferred to P. maximum and S. plicatilis at the beginning of various instars starting from the second instar stage. Survival was assessed at the end of each instar and the weights of pupae and adults compared.

The effect of temperature on the rate of larval and pupal development was investigated by rearing larvae on the five species of grass in an outdoor cage.

In order to develop an effective strategy for controlling the outbreaks of the armyworm the need for understanding its food plant preferences was realised. Densities of larvae on various host plants in outbreak localities were determined and compared. Emergence weights and wing lengths of moths from different localities and stands of host plant species were compared to each other. Choice experiments were carried out both in the field cage and laboratory to confirm laboratory and field results. The nitrogen levels for Z. mais, C. dactylon, P. clandestinum, P. maximum and S. plicatilis were determined and these grass species were tested for cyanide.

Wing length and wing areas for laboratory and outbreak moths were measured and compared. The relation between the forewing length, forewing area, the product of the forewing length and width and the product of the length and width of the pupal thorax and pupal weights were determined in order to estimate the latter when direct weighing is not possible.

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GENERAL INTRODUCTION

The caterpillar of Spodoptera exempta (Walk.) is known as the armyworm from its habit of moving across country in vast swarms in search of fresh food after it has exhausted the local food supply during a period of outbreak (Brown, 1962; Hattingh, 1941). Sometimes, the movement occurs before the local food supply is actually depleted so that some authors consider it to be a response to general mutual stimulation caused by very high larval densities (Brown and Dewhurst, 1975). It is also a movement in search of pupation sites.

In 1856 it was described under the name Agrotis exempta (Walker, 1856) but in 1909, it was identified as Laphygma exempta (Hampson, 1909). With no important differences between the genera Laphygma and Spodoptera they were combined in 1958 under the latter name which had the priority (Zimmerman, 1958).

As a result of the damage it does to graminaceous crops and grazing S. exempta has been given a variety of common names. These include the "common army worm", "mystery worm", "army mystery worm", "true mystery worm", South African mystery worm","swarming caterpillar", "variegated armyworm", "leaf eating grass worm" and "nut grass armyworm" after one of its favourite local food

plants. There are many vernacular names used in Africa, reflecting its wide recognition as a pest. The name "mystery armyworm" expresses the reaction of farmers to seemingly sudden appearance and disappearance of the outbreak of caterpillars. The African armyworm is, however, most appropriate because of the various species of caterpillars known as armyworms in different parts of the world. It is best represented in Africa which appears to be its true home (Brown, 1962). There are records of S. exempta from most of the African countries including Morocco, Algeria, Tunisia, Libya, Egypt, Mauritania, Senegal, Gambia, Mali, Niger, Chad, Sudan Guinea, Sierra Leone, Liberia, Ivory Coast, Upper Volta, Ghana, Togo, Nigeria, Cameron, Central African Republic, Gabon, Zaire, Rwanda, Buruni, Ethiopia, Somalia, Kenya, Uganda, Tanzania, Angola, Zambia, Zimbabwe, Malawi, Mozambique, South West Africa, Botswana, Swaziland, Lesotho and South Africa. There are also records of the pest in the Indian Ocean Islands of Socotra, Pemba, Zanzibar, Mafia, Aldabra, Comoro, Malagasy, Seychelles, Rodrigues, Mauritius and Reunion as well as the Atlantic Ocean Islands of Madeira, Fernando Po, Principe, Sao Tome, Ascension, St. Helen and Canary Islands. In the western Arabian Peninsula it has been reported from Western Saudi Arabia, Yemen Arab Republic and P.D.R. Yemen (Brown, 1962; Brown and Dewhurst, 1975). Elsewhere it has been reported from Java, Hawaii,

Philippine Islands and Queensland (Brown, 1962) and Papua New Guinea (Baker, 1978).

Frequently only one outbreak generation occurs in one place. This may be widespread (Brown, 1962; Brown and Swaine, 1966) and may be the cause of devastating damage to crops and pastures in as little as eight or nine days (Hudson, 1943). Sometimes outbreaks may be repeated in the same locality (Whellan, 1958) or with the main attach occurring during the second generation (Smith and Caldwell, 1947) but three succeeding generations have also been reported (Khasimuddin and Lubega, 1979; Rose, 1975).

The larval outbreaks tend to be associated with the beginning of the rains so that in East Africa they often begin in Southern Tanzania in December or January and progressively move into Kenya in March and June. This progressive northward movement during which cereals and pasture are infested is attributed to long distance downwind displacement of successive moth populations (Brown and Swaine, 1966). In Southern Africa similar north to south progressive movement of outbreaks is known (Faure, 1943; Whellan, 1954). Circumstantial evidence, from light traps distributed throughout East

Africa and from field observations of outbreak of larvae, indicates that long-distance migrations occur between moth emergence and the next breeding areas which are usually in the vicinity of seasonal passage of low-level wind convergence such as the Inter-Tropical Convergence Zone or the African Rift Convergence Zone (Brown et al., 1969; Haggis, 1971).

An increase in numbers of moths caught in light traps has been found to be followed by an increased probability of infestation of crops by the larvae occurring two to four weeks later at distances up to 200 km from the traps (Betts and Odiyo, 1968). Large light trap catches may therefore represent populations in transit and not simply evidence of breeding or local emergence. Moths are physiologically capable of flying over distances which are involved in such long distance migrations (Aidley, 1974).

Most female moths in light traps are unfertilized (Brown and Swaine, 1966) suggesting that mating takes place in the area of oviposition. Published references have quoted the preoviposition period as usually ranging from two to seven days although oviposition may take place on the night after emergence (Brown, 1962). In migratory species the preoviposition period often limits the time and therefore the geographical distance separating one generations of

larvae from the next. In greenhouses at Muguga at 6,800 ft at temperatures approximating to those in the field in East Africa during the local outbreak period ranges from two to four days (Brown et al. 1969). Laboratory-bred males require at least 48 hours while wild caught males require 24-36 hours to become sexually mature after emergence at 25°C. Corresponding females take 60 and 40 hours repectively (Khasimuddin, 1978). At lower temperatures both the preoviposition period and the adult longevity are longer. The average adult lifespan varies widely with the temperature of the locality, for instance in an experiment it varied from 10.2 days at a mean temperature of 18.3°C at Nairobi to 7.1 days at 23.0°C at Mbita Point on Lake Victoria and 4.8 days at 25.2°C at Msabaha near Mombasa (Persson, 1981).

Moths emerge between dusk and midnight and make peak flights one to two hours later and again at dawn, but many remain in the habitat until the following night when they emigrate from the area as dusk falls on the day following emergence (Rose and Dewhurst, 1979). Similarly, the flight activity in the laboratory is highest on the second might (Gatehouse and Hackett, 1980). Studies of flight by radar at field emergence sites suggest that many moths also leave the area downwind on the night of emergency (Riley et al., 1981). Numbers of moths caught by pheromone traps are usually much lower than those caught in light traps but they may be higher

when the moths have settled in the area (Rose and Odiyo, 1979). It is therefore highly probable that some moths migrate long distances during the preoviposition period.

Eggs are deposited in irregular masses sometimes covered with black down from the female body in one, two or three layers superimposed on one another (Hattingh, 1941). The number of eggs varies (Hattingh, 1941; Whellan, 1954); for example in three Kenyan localities females in the colder locality (Nairobi) laid more eggs than those at Msabaha (Mombasa) (Persson, 1981). They are laid on young grass or maize although sometimes the females are not very particular where they lay their eggs (Whellan, 1958). The eggs may be laid on tall plants with mature foliage unsuitable for young larvae or on non host plants from which young larvae disperse on silken threads (Brown, 1962).

When the larvae are reared in groups or singly, the former all seem to pass through six instars while most of the latter pass through five instars (Matthee, 1946). On maize diet (David et al., 1975) some singly reared larvae pass through five instars. In three successive generations from an outbreak, larvae passed through six instars, although there were variations in size (Rose, 1975).

The colours of the larvae are very variable as a result of differences in larval density and this has been compared to "phase change" in the locusts. They have been classified into the darker phase gregaria (outbreak phase), the paler phase solitaria (solitary phase) and the intermediate colour forms (phase transiens) (Faure, 1943). The variation affects characters involving behaviour, physiology (including colour) and morphology (Uvarov, 1961) and the terms active and passive (Whellan, 1954) are sometimes used to emphasize differences in behaviour. It has been suggested that although most of the moths of high-density larvae which are black migrate, the smallest of them lay eggs locally to produce caterpillars of a lower density population with a proportion of passive, non-black caterpillar (Rose, 1975). Sometimes, depending on the density, both black and non-black caterpillars may be present in the first generation (Khasimuddin and Lubega, 1979). In East Africa the period between July and October or November is characterised by virtual absence of outbreaks of larvae but evidence from light and pheromone traps shows that, though reduced in numbers, some moths are caught in some localities throughout the year (Brown and Swaine, 1966;

Brown et al., 1969; Odiyo, 1979, 1981). This may be explained by the presence of places in parts of Eastern Africa where low density populations of moths and caterpillars persist. Numbers then build up with favourable conditions and moths are concentrated by weather patterns so that oviposition is concentrated in one place and caterpillars develop to cause outbreaks (Rose, 1979).

Temperature greatly influences the duration of the stages of the life cycle (Brown et al., 1969; Persson, 1981) but even at the optimum temperature for development, S. exempta is unable to survive the five or six months of the year during which plant growth is inadequate to support the larvae. Extensive field and laboratory studies carried out in East Africa have not produced any evidence for diapause (Brown et al., 1969) although its occurrence had been suggested in Angola (Fonseca et al., 1965). An extension of pupal duration has been reported in East Africa (Khassimudin, 1977) but manipulation of conditions for larval development has so far failed to induce diapause.

Phenotypic differences between moths exist. For instance, mean winglengths of populations vary with the localities of outbreaks and between populations arriving at the same place at different times (Aidley and Lubega, 1979). These authors have used winglength variation to indicate migration of moths from different sources. A search for true genetic variations brought into light

that the frequency of six polymorphic alleloenzymes was similar in populations over a maximum distance of 2,000 miles between Kenya, Tanzania and Zimbabwe (Den Boer, 1978). This suggested that extensive mixing of populations by migration was occurring not only in the north moving wave in East Africa but also between this population and the one which appears in southern part of the continent.

The larvae are almost rigidly confined to feeding on the family Gramineae and the related Cyperaceae. The latter are weeds of cultivation and grasslands and are usually unimportant components of the diet. The former include cereals and grass in pasture or savannah (Brown, 1970). The list of cultivated graminaceous plants reported as food plants of S. exempta (Brown, 1962; Table 4) is presented in appendix 1. Pennisetum typhoides, the bulrush millet (known as "babala" in South Africa) has lately been added to that list and so has Eragrotis tef (E. Abyssinia) which is an important food crop in Ethiopia. Panicum miliaceum, the common millet, is mistakenly listed in Table 3 as uncultivated (Brown, 1962). The list of wild and fodder grass reported as eaten by S. exempta (Brown, 1962; Table 3) is presented in appendix 2.

An additional list showing some degrees of preference and some few species which were not eaten at all (Bogdan, 1963) is presented in Appendix 3. The list of plants, other than Gramineae, reported as eaten by S. exempta is presented in appendix 4. They include Compositae, Convolvulaceae, Iridaceae, Leguminosae, Liliaceae, Musaceae, Rubiaceae and Solanaceae. Additional reports include Acidanthera laxiflora (Iridaceae), Oxygonum sinuatum (Polygonaceae), Alternanthera pungens (Amaranthaceae), Carpobrotus edulis (Ficoidaceae) as as well as another plant which was probably Tribulus terrestris (Zygophyllaceae), although in one Kenya outbreak where some grass still remained this plant was not eaten (Brown and Dewhurst, 1975), and the dwarf variety of coconut, Cocos nucifera (Palmae) (Yarro et al., 1981). S. exempta rarely attacks dicotyledons and it is likely the above list includes misidentifications of larvae as well as records of plants attacked under exceptional conditions when caterpillars are swarming.

The basis for the oligophagy is thought to be a combination of strong intolerance to chemical feeding inhibitors and a very strict requirement for a well-balanced complex of feeding stimulants and biting

incitants (Ma and Kubo, 1977). The larvae have sensilla on the maxilla with mechanoreceptors and chemereceptors but the range of sensitivity is similar to that in sensilla of larva of S. littoralis, S. litura and S. frugipera (Ma, 1977a). Some African plants like Warburgia ugandense have a group of related sesquiterpenoids (Nakanishi and Kubo, 1977). Warbuganal is a dialdehyde that strongly suppresses the feeding response of larvae of S. exempta and S. littoralis (Mainwald et al., 1978) possibly by reaction between the aldehyde groups of Warburganal and - SH groups in the chemoreceptor membranes of sensilla (Ma, 1977b).

Accounts of its economic importance in relation o to the different categories of host plants attacked have been given by Brown (1970, 1972) and Brown and Mohamed (1972). Farmers use chemical control on cultivated crops but not on most grasslands in East Africa (Brown, 1970). A high proportion of outbreaks are on grasslands and many infestations in the more remote areas go unreported. Therefore, even if the farmers were able to effectively control the pest in their farms they cannot effectively reduce the overall population. This can only be achieved by national and international organizations.

In S. exempta, predators and parasites (at least during outbreak conditions) have little effect on mortality (Brown, 1970) and a polyhedrosis virus is the most important cause of mortality (Brown and Swaine, 1965). When it appears, the virus spreads quickly through the whole population with larval mortality increasing rapidly (Persson, 1981). Nuclear polyhedrosis is characterised by liquefaction of the body contents of a caterpillar and the skin becoming thin and fragile and bursting after death thus liberating the fluid over the plants so that it infects other larvae. The larvae die in a typical position of larvae attacked by a nuclear polyhedrosis virus, hanging upside down from one or two pairs of prolegs. Infected larvae tend to move upwards (Odindo, 1977).

As S. exempta is the most important armyworm in Africa and one of the most important causes of loss to cereal crops and pasture a thorough understanding of its food preferences is of paramount importance in developing effective control strategies. The wild grass species are the natural food plants of this indigenous insect and their study in relationship to development of the armyworm population is essential in understanding its life system. For much of the time the larvae in natural grasses are probably solitary and are therefore greeen,

sluggish and inconspicuous (Hattingh, 1941; Faure, 1943; Rose, 1975, 1979). They are difficult to identify as S. exempta larvae as they differ greatly in appearance and behaviour from the outbreak caterpillars known to farmers and are also similar to other Spodoptera species.

Cynodon dactylon appears to be the most favoured grass species generally (Harris, 1944; Smee, 1943) especially by younger larvae. Outbreaks frequently start on this grass species (Hattingh, 1941) and since in its absence other species are eaten, some degree of preference can be established. There is some evidence that C. dactylon is preferred to Zea mais for oviposition (Persson, unpublished) and as the eyes of S. exempta moths are adapted for colour vision they may be important in the selection of oviposition sites (Langer et al., 1979). The localization of outbreaks within the general area of wind convergence (Brown and Swaine, 1966; Brown et al., 1969; Rose and Law, 1976) stand to support the selective ability of the female moth.

The work reported in this thesis was designed to establish the criteria for the importance of some selected grass species with respect to the performance

of S. exempta. The parameters examined include the duration of development stages, larval survival, weights of pupae and adults within twelve hours of pupation and emergence, wing size and fecundity. Advantage was taken of larval outbreaks where larval densities on dominant grass species were determined. Field cage and laboratory choice experiments were designed to closely examine the observations made in the field. The role of the less preferred host plants and the older leaves was also investigated. Phenotypic variations in relation to the larval host plants were examined so that this could be evaluated for use in pinpointing the origin of moth populations and therefore strengthening the forecasting system.

CHAPTER 1

GROWTH AND DEVELOPMENT OF THE AFRICAN ARMYWORM SPODOPTERA EXEMPTA (WALK.) AS OBSERVED ON SOME SPECIES OF GRAMINEAE

INTRODUCTION

The African armyworm, S. exempta (Walk.) is a sporadic and seasonal pest of various graminaceous crops and grasslands (Brown, 1962; Brown, 1970; Brown and Mohamed, 1972; Hatt[illegible]gh, 1941; Whellan, 1954). It also feeds on the family Cyperaceae (Faure, 1943) which is closely related to the Gramineae. Under exceptional conditions S. exempta can feed on plants belonging to families other than the Gramineae and the Cyperaceae but there is no doubt that the family Gramineae, being the largest in terms of species and biomass within the range of occurrence of the African armyworm, provides the bulk if not all of the larval food requirements under normal conditions. Extensive larval outbreaks which account for the pest status of S. exempta coincide with the new growth of Gramineae at the onset of the rain season as a result of moth populations being concentrated in areas of wind convergence so that the arrival of moths coincides with

that of rains (Brown and Swaine, 1966; Brown et al., 1969).

It has for a long time been believed that the female moth contributes little or nothing to the determination of the host plant of the next generation because it is unselective with regard to the species of the plant on which it oviposits (Hattingh, 1941) although the larvae are to some extent selective as to the grass species they attack (Bogdan, 1963; Brown, 1970; Hattingh, 1941). The preference is relative since the less preferred grass species are equally accepted in the absence of the preferred ones (Brown, 1970). Recently it has been shown that in field cages moths prefer Stargrass, Cynodon dactylon (L.) Pers. to maize, Zea mais L. for oviposition (Persson, unpublished data).

Since the African armyworm is a major pest of important food crops, it is important to identify those host plants which contribute to the build up of its populations. Most of the observations in the field cannot be conclusive because the larvae move freely between various host plant species. Under high density conditions, some larvae may be forced to feed on the less preferred host plants making the host preference more difficult to detect.

The present investigations were undertaken to study the survival, growth rate, pupal and adult weights and the reproductive potential of the African armyworm when larvae are fed on some selected grass species throughout the larval life.

MATERIALS AND METHODS

Newly hatched first instar larvae used in these experiments were all obtained from an insectary culture of gregarious phase caterpillars maintained on Z. mais. They were transferred into two pound kilner jars containing leaves of maize, Zea mais L.; Star grass, Cynodon dactylon (L) Pers; Kikuyu grass, Pennisetum clandestinum Chiov.; Guinea grass, Panicum maximum Jacq.; and Setaria plicatilis (Hochst.) Hack.; separately. Four hundred first instar larvae were introduced on each host plant in groups of forty per jar forming ten replications. The food was supplied without limitation once or twice daily depending on the larval density and age. Leaves were washed in running water and drained to avoid differences in humidity in jars. The jars were stoppered with filter papers held in position by metallic or plastic rings to prevent larvae from escaping. The rearing was carried out in an insectary at 25°C and 70% R.H. although the actual humidity in the jars was probably higher due to transpiration.

All jars used in the experiment were washed with soap and sterilized in 5% sodium hydroxide and 2% tetramide solution for twelve and six hours, respectively. They were then rinsed in running water and heat sterilized at 100°C in an oven. All jars in which larval mortality had occurred were replaced by clean and sterile ones.

Each morning as food was replenished the larvae were classified into instars and when at least half of the larvae in any one jar had moulted into the next instar that day was taken as the end of the duration of the previous instar and the larval mortality during that instar was estimated. This necessarily meant that some of the larvae which died during a given instar actually belonged to the previous instar. The larval durations of all individuals which reached the pupal stage were recorded. Each pupa was weighed within twelve hours of pupation and placed singly in a one ounce plastic vial plugged with cotton wool to prevent the moth from escaping. The sex of pupae was used in inferring the sex of larvae. Pupal duration of each pupa was recorded and adults were weighed within twelve hours of emergency and after voiding meconium. Well formed adults were paired immediately after the weights were taken. They were kept in kilner jars and fed on 10% sucrose solution placed in small plastic containers with pieces of cotton wool. The sucrose solution was changed daily.

The number of eggs laid daily by each female and the adult longevity for each individual was recorded. An analysis of variance was performed on the data.

The growth index values were calculated for each host plant by dividing the percent survival (Pant and Dang, 1969) or the natural logarithim of the percent survival (Howe, 1971) by the developmental duration in days. Both methods were employed to compare the values obtained by dividing the percent pupation and emergence by larval and the combined larval and pupal duration, respectively.

The reproductive index values were obtained by working out the mean number of eggs produced for a unit weight (mgm) of both the female pupa ~~and adult~~.

In a separate experiment the percent egg hatch for moths reared on each host plant was estimated by counting the number of larvae and eggs which failed to hatch for each female. Twelve well-formed female moths from each host plant were mated and the date of oviposition and size of each egg batch was recorded. Assuming the sex ratio of 1:1 the number of female eggs per batch was estimated by dividing the number of eggs per batch by two. This information was used in calculating the mean number of female eggs per day. The percent survival of the

pupal and adult stages was based on the results from the rearing experiments. The survival during the adult stage was based on the twelve females for each host plant. The results were used in calculating population growth rates on each host plant.

Whenever necessary an analysis of variance (Sokal and Rohlf, 1969) was carried out on the data, and the mean values which were significantly different from each other were determined by Tukey's pairwise comparison test (Gill, 1978) at the 5% level of significance. The probability values for the differences between sexes in the same treatment are given in the tables but the probability values for the differences between host plants are given in the text. Since the number of instars varied with the host plants, larval survival comparisons were carried out between the larvae which went through same number of moults.

RESULTS

The mean numbers of larvae surviving at the beginning of each instar stage are presented in Table 1 and the percentages of the total mortality that occurred at each developmental stage are presented in Table 2 and Figure 1. Large numbers of larvae on all the

five grass species died during the first instar stage. Nevertheless, there were some differences in survival for instance at the beginning of the second instar stage. The larval survival was significantly ($P<0.5$) lower in samples reared on P. clandestinum grass than on samples reared on Z. mais. The larval survival on C. dactylon was of intermediate value and no significant difference was detected when compared to the samples on Z. mais and P. clandestinum. This trend in survival continued up to the beginning of the fourth instar stage. There was, however, high mortality during the fourth instar stage in samples reared on P. clandestinum and to some extent in those reared on Z. mais. Larvae reared on C. dactylon experienced a lower mortality during that instar stage so that at the beginning of the fifth instar stage significantly ($P<.05$) larger numbers of larvae survived on both Z. mais and C. dactylon than on P. clandestinum.

The larvae on P. maximum experienced high mortality during the second instar stage and to a lesser extent during the third instar stage. Mortality was lower during the fourth and fifth instar stages but higher during the last instar. On the other hand larvae on S. plicatilis suffered comparatively lower mortality during the second, fourth and seventh instar stages. There was, however, high mortality during the third, fifth and sixth instar stages.

Larval development was more synchronised in samples reared on Z. mais, C. dactylon and P. clandestinum than in samples on P. maximum and S. plicatilis. Some of the larvae which died in a given instar stage on the latter two host plants actually belonged to the previous instar.

Comparison of samples reared on all the five grass species showed a significantly higher survival ($P<.05$) among larvae reared on Z. mais and C. dactylon than among larvae on the rest of the grass species, at the time of pupation and adult emergence.

The majority of those larvae which died became inactive a day before death. On being disturbed they regurgitated a creamy, rather than the greenish, liquid regurgitated by healthy larvae. The colour of the integument of the healthy gregarious larvae fed on maize or grass changed from dark velvety and olive to light grey. The dead larvae were often found hanging upside down from the kilner jar tops. Their integuments were very tender even before death and could easily be punctured to produce the creamy mass. These symptoms closely resemble those described for nuclear polyhedrosis virus of the African armyworm (Brown and Swaine, 1965; Odindo, 1977).

A smaller percentage of larvae died after three to five days of initial diagnosis of infection. The larval colour turned to light grey and though the integument remained tough, it was wrinkled. The faeces were semi-liquid as opposed to the semi-solid ones produced by healthy larvae. No identification was attempted but there were indications that they could have died of bacterial infection.

In still fewer cases particularly in samples reared on P. clandestinum some previously healthy-looking larvae were found dead the next morning. They had a profuse growth of white fungal hyphae on the integument. A small proportion of larval mortality in S. exempta is known to be c used by fungi (Persson, 1981; Whellan, 1954). Although the fungus was not identified, a Beauveria species is known to be a killer (Rose, personal communication).

Larval duration

Larval duration (Table 3) varied significantly ($P<.001$) with the grass species on which the larvae fed. Larvae fed on Z. mais developed significantly ($P<0.05$) faster than those fed on other host plants. Those fed

on C. dactylon developed significantly ($P<0.05$) faster than those fed on P. clandestinum. The lowest rate of larval development was recorded among larvae reared on P. maximum and S. plicatilis. Males had slightly shorter larval duration than females except for those reared on C. dactylon although the difference was significant ($P<0.05$) only for the sample reared on Z. mais.

Pupal duration

Pupal duration varied significantly ($P<.001$) with the larval host plant (Table 4). Among the females the pupae formed from the larvae which fed on S. plicatilis developed fastest. This however does not differ significantly from that of pupae that developed from larvae reared on C. dactylon.

Pupal duration of the latter was comparable to that of pupae formed from larvae fed on Z. mais. Larvae fed on P. clandestinum and P. maximum formed pupae which had the longest pupal duration. Male pupae produced by larvae reared on S. plicatilis and Z. mais developed significantly ($P<0.05$) faster than the others. Females completed the pupal life significantly ($P<.001$) earlier than males. However, further analysis of the pupal duration of male and

TABLE 1

SURVIVAL OF THE AFRICAN ARMYWORM, *S. EXEMPTA* DURING THE DEVELOPMENT TO ADULT EMERGENCE AT 25°C AND 70% R.H.
(MEAN ± S.E.*, N = 10 JARS PER TREATMENT)

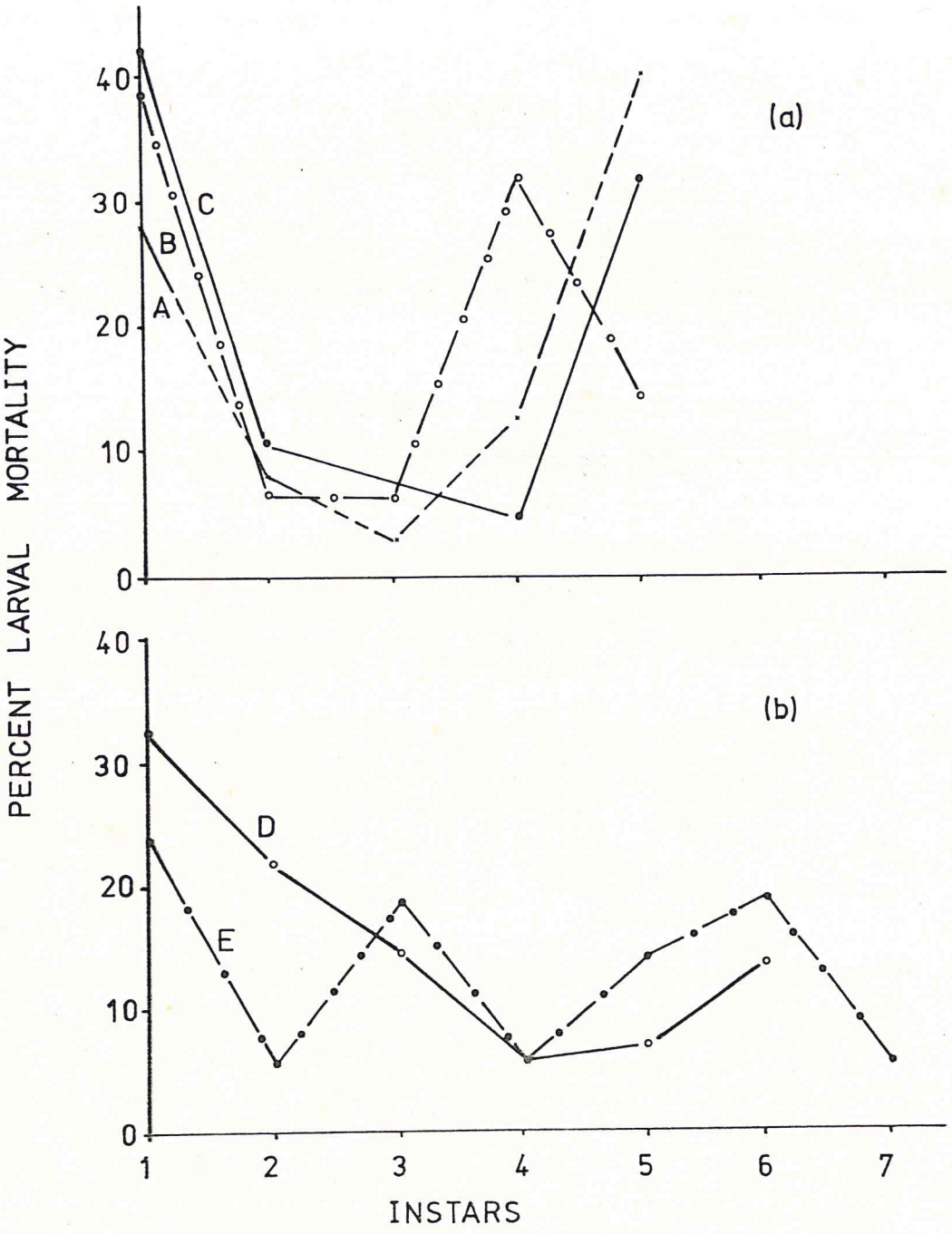
	HOST PLANT				
Instar	*Z. mais*	*C. dactylon*	*P. clandestinum*	*P. maximum*	*S. plicatilis*
1	40	40	40	40	40
2	32.22 ± 1.85a	29.33 ± 2.68ab	26.33 ± 1.97b	28.00 ± 1.58	31.33 ± 2.75
3	30.00 ± 1.59a	26.67 ± 2.90ab	24.00 ± 1.06b	19189 ± 1.98	29.22 ± 1.83
4	29.22 ± 1.59a	24.67 ± 2.63ab	21.78 ± 1.13b	14.56 ± 2.02	22.44 ± 2.91
5	25.67 ± 2.20a	23.44 ± 2.70a	10.44 ± 1.84b	12.44 ± 1.80	20.44 ± 3.09
6	-	-	-	9.78 ± 1.58	15.22 ± 3.33
7	-	-	-	-	8.22 ± 3.07
Pupal Stage	14.44 ± 2.53a	15.33 ± 2.24a	5.33 ± 2.02b	4.67 ± 1.08b	6.22 ± 2.80b
Adult Stage	12.12 ± 2.43a	14.67 ± 3.40a	4.78 ± 2.00b	2.89 ± 1.09b	3.50 ± 1.14b
% Pupation	36.1	38.33	13.33	11.68	15.55
% Emergence	30.3	36.68	11.95	7.23	8.75

* Figures followed by different letters are significantly different from each other ($P<0.05$)

TABLE 2

MORTALITY AT VARIOUS STAGES EXPRESSED AS PERCENTAGE OF THE TOTAL MORTALITY IN SAMPLES OF LARVAE REARED ON EACH GRASS SPECIES

INSTAR	HOST PLANT				
	Z. mais	C. dactylon	P. clandestinum	P. maximum	S. plicatilis
1	28.01	42.12	38.81	32.34	23.75
2	7.99	10.50	5.62	21.85	5.78
3	2.81	7.90	6.30	14.36	18.58
4	12.78	4.86	32.20	5.71	5.48
5	40.42	32.02	14.51	7.17	14.30
6	-	-	-	13.77	19.18
7	-	-	-	-	5.48
Pupal Stage	7.99	2.60	1.56	4.80	7.45



A-Z.mais. B-P.clandestinum. C-C.dactylon.

D-P.maximum. E-S.plicatilis.

female moths from larvae reared on the same grass species showed that only the females produced by larvae reared on C. dactylon had significantly ($P<0.05$) shorter pupal duration.

The Period from larval hatching to adult emergence

This consists of the larval and pupal duration (Table 5) and also indicates that there were significant ($P<.001$) differences between the development periods on the various host plants. The rate of development during the larval stage was highest among individuals fed on Z. mais. C. dactylon and P. clandestinum ranked second and third, respectively, and they were significantly different from each other. Females reared on Z. mais and C. dactylon had comparable development periods.

The developmental period was longest on S. plicatilis although it was not significantly different from that for individuals reared on P. maximum. Females reared on star grass emerged significantly earlier than their males.

Growth rate

Growth indices (S/T) in relation to the percentage pupation and the larval duration (Table 6) showed that Z. mais and C. dactylon were far more suitable in supporting the development of the African armyworm than the other host plants. C. dactylon had a slightly lower growth index than Z. mais. S. plicatilis had the lowest growth index suggesting that it is the poorest grass species in supporting the development of S. exempta. P. clandestinum was inferior to P. maximum but when the indices were calculated on the basis of log S/T they had comparable values.

Z. mais and C. dactylon retained their superiority when the growth indices were based on percentage emergence and combined larval and pupal durations (Table 7). The higher mortality suffered by pupae formed from larvae fed on Z. mais resulted in C. dactylon being slightly superior to the former. Similar pupal mortality resulted in P. maximum having the lowest growth index. P. clandestinum had higher value than S. plicatilis. Indices based on log S/T for C. dactylon and Z. mais were equal and the other host plants were of the same order.

TABLE 3

THE MEAN LARVAL DURATION (DAYS) OF LARVAE BEARED ON THE FIVE SPECIES OF GRASS (n = 60)

HOST PLANT	FEMALES MEAN ± S.E.	MALES MEAN ± S.E.*	P
Z. mais	15.53 ± 0.30a	14.47 ± 0.20a	<0.05
C. dactylon	16.42 ± 0.35b	16.93 ± 0.37b	NS
P. clandestinum	18.40 ± 0.37c	18.27 ± 0.38c	NS
P. maximum	21.22 ± 0.49d	22.12 ± 0.51d	NS
S. plicatilis	21.23 ± 0.42d	22.03 ± 0.41d	NS

* Figures followed by different letters in each colum are significantly different from each other (P<0.05).

TABLE 4

THE MEAN PUPAL DURATION (DAYS) OF GROUPS REARED ON FIVE SPECIES OF GRASS (n = 60)

HOST PLANT	FEMALES MEAN + S.E.	MALES MEAN + S.E.*	P
Z. mais	9.63 ± 0.13b	9.85 ± 0.13a	NS
C. dactylon	9.53 ± 0.14ab	10.27 ± 0.13c	<0.05
P. clandestinum	10.02 ± 0.18c	10.13 ± 0.13c	NS
P. maximum	10.12 ± 0.12c	10.33 ± 0.11c	NS
S. plicatilis	9.33 ± 0.11a	9.67 ± 0.11a	NS

* Figures followed by different letters in each column are significantly different from each other (P<0.05)

TABLE 5

COMBINED LARVAL AND PUPAL DURATION (DAYS) OF INDIVIDUALS REARED ON FIVE SPECIES OF GRASS (n = 60)

HOST PLANT	FEMALES MEAN ± S.E.	MALES MEAN ± S.E.*	P
Z. mais	25.23 ± 0.31a	24.50 ± 0.25a	NS
C. dactylon	25.90 ± 0.39a	27.05 ± 0.40b	<0.05
P. clandestinum	28.42 ± 0.43c	28.08 ± 0.41c	NS
P. maximum	30.67 ± 0.41d	31.20 ± 0.46d	NS
S. plicatilis	31.33 ± 0.49d	32.35 ± 0.61d	NS

* Figures followed by different letters in each column are significantly different from each other (P<0.05)

Pupal Weights

Pupal weights (Table 8) also varied significantly (P<.001) with the larval food plants. The largest pupae were formed from larvae reared on Z. mais, C. dactylon and P. clandestinum with females being slightly larger, Pupae of both sexes formed from larvae reared on S. plicatilis had the lowest weights. Those formed from larvae fed on P. maximum had intermediate weights and were significantly different from the other two groups. Larvae reared on P. maximum and S. plicatilis formed pupae in which males were slightly larger than females but the weight differences between sexes from the same host plant were not significant in any case.

Adult emergence weights

There were significant (P<.001) variations in emergence weights (Table 9) of adults from the larvae reared on various host plants. The females could be divided into four groups which consisted of individuals reared on Z. mais and C. dactylon, P. clandestinum, P. maximum and S. plicatilis.

Females reared on Z. mais and C. dactylon were not significantly different from each other but were significantly larger than females reared on the other host plants which differed significantly (P<0.05)

TABLE 6

GROWTH INDICES OF *S. EXEMPTA* ON VARIOUS HOST PLANTS IN RELATION TO LARVAL DURATION (T) AND PERCENTAGE PUPATION (S).

HOST PLANT	LARVAL DURATION IN DAYS (T)	PERCENTAGE PUPATION (S)	ST	LOG S/T
Z. mais	15.00	36.10	2.41	0.24
C. dactylon	16.68	38.33	2.30	0.22
P. clandestinum	18.34	13.33	0.73	0.14
P. maximum	21.67	20.55	0.95	0.14
S. plicatilis	21.63	11.68	0.5[illegible]	0.11

TABLE 7

GROWTH INDICES OF S. EXEMPTA ON VARIOUS HOST PLANTS IN RELATION TO COMBINED LARVAL AND PUPAL DURATION (T) AND PERCENTAGE EMERGENCE (S)

HOST PLANT	LARVAL + PUPAL DURATION (T)	PERCENTAGE EMERGENCE (S)	ST	LOG S/T
Z. mais	24.87	30.55	1.23	0.14
C. dactylon	26.48	36.68	1.39	0.14
P. clandestinum	28.25	11.95	0.42	0.09
P. maximum	30.94	7.23	0.23	0.06
S. plicatilis	31.84	9.00	0.28	0.07

among themselves. Males showed a similar pattern except that there was no significant difference between the males reared on P. clandestinum and those reared on Z. mais and C. dactylon. While the differences in female and male weights of moths reared on Z. mais, C. dactylon and P. clandestinum were quite large, those between female and male moths reared on the poorer host plants were smaller. In fact the differences between male and female emergence weights were not significant in the group reared on S. plicatilis although the females were slightly larger.

Adult longevity and fecundity

Adults varied significantly ($P<.001$) in their longevity (Table 10) when reared on different host plants. The adults formed from larvae which fed on Z. mais had significantly ($P<0.05$) shorter adult life span than those formed from larvae fed on the wild grass species. The latter did not differ significantly among themselves. The males lived significantly ($P<.001$) longer than females except those reared on C. dactylon.

As can be seen from the large standard errors (Table 11) female moths were extremely variable in the number of eggs they laid and no significant differences

between treatments were observed. However, the trend clearly showed that the female moths formed from larvae which fed on Z. mais and C. dactylon laid the largest number of eggs. The smaller female moths formed from larvae reared on S. plicatilis and P. maximum laid lower numbers of eggs while those from larvae reared on P. clandestinum laid larger numbers of eggs than females reared on P. maximum and S. plicatilis but they were inferior to females from larvae that were reared on C. dactylon and Z. mais.

The reproductive index values of both pupae and adult moths did not vary significantly between the moths reared on different host plants. The mean reproductive period varied from four to five days without much variation between the moths reared on the different grass species.

The females first laid eggs on the first night after emergence but the batches of eggs were extremely small and usually did not hatch. The largest batches were laid between the second and the fifth night after emergence (Figure 2b). After the sixth night following emergence the batch size dropped very rapidly with the last batch being laid on the twelveth night. Female survival was quite high during the first four days of emergence but soon after that the percent mortality steadily increased

(Figure 2a). Ten days after emergence only thirteen percent of the original females remained alive but since they did not lay any eggs they were of no reproductive value.

Life and fertility tables, the net reproductive rates and the capacity for increase in S. exempta populations on various host plants

(a) The percent survival at the start of each stage of development

The mean numbers of eggs laid, the mean egg hatch and the mean percent egg hatch are presented in Table 12. This table shows that mean numbers of eggs oviposited are generally higher than those presented in Table 11 but the variations between females were just as high. The egg viability was highest among the females reared on C. dactylon and lowest among those reared on P. maximum but the differences were not significant. There were larger variations in percent egg hatch in the groups of females reared on P. maximum, S. plicatilis and P. clandestinum than in the groups reared on C. dactylon and Z. mais.

TABLE 8

PUPAL WEIGHTS (mgm) OF *S. EXEMPTA* REARED ON FIVE SPECIES OF GRASS (n = 60)

HOST PLANT	FEMALES MEAN ± S.E.	MALES MEAN ± S.E.
Z. mais	181.21 ± 3.95a	171.16 ± 3.21a
C. dactylon	180.80 ± 2.67a	178.00 ± 2.71a
P.clandestinum	181.21 ± 3.48a	175.29 ± 3.34a
P. maximum	146 ± 3.58b	155.09 ± 3.50b
S. plicatilis	123.58 ± 3.53c	126.40 ± 2.89c

* Figures followed by different letters in each column are significantly different from each other ($P<0.05$)

TABLE 9

EMERGENCE WEIGHTS (mgm) OF ADULT S. EXEMPTA REARED ON FIVE SPECIES OF GRASS (n = 60)

HOST PLANT	FEMALES MEAN + S.E.	MALES MEAN + S.E.*	P
Z. mais	93.58 ± 2.04a	79.34 ± 1.84a	<0.05
C. dactylon	91.24 ± 1.82a	80.59 ± 1.43a	<0.05
P. clandestinum	84.50 ± 2.10b	74.91 ± 1.73a	<0.05
P. maximum	77.82 ± 1.51c	69.07 ± 1.62c	<0.05
S. plicatilis	58.60 ± 1.63d	56.75 ± 1.28d	NS

* Figures followed by different letters in each column are significantly different from each other (P<0.05)

TABLE 10

MEAN LONGEVITY OF S. EXEMPTA ADULTS FROM LARVAE REARED ON VARIOUS HOST PLANTS (n = 60)

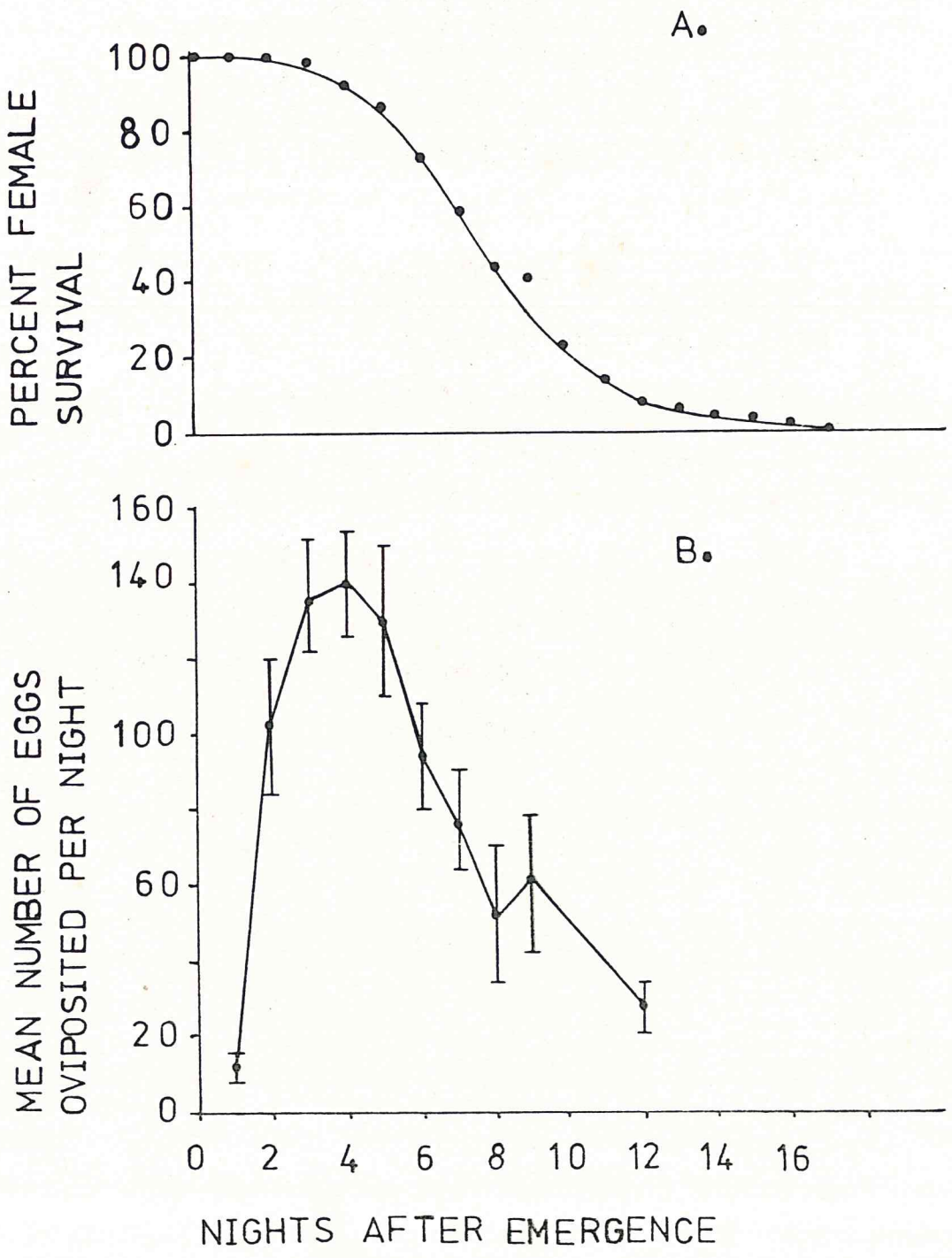
HOST PLANTS	LONGEVITY (DAYS ± S.E.)*		
	MALES	FEMALES	P
Z. mais	10.23 ± 0.15a	8.25 ± 0.31a	<0.05
C. dactylon	11.42 ± 0.48b	10.07 ± 0.49b	NS
P.clandestinum	12.23 ± 0.54b	10.25 ± 0.39b	<0.05
P. maximum	12.90 ± 0.48b	9.93 ± 0.44b	<0.05
S. plicatilis	12.25 ± 0.54b	10.32 ± 0.50b	<0.05

* Figures followed by different letters in each column are significantly different from each other (P<0.05)

TABLE 11

FERTILITY, REPRODUCTIVE INDICES AND EGG LAYING DURATION OF *S. EXEMPTA* (n = 30 FOR EACH HOST PLANT)

HOST PLANT	MEAN NUMBER OF EGGS PER FEMALE	PUPAL REPRODUCTIVE INDEX (EGGS/mgm)	ADULT REPRODUCTIVE INDEX (EGGS/mgm)	MEAN EGG LAYING DURATION (DAYS)
Z. mais	679.33 ± 53.93	4.01	8.47	4.83 ± 0.33
C. dactylon	673.43 ± 35.62	4.33	8.67	5.03 ± 0.30
P. clandestinum	637.73 ± 53.06	3.52	7.48	5.23 ± 0.46
P. maximum	541.97 ± 53.08	3.65	7.40	4.00 ± 0.22
S. plicatilis	540.00 ± 45.46	4.36	8.97	4.30 ± 0.34


A.
PERCENT FEMALE SURVIVAL
100
80
60
40
20
0
B.
MEAN NUMBER OF EGGS OVIPOSITED PER NIGHT
160
140
100
60
20
0
0
2
4
6
8
10
12
14
16
NIGHTS AFTER EMERGENCE

(b) Life and fertility tables

The following columns (Devy, 1947) have been used in constructing the life and fertility tables,

x - the pivotal age for the age class (Days)

l_x - the proportion surviving at the beginning of age class out of the original numbers e.g. l_x for the larval stage is equal to the percent egg hatch and l_x for pupal and adult stages were obtained by multiplying the percent survival obtained in Table 1 by the percent egg hatch. For the rest of the adult life l_x values were obtained by multiplying the l_x value at the beginning of the adult stage by the percent survival for adults in any given group of females (Table 13).

m_x - The number of females produced per female in each age interval. It was obtained by dividing the mean number of larvae hatched from eggs oviposited in each age interval by two (assuming that the sex ratio is 1:1).

The number of times the population will multiply per generation or the net reproductive rate, R_o is

$$R_o = \Sigma l_x m_x$$

The cohort generation time T_c, is the mean age of the females in the cohort at the birth of female offspring or the pivotal age where $l_x m_x = 0.5R_o$ was calculated as

$$T_c = \Sigma x l_x m_x / R_o$$

Finally the capacity for increase r_c which is an estimate of the intrinsic rate of natural increase r_m is calculated as $r_c = \log_e R_o / T_c$.

The values for the net reproductive rate R_o are presented in Tables 14-18. The group of moths reared on Z. mais had the highest net reproductive rate while the group reared on P. maximum had the lowest. Among the groups reared on wild grass species those reared on C. dactylon had the highest net reproductive rate, and though not as high was close to that for the group reared on Z. mais. The group reared on C. dactylon had the shortest cohort generation time and that on P. maximum had the longest (Table 19). Similarly, the capacity for increase was highest in the group reared on C. dactylon and lowest in the group reared on P. maximum while r_c for the moths reared on Z. mais was very close to that of moths reared on C. dactylon.

TABLE 12

MEAN NUMBER OF EGGS OVIPOSITED, MEAN EGG HATCH AND MEAN PERCENT HATCH ± S.E.

HOST PLANT	N	MEAN NUMBER OF EGGS OVIPOSITED ± S.E.	MEAN EGG HATCH ± S.E.	% HATCH ± S.E.
Z. mais	30	850.07 ± 54.34	761.00 ± 48.82	89.80 ± 1.68
C. dactylon	23	814.22 ± 43.84	748.87 ± 44.63	91.16 ± 1.33
P. clandestinum	22	858.86 ± 54.30	753.91 ± 49.42	88.71 ± 2.62
P. maximum	15	692.00 ± 63.29	614.27 ± 70.38	86.36 ± 3.86
S. plicatilis	19	653.32 ± 53.05	611.47 ± 55.39	92.33 ± 2.51

TABLE 13

THE PERCENT SURVIVAL IN ADULTS OF *S. EXEMPTA* REARED ON VARIOUS HOST PLANTS

HOST PLANT	DAYS AFTER EMERGENCE										
	1	2	3	4	5	6	7	8	9	10	11
Z. mais	100	100	100	92	83	75	67	50	33	33	0
C. dactylon	100	100	100	100	100	42	33	8	0	0	0
P. clandestinum	100	100,	100	83	83	75	67	42	33	33	0
P. maximum	100	100	100	100	75	58	33	25	17	0	0
S. plicatilis	100	100	100	100	100	75	75	58	42	8	0

TABLE 14

LIFE AND FERTILITY TABLE FOR S. EXEMPTA ON Z.MAIS

AGE_x (DAYS)	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.00	-	-	-
3	0.90	-	-	-
19	0.32	-	-	-
30	0.27	2.21	0.60	18.00
31	0.27	109.46	29.55	916.05
32	0.27	97.63	26.36	843.52
33	0.27	127.73	34.49	1138.17
34	0.25	70.15	17.54	596.36
35	0.23	49.29	11.34	396.78
36	0.20	50.86	10.17	366.19
37	0.18	55.75	10.04	371.48
38	0.14	34.00	4.76	180.88
39	0.09	10.50	0.95	37.05
			R_o =145.80	4864.48

TABLE 15

LIFE AND FERTILITY TABLE FOR *S. EXEMPTA* ON ON *C. DACTYLON*

AGE (DAYS)	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.00	-	-	-
3	0.91	-	-	-
19	0.33	-	-	-
29	0.28	1.79	0.50	14.50
30	0.28	105.21	29.46	883.80
31	0.28	137.13	38.40	1190.40
32	0.28	106.58	29.84	954.88
33	0.28	56.73	15.88	524.04
34	0.12	75.60	9.07	308.38
35	0.09	19.38	1.74	60.90
36	0.02	19.00	0.38	13.68
		R_o =	125.27	3950.58

TABLE 16

LIFE AND FERTILITY TABLE FOR S. EXEMPTA ON P. CLANDESTINUM

AGE (DAYS)	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.00	-	-	-
3	0.89	-	-	-
21	0.14	-	-	-
31	0.08	5.13	0.41	12.71
32	0.08	75.67	6.05	193.60
33	0.08	78.54	6.28	207.24
34	0.08	79.70	6.38	216.92
35	0.08	90.90	7.27	254.45
36	0.06	40.50	2.43	87.48
37	0.05	25.00	1.25	46.25
38	0.30	10.20	0.31	11.78
39	0.01	5.00	0.05	1.95
			R_o = 30.43	1032.38

TABLE 17

LIFE AND FERTILITY TABLE FOR S. EXEMPTA ON S. PLICATILIS

AGE (DAYS)	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.00	-	-	-
3	0.92	-	-	-
24	0.14	-	-	-
34	0.08	18.21	1.46	49.64
35	0.08	58.13	4.65	162.75
36	0.08	91.21	7.30	262.80
37	0.08	56.13	4.49	166.13
38	0.08	50.23	4.02	152.76
39	0.08	27.50	2.20	85.80
40	0.06	18.83	1.13	45.20
41	0.06	1.17	0.07	2.87
42	0.05	14.67	0.73	30.66
43	0.03	0.85	0.26	11.18
			R_o = 26.31	969.79

TABLE 18

LIFE AND FERTILITY TABLE FOR S. EXEMPTA ON P. MAXIMUM

AGE (DAYS)	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	1.00	-	-	-
3	0.86	-	-	-
24	0.10	-	-	-
34	0.06	7.86	0.47	15.98
35	0.06	66.67	4.00	140.00
36	0.06	85.33	5.12	184.32
37	0.06	63.38	3.80	140.60
38	0.06	26.28	1.58	60.04
39	0.05	24.00	1.20	46.80
40	0.04	43.00	1.72	68.80
41	0.02	31.83	0.64	26.24
42	0.02	10.00	0.20	8.40
43	0.01	11.25	0.11	4.73
			R_o = 15.84	695.88

TABLE 19

THE NET REPRODUCTIVE RATE (R_o), THE COHORT GENERATION TIME (T_c) AND THE CAPACITY FOR INCREASE (r_c) FOR *S. EXEMPTA* POPULATIONS ON VARIOUS GRASS SPECIES

HOST PLANT	$R_o(\Sigma l_x m_x)$	$T_c(\Sigma x l_x m_x / R_o)$	$r_c(\log_e R_c / T_c)$
C. dactylon	125.27	31.54	0.153
Z. mais	145.80	33.36	0.149
P. clandestinum	30.43	33.93	0.101
S. plicatilis	26.31	36.86	0.089
P. maximum	15.84	43.93	0.063

DISCUSSION

The rate of development of larvae of the African armyworm, S. exempta was highest on Z. mais but among the wild grass species, C. dactylon was superior. P. maximum and S. plicatilis can support larval development but the larvae grow at lower growth rates. Except for the larvae on C. dactylon, males had a slightly faster larval development than females. This could be due to males feeding faster than females or due to females having greater food requirement than males so that at similar feeding rates, females take slightly longer time to complete the larval life. In the related Spodoptera litura F. female larvae digest higher amounts of food at 15°C, 20°C although the trend is reversed with the rise in temperature which is clearly evident at 30°C (Bhat and Bhattacharya, 1973).

The larval stage is the most susceptible to mortality factors. A large proportion of larvae died at the first instar stage. Some of them died on the first day after hatching and refusing to feed. Others fed but died later and in fact some of them remained in the first instar and died after the healthy larvae of their age were long in the second instar. The high

mortality of the first instar larvae was common to all the larval groups irrespective of the host plant. While high mortality occurred through out the larval life in the groups on P. maximum and S. plicatilis; second, third and fourth instar larvae experienced relatively low mortality on Z. mais and C. dactylon. In the latter group larval mortality was, however, high during the fifth instar. Larvae on P. clandestinum experienced the highest mortality during the first and fourth instar stages. In some cases, particularly on S. plicatilis moulting was not well synchronised resulting in a proportion of the sick larvae dying long after the healthy ones had moulted into the next instar. Therefore some of the larvae recorded dead during the third instar actually belonged to the second instar.

The integuments of most of the dead larvae were delicate and on tearing a creamy mass of haemolymph propbably containing polyhederal inclusion bodies (Odindo, 1977) was produced. Larvae could have been infected through feeding on food contaminated by nuclear polyhedrosis virus although this virus can also be transovarially transmitted (Brown and Swaine, 1965) and this could have been the cause of death for most of the larvae which died during

the first instar stage. The effect of viral infection on the larvae is probably dependent on the initial dose of the viral particles, quantity and quality of larval food and conditions of humidity and temperature. Larvae which feed on nutritionally suboptimal food supply or kept at high densities, or under unsuitable conditions of temperature and humidity are likely to be weaker and therefore vulnerable to virus attack.

A small proportion of larvae which died three to five days after the initial diagnosis of an infection produced semi-liquid faeces but their integuments, though wrinkled, remained tough and more difficult to puncture. These were probably killed by bacteria. In still fewer cases, particularly among the larvae reared on P. clandestinum previously healthy-looking larvae were found dead next morning with profuse growth of white fungal hyphae on the integument.

C. dactylon, Z. mais and P. clandestinum had the highest nitrogen levels in the youngest leaves. P. maximum and S. plicatilis and the older leaves of the more suitable host plants had the lowest levels of nitrogen (Chapter 3). Despite its similarity to C. dactylon and Z. mais in nitrogen level, the larval mortality on P. clandestinum was much higher. Thus, the

nitrogen level by itself is not necessarily indicative of the suitability of a plant as a host because it neither distinguishes between strictly nutritive substances and other substances nor does it show the amount of nutritive material that the larvae derive from the food stuff by digestion (House, 1969). The quantitative imbalance of nutrients or poor rate of food consumption by insects can also be responsible for unsuitability of host plants (Waldbauer, 1968; House, 1969). The resistance of some host plants to Spodoptera eradania (Cramer) is known to be due to hard texture or to the fish-like spines of those plant species (Soo Hoo and Fraenkel, 1966).

The caterpillars reared on Z. mais, C. dactylon and P. clandestinum went through five instars although previously it had been reported that under similar conditions the larvae went through six instars on these host plants (Ma, 1974). The differences in the number of instars could have resulted from the differences in the age of the leaves fed on. The distribution of mortality among the larvae which went through five instars was U-shaped with highest rate of death occurring during the first and the last instar. Similar results were obtained with the larvae which went through five instars except that

high mortality during the last instars can also occur during the fourth as in the case of the population reared on P. clandestinum.

Larvae reared on P. maximum and S. plicatilis went through six instars respectively with the highest mortality of larvae occurring during the first instar. Even so, the percent mortality during the second and third instar stages was much higher than it was on the host plants on which the larvae went through five instars. Consequently, the percent larval mortality during the last instars was much lower than in the five instar group and therefore the mortality distribution was not U-shaped.

Though small, there were variations in durations of pupal development. Pupae formed from larvae reared on Z. mais and S. plicatilis had the shortest pupal duration. Since these host plants were very different in their ability to support larval growth and development, the similarity in the pupal duration suggests that the host plants affect the larvae differently from the pupae. Similar observations have been made with regard to Prodenia litura F. (Pandey and Srivastava, 1967). Pupal development is probably governed by intrinsic physiological factors. Females had a significantly shorter pupal duration but the comparison of the period from hatching of eggs to adult emergence did not show significant differences between the sexes.

Larvae fed on Z. mais, C dactylon and P. clandestinum formed larger pupae and though the differences were not significant females were larger than the males. Those fed on P. maximum and S. plicatilis formed smaller pupae, and in this case females were slightly smaller than males. Thus, host plants vary in their effects on larvae and they affect sexes differently. Except for those reared on S. plicatilis females weighed significantly more than males at emergence. The greater females weights could be attributed to eggs although differences in adult behaviour could result in females not voiding all of the meconium. Pupal and adult weights used were for the same individuals and therefore the possibility of smaller females having died does not arise. Adults from larvae reared on P. clandestinum had lower weights than expected for their pupal weights, suggesting that water content of the larval host plant may influence' pupal water content. The water content of P. clandestinum and Z. mais are comparable (Chapter 3) but the late instar stages of larvae reared on latter fed on older leaves whereas this procedure cannot be as easily followed with P. clandestinum.

Females were extremely variable in the total number of eggs they laid. However, the reproductive index values suggest that the number of eggs laid is a function of the weight of the female pupa or adult. The short reproductive period is consistent with the synchrony in the larval development under optimum conditions of growth. A prolonged reproductive period would have been wasteful, as the older larvae would deplete the food resources and most of the younger larvae would die of starvation. Those which survive, if at all, would need a much longer time feeding and would only produce small moths due to scarcity of food.

The net reproductive rate R_o is in all cases in excess of one implying that on all the five species of host plants population growth is possible. C. dactylon and Z. mais are, however, far more important food plants in bilding up the African armyworm populations since the R_o values for populations on these host plants are much higher than those for populations on P. clandestinum, S. plicatilis and P. maximum. The net reproductive rates are probably sufficient in estimating the increase in populations of the African armyworm since apart from outbreak populations and several successive generations (Khasimuddin and Lubega, 1979; Rose, 1975) no resident

populations with known age distribution have been established.

Even so, field searches for low density populations in South Africa have resulted in some solitary-phase caterpillars being found during several months of each wet season when grasses were suitable (Faure, 1943; Matthee, 1952). Solitary-phase caterpillars have also been found in East Africa (Rose, unpublished observation). Furthermore, low numbers of moths continue being caught by light and pheromone traps in East Africa even during the period of virtual absence of outbreaks (Brown and Swaine, 1966; Brown et al., 1969). These probably come from inconspicuous caterpillars, either in low densities scattered in seasonally green grasses or in denser populations where grasses are green and temperatures are favourable most of the year. Such populations are possibly the origin of the first outbreaks (Rose, 1979). It is possible that under low density conditions the generations are overlapping. The growth potential of such populations can be described by the parameter r whose maximum value is r_m under given climatic and food conditions (Messenger, 1964; Watson, 1964). The parameter r_m is variously termed the intrinsic rate of natural increase, the Malthusian parameter, the innate capacity for increase or various combinations of these (Leslie and Ranson, 1940; Birch, 1948; Caughley and Birch, 1971). An

approximate r_m, the capacity for increase (r_c) has long been used in insect ecology and the present results show that at least in the laboratory, the capacity for increase r_c is highest in populations reared on C. dactylon and Z. mais and lowest in the populations on P. maximum and S. plicatilis.

The laboratory results may not be exactly representative of what happens in the field where the population increase is limited by food, temperature, predation, parasitism and disease. At the beginning of the outbreak season, however, tender grass is available in abundance and temperature is favourable. Predation, parasitism and disease may reduce the population considerably but their effect may be counterbalanced by the usually high density of outbreak larvae and rapid development of immature stages. Moreover, outbreaks usually take place in areas where there had not been previous outbreaks during the season, and therefore predators and parasites would not be expected to be as high in numbers as if the population had been resident.

SUMMARY

Five species of the grass family were used to study the development of the African armyworm *S. exempta*. The rate of larval development and survival, percent pupation and adult emergence as well as the net reproductive rates and the capacities of increase were highest on *C. dactylon* and *Z. mais.* These host plants are therefore very important in building up the population of the African armyworm to pest status during the outbreak season. The dry season populations may be sustained on *C. dactylon* in scattered but not necessarily permanent areas in the highlands of East Africa, river beds and flood plains where this grass species is widespread.

CHAPTER 2

THE INFLUENCE OF TEMPERATURE AND THE HOST PLANT SPECIES ON THE DEVELOPMENT OF THE AFRICAN ARMYWORM SPODOPTERA EXEMPTA (WALK.)

INTRODUCTION

Characteristic sudden appearance of outbreaks of the African armyworm larvae at the beginning of the rainy season is experienced during the first half of the year in Eastern (Brown, 1970) and Southern Africa (Hattingh, 1941). Outbreak populations virtually disappear during the rest of the year. Adult moths are dispersed and brought together by wind currents (Brown and Swaine, 1966; Brown et al., 1969; Rose and Law, 1976) but no permanent breeding habitats are known except that several generations can survive in the same locality (Rose, 1975; Khasimuddin and Lubega, 1979). Light trap data (Odiyo, 1979) show that low density populations persist throughout the year in places which may not be permanent habitats within the range of distribution.

Climate is one of the factors which controls the population of the species (Brown et al., 1969, Hattingh, 1941; Persson, 1981) but how the changes in ambient

temperature interact with host plants of the larvae is not known. This investigation was carried out to find out the effect of changing ambient temperature on the development of S. exempta on some host plants.

MATERIALS AND METHODS

Larvae of S. exempta from insectary stock were reared in groups of twenty in 16cm high cylindrical wire cages with diameters of 12cm. Each cage was placed in a bag of muslin cloth in an outdoor 5x5x3m screen cage at ICIPE, Chiromo campus. Larvae were reared on maize, Zea mais L; star grass, Cynodon dactylon (L.) Pers.; Kikuyu grass, Pennisetum clandestinum Chiov. and Setaria plicatilis (Hochst.) Hack. throughout the larval life. Each cage was fitted with an elastic rubber band which held a plastic vial containing water in position. The cut ends of grass leaves were immersed in water to minimise wilting.

The study was carried out between June 1978 and July 1979 but due to larval mortality it was not possible to have data for some months. Larval survival was lowest on P. maximum and therefore this host plant was excluded in the figures. Each host plant was replicated five times for each month.

The larval duration for each individual was recorded at the time of pupation and as pupae were kept singly the pupal duration was also recorded.

The average ambient temperature to which each individual was exposed during its development period was estimated from daily minimum and daily maximum temperatures average for development period. Pupal and adult weights were taken within twelve hours of pupation and emergence respectively and for each individual the adult longevity was recorded.

RESULTS

The mean ambient temperatures (Table 20) under which the larvae developed on each host plant ranged from about 16°C in June 1978 to about 20°C in January, 1979. Larval duration (Table 21) varied from 35 days on Z. mais to 43 days on S. plicatilis in June 1978. In January 1979 it varied from 20 days on Z. mais to 23 days on S. plicatilis. The results show that both the ambient temperature and the host plant have an effect on the rate of larval development (Figure 3). The difference between the rates of development on Z. mais and S. plicatilis was greater during the colder

months than during the warmer ones. Thus under low temperature conditions the influence of the host plant on the rate of development of larvae is greater than under the warmer temperature conditions. The larval development on Z. mais at temperatures below 20°C was faster than that on the other host plants. As the temperature increased the rate of growth on Z. mais was comparable to that for larvae on C. dactylon and P. clandestinum. Larvae on S. plicatilis, C. dactylon and P. clandestinum developed at similar rate under lower temperature regimes but S. plicatilis was inferior to the other two host plants under higher temperature.

The regression (Table 22) of the temperature on percent development per day is in all cases highly significant ($P<0.001$). Comparison with results obtained under constant temperature (Hattingh, 1941) shows that for any given temperature the rate of development was higher under the average ambient temperature than at constant temperature (Figure 4). The mean monthly maximum and minimum temperatures (Table 23) show large differences between them but do not show how the temperature varied during any one given day. Since the regression based on the mean ambient temperature of the pooled data for all the four host plants was lower than that for data obtained under constant temperature (Hattingh, 1941) the actual mean temperatures must have

TABLE 20

MEAN AMBIENT TEMPERATURE AND STANDARD ERRORS DURING THE LARVAL DEVELOPMENT

(C ± S.E.)

MONTH		HOST PLANT				
		Z. mais	C.dactylon	P.clandestinum	P. maximum	S.plicatilis
June '1978)	M	15.81 ± 0.05	15.89 ± 0.01	16.01 ± 0.02	-	16.04 ± 0.04
	F	15.88 ± 0.06	15.77 ± 0.04	16.12 ± 0.03	15.88 ± 0.04	-
July (1979)	M	-	15.95 ± 0.09	15.95 ± 0.04	-	15.98 ± 0.03
	F	-	15.96 ± 0.04	15.98 ± 0.04	15.98 ± 0.04	-
August (1978)	M	16.58 ± 0.06	16.0 ± 0.10	16.85 ± 0.07	-	16.83 ± 0.08
	F	16.77 ± 0.03	16.74 ± 0.01	16.76 ± 0.01	-	16.77 ± 0.03
September (1978)	M	-	-	19.03 ± 0.01	-	19.03 ± 0.01
	F	-	19.03 ± 0.01	19.03 ± 0.01	-	19.03 ± 0.01
January (1979)	M	20.15 ± 0.02	20.14 ± 0.03	20.15 ± 0.02	-	20.07 ± 0.07
	F	20.19 ± 0.02	20.09 ± 0.0	20.13 ± 0.05	-	20.03 ± 0.05
July (1979)	M	15.69 ± 0.01	15.72 ± 0.02	15.69 ± 0.01	15.69 ± 0.02	15.60 ± 0.03
	F	15.68 ± 0.02	-	15.64 ± 0.02	15.72 ± 0.00	15.62 ± 0.01

TABLE 21

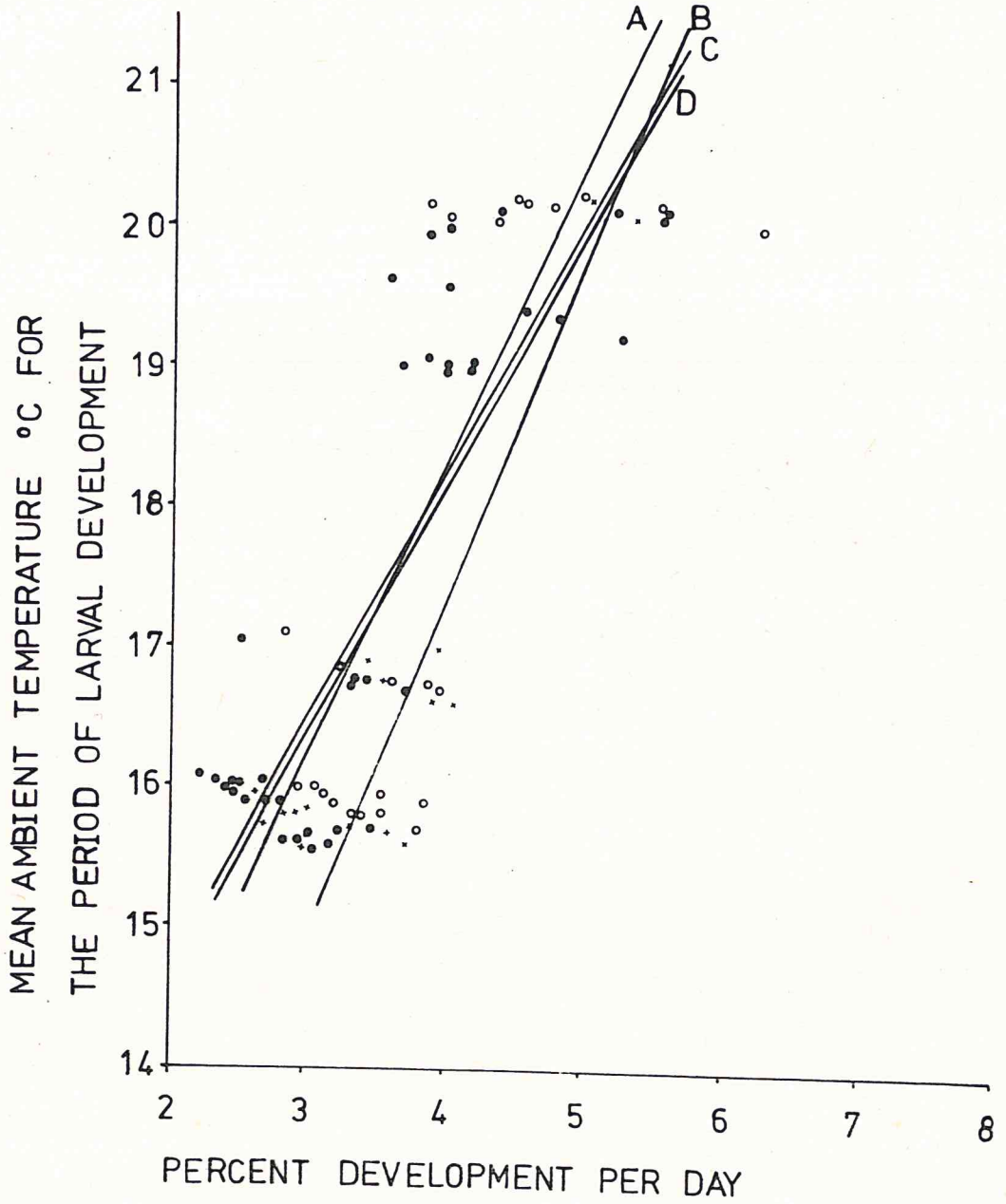
MEAN LARVAL DURATION (DAYS) AND STANDARD ERRORS FOR LARVAE REARED ON DIFFERENT GRASS SPECIES IN A FIELD CAGE AT CHIROMO

MONTH		HOST PLANTS				
		Z. mais	C. dactylon	P. clandestinum	P. maximum	S. Plicatilis
June 1978	M	35.5±1.31(6)*	37.1±0.81(10)	40.6±0.85 (10)	-	43.0 (1)
	F	34.67±1.67(3)	35.9±0.84(10)	41.0±1.13 (6)	37.0 (1)	-
July 1978	M	-	33.5±3.50 (2)	35.5±0.65 (4)	-	34.0 (1)
	F	-	33.0 (1)	39.0±1.15 (1)	35.0 (1)	-
August 1978	M	26.31±0.24(3)	29.5±2.18 (4)	32.17±1.97(6)	-	31.0±1.53(3)
	F	28.3±0.62(10)	28.75±0.75(4)	30.0 ±0.58(3)	-	30.2±0.2 (5)
September 1978	M	-	-	24.8±0.20 (5)	-	24.0 (1)
	F	-	25.0 (1)	25.8 ±0.58(5)	-	25.0 (1)
January 1979	M	21.17±0.60(6)	20.0±0.77(6)	20.33±1.20(3)	-	22.0±3.0 (2)
	F	20.19±0.02	20.25±0.98(8)	22.67±0.33(3)	-	23.33±2.19(3)
July 1979	M	29.62±0.99(13)	30.0 (1)	31.4 ±0.82(10)	30.67±2.26(6)	32.5 ±0.5 (4)
	F	29.67±0.71(6)	-	32.0 ±0.58(4)	30.0 ±0 (2)	33.0 ± 1.0(2)

*The number of individuals on which the mean and the standard error are based is in parenthesis.

PLATE

of *S. exemplta* larvae on various planes at ambient temperature.



A •—S.plicatilis

B •—Z.mais

C •—P.clandestinum

D •—C.dactylon

been higher than the average of the minimum and maximum temperature. The regression for the pooled data is

$$y = 1.76x + 10.91$$

whereas that for data from constant temperature conditions is

$$y = 2.15x + 14.45$$

where y is the temperature (^{o}C) and x is the percent development per day.

The rate of development of pupae was variable (Table 25). At lower temperature the pupae formed from larvae reared on C. dactylon had the highest rate of pupal development whereas at higher temperatures those formed by the larvae reared on Z. mais had the highest rate of development. The group of pupae formed from larvae reared on P. clandestinum had the lowest rate of development particularly at higher temperatures (Figur 25). The mean temperatures ranged from about 16^{o}C in June, 1978 to about 19.5^{o}C in January 1979 (Table 24).

TABLE 22

THE RELATIONSHIP BETWEEN MEAN AMBIENT TEMPERATURE ^{o}C AND THE PERCENT LARVAL DEVELOPMENT PER DAY ON THE SAME HOST PLANT

HOST PLANT	N	REGRESSION	r	r^2	a
Z. mais	60	2.26	0.89	0.80	8.47
C. dactylon	41	1.77	0.89	0.80	11.11
P. clandestinum	66	1.72	0.83	0.70	11.37
S. plicatilis	23	2.12	0.86	0.74	9.90
Pooled data	188	1.76	0.83	0.69	10.91
Barley*	5360	2.15	0.97	0.95	14.45

* Based on data by Hattingh (1941)

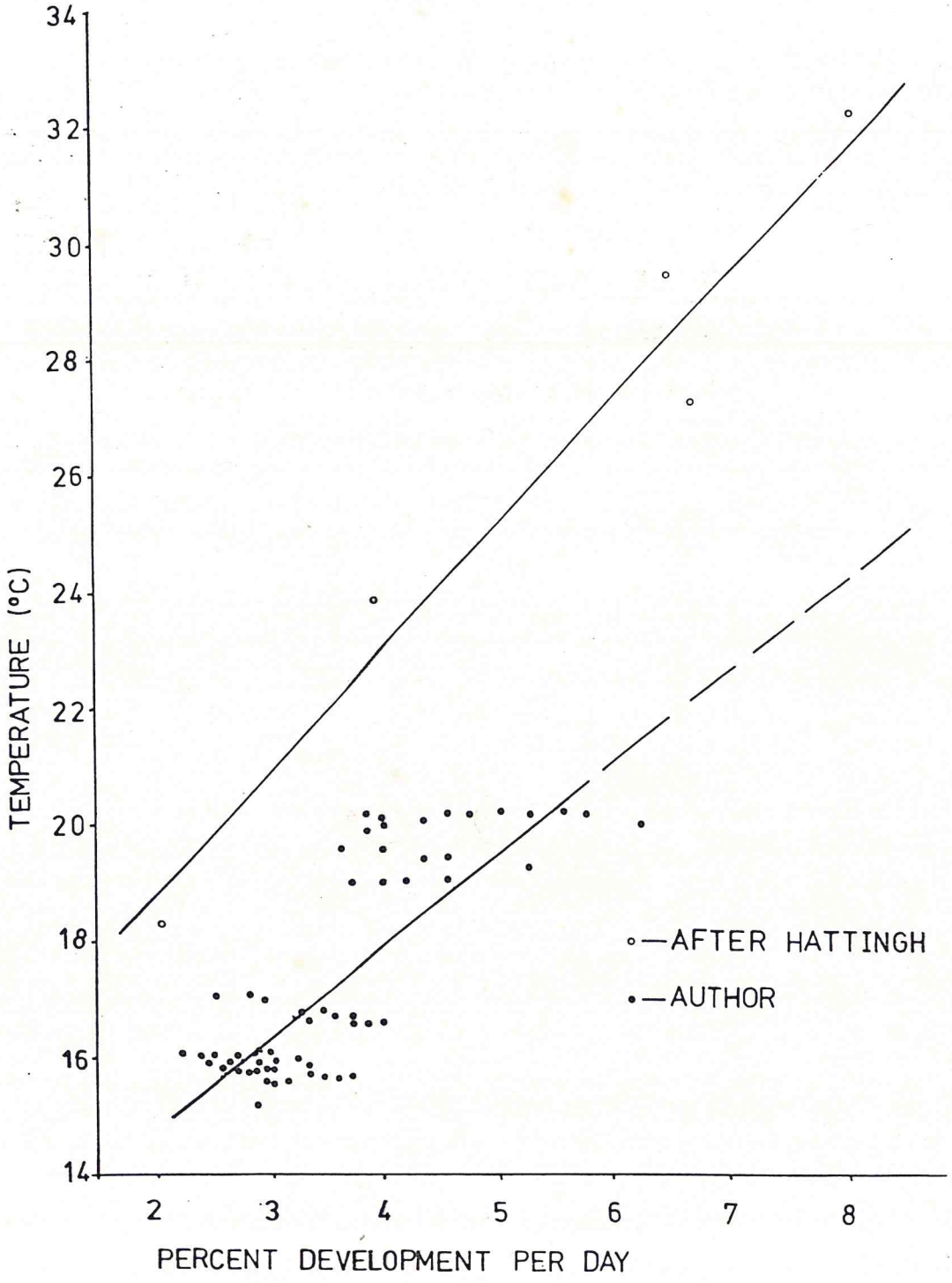
TABLE 23

MEAN MONTHLY MAXIMUM AND MINIMUM TEMPERATURE

($^{o}C \pm$ S.E.)

MONTH	MEAN MAXIMUM TEMPERATURE	MEAN MINIMUM TEMPERATURE
JUNE (1978)	21.43 ± 0.40	12.07 ± 0.24
JULY (1978)	20.86 ± 0.40	11.30 ± 0.29
AUGUST (1978)	21.89 ± 0.39	11.22 ± 0.24
SEPTEMBER (1978)	24.41 ± 0.33	11.51 ± 0.35
OCTOBER (1978)	24.30 ± 0.35	13.45 ± 0.24
JANUARY (1979)	25.14 ± 0.24	13.56 ± 0.25
FEBRUARY (1979)	25.91 ± 0.24	13.74 ± 0.26
JULY (1979)	20.73 ± 0.43	10.78 ± 0.28

FIGURE 4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TEMPERATURE (°C)
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PERCENT DEVELOPMENT PER DAY
°—AFTER HATTINGH
•—AUTHOR

Larvae reared in June pupated towards the end of July 1978 with pupal duration varying from 23 days on S. plicatilis to about 27 days on Z. mais but in January 1979 it varied from 12 days on Z. mais to 21 days on S. plicatilis (Table 25).

The regression of the average ambient temperature on the development per day (Table 26) was highly significant in each case ($P<0.001$). The regression for the pooled data was also highly significant ($P<0.001$) but the slope was lower than that for the results from constant temperature conditions (Hattingh, 1941) meaning that for a given temperature the development rate was lower under constant temperature conditions (Figure 6). This is again attributed to the fact that the average ambient temperature does not give details of variation in temperature for a given day.

The regression for the pooled data is

$$y = 0.90x + 13.05$$

and that for the data from constant temperature conditions is

$$y = 1.29x + 12.37$$

where y is the temperature (^{o}C) and x is the percent development per day.

TABLE 24

MEAN AMBIENT TEMPERATURE AND STANDARDARD ERRORS DURING THE PUPAL DEVELOPMENT PERIOD

MONTH		Z. mais	C.dactylon	P.clandestinum	P. maximum	S. plicatilis
June (1978)	M	16.15±0.01	16.15 ± 0.01	16.19 ± 0.12	-	16.43±0.02
	F	16.07±0.01	15.91 ± 0.05	16.32 ± 0.13	16.13±0.02	-
July (1978)	M	-	16.96 ± 0.25	17.09 ± 0.00	-	-
	F	-	16.82 ± 0.05	17.11 ± 0.08	17.09±0.06	-
August(1978)	M	17.61±0.04	17.70 ± 0.04	17.64 ± 0.00	-	17.64±0.03
	F	17.66±0.01	17.66 ± 0.02	17.64 ± 0.00	17.81±0.02	17.67 ± 0.01
September(1978)	M	-	-	19.34 ± 0.02	-	19.39 ±0.03
	F	-	19.37 ± 0.04	19.33 ± 0.05	-	19.37 ± 0.20
January (1979)	M	19.59±0.06	19.50 ± 0.09	19.71 ± 0.09	-	19.35 ± 0.04
	F	19.63±0.00	19.57 ± 0.08	19.48 ± 0.17	-	19.50 ± 0.25
July (1979)	M	16.85±0.09	16.95 ± 0.08	16.85 ± 0.04	16.92±0.02	
	F	16.75±0.08	-	16.96 ± 0.03	16.77±0.04	17.00 ± 0.05

TABLE 25

MEAN PUPAL DURATION (DAYS) AND STANDARD ERRORS IN FIELD CAGE AT CHIROMO

MONTH		Z. mais	C. dactylon	P.clandestinum	P. maximum	S.plicatilis
June 1978	M	27.0±0.41 (4)*	25.9 ± 0.31(10)	25.0 ± 1.0 (3)	-	23.0 (1)
	F	27.33±1.73(3)	24.6 ± 0.98(10)	25.0 ± 0.58(3)	24.0 (1)	-
July 1978	M	-	23.0 ± 1.0 (2)	23.5 ± 0.5 (4)	-	-
	F	-	21.0 (1)	22.0 ± 0.58(3)	24.0 (1)	-
August 1978	M	17.3±0.62(10)	16.33± 0.77(10)	18.67±0.38 (3)	-	18.0 (1)
	F	17.0±0.68(3)	17.5 ± 0.5 (2)	17.5 ± 0.5 (2)	17.0 (1)	17.0±0(4)
September1978	M	-	-	15.75±0.48 (4)	-	15.0 (1)
	F	-	15.0 (1)	14.6 ±0.51 (5)	-	15.0±0.00(2)
January 1979	M	12.0±1.65(6)	15.8 ± 1.11(5)	13.0 ±1.0 (2)	-	21.0 (1)
	F	13.33±0.33(3)	15.25±0.47 (4)	15.5 ± 1.5 (2)	-	15.5±0.5(2)
July 1979	M	25.0 ± 37 (6)	26.0 (1)	25.17±0.40 (6)	25.0±0.37(6)	22.67±0.88(3)
	F	23.0 (1)	-	24.5 ± 0.5 (4)	23.0 (1)	24.0 (1)

*The number of individuals on which the mean and the standard error are based is in parenthesis.

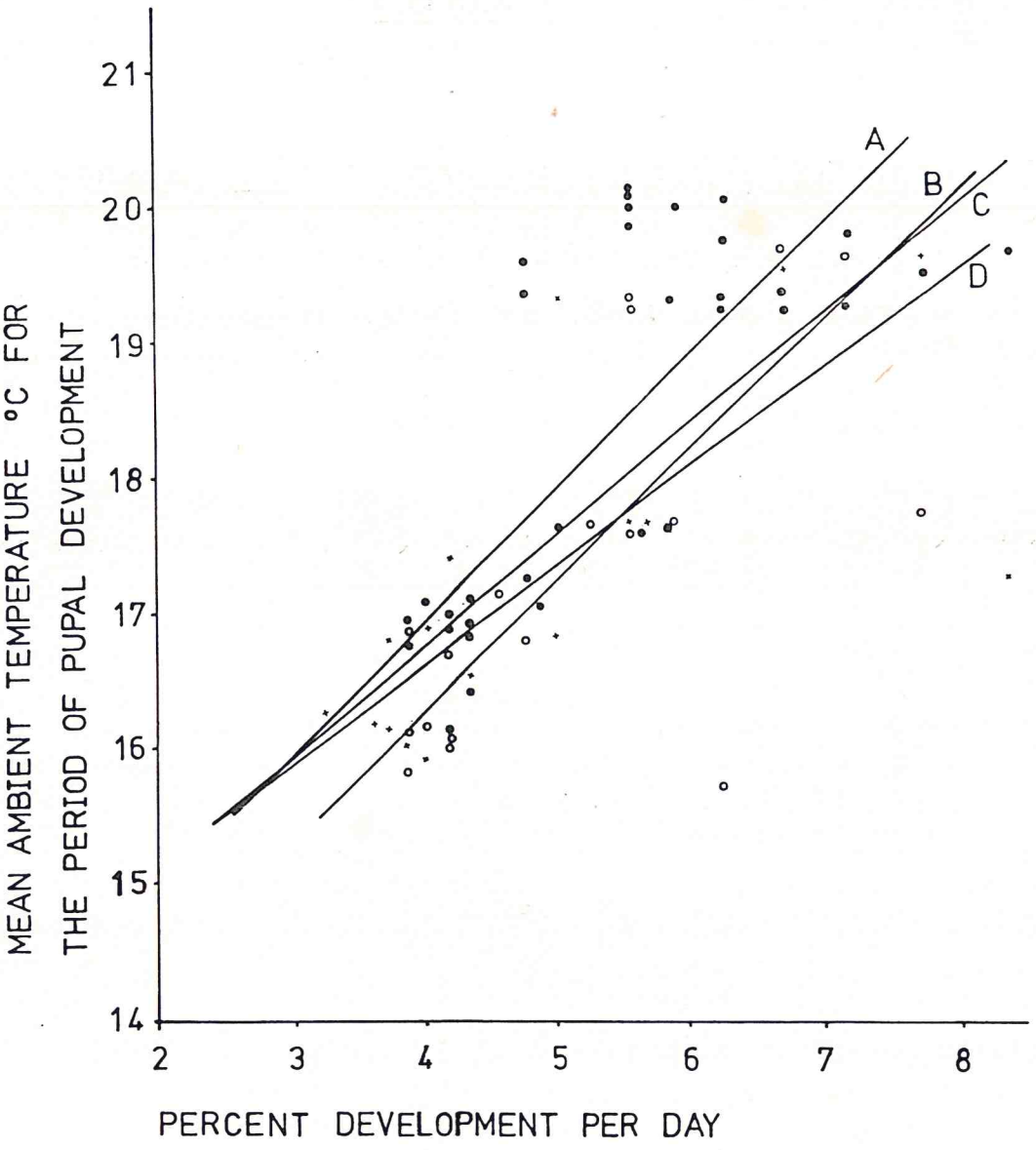
TABLE 26

THE RELATIONSHIP BETWEEN MEAN AMBIENT TEMPERATURE AND THE PERCENT PUPAL DEVELOPMENT PER DAY ON SOME HOST PLANTS

HOST PLANT	N	REGRESSION	r	r^2	a
Z. mais	43	0.74	0.85	0.72	13.66
C. dactylon	36	0.96	0.84	0.71	12.44
P. clandestinum	51	0.98	0.81	0.67	12.01
S. plicatilis	16	0.82	0.71	0.51	13.48
Pooled data	146	0.90	0.80	0.64	13.05
Barley*	140	1.29	0.98	0.96	12.37

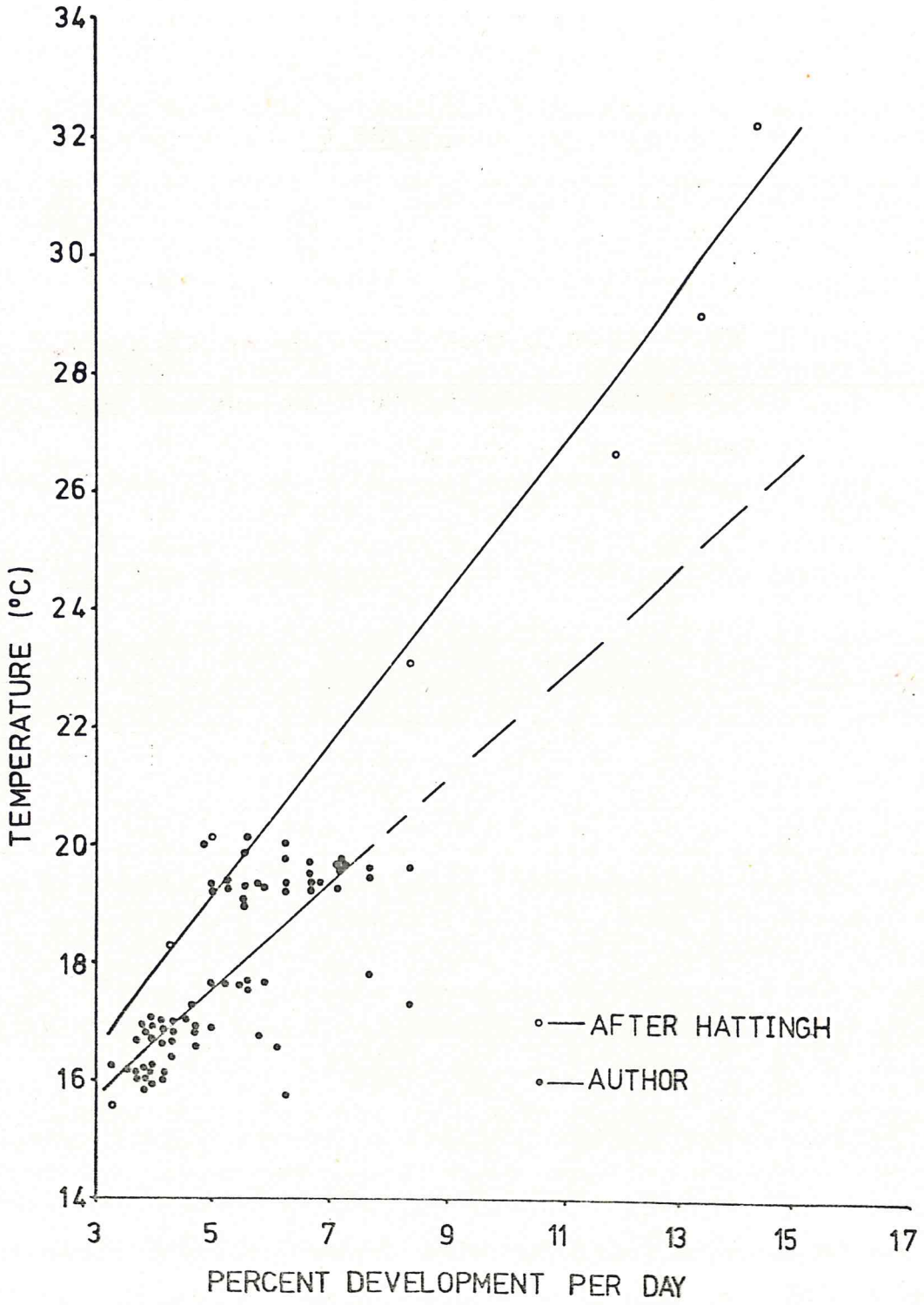
*Based on data by Hattingh (1941).

Fig. 3(b)



A •—P.clandestinum B ∘—C.dactylon

C ·—S.plicatilis D •—Z.mais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TEMPERATURE (°C)
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PERCENT DEVELOPMENT PER DAY
AFTER HATTINGH
AUTHOR

As expected the period from egg hatching to pupation (Table 27) was longest in the group that was reared starting June, 1978 and shortest in the group which was reared starting January, 1979. During the coldest period it took over two months while during the warmest period it took just above one month. Although there were some differences with respect to the host plants the ambient temperature was far more important in determining the length of the development period.

Pupal weights varied with months when rearing took place (Table 28). The highest pupal weights were recorded in the groups reared starting July, 1979 followed by those reared starting September, 1978 and June 1978. The humbers of individuals in consideration were, however, lower in September 1978 than in June 1978 and July 1979. Larvae reared in January, 1979 produced the smallest pupae. With the present data no concrete conclusion can be made but the results suggest that larvae reared during the cold months produce larger pupae than those reared during the warm months when the growth rate is highest.

Most moths formed from larvae reared starting June1978 died between the second and the eleventh day

after emergence (Table 29) although some moths survived for a longer period with the last one dying on the twenty fourth day.

Those formed from larvae reared starting August 1978, started dying from the fifth to the twelveth day while the group from larvae reared starting January 1979 started dying mostly between the seventh day and the twentieth day. The result suggest that under higher temperature conditions moths live longer than under low temperature conditions.

TABLE 27

COMBINED LARVAL AND PUPAL DURATION IN A FIELD CAGE AT CHIROMO A(DAYS ± S.E.)

MONTH	SEX	HOST PLANT				
		Z. mais	C. dactylon	P.clandestinum	P. maximum	S. plicatilis
June 1978	M	64.25 ± 0.75(4)*	63.0 ± 0.37(10)	64.67±0.37(3)	-	66.0 (1)
	F	62.0 ± 3.51 (3)	60.5 ± 1.31(10)	65.0 ±2.31(3)	61.0 (1)	-
July 1978	M	-	56.5 ± 2.5 (2)	59.0 ± 1.08(4)	-	-
	F	-	54.0 (1)	61.0 ± 1.0 (3)	-	-
August 1978	M	43.6 ± 0.64(10)	46,67±1.45(3)	47.67±0.33 (3)	-	48.0 (1)
	F	44.33± 1.73(3)	46.0 ± 2.0(2)	48.0 ± 0.0(2)	-	47.25±0.25
September 1978	M	-	-	40.75± 0.48(4)	-	39.0 (1)
	F	-	40.0 (1)	40.40± 0.75(5)	-	40.0 (1)
January 1979	M	36.17±1.01(6)	37.8 ± 1.91(5)	32.5 ± 1.41(2)	-	46.0 (1)
	F	33.33±0.33(3)	37.0 ± 2.38(4)	38.5 ± 1.5(2)	-	37.5 (2)
July 1979	M	54.88±1.20(8)	56.0 (1)	55.17±0.40(6)	55.67±0.49(3)	-
	F	53.0 ±0.82(7)	-	56.25±0.48(4)	56.0 (1)	-

*The number of individuals on which the mean and the standard deviation is based is in parenthesis.

TABLE 28

PUPAL WEIGHTS OF INDIVIDUALS REARED IN A FIELD CAGE AT CHIROMO (mg)

MONTH	SEX	HOST PLANT				
		Z. mais	C. dactylon	P.clandestinum	P. maximum	S. plicatilis
June 1978	M	169.24±10.31(6)	171.71±3.35(10)	189.31±5.86(8)	-	171.90 (1)
	F	172.09±13.61(10)	169.49±5.7[illegible](10)	183.57±6.72(5)	166.26 (1)	-
July 1978	M	-	168.35±20.45(2)	168.22±7.20(4)	-	184.2 (1)
	F	-	155.61 (1)	195.41±12.91(3)	186.93 (1)	-
August 1979	M	153.16±7,14(13)	158.18±13.16(4)	160.92±12.91(6)	-	153.5 (11
	F	167.75±5.02(10)	161.18±26.44(4)	177.8±3.03 (3)	-	108.9 (1)
September 1978	M	-	-	181.93±5.72(4)	-	153.5 (1)
	F	-	219.9 (1)	175.85±29.99(4)	-	108.9 (1)
January 1979	M	141.54±10.43(6)	174.29±17.92(6)	143.57±11.56(3)	-	135.41±1.53(2)
	F	147.99±2.29(5)	173.45±9.05(8)	162.84±10.81(3)	-	141.56±9.54(3)
July 1979	M	203.82±3.94 (3)	186.19 (1)	187.77±6.62(10)	172.67±8.87(6)	159.41±5.79(4)
	F	214.56±5.59(6)	-	195.10±12.31(6)	180.75±12.66(6)	159.68±8.98(2)

*The number of individuals on which the mean and the standard error are based is in parenthesis.

TABLE 29

MOTH LONGEVITY IN AN OUTDOOR FIELD CAGE AT CHIROMO

(DAYS)

	June (1978)		July (1978)		August (1978)		Sept. (1978)		Jan. (1979)		July (1979)	
Sex	F	M	F	M	F	M	F	M	F	M	F	M
Date of death after emergence												
1												
2	1	1						1				
3	2			1				1		1		
4	2						2	1				
5	3	2		1	3	5	2		1			
6		3			1	2						
7	3		1	1	2					2		
8				2	1				1	2	1	3
9	1	3							1	2		
10	1			1	1				1	1	2	2
11		1		1	2	1			2		1	2
12						1			1	3	2	4
13	1											
14	1	1							2	1	1	
15					1				2	2		
16		1							1			1
17									1	1		1
18										1	1	
19												
20		1	1							1		
21												
22												
23	1											
24			1									1
25												

DISCUSSION

The developmental times of both larvae and pupae of S. exempta vary with host plants of the larval stage but they are also much influenced by temperature. The rate of development of an immature stage is the reciprocal of developmental period and when this is multiplied by 100, it gives an estimate of percent development per day. When the ambient temperature was regressed against the percent development per day the coefficients of determination were in all cases above 70%. If a sufficiently wide range of temperature were used the relationship would have been described by the logistic curve (Lamb and Loschiavo, 1981) but the range of temperature used in this investigation was small. The relationship can therefore be described accurately by a linear equation.

In field situation temperature fluctuates and the mean or average temperature for the development period of a given individual is just an estimate and so is the relationship between the developmental period and temperature. Under constant temperature conditions, (Hattingh, 1941) higher correlation was obtained. Moreover, for a given temperature the rate of development was higher for both larvae and pupae under average ambient temperature than under constant temperature.

This is explained by the fact that the minimum temperature for at least some days may have been for only a short period but this is not taken into account in calculating the average temperature. The actual mean temperature is therefore probably higher than the calculated average. Furthermore it may be that the high day time temperature has more influence on the rate of development than the low night temperature.

Using the regression lines it was possible to estimate the theoretical threshold temperature as the value at which the line intersected the temperature axis. Apparent threshold temperature values for larval stage were 10.91^{o}C and 14.45^{o}C under ambient and constant temperature conditions respectively and those for pupal stage were 13.05^{o}C and 12.35^{o}C. In some cases the daily minimum temperatures were lower than 10^{o}C and this suggests that larvae can survive at temperature below the threshold under constant temperature conditions so long as such low temperature conditions do not persist. The critical factor is probably the time the immature stage is subjected to such low temperature and this may vary with the stage of development.

In East African outbreaks of larvae occur at the time when the food plants are germinating and the temperature is favourable for growth. Unlimited supply of tender and nutritious food in combination with high temperature probably results in rapid development of both larvae and pupae leading to the widespread outbreaks of larvae. As the season advances both the food supply and ambient temperature decline and this possibly leads to reduction of the number and size of outbreaks.

During the dry season it may be possible to find isolated small populations in river beds, flood plains, and the highlands. The East African highlands seem to have suitable habitats for survival of low density populations of S. exempta because patches of C. dactylon grow throughout the year. Moths and caterpillars are present during the off-season in Kenya particularly in the C. dactylon pasture in the uplands where grass is green throughout the year (Rose unpublished data).

In low temperature habitats like Nairobi, survival is erratic with some generations failing to produce adults whereas at the coast all generations survive (Persson, 1981). Therefore although populations of armyworm exist in the highlands their habitats are probably not permanent. The survival within each habitat is probably dependent on the food conditions and also the

temperature in the grass as this may not be similar to the air temperature.

The prolonged development period of the immature stages necessarily results in the reduction of the number of generations per year. In field situation the development period may be further prolonged by a decline in the quantity and quality of food as a result of climatic changes.

SUMMARY

In field situation fluctuation in temperature greatly influences the rate of development of immature stages of S. exempta. The rate of development is much lower during the cold season than during the warm season. Low temperatures coupled with a decline in food quantity and quality during the later half of the year probably suppress the population of the pest. Tender food and high temperatures during the first half result in fast development of immature stages and high rate of population growth and the spread of outbreaks. High temperatures during part of the day may have greater influence on the rate of development than the minimum temperature experienced for only short periods.

CHAPTER 3

HOST PLANT PREFERENCE OF THE AFRICAN ARMYWORM SPODOPTERA EXEMPTA (WALK.)

INTRODUCTION

Pasture grass and cultivated cereals which provide the most if not all of the food requirements of the caterpillars of the African armyworm, S. exempta (Brown and Mohamed, 1972) belong to the family gramineae. The gramineae is a large family of flowering plants with an estimated six hundred genera and more than seven thousand and five hundred species (Langer, 1972). The caterpillars also feed on the family Cyperaceae (Faure, 1943) but as outbreaks of the caterpillars can be very extensive (Brown et al.; 1969; Khasimuddin and Lubega, 1979) they obtain most of their food requirements from pasture grass and cultivated cereals. Even so, it is unlikely that such a large number of species of grass are eaten with same acceptability by the caterpillars although preferences may not be evident under high density conditions.

At an outbreak observed in South Africa, a field on which Panicum miliaceum was growing, was very severly attacked whereas in an adjoining field Setaria italicum hardly suffered any damage but where the latter grew alone it was badly attacked (Hattingh, 1941). Observations made at other outbreak sites in the Tzanee district of South Africa during 1937 and 1939 (Hattingh, 1941) established that outbreaks started in uncultivated areas, mainly on Cynodon dactylon from which it spread to Z. mais. It was further observed that under most conditions at least the young stages of the armyworm prefer C. dactylon to all other grass species including the cereals. The armyworm preference for C. dactylon was further demonstrated by the collection of solitary larvae from fields where it was dominant (Faure, 1943; Matthee, 1952) and by the observation that it was one of the main grass species attacked by the three successive generations at a site in Zimbabwe (Rose, 1975).

Other grass species preferred by S. exempta include Eleusine indica Gaerth, E. coracana Gaertn, Urochloa panicoides Beauv. and species of Setaria and Branchiaria (Whellan, 1954). In addition to C. dactylon, other main grass species in the paddock where the three successive generations were observed included E. indica, U. panicoides, Sporobolus pyramidalis Beauv., Setaria pallidifusca (Schumach) Stapf & Hubbard and Digitaria abyssinica (Hochst ex A. Rich) Stapf.

C. dactylon is widely distributed in river beds and in flood plains in Eastern, Central and Southern Africa. It grows well in the highlands of Kenya, Tanzania and Ethiopia where its leaves remain suitable as food for larvae of S. exempta for most of the year. S. exempta being the most important armyworm species in Africa and one of the most severe pests in the world (Brown and Dewhurst, 1975), detailed information regarding its food preferences and identification of food plants which contribute most significantly to the building of field populations to pest status is of immediate relevance to the development of a management programme for limiting future armyworm outbreaks.

MATERIALS AND METHODS

During the armyworm outbreak season of 1979 there were a number of outbreaks but only a few of them were visited and studied. Areas of pure stands of representative grass species in any one given locality were identified. In each stand larval density was determined by counting larvae in randomly selected one square metre quadrats. The quadrats used for determination of pupal densities were similarly selected,

marked and the pupae were carefully dug out and counted. The mean densities of both larvae and pupae on each grass species were based on counts from ten quadrats.

Pupae collected from the field were taken to the laboratory and kept until emergence. Moths were weighed within twelve hours of emergence and after voiding meconium. They were then dried in an oven at 100°C to constant weights which were recorded. The weights of moths from various grass species within each locality were tested for differences by an analysis of variance. In a separate analysis of variance, weights for moths from C. dactylon stands at Athi River, Taveta and Kajiado were tested for differences.

Five species of Gramineae namely maize, Zea mais; star grass, C. dactylon; Kikuyu grass, Pennisetum clandestinum; Guinea grass, Panicum maximum and Setaria plicatilis were planted randomly in ten one metre quadrats in such a way that the plants had comparable percentage cover. First instar larvae were introduced into the cages at the early stage of plant growth. The larvae on each host plant were counted after every two days at mid-day so that for each instar two counts of larvae were made for each cage. Host plants were tested for differences in larval densities.

Further choice experiments were carried out in the laboratory by placing one centimetre long pieces of each of the five grass species in separate clusters around the periphery of moist filter papers on wax at the bottom of two pound kilner jars. Ten replicates, each with twenty larvae of each instar were prepared. Except for the first instar, larvae were initially reared on Z. mais and soon after moulting into the appropriate instar they were placed in the centre of filter papers. Since newly hatched larvae and generally early instars are strongly attracted to light (Hattingh, 1941), jars containing early instars were carefully covered with pieces of cloth so that the light intensity was more or less uniform. Mean numbers of larvae on each host plant were recorded and an analysis of variance was carried out to test for differences between host plants.

An additional choice experiment was carried out in the laboratory using newly moulted fifth instar larvae which had been reared on Z. mais during the previous instars. This was the last instar since the larvae of the African armyworm go through five instars when fed on good quality leaves of Z. mais under insectary conditions. Pieces of leaves of the five grass species were arranged on a bench in clusters around ten circles with radii of ten centimetres. The numbers of larvae on each of the host plants were recorded hourly for five hours.

Samples of leaves of the grass species used in these choice tests were harvested at about nine o'clock in the morning. The leaves were dried in an oven at 30°C to constant weight and then stored in the dark. Nitrogen content of each sample was determined using the Micro Kjeldahl method (Bailey, 1967). In addition, - leaves of the five species of grass were screened for cyanide by crushing about 0.1g of leaves in a tube into which a strip of filter paper previously dipped in alkaline sodium picrate solution (Feigl and Anger, 1966) was suspended. A few drops of chloroform were added in the glass tube which was stoppered immediately. The presence of cyanide was detected by the yellow paper turning brown.

The water content of the leaves was determined by weighing young fresh leaves usually fed to the first and the second instar larvae as well as those from plants just before flowering and after flowering and then drying them to constant weights. Twenty replicates each weighing 2g were taken for each growth stage for each grass species. The leaves were harvested from the same site at Chiromo so that variation due to soil moisture does not arise.

RESULTS

Larval densities on pure stands of grass species in larval outbreak localities

In all the outbreak localities visited the larval densities were significantly higher ($P<0.05$) in pure stands of *C. dactylon* than on all other examined species of grass (Table 30). The densities on other grass species varied with the locality. At Athi River *Themida triandra* Forsk and *Aristida keniensis* Henrard ranked second and third respectively with regard to larval densities. *Pennisetum mezianum* Leeke and *P. maximum* had intermediate larval densities between *T. triandra* and *A. keniensis* and the difference in densities was not significant. At Ngong Race Course a species of *Digitaria* was second to *C. dactylon* and *T. triandra* ranked third. The differences between the three host plants were significant. On Magadi Road the larval density on *P. mezianum* and *A. keniensis* ranked second and fifth respectively. In between these were *P. maximum* and *Cenchrus ciliaris* L. on which the larval densities were not significantly different. The densities on *P. mezianum* and *A. keniensis* were, however, significantly different from the densities on *P. maximum* and *C. ciliarias*. At Kajiado

the density on C. dactylon was significantly higher than densities on the other grass species ($P<0.05$) but the larval densities on the other grass species were of similar magnitudes.

The larval densities on C. dactylon were highest at the outbreak sites on Magadi Road and Athi River and lowest at Kajiado and Ngong Race Course. However, the proportions of larvae on C. dactylon were highest at Kajiado and Ngong Race Course. The growth of grass was, however, better on Magadi Road and Athi River than at Kajiado and Ngong Race Course.

When the outbreak site on Magadi Road was visited for the second time, the moths had emerged but there was yet a second outbreak which could have been a second generation or a totally new outbreak due to in coming moths. Larvae were in the late third instar and the density was about $400/m^2$. These larvae later died out due to starvation resulting from drought.

An armyworm outbreak near Nyandarua was entirely confined to a farm of young wheat Triticum vulgare. Surrounding grass species and nearby farms of older wheat were not infested at all. Similar observations were made at Kakamega where most larvae were confined to young maize farms.

The pupal densities in pure stands of grass species in larval outbreak localities

The pupal densities in pure stands of selected grass species are presented in Table 31. The only site where both larval and pupal densities were determined in these investigations is Athi River. Taveta was visited when most of the larvae had already pupated. There were two outbreaks at Kajiado but the one for which the larval density was determined had a very low pupal density and therefore no attempt was made to determined it. The other outbreak for which the pupal density was determined was visited after pupation.

In all the outbreak sites considered, the pupal density in C. dactylon stands was significantly ($P<0.05$) higher than the densities in other stands. The comparison between larval and pupal densities at Athi River showed that the pupal density in the A. keniensis stand was significantly ($P<0.05$) higher than the density in P. mezianum stand. Similarly a bare piece of land at Taveta had a significantly ($P<0.05$) higher pupal density than a stand of P. mezianum. Though not significant, the pupal density in that bare piece of land was higher than the density in a stand of P. maximum. At Kajiado C. dactylon was concentrated around termite mounds but the mixture of T. triandra and P. mezianum was dominant in the area away from the termite mounds.

TABLE 30

DENSITIES OF *S. EXEMPTA* LARVAE ON PURE STANDS OF SOME GRASS SPECIES IN OUTBREAK LOCALITIES

LOCALITY	GRASS SPECIES	MEAN + S.E./M^{2*}	PERCENTAGE
ATHI RIVER	*Cynodon dactylon*	136.70 ± 3.69[a]	35.60
(23.2.1979)	*Themida triandra*	88.80 3.41[b]	23.14
	Pennisetum mezianum	68.00 3.56	17.70
	Panicum maximum	56.90 3.04[c]	14.81
	Aristida keniensis	33.70 1.44	8.77
NGONG RACE COURSE	*C. dactylon*	51.20 2.83[a]	57.33
	Digitaria sp.	17.80 1.65[b]	19.93
(8.3.1979)	*T. triandra*	10.60 1.60[c]	11.87
MAGADI ROAD	*C. dactylon*	154.30 2.44[a]	41.50
(2.3.1979)	*P. mezianum*	82.20 2.39[b]	27.50
	P. maximum	64.50 4.20	17.35
	Cenchrus ciliaris	58.70 1.33[c]	15.79
	A. keniensis	12.10 0.99[d]	3.25
KAJIADO	*C. dactylon*	11.00 1.69[a]	69.18
(8.3.1979)	*T. triandra*	2.10 0.43[b]	13.21
	P. mezianum	1.40 0.34[b]	8.81
	Digitaria sp.	0.90 0.30[b]	5.66
	A. keniensis	0.50 0.17[b]	3.14

*For each locality, figures followed by different letters differ significantly ($P<0.05$) (Turkey's pairwise test).

The high pupal densities on bare land and in areas with low larval density suggest that larvae move considerable distances in search of suitable pupation sites where they can enter the ground easily to construct earthen cocoons. These may be cracks or soft soil often in shady areas under grass tufts or trees. At an outbreak site in the Shimba Hills which had previously been burnt pupae were at high densities under trees. However, as suggested by dead parts of pupae left behind, a large proportion of pupae had been eaten by an unidentified predator.

C. dactylon at Kajiado was found to be growing on the old parts of termite mounds and both at Athi River and on Magadi Road it was on the road sides indicating that this grass species grows in disturbed areas (Hattingh 1941) where larvae can easily dig into the soil to form cocoons and hence the higher pupal densities in stands of C. dactylon. As a result of the suitability of sites covered by this host plant larvae in search of pupation sites could move from could move from sites with other host plants to areas where C. dactylon is dominant within the same outbreak locality. The density of pupae in C. dactylon stands can therefore be as high as or higher than the larval

density, and this makes pupal density unsuitable as an index of host plant preference.

Larval densities on host plants in field cages

The results (Table 32) were analysed separately for each instar. In all instars the mean larval densities (Figure 7) on C. dactylon were higher than the densities on the other host plants except during the fourth instar when the mean density on C. dactylon was found to be equal to the mean density on P. clandestinum. P. maximum and S. plicatilis had the lowest larval densities during the first and second instar stages. The densities of the first instar larvae on Z. mais and P. clandestinum were intermediate but during the second instar the larval density on the former was significantly lower ($P<0.05$) than the density on the latter. In fact the density of larvae on Z. mais continued to fall and was even significantly ($P<0.05$) lower than the density on S. plicatilis during the third instar stage. The latter host plant also had significantly higher larval density ($P<0.05$) than P. maximum. During the fourth instar stage the densities on Z. mais and P. maximum were not significantly different. The density of larvae on P. clandestinum dropped during the fifth instar stage and was significantly ($P<0.05$) lower than the

TABLE 31

DENSITIES OF S. EXEMPTA PUPAE IN PURE STANDS OF SOME GRASS SPECIES IN OUTBREAK LOCALITIES

LOCALITY	GRASS SPECIES	MEAN + S.E./M^2		PERCENTAGE
TAVETA	C. dactylon	107.80	3.54^a	45.05
(19.2.1979)	Bare land	57.30	0.86^b	23.94
	P. maximum	49.00	2.22^b	20.48
	P. mezianum	25.00	1.13^c	10.53
ATHI RIVER	C. dactylon	122.00	5.88^a	51.28
(27,2.79)	T. triandra	49.00	2.35^b	20.60
	A. keniensis	35.10	6.35^c	14.75
	P. maximum	25.00	0.88^c	10.51
	P. mezianum	6.80	1.55^d	2.86
KAJIADO	C. dactylon	136.80	5.97^a	78.35
(2.3.79)	T. triandra and P. mezianum	37.8	4.14^b	21.65

For each locality, values followed by different letters differ significantly ($P<0.05$).

density on C. dactylon. The other host plants had much lower densities which did not differ significantly between themselves. During the sixth instar stage there was a significant increase in the larval density on Z. mais but the densities on the other host plants remained much lower with differences between them remaining insignificant.

The results suggest that in field cages all larval instars prefer C. dactylon to the other host plants to which it was compared. Larvae move a lot between adjacent host plants rejecting the less palatable and moving on to the more palatable plants. As Z. mais grows much taller than any of the other host plants tested in this study, larvae on the higher parts of this plant can easily fall on to the shorter host plants when disturbed for instance by wind. Its leaves also rapidly become tougher with height and hence unsuitable as food for the younger larvae. This is probably why the larval density was unexpectedly low on this host plant during the third to fifth instar stages. The increase in the larval density on Z. mais during the last instar could be explained by the greater mobility of the sixth instar larvae and their ability to feed on tougher leaves.

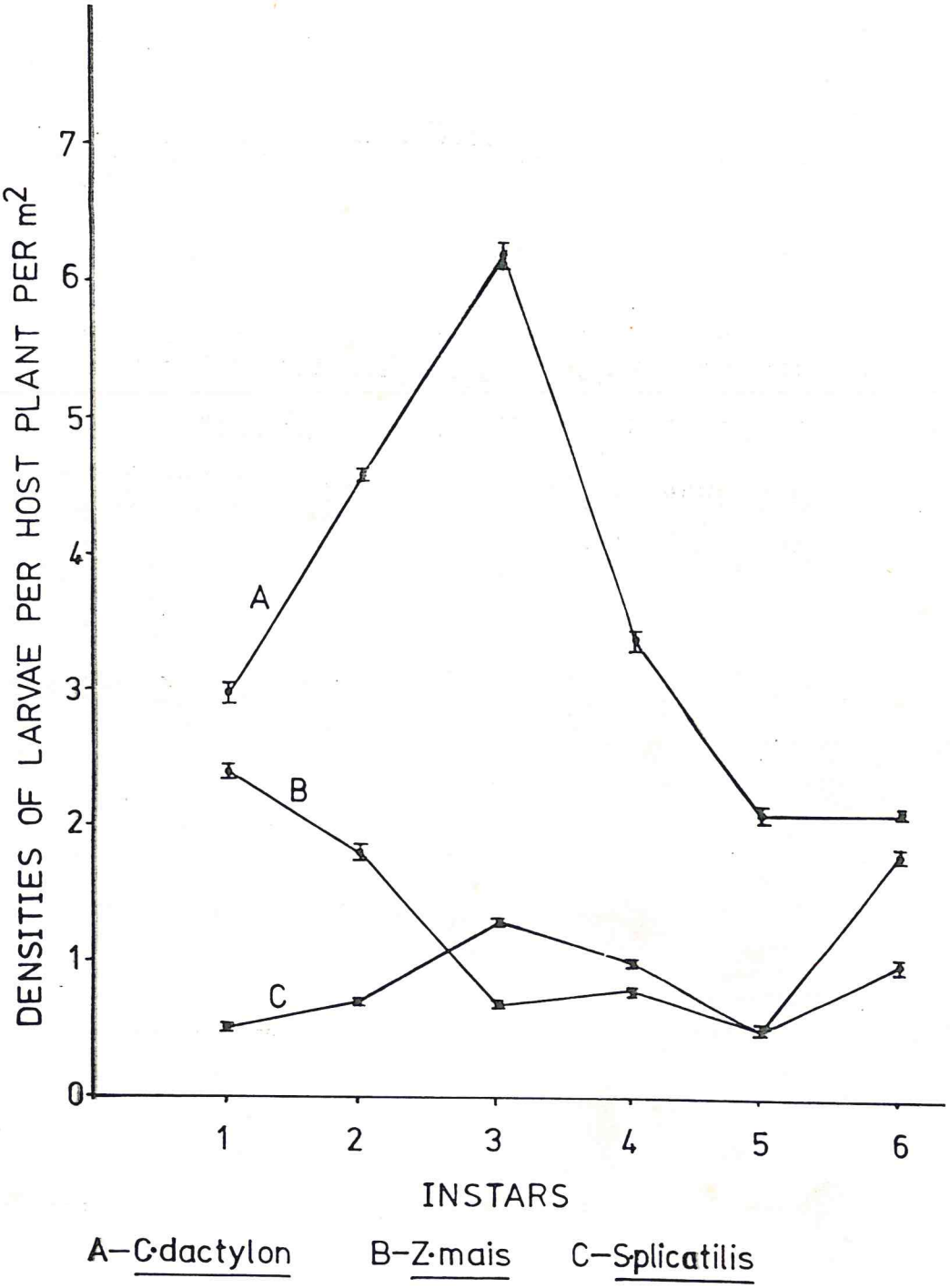
TABLE 32

DENSITIES OF LARVAE ON HOST PLANTS IN FIELD CAGES (MEAN ± S.E.*)

Instars	HOST PLANTS				
	C. dactylon	Z. mais	P. clandestinum	S. plicatilis	P. maximum
1	3.50 ± 0.07^{a}	2.40 ± 0.52^{b}	2.10 ± 0.46^{b}	0.50 ± 0.22^{c}	0.30 ± 0.15^{c}
2	4.60 ± 0.50^{a}	1.80 ± 0.59^{c}	3.50 ± 0.43^{b}	0.70 ± 0.30^{d}	0.70 ± 0.26^{d}
3	6.20 ± 0.84^{a}	0.70 ± 0.21^{d}	1.70 ± 0.52^{b}	1.30 ± 0.26^{c}	0.30 ± 0.15^{e}
4	3.40 ± 0.92^{a}	0.80 ± 0.29^{c}	3.40 ± 0.58^{a}	1.00 ± 0.37^{c}	0.40 ± 0.31^{c}
5	2.10 ± 0.50^{a}	0.50 ± 0.31^{c}	1.70 ± 0.40^{b}	0.50 ± 0.22^{c}	0.60 ± 0.27^{c}
6	2.10 ± 0.41^{a}	1.80 ± 0.49^{b}	0.90 ± 0.30^{c}	1.00 ± 0.45^{c}	0.80 ± 0.33^{c}

*For each instar, values followed by different letters differ significantly from each other ($P<0.05$).

FIGURE 7



A–C.dactylon B–Z.mais C–Splicatilis

Choice of host plants by different instars in Kilner jars

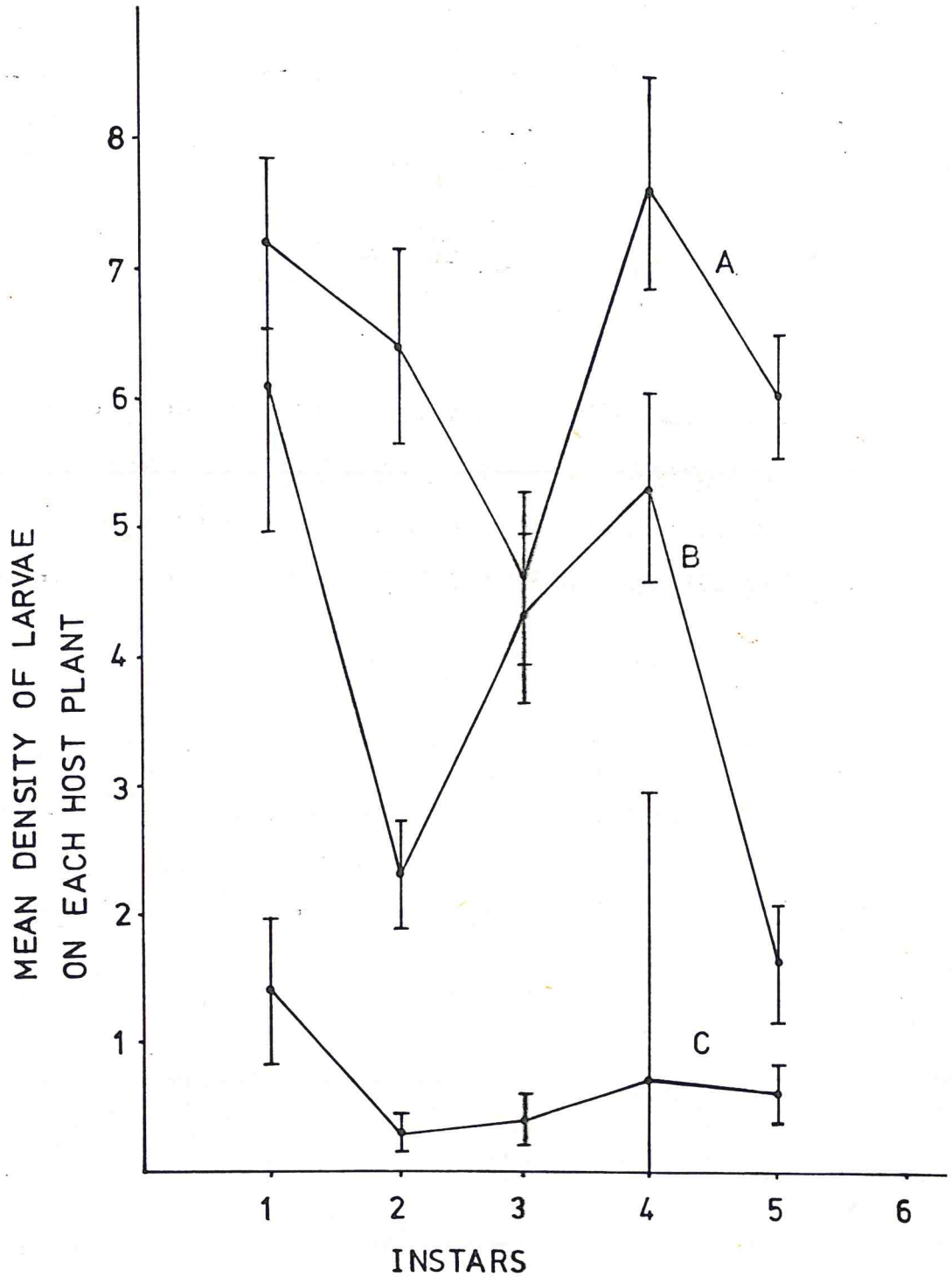
The choice experiments in jars showed differences in food preferences (Table 33). In all cases *C. dactylon* had a higher number of larvae than the other host plants and this was significant ($P<0.05$) except with regard to *Z. mais* during the first instar stage (Figure 8). The differences in the number of larvae on the other host plants were not significant. The results with the second instar larvae were similar to those obtained for the first instar larvae except that the mean number of larvae on *C. dactylon* was significantly higher than that on *Z. mais*. With regard to the third instar larvae, only the mean number of larvae on *S. plicatilis* was significantly lower ($P<0.05$) than the other means although *C. dactylon* and *Z. mais* remained superior to *P. clandestinum* and *P. maximum*. At the fourth instar stage the mean number of larvae on *C. dactylon* was significantly higher ($P<0.05$) than the mean numbers of larvae on the other host plants except *Z. mais*. The latter host plant was significantly ($P<0.05$) preferred to the others except *P. clandestinum* which had a significantly ($P<0.05$) higher number of larvae than *S. plicatilis*. The latter was significantly less ($P<0.05$) preferred to *P. maximum*.

TABLE 33

NUMBERS OF LARVAE OF VARIOUS INSTARS ON SELECTED GRASS SPECIES IN CHOICE EXPERIMENT IN KILNER JARS (MEAN ± S.E.)*

	HOST PLANTS				
INSTARS	C. dactylon	Z. mais	P. clandestinum	P. maximum	S. plicatilis
1	7.20 ± 0.65^{a}	6.10 ± 1.12^{a}	0.20 ± 0.13^{b}	0.40 ± 0.22^{b}	1.40 ± 0.56^{b}
2	6.40 ± 0.75^{a}	2.30 ± 0.42^{b}	0.90 ± 0.30^{c}	1.10 ± 0.31^{c}	0.30 ± 0.15^{c}
3	4.60 ± 0.68^{a}	4.30 ± 0.66^{a}	2.60 ± 0.51^{a}	2.60 ± 0.62^{a}	0.40 ± 0.20^{b}
4	7.70 ± 0.86^{a}	5.30 ± 0.73^{ab}	3.60 ± 0.76^{bc}	3.60 ± 0.58^{c}	0.70 ± 2.22^{d}
5	6.00 ± 0.47^{a}	1.60 ± 0.45^{c}	3.40 ± 0.58^{b}	1.20 ± 0.13^{c}	0.60 ± 0.22^{c}

* For each instar values followed by different letters are significant ($P<0.05$).



A- C.dactylon B- Z.mais C- S.plicatilis

The fifth (in this case the last) instar larvae showed significant ($P<0.05$) preference for *C. dactylon* to the other host plants and *P. clandestinum* was significantly preferred to the other three host plants which did not show significant differences between themselves.

Choice of host plants by fifth instar larvae in Kilner jars over time

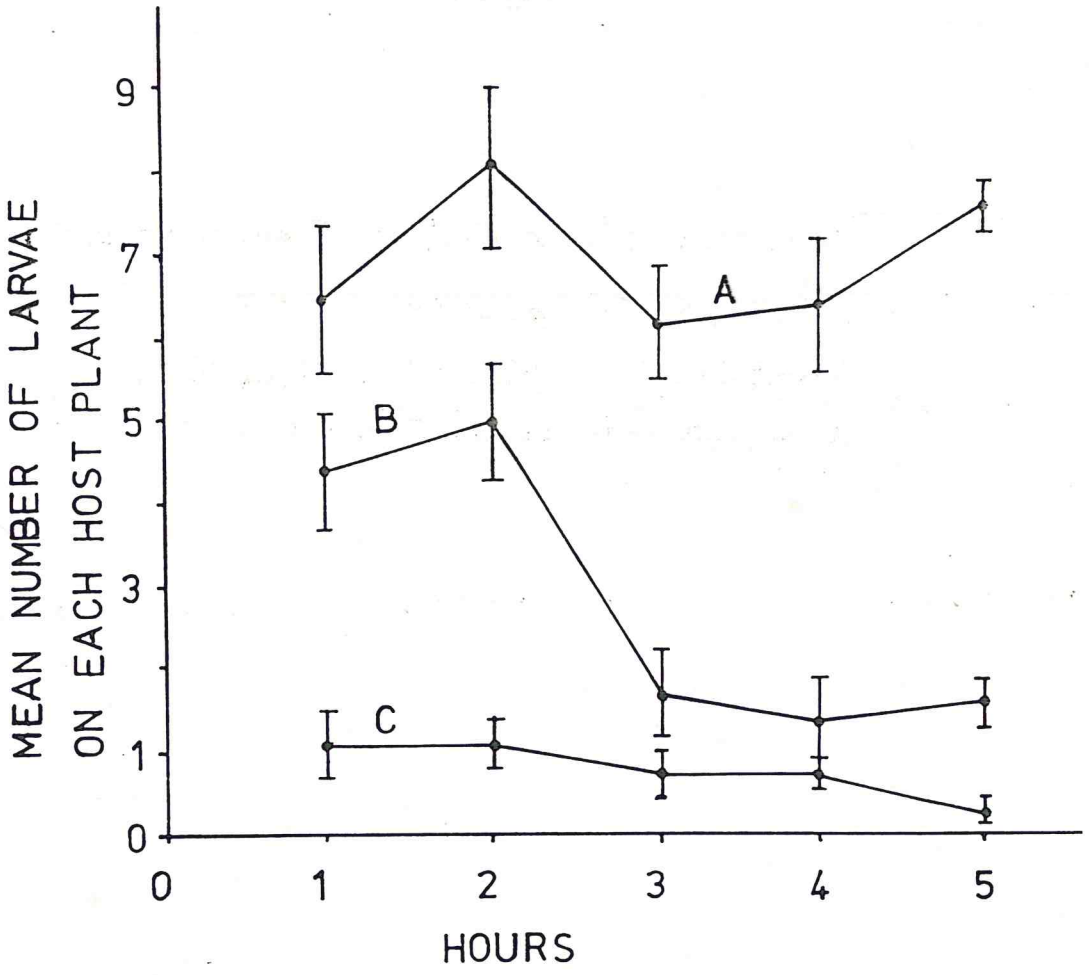
Newly moulted fifth instar larvae (Table 34) showed a higher count on *C. dactylon* but this was significant ($P<0.05$) only when compared to the larval count on *S. plicatilis* after one hour. After the second hour, however, the preference for *C. dactylon* was more clearly pronounced and was significantly ($P<0.05$) higher than for other host plants except *Z. mais* (Figure 9). The mean numbers of larvae on *Z. mais*, *P. clandestinum* and *P. maximum* were comparable but were significantly higher ($P<0.05$) than that of larvae on *S. plicatilis*. The preference for *C. dactylon* to other host plants after the third and fourth hours remained significant ($P<0.05$). Among the other host plants *P. clandestinum* was significantly preferred ($P<0.05$) and the difference between *Z. mais*, *P. maximum* and *S. plicatilis*

TABLE 34

NUMBERS OF FIFTH INSTAR LARVAE ON SELECTED HOST PLANTS AT HOURLY INTERVALS (MEAN ± S.E.)*

TIME	HOST PLANTS				
(hours)	C. dactylon	Z. mais	P. clandestinum	P. maximum	S. plicatilis
1	6.50 ± 0.89^{a}	4.40 ± 0.72^{a}	4.50 ± 0.70^{a}	4.30 ± 0.60^{a}	1.10 ± 0.41^{b}
2	8.10 ± 0.95^{a}	5.00 ± 0.71^{ab}	3.90 ± 0.57^{b}	3.70 ± 0.97^{b}	1.10 ± 0.28^{c}
3	6.20 ± 0.66^{a}	1.70 ± 0.52^{c}	3.60 ± 0.31^{b}	1.30 ± 0.21^{c}	0.70 ± 0.15^{c}
4	6.40 ± 0.80^{a}	1.40 ± 0.52^{c}	2.90 ± 0.31^{b}	0.90 ± 0.18^{c}	0.70 ± 0.26^{c}
5	7.60 ± 0.31^{a}	1.60 ± 0.31^{b}	1.60 ± 0.43^{b}	0.90 ± 23^{bc}	0.30 ± 0.15^{c}

*For each hour, the values followed by different letters are significantly different from each other ($P<0.05$).



A–C.dactylon

B–Z.mais

C–S.plicatilis

were not significant. Five hours later, C. dactylon remained significantly superior ($P<0.05$) to other host plants but the differences between Z. mais, P. clandestinum and P. maximum were insignificant. Although the difference between S. plicatilis and P. maximum was not significant the former was again the least preferred.

C. dactylon was definetely the preferred host and although the larvae were moving from one host plant to another they stayed much longer on C. dactylon as evidenced by the accumulation of frass in and around the clusters of the pieces of leaves of C. dactylon. Most of the larvae on C. dactylon were feeding whereas some of those which were on the other grass species particularly those on P. clandestinum were not feeding.

Emergence weights of moths from outbreak pupae

Male moths from the pure stand of C. dactylon at Athi River weighed significantly ($P<0.05$) more than the males from the other host plants (Table 35). Among females, those from the C. dactylon and T. triandra stands had significantly ($P<0.05$) higher weights than those from the A. keniensis stand.

TABLE 35

THE EMERGENCE WEIGHTS OF S. EXEMPTA MOTHS FROM THREE OUTBREAK LOCALITIES

LOCALITY	HOST PLANT	WEIGHTS ± S.E.*	
		MALES	FEMALES
Taveta	C. dactylon	67.71 ± 2.31^{a}	74.08 ± 2.35^{a}
	P. maximum	65.61 ± 1.35^{ab}	70.08 ± 1.90^{ab}
	Bare land	61.06 ± 1.95^{b}	65.06 ± 2.52^{b}
Athi River	C.dactylon	92.82 ± 2.30^{a}	95.42 ± 2.79^{a}
	T. triandra	76.83 ± 3.39^{b}	94.08 ± 3.00^{a}
	A.keniensis	75.79 ± 2.98^{b}	83.63 ± 2.40^{b}
	P. maximum	70.99 ± 3.02^{b}	72.96 ± 2.54^{c}
Kajiado	C.dactylon	64.11 ± 2.56^{a}	64.22 ± 2.06^{a}
	P. mezianum & T. triandra	50.59 ± 2.93^{b}	55.59 ± 2.13^{b}

For each locality and sex, the values followed by different letters are significantly different from each other (P<0.05).

The latter moths weighed significantly more than the moths from the P. maximum stand. Females weighed more than males within stands but this was significant only in the sample collected from the A. keniensis stand.

Like at Athi River, the moths from the C. dactylon stand at Taveta weighed more than the moths from the other stands but this was significant ($P<0.05$) only when compared to the moths which emerged from the pupae dug from the bare land. The emergence weights of the latter did not differ significantly from those of moths from the P. maximum stand. Female moths from the C. dactylon stand weighed significantly ($P<0.05$) more than males but the moths from the other stands did not differ significantly between sexes.

Similarly, the moths from the C. dactylon stand at Kajiado were significantly ($P<0.05$) larger than the moths from the mixture of T. triandra and P. maximum. The difference between sexes were significant in both stands.

Dry weights of moths (Table 36) from C. dactylon stand at Athi River were significantly ($P<0.05$) higher than the dry weights of the other moths from the same site. Males from T. triandra, A. keniensis and

P. maximum did not differ significantly in their weights. The dry weights of females from C. dactylon and T. triandra did not differ significantly from each other but they were significantly ($P<0.05$) higher than those for females from the A. keniensis and P. maximum stands. As for the differences between sexes females weighed significantly ($P<0.05$) more than their males except for those from the P. maximum stand.

Dry weights of moths within individual sites at Taveta and Kajiado showed no variation with respect to host plants but females weighed significantly ($P<0.05$) more than the males.

Variation in moth weights in relation to outbreak sites

The data on densities of larvae and pupae as well as the results from the choice experiments suggest the importance of C. dactylon in sustaining and building up field populations of the African armyworm. It was therefore found desirable to assess its suitability in different outbreak sites. Table 35 gives weights of the moths at emergence and Table 36 their dry weights. Comparisons between weights at emergence and between dry weights of moths from pure stands of C. dactylon at Athi River, Taveta and Kajiado showed that differences due to outbreak sites were highly significant ($P<0.001$). Moths

TABLE 36

DRY WEIGHTS OF MOTHS OF *S. EXEMPTA* FROM THREE LARVAL OUTBREAK LOCALITIES (mg)

LOCALITY	HOST PLANT	WEIGHTS ± S.E.*	
		MALES	FEMALES
Taveta	*C.dactylon*	27.29 ± 1.21	33.66 ± 1.31
	P.maximum	26.96 ± 0.76	33.25 ± 2.96
	Bare land	24.24 ± 1.37	28.91 ± 1.95
Athi River	*C.dactylon*	39.49 ± 1.18^{a}	43.86 ± 1.90^{a}
	T.triandra	32.62 ± 1.02^{b}	41.60 ± 1.23^{a}
	A.keniensis	31.34 ± 1.48^{b}	36.34 ± 1.38^{b}
	P. maximum	29.51 ± 1.38^{b}	32.25 ± 1.35^{b}
Kajiado	*C.dactylon*	21.51 ± 1.38	29.77 ± 1.14
	P. mezianum & *T. triandra*	22.25 ± 1.20	26.42 ± 0.93

*For each sex in each locality, the values followed by different letters are significantly different from each other ($P<0.05$).

from Athi River had the highest weights while those from Kajiado had the lowest. Athi River experienced the highest rainfall whereas Kajiado received the lowest (Tables 71 and 72). The differences in rainfall probably influenced quality and quantity of C. dactylon available within the outbreak sites. Larvae which fed on luxuriant C. dactylon at Athi River thus formed the largest moths whereas those on poor C. dactylon at Kajiado formed the smallest adults.

Nitrogen contents of selected host plants of the African armyworm

Nitrogen content differs considerably between species with young C. dactylon having the highest (Table 37) Z. mais and P. clandestinum had much higher nitrogen contents than S. plicatilis, P. maximum and C. maranguensis. The analysis on leaves from the third node of six leaf stage Z. mais plants showed that the nitrogen level decreased from the terminal to the basal end. In leaves of C. dactylon, Z. mais and P. clandestinum the nitrogen content decreased drastically with age but this change was not as obvious in leaves of P. maximum and S. plicatilis. Among the young leaves of the host plants examined, those of C. maranguensis had the lowest nitrogen content.

The test for cyanide was positive only with C. dactylon and although on account of HCN it was found to be strongly cyanogenic, the amount of nitrogen allocated to HCN was relatively small (Table 38).

Variation in the leaf water content between selected grass species at different growth stages

Z. mais and P. clandestinum had significantly ($P<0.05$) higher water content than C. dactylon, P. maximum and S. plicatilis both at young and older age (Table 40). However, significant ($P<0.05$) differences between water content of young leaves of the latter host plants were also observed with C. dactylon and S. plicatilis having the highest and the lowest water content respectively. Similar trends were observed in the older leaves except that the difference between C. dactylon and P. maximum did not reach a significant level. All the grass species examined showed a significant ($P<0.05$) decrease in water content with age although this was more evident in Z. mais, P. clandestinum and C. dactylon. The fall in the water content of S. plicatilis and P. maximum was not so drastic.

TABLE 37

NITROGEN CONTENT OF LEAVES OF SOME HOST PLANTS OF S.EXEMPTA EXPRESSED AS PERCENT DRY WEIGHTS

(MEAN ± S.E.)

GROWTH CONDITION	NODE	C. dactylon	Z. mais	P.Clandestinum	S.plicatilis	P. maximum	C.maranguensis
4 leaf stage	3		4.06±0.07				
6 leaf stage	3		3.72±0.06				
6 leaf stage basal 1/3	3		3.47±0.04				
middle 1/3	3		3.86±0.045				
Terminal 1/3	3		4.06±0.03				
Young Plant	1	4.57 ± 0.03		4.31±0.01	2.92 ± 0.02	2.67 ± 0.03	2.10 ± 0.13
	2	4.28 ± 0.02		3.89±0.06			2.02 ± 0.11
	3	4.16 ± 0.02		3.71±0.01			2.00 ± 02
	4			3.51±0.01			1.73 ± 0.01
Before flowering	1	3.17 ± 0.02	2.73±0.03		2.69 ± 0.02	2.53 ± 0.02	
	2	2.90 ± 0.02			2.94 ±0.03	2.47 ± 0.03	
	3	2.72 ± 0.01			2.90 ± 0.02	2.42 ± 0.03	
	4	2.57 ± 0.02					
	5	2.40 ± 0.02					
Flowering		2.96 ±0.03	2.54±0.04	3.3 ± 0.02	3.00 ± 0.01	2.56 ± 0.03	
		2.97 ± 0.03		3.15 ±0.02	3.03 ± 0.01	2.43 ± 0.02	
		2.96 ± 0.02		3.01±0.01	2.75 ± 0.03	2.29 ± 0.02	
		2.91 ± 0.03		2.89 ± 0.02			
		2.68 ± 0.04					

TABLE 38

HCN DETERMINATION ON C. DACTYLON

GROWTH CONDITION	NODE	HCN % DRY WT.	N IN HCN % DRY WT.
Young plants	1	0.03	0.015
	2	0.05	0.025
	3	0.14	0.07
Mature Plants Before flowering	1	0.01	0.005
	2	0.02	0.01
	3	0.05	0.025
	4	0.07	0.035
	5	0.02	0.02
Mature dry seasons plants	1	0.02	0.01
	2	0.02	0.01
	3	0.025	0.012
	4	0.07	0.035

TABLE 39

VARIATION IN THE LEAFT WATER CONTENT BETWEEN SELECTED GRASS SPECIES AT DIFFERENT GROWTH STAGES

GRASS SPECIES	% WATER CONTENT (MEAN ± S.E.)*	
	YOUNG LEAVES	OLDER LEAVES
Z. mais	88.03 ± 0.27^{a}	82.15 ± 0.42^{a}
P. clandestinum	87.08 ± 0.34^{a}	80.95 ± 0.61^{a}
C. dactylon	82.60 ± 0.40^{b}	77.38 ± 0.25^{b}
P. maximum	80.23 ± 0.66^{c}	77.20 ± 0.68^{b}
S. plicatilis	77.53 ± 0.80^{d}	75.25 ± 0.49^{c}

* For each growth stage, values followed by different letters differ significantly ($P<0.05$).

DISCUSSION

Determination of larval densities on stands of various grass species in outbreak localities has shown that C. dactylon is preferred to other grass species. The proportion of larvae on C. dactylon was higher in localities where the conditions for growth of grass was harsher. In some localities extensive outbreaks were observed on burnt grasslands and monocultures such as T. vulgare and Z. mais. The occurrence of outbreaks of larvae of the African armyworm on C. dactylon and burnt grasslands is in agreement with earlier observations made in South Africa (Hattingh, 1941).

It is known that within the general area of wind convergence (Brown and Swaine, 1966; Brown et al., 1969; Rose and Law, 1976) the armyworm outbreaks are localized by mechanisms which are not yet fully understood although it is believed that this is partly due to weather patterns and topography (Rose, pers. comm.).

The examination of selected grass species revealed that there are considerable variations in nitrogen and water content of leaves with respect to grass species and leaf age. Young C. dactylon leaves had the highest nitrogen content and although its water content was lower than that of Z. mais and

P. clandestinum the results that the grass species with higher water content are also rich in nitrogen and that the younger the leaves, the higher the nitrogen and water content. The chemical composition of leaves and their fibre contents generally differ with age (Fraenkel, 1953). The examination of Z. mais leaves has further shown that the nitrogen content decreases from the tip to the base of leaves. It is, however, uncertain whether it is the fibre or water content which is more important.

The larvae of Spodoptera eridania Cram, for instance have more difficulty eating and processing tree leaves than herb leaves (Soo Hoo and Fraenkel, 1966), but whether this is due to the high fibre content or the low water content of tree leaves is not known.

However, leaf nitrogen content can have a significant influence on the growth of lepidopterous larvae (Slansky and Feeny, 1977). It is correlated to leaf water content, though less strongly to the larval growth rate (Scriber and Feeny, 1979). Furthermore, the proportions of the essential nutrients in the food stuff contribute to the nutritional quality than do the absolute amounts of nutrients (House, 1969). Even if moths were unselective with respect to the oviposition sites (Hattingh, 1941) large variations in the nutritional qualities between grass species, their growth

stages, changes in their chemical composition and fibre content would result in differences in larval growth rates and survival. In outbreak areas or stands within outbreak areas where grass quality is nutritionally suboptimal, larval mortality may result in the extinction of the outbreak or in a low density of larval population. On the other hand, late instar larvae can undertake short distance migration from the preferred to the less preferred host plants. As long as no grass species is depleted the resulting distribution of larvae on the various grass species within reach should reflect food preferences.

Movement of larvae during the feeding stage should not be confused with the movement in search of pupation sites. The latter results in mixing of larvae from various grass stands and the resulting pupal densities and adult weights at emergence, unlike larval densities cannot be used as indices of food preference. They may, however, be used in comparing moths from outbreak sites which are far enough from each other.

Burnt, over-grazed land mowed grassland and cereal farms in which high density outbreaks of larvae are often reported all have new growth of nutritious

food at the onset of the outbreak season. C. dactylon continues to produce new nodes and tillers with young, tender and nutritious leaves as the season advances. Taking into account that the wind dispersal of the early instar larvae is a passive mechanism which is useful in so far as the regulation of density is concerned, the recognition of suitable sites of oviposition by females can not be ruled out. Recent work on the visual system of the armyworm moths (Langer et al., 1979) has revealed that the compound eye of S. exempta is tetrachromatic, sensitive to u.v., blue, green and red lights. Such a sensitive colour detector with a high discrimination power, unusual in that it is sensitive in the long wavelength part of the spectrum may be important in the slection of oviposition sites within the general area of wind convergence. If gravid females are capable of recognising young grass on the basis of colour patterns, the this may be more critical at the time of germination as the differences in growth stages of grass species become more pronounced with the advance of the season. In captivity, at least, the preference for C. dactylon to Z. mais for oviposition has been demonstrated (Persson, unpublished data). In the citrus butterfly Papilio demoleus L. the combination of colour, odour and contact stimuli elicit the oviposition response (Saxena and Goyal, 1978). It is also possible that within the

proximity of the grass species the orientation of the moths is further influenced by odours emanating from the surrounding grass species.

The suggestion that females may be selective with respect to the ovipositional sites was strengthened by consistently higher densities on larvae on C. dactylon in outbreak sites. The basis for this preference is not known, but in young Z. mais, sucrose and adenosine have been shown to be the principal water-soluble feeding stimulants (Ma and Kubo, 1977) and are present above the thresholds of chemoreceptors whose sensitivity is specifically geared towards a capacity to detect them (Ma, 1977a). The preference for Z. mais to cassava Manihot esculenta increased with larval experience on Z. mais as a host plant (Ma, 1976). In the present experiments the preference for C. dactylon to Z. mais was retained even by larvae reared on Z. mais through to the penultimate instar. This suggests that C. dactylon either possesses a stronger combination of stimulants or of weaker feeding inhibitants than Z. mais.

In addition to superiority in nitrogen content, the leaves of C. dactylon are highly cyanogenic. Cyanogenesis is believed to be an effective defence for

plants against attack by a variety of animals including insects (Jones, 1962; Parsson and Rothschild, 1964; Rehr et al. 1973; Blau et al., 1978). Since the larvae of the African armyworm eat and prefer C. dactylon, it can be suggested that S. exempta has fully evolved counteradaption to any barrier that cyanogenesis may have presented to its ancestors. Among other insects the common blue butterfly Polyommatus icarus (Rott) oviposits on both cyanogenic and acyanogenic strains of Lotus corniculatus and the newly hatched larvae readily feed on both strains (Lane, 1962). Larvae of polyphagous southern armyworm Spodoptera eradania feed on both strains of L. corniculatus and as long as leaves are of similar age there is no difference in growth rates or nitrogen utilization (Scriber, 1978; Scriber & Feeny, 1979). The basis of the cyanide tolerance is unknown but S. eridania possesses an extremely high microsomal mixed function oxidase activity which could be involved in detoxifying naturally encountered food plants (Krieger et al., 1971). It has the capacity for rapid induction of mixed function oxidases upon exposure to secondary plant chemicals in its diets (Brattsten et al., 1977). Even more interesting is that low concentrations of cyanogenic glycosides in combination with glucose elicit strong biting responses in the Mexican bean beetle Epilachna varivestis (Nayar and Fraenkel, 1963).

Under certain conditions the larvae of S. exempta can feed on cut foliage of cassava, Manihot esculenta (Ma, 1976). Since both M. esculenta and C. dactylon are cyanogenic they may contain cyanogenic sugars possibly glycosides which by themselves or in the presence of other sugars elicit stronger feeding or biting response by S. exempta larvae.

SUMMARY

The distribution of larvae of S. exempta in the outbreak sites and the results from choice experiments in the laboratory and field cages have consistently shown that they prefer C. dactylon. The higher larval density on this grass species in outbreak sites strongly suggests that the female moths may be selecting it for oviposition although this could have resulted from differences in larval mortality during the early instars. This problem could be resolved by counting egg batches and monitoring the larval survival on various grass species. The basis for the preference by the caterpillars for C. dactylon needs to be investigated and so does the adaptive mechanism which S. exempta has evolved to counteract the barriers presented by cyanogenesis. This would result in greater understanding of the relationship between S. exempta and C. dactylon as its host plant not only during the outbreak, but also during the off-season.

CHAPTER 4

THE ROLE OF THE LESS-PREFERRED HOST PLANTS AND THE INFLUENCE OF LEAF AGE ON THE GROWTH AND DEVELOPMENT OF THE AFRICAN ARMYWORM, *SPODOPTERA EXEMPTA* (WALK.)

INTRODUCTION

Although the larvae of the African armyworm *Spodoptera exempta* (Walk.) have been reported feeding on plants of both monocotyledon and dicotyledon families in East Africa (Brown, 1962) they are almost rigidly confined to the Gramineae and Cyperaceae, and only in rare instances are dicotyledons or even other families of monocotyledon eaten (Brown and Dewhurst, 1975). It is likely that the larvae of other armyworm species are frequently mistaken for *S. exempta* and therefore some plants are probably incorrectly reported as hosts for *S. exempta*

Even among the Gramineae, there are some degrees of preference and a few species which are not eaten at all (Bogdan, 1963). Larval outbreaks are localized within the general area of wind convergence (Brown and Swaine, 1966; Brown *et al.*, 1969; Rose and Law, 1976)

by a mechanism which is not fully understood although it seems that the female moths are able to select the host plants on which they oviposit eggs (Persson, unpublished observations). This is also suggested by the highly sensitive visual system of the moths (Langer et al., 1979).

In outbreak localities the larval densities were highest on Cynodon dactylon (L.) Pers. and in subsequent experiments, strong preference by larvae for this host plant has been demonstrated (Chapter 3). They developed significantly faster and produced higher yields of adults than the larvae reared on other wild grass species. The resulting moths were larger and oviposited more eggs than the smaller ones which were for instance produced by larvae reared on Panicum maximum Jacq. and Setaria plicatilis (Hochst.) Hack. (Chapter 1).

In field situation, however, these grass species form mixed or adjacent populations with leaves varying tremendously in age, texture and therefore nutritional qualities. Thus, even though the caterpillars have preferences they have to move to the less preferred grass species on the depletion of the former. Similarly, when the young leaves have all been eaten the larvae will have to feed on the older ones. The effect of these

interactions were studied by switching larvae of various instars from C. dactylon to P. maximum and S. plicatilis. Other separate larval samples were fed on leaves from the three uppermost nodes of C. dactylon throughout the larval life.

MATERIALS AND METHODS

Larval development and survival in relation to leaf age

Development and survival of S. exempta larvae from an insectary culture maintained at 25°C and 70% R.H. were investigated on the leaves from the three uppermost nodes of young C. dactylon. Larvae in groups of twenty per one pound kilner jar were introduced on leaves from each node separately in fifteen replicates..

The numbers of larvae surviving at the beginning of each instar and those larvae which died in each instar were recorded. This information was used to calculate the mean numbers of larvae which survived in each instar and the distribution of percent mortality.

The pupal weights and the weights of adults at emergence were taken within twelve hours of pupation and emergence

respectively. After the fresh weights were taken the adults were killed using chloroform vapour, dried at 100°C to constant weights and then dry weights recorded.

Effect of switching larvae from C. dactylon to P. maximum and S. plicatilis

First instar S. exempta larvae obtained from insectary culture as described above were reared on young C. dactylon in groups of twenty in one pound kilner jars. A sample of freshly-moulted second instar larvae from this lot were transferred to P. maximum and S. plicatilis at a density of twenty larvae per kilner jar. Another lot was transferred into clean jars but continued to feed on C. dactylon. The larvae in the remaining kilner jars into which first instar larvae were introduced were fed daily but otherwise left undisturbed. Early third, fourth and fifth instar larvae from these jars were transferred to P. maximum and S. plicatilis as well as setting up controls as described for the second instar larvae.

The number of larvae surviving and those which died in each instar were recorded and the mortality during the early instars, the last instar, the prepupal stages was

converted into percentages of the total mortality. The percent emergence of each sample on each host plant was also calculated. Pupal weights, adult weights at emergence as well as dry weights of moths were taken and recorded as described in the previous section.

RESULTS

The survival of S. exempta larvae separately reared on leaves from three nodes of young C. dactylon

The numbers of larvae which survived in each instar are presented in Table 40. All samples suffered high mortality during the first instar and although the survival was highest on the youngest leaves and lowest on the oldest leaves the differences were not significant. However, except for the fifth instar stage the larval survival in the other instars was significantly higher ($P<0.05$) on the youngest leaves than on the older leaves from the third node. Larval survival on the leaves from the middle nodes was of intermediate value and was not significantly different from the survival on both leaves from the uppermost and the third node. The late fifth instar larvae on the youngest leaves suffered higher mortality and rendered differences in survival during this instar insignificant.

Distribution of percent mortality of larvae reared on the uppermost and the middle nodes was typically U-shaped (Table 41 and Figure 10). The highest mortality of between thirty one and thirty three percent occurred during the first and the fifth (last) instar stages while only between seven to ten percent of the mortality occurred during the intermediate instars.. On the leaves from the third node about forty and thirteen percent of all the larvae died during the first and second instar stages respectively. As a result of high mortality during the first two instars the percent mortality during the last instar was substantially lower.

Pupal mortality was much lower than the larval mortality although the pupae formed from larvae reared on the leaves from the middle and the third nodes suffered higher mortality than those formed from larvae reared on the leaves from the uppermost node. On account of this, significantly more ($P<0.05$) moths emerged from the pupae formed from larvae that were reared on the leaves from the uppermost node than those reared on leaves from the third node (Table 40). The number of moths resulting from the larvae reared on the leaves from the middle nodes

TABLE 40

THE SURVIVAL OF S. EXEMPTA LARVAE ON LEAVES OF C. DACTYLON FROM THREE DIFFERENT NODES (MEANS ± S.E.)
(N = 15 JARS OF EACH TREATMENT)

INSTAR	NODE		
	1	2	3
1	16.2 ± 0.79^{a}	14.2 ± 0.79^{a}	13.0 ± 0.93^{a}
2	15.2 ± 0.61^{a}	12.93± 1.14^{ab}	10.67± 0.77^{b}
3	13.6 ± 0.84^{a}	11.53± 1.09^{ab}	9.33 ± 1.06^{b}
4	11.87± 0.84^{a}	9.6 ± 1.05^{ab}	7.87 ± 1.03^{b}
5	6.6 ± 1.04^{a}	4.4 ± 0.74^{a}	4.13 ± 0.81^{a}
Pupal stage	6.13± 0.99^{a}	3.47± 0.99^{a}	3.13 ± 0.73^{b}

For each instar figures followed by different letters are not significantly different from each other ($P<0.05$).

TABLE 41

PERCENT MORTALITY OF S. EXEMPTA REARED ON LEAVES FROM THE THREE UPPERMOST NODES OF C. DACTYLON (MEAN ± S.E.)

INSTAR	NODES		
	1	2	3
1	33.5 ± 7.49	33.97 ± 7.38	40.87 ± 5.45
2	7.81 ± 2.36	8.89 ± 1.84	13.15 ± 4.31
3	9.89 ± 3.94	8.65 ± 2.3	9.05 ± 2.82
4	10.80 + 4.00	11.30 ± 4.15	8.23 ± 3.58
5	34.20 ± 5.18	31.45 ± 5.25	22.44 ± 3.75
Pupal stage	3.80 ± 1.15	5.74 ± 1.91	6.26 ± 1.72

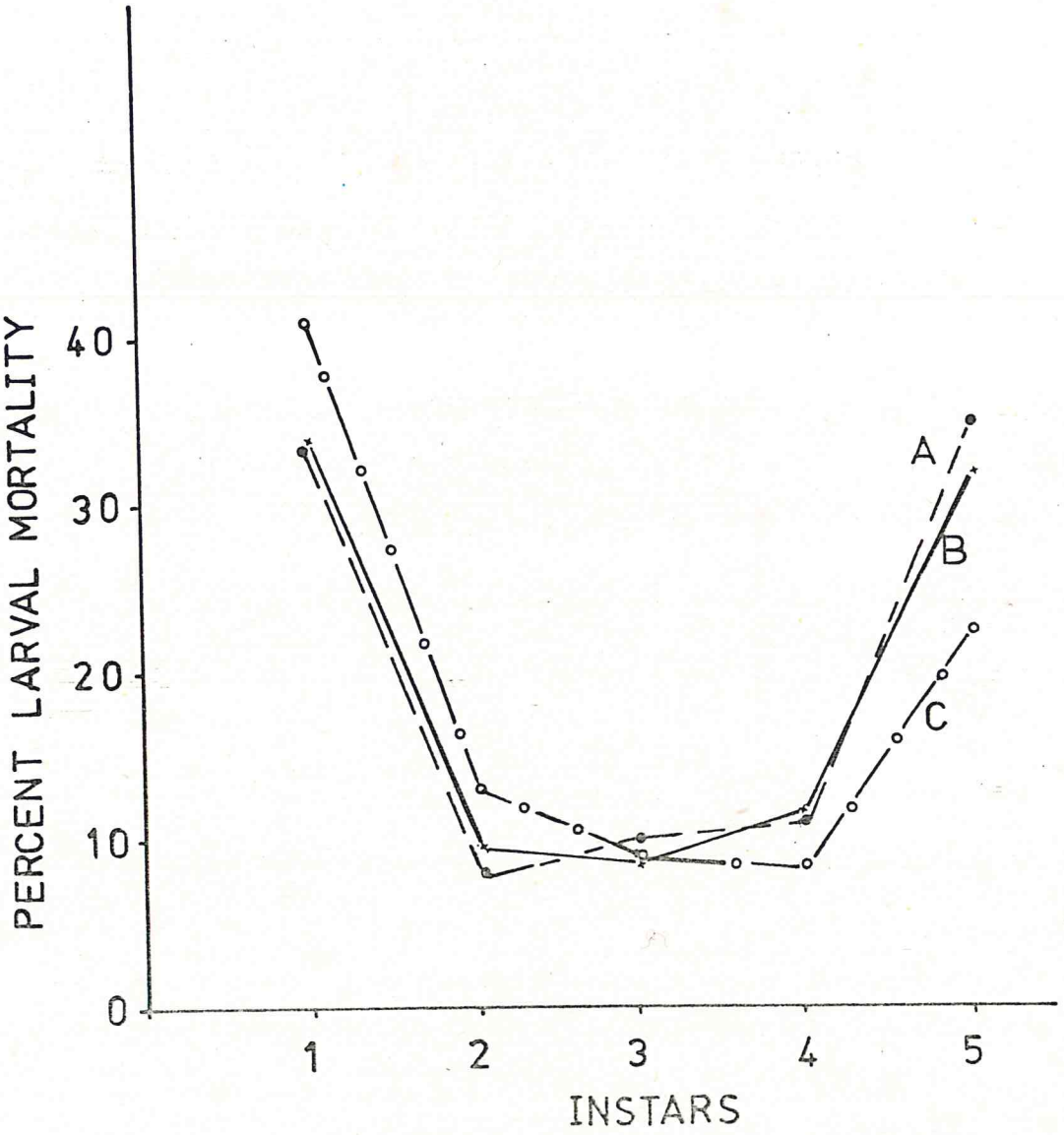
Percent mortality distribution of [illegible]

Larvae reared separately on young C. [illegible]

leaves from the three uppermost nodes.

A - First node

B - [illegible] node


PERCENT LARVAL MORTALITY
40
30
20
10
0
1
2
3
4
5
INSTARS
A
B
C

was not significantly different from the numbers which emerged from the group reared on the leaves from uppermost and the third node.

Pupal weights, adult weights at emergence and adult dry weights of S. exempta on leaves from three uppermost nodes of C. dactylon.

Pupal weights, adult weights at emergence and adult dry weights (Table 42) of moths which resulted from larvae reared on the leaves from the middle and the third node were significantly higher ($P<0.05$) than those of individuals formed from larvae which fed on the youngest leaves from the uppermost node. In all cases the differences between the weights of insects which were fed on leaves from the middle and third node were not significant. The consistently higher survival of larvae in jars with youngest and more nutritious leaves resulted in higher densities of larvae in these jars and this was probably responsible for the lower weights.

The survival of larvae switched to S. plicatilis and P. maximum in comparison to those left on C. dactylon

The number of larvae surviving (Table 43) on C. dactylon shows that although larval mortality was low during the earlier instars it was extremely high during the last instar. On P. maximum and S. plicatilis very few larvae died during the instar at which the larvae were switched on to them. During the subsequent instars, however, larval mortality increased accounting for higher percent mortality than that for the larvae which died during the last instar except for the sample that was transferred on to S. plicatilis at the fourth instar stage. On the other hand, larvae which died during the last instar on C. dactylon accounted for a higher percent mortality than those which died during the earlier instars (Table 44).

In larvae which were transferred during the fifth instar stage, the highest mortality occurred during the same instar on C. dactylon and S. plicatilis while on P. maximum it occurred during the prepupal stage.

Larvae transferred on to the other host plants and the controls which remained on C. dactylon at the fifth instar stage went through five instars whereas the other samples went through six instars.

TABLE 42

PUPAL, EMERGENCE AND ADULT DRY WEIGHTS OF S. EXEMPTA FED ON LEAVES FROM THREE UPPERMOST NODES OF C. DACTYLON (MEANS ± S.E.*)

NODE	SEX	WEIGHTS (mg)		
		PUPAL	EMERGENCE	DRY ADULT
1	Females	132.33 ± 3.45[b]	67.56 ± 2.24[b]	30.10 ± 1.10[b]
	Males	124.11 ± 3.25	55.84 ± 1.46	23.83 ± 0.93
2	Females	150.87 ± 4.18[a]	81.15 ± 2.35[a]	37.15 ± 1.21[a]
	Males	153.90 ± 3.69	77.40 ± 2.78	34.27 ± 1.32
3	Females	151.33 ± 3.61[a]	77.82 ± 3.24[a]	36.45 ± 1.25[a]
	Males	150.12 ± 3.11	59.53 ± 1.62	30.86 ± 1.15

* For both sexes, the weights followed by different letters in each stage of development are significantly different from each other ($P<0.05$).

TABLE 13

SURVIVAL OF SPODOPTERA EXEMPTA ON TRANSFERRING LARVAE FROM C. DACTYLON TO P. MAXIMUM AND S. PLICATILIS AT VARIOUS INSTARS (MEANS ± S.E.)

Instar at which larvae switched	Host Plant	Subsequent instars					Pupal Stage	Adult Stage
		2	3	4	5	6		
2	C.dactylon	20	18.40±0.40	15.80±0.97	15.80±0.97	15.60±1.03	4.60±0.81	3.00±0.32
	P.maximum	20	18.60±0.75	16.40±1.44	13.00±1.87	8.60±1.21	4.00±1.26	3.20±0.86
	S.plicatilis	20	19.20±0.49	13.00±1.86	9.20±2.78	7.80±2.82	3.20±1.46	2.40±1.03
3	C.dactylon		20	19.00±0.77	18.80±0.97	18.40±0.87	3.80±1.16	2.60±0.93
	P.maximum		20	18.20±0.58	16.00±1.22	13.60±1.99	3.60±1.10	3.00±1.10
	S.plicatilis		20	19.20±0.20	16.80±1.28	13.40±1.94	4.20±0.66	3.20±0.97
4	C.dactylon			20	19.00±0.00	18.00±0.63	3.80±1.36	3.40±1.21
	P.maximum			20	19.20±0.20	14.40±1.44	5.00±0.95	3.80±0.86
				20	17.00±1.00	15.00±1.07	1.8 ±0.86	2.20±0.56
5	C.dactylon				20	-	6.20±0.45	5.20±0.44
	P.maximum				20	-	6.40±3.04	6.10±2.73
	S.plicatilis				20	-	3.80±1.46	3.20±1.39

TABLE 44

PERCENT MORTALITY DISTRIBUTION OF S. EXEMPTA ON TRANSFERRING LARVAE FROM C. DACTYLON TO P. MAXIMUM AND S. PLICATILIS AT VARIOUS INSTARS.

Instar at which transferred	Host plant	% Mortality during the various stage			
		Other Instars	Last Instar Stage	Prepupal Stage	Pupal Stage
2	C.dactylon	26.0 ± 6.07	55.2 ± 10.21	9.2 ± 1.39	9.6 ± 3.17
	P. maximum	67.4 ± 5.79	23.0 ± 5.50	4.4 ± 4.40	5.2 ± 3.71
	S. plicatilis	65.4 ±14.49	17.6 ± 5.78	12.4 ± 6.50	4.6 ± 2.82
3	C. dactylon	9.0 ± 4.89	6o.0 ±11.02	23.8 ±11.10	7.2 ± 3.38
	P. maximum	37.8 ±10.58	45.6 ±12.22	16.6 ± 6.99	0
	S.plicatilis	39.8 ±12.23	29.4 ±10.16	25.4 ±11.32	3.8 ± 2.22
4	C.dactylon	11.8 ± 1.97	49.8 ± 4.53	35.8 ± 2.75	2.6 ± 1.74
	P. maximum	34.8 ± 9.13	31.8 ± 8.30	26.0 ± 9.61	7.4 ± 1.44
	S.plicatilis	28.2 ±11.45	56.0 ±10.80	12.6 ± 3.34	3.2 ± 2.40
5	C.dactylon	-	84.6 ± 6.20	8.0 ± 5.80	7.4 ± 3.76
	P. maximum	-	37.0 ±19.27	50.6 ±16.55	12.4 ± 9.50
	S.plicatilis	-	95.2 ± 3.34	1.2 ± 1.2	3.6 ± 2.29

There was a great deal of variation in the numbers of moths that emerged from each jar and no significant differences were detected in percent emergence (Table 45).

Weights of individuals resulting from larvae previously reared on C. dactylon and then switched to P. maximum or S. plicatilis

Weights of pupae (Table 46) formed from larvae initially reared on C. dactylon and then transferred either to S. plicatilis and P. maximum or left on C. dactylon showed highly significant ($P<0.001$) variations in all the four treatments. Larvae left on C. dactylon formed pupae which weighed significantly more ($P<0.01$) than those formed from larvae transferred on to P. maximum and S. plicatilis. Those formed from larvae transferred on to P. maximum at various instars except the second, weighed significantly more ($P<0.01$) than those from larvae switched to S. plicatilis. Male pupae formed from larvae transferred on to S. plicatilis at second instar stage weighed more than those formed from those transferred on to P. maximum. When results for both sexes were analysed collectively the difference was not significant.

TABLE 45

PERCENT EMERGENCE OF S. EXEMPTA WHEN LARVAE WERE SWITCHED FROM C. DACTYLON TO P. MAXIMUM AND S. PLICATILIS AT VARIOUS INSTARS

Instar at which transferred	Host Plant		
	C. dactylon	P.maximum	S. plicatilis
2	15.0 ± 1.58	16.0 ± 4.30	3.0 ± 2.55
3	13.0 ± 4.64	15.0 ± 5.48	16.0 ± 4.85
4	17.0 ± 6.04	19.0 ± 4.30	11.0 ± 2.92
5	26.0 ±11.11	28.0 ±13.66	16.0 ± 6.96

TABLE 46

PUPAL WEIGHTS OF INDIVIDUALS PREVIOUSLY REARED ON *C. DACTYLON* BUT SWITCHED TO *P. MAXIMUM* OR *S. PLICATILIS* AT VARIOUS INSTARS (mg) + S.E.

INSTARS AT SWITCHING		HOST PLANTS		
		C. dactylon	*P. maximum*	*S. plicatilis*
2	Females	167.83 ± 4.95^{a}	130.45 ± 5.61^{b}	125.63 ± 4.97^{b}
	Males	157.76 ± 5.20	110.09 ± 2.02	126.84 ± 4.10
3	Females	170.08 ± 6.19^{a}	144.84 ± 3.74^{b}	108.10 ± 6.53^{c}
	Males	161.14 ± 6.66	137.78 ± 3.90	96.91 ± 6.10
4	Females	169.81 ± 4.30^{a}	132.62 ± 4.37^{b}	103.17 ± 3.88^{c}
	Males	166.71 ± 3.93	129.15 ± 2.39	95.42 ± 6.07
4	Females	169.81 ± 4.30^{a}	132.62 ± 4.37^{b}	103.17 ± 3.88
	Males	166.71 ± 3.93	129.15 ± 2.39	95.42 ± 6.07
5	Females	176.72 ± 4.34^{a}	126.38 ± 3.99^{b}	106.73 ± 7.18^{c}
	Males	176.13 ± 4.74	126.00 ± 5.81	119.26 ± 5.81

Irrespective of sex, the weights followed by different letters for each stage of transfer of larvae are significantly different from each other ($P<0.01$).

Adult weights at emergence (Table 47) followed trends similar to those of pupal weights except that the difference between mean weights for moths formed from the fifth instar larvae transferred on to P. maximum and S. plicatilis was not significant. The comparisons between dry weights (Table 49) still showed significant differences ($P<0.01$) between C. dactylon on the one hand and P. maximum and S. plicatilis on the other hand. Significant difference between the latter host plants was found only with regard to moths which emerged from the larvae transferred on to them at the early third instar stage.

The within-host comparisons of weights of individuals transferred to the three hosts at various instars

At the 5% level of significance the pupal weights adult weights at emergence and adult dry weights (Tables 46, 47 and 48) of S. exampta kept feeding on C. dactylon showed no significant differences with respect to the instars at which the densities were made up to twenty per kilner jar. Female pupae and moths weighed more than males although the differences were not significant except in adults formed from larvae whose density per

ADULT WEIGHTS TABLE 47

ADULT WEIGHTS AT EMERGENCE FOR INDIVIDUALS PREVIOUSLY REARED ON C. DACTYLON BUT TRANSFERRED TO P. MAXIMUM OR S. PLICATILIS AT VARIOUS INSTARS

(MEANS ± S.E.)*

INSTAR at SWITCHING		HOST PLANTS		
		C. DACTYLON	P. MAXIMUM	S. PLICATILIS
2	Females	78.28 ± 2.87[a]	61.41 ± 3.38[b]	56.78 ± 2.80[b]
	Males	79.93 ± 2.22	50.18 ± 1.34	56.11 ± 1.79
3	Females	84.16 ± 2.39[a]	67.68 ± 2.33[b]	53.24 ± 2.90[c]
	Males	79.10 ± 2.46	61.01 ± 2.13	47.90 ± 1.60
4	Females	88.10 ± 3.69[a]	60.78 ± 3.44[b]	47.82 ± 2.26[c]
	Males	78.76 ± 1.55	58.77 ± 1.15	47.22 ± 3.30
5	Females	86.06 ± 2.26[a]	62.79 ± 2.32[b]	56.98 ± 3.22[b]
	Males	81.08 ± 2.25	53.48 ± 2.34	51.59 ± 3.24

* For both sex, the weights followed by different letters for each stage of transfer of larvae are significantly different from each other ($P \leq 0.01$).

TABLE 48

ADULT DRY WEIGHTS FOR INDIVIDUALS PREVIOUSLY REARED ON *C. DACTYLON* BUT TRANSFERRED TO *P. MAXIMUM* OR *S. PLICATILIS* AT VARIOUS INSTARS (MEANS ± S.E.)*

INSTARS AT SWITCHING		HOST PLANTS		
		C. DACTYLON	P. MAXIMUM	S. PLICATILIS
2	Females	37.37 ± 1.44[a]	26.58 ± 2.05[b]	26.31 ± 1.01[b]
	Males	38.22 ± 1.32	20.69 ± 0.62	22.49 ± 0.63
3	Females	40.99 ± 2.07[a]	28.95 ± 1.15[b]	22.28 ± 0.90[c]
	Males	35.49 ± 1.07	24.65 ± 0.68	18.24 ± 0.76
4	Females	39.48 ± 1.62[a]	25.41 ± 0.95[b]	24.14 ± 2.08[b]
	Males	32.93 ± 0.70	25.25 ± 1.54	20.48 ± 1.17
5	Females	40.24 ± 1.54[a]	21.20 ± 0.94[b]	19.26 ± 1.92[b]
	Males	33.07 ± 1.56	24.77 ± 1.12	22.25 ± 2.01

* For both sexes the weights followed by different letters for each stage of transfer of larvae are significantly different from each other ($P<0.01$).

kilner jar was made up to twenty at the fourth instar stage. Female dry weights were significantly higher ($P<0.01$) than male weights except for the individuals developing from larvae whose density was made up to twenty at the second instar stage.

Pupal weights of samples transferred to S. plicatilis (Table 46) varied with the stage at which the larvae were transferred. Those from larvae that were transferred at the early second instar stage weighed significantly more ($P<0.05$) than the others. Comparisons between the other treatments showed that the larvae which were switched at the early fifth instar stage developed into larger male pupae and therefore the overall mean for both sexes was significantly larger ($P<0.05$) than the means for individuals transferred at the fourth stage. However, the two means did not differ significantly from that for pupae formed from larvae that were transferred at the third instar stage. The adult weights at emergence (Table 47) showed similar trends except for individuals developing from larvae which were switched to S. plicatilis at the early second and fifth instar stages. The weights at emergence of these individuals were not significantly different from each other.

Dry adult weights (Table 48) were variable but the differences with respect to the instar at which the larvae were transferred to S. plicatilis were not significant although dry weights of individuals transferred at the early second instar were slightly higher possibly due to the lower larval densities during the last instar (Table 40). If this is so, the result suggest that at low densities on less suitable host plants, the last instar larvae consume larger quantities of food since they suffer less disturbance from each other and are to some extent capable of compensating for the unsuitable qualities of the host plant. Similar results were observed in the mean pupal weights (Table 46).

Significant ($P<0.01$) variations were found between the weights of pupae formed from larvae transferred to P. maximum at the various instar stages. Weights of pupae formed from larvae, which were transferred at the early third instar stage were significantly higher ($P<0.05$) than those for individuals transferred at other stages transferred at the fourth instar stage developed into significantly larger ($P<0.05$) pupae than those transferred at the early second instar stage but the pupal weights of these two treatments were

comparable to the pupal weights of the sample transferred at the fifth instar stage. Adult weights at emergence gave similar results except that the differences between individuals transferred to P. maximum at the early third and fourth instar stages was not significant. Similar results were obtained for adult dry weights with the exception that individuals transferred to P. maximum at the second instar stage weighed slightly more than those from larvae transferred to this host at the fifth instar stage and their weights were not significantly different from those for moths formed from larvae transferred at the fourth instar stage.

Female pupae were slightly larger than male pupae but this was only significant ($P<0.05$) in the treatment in which larvae were switched at the second instar stage. Females had higher weights at adult emergence than males but this was only significant ($P<0.05$) in individuals developing from larvae which were switched to this host at the third instar stage. Except for the individuals developing from larvae transferred to P. maximum at the fourth instar stage the female dry weights were significantly higher ($P<0.05$) than male dry weights.

The low weights of pupae formed from larvae which were on P. maximum at the second instar stage despite the lower larval density during the last instar could be explained by variability in quality of the leaves of P. maximum on which the larvae fed.

DISCUSSION

The distribution of mortality is U-shaped for larvae fed on leaves from the uppermost and the second nodes of C. dactylon. In larvae fed on leaves from the third node from the top, percent mortality was lower during the last instar because a substantially larger number of larvae died during the second instar. Similarly, the results obtained from experiments on which larvae were transferred on to less suitable host plants showed that among larvae which continued to feed on C. dactylon mortality was higher during the last instar than during the earlier instars. On the other hand, larvae were switched to S. plicatilis and P. maximum suffered higher mortality before reaching the last instar. In these samples, low mortality during the last instar was often follwed by high mortality of the prepupae.

In most insects the highest mortality occurs in the early stages of development particularly during the first larval instar. In S. exempta mortality is equally high during the first and the last instar in larvae reared on young leaves of suitable host plants such as C. dactylon. On the less suitable host plants such as S. plicatilis, P. maximum and even older leaves of the usually suitable host plants, larvae continue to die during the intermediate instars resulting in much lower percent larval mortality during the last instar.

Mortality during the first instar stage could be related to the quality of larvae, for instance, they could die of nuclear polyhedrosis virus transmitted from parents to offpring (Brown and Swaine, 1965). Since the samples reared on the leaves from three nodes of C. dactylon and on the other host plants in earlier experiments suffered equally high mortality during the first instar, the quality of leaves is probably important at this stage. Plant factors such as morphology, digestibility, deficiencies of primary plant chemicals and presence of toxic substance could also result in high mortality of the early instars. Mortality during the later instars often results from

deficiencies in the primary plant chemicals (Gerber and Obadofin, 1981). Young leaves of S. plicatilis and P. maximum have lower nitrogen content than those of C. dactylon and although the optimum quantity of nitrogen is not known, it is possible that dificiencies in this nutrient and in other primary plant substances could have contributed to the larval mortality during the intermediate instars among the larvae on S. plicatilis and P. maximum.

The foliage of S. plicatilis and P. maximum, being coarser than that of C. dactylon, may have been consumed in sub-optimal quantities resulting in weaker larvae which are more susceptible to nuclear polyhedrosis virus. The resistance of some plants to Spodoptera eridania is known to be due to their hard texture (Soo Hoo and Fraenkel, 1966).

Mortality was highest during the last instar stage in larvae which otherwise had previously good survival in both the leaf age experiments and those in which larvae were transferred on to less suitable host plants. Since most of the larvae which died showed symptoms similar to those of nuclear polyhedrosis virus, the results indicate that under laboratory conditions mortality due to virus is greater with higher

larval density (Brown and Swaine, 1965). However, high mortality during the last larval instar has not been observed under suitable outbreak conditions suggesting that the larval mortality may be more severe during the early instars and particularly the first instar. If this is so, larvae which start on young foliage of the preferred grass species and then due to depletion, move on to coarser and less nutritious species, survive better than those which start on the latter.

Although the second, third, fourth and fifth instar larvae switched from C. dactylon to P. maximum and S. plicatilis showed an improved percent larval survival, the resulting pupae and adults remained just as small as those reared on these host plants from the beginning. Since this was so irrespective of the instar at which larvae were transferred to the less preferred hosts, it suggests that the quality and quantity of foliage consumed during the ultimate instar determines the weight of the pupa or adult. Digestibility, consumption rates or respiratory costs were not determined but P. maximum and S. plicatilis have lower nitrogen content than C. dactylon and this together with possible deficiences in other primary plant substances could be responsible for the smaller weights. The growth of larvae of Pieris rapae

is affected by nitrogen levels in crucifers (Slansky and Feeny, 1977). Similarly young leaves of hosts of Leptinotarsa decelineata (Say), Plutela maculipennis Curtis and Phaedon cochleariae Fabricius have higher amounts of amino acids and proteins than old leaves and are therefore nutritionally superior (Cibula et al., 1967; Taylor and Bardner, 1968).

Assuming that the young leaves are nutritionally superior, larvae fed on the youngest leaves of C. dactylon would have been expected to form the largest pupae and moths but these were smaller than those developing from larvae that fed on older leaves. This suggests that due to the high survival up to the last instar, the larval density was too high and that disturbances between larvae could have lowered food consumption resulting in smaller pupae and adults.

These results suggest that although the preference of S. exempta for C. dactylon is maintained throughout the larval life the less preferred host plants are more tolerated by the older larvae than by the younger ones. Furthermore the larval density and the leaf age may affect the food consumption, larval survival and the quality of the resulting pupae and adults. It can thus be concluded that the rank order of food preference of S. exempta can be influenced by larval age, density and leaf age.

SUMMARY

Survival of S. exempta larvae is highest on the youngest foliage of C. dactylon. Transferring the subsequent instars to the less preferred S. plicatilis or P. maximum results in higher larval survival than when larvae are fed on these grass species throughout the larval life. Their pupal and adult weights are, however, lower than those for individuals left on C. dactylon irrespective of the stage at which they are transferred suggesting that the pupal and adult weights are largely dependent on the species of grass consumed during the last instar. Lower weights can also result from high density even if the larvae are on the preferred host. High density larvae may, however, move on to the less preferred host plants on depletion of the preferred grass species and though the resulting pupae or adults are smaller good survival is achieved.

CHAPTER 5

MOULTING AND DEVELOPMENT OF LARVAE OF THE AFRICAN ARMYWORM *SPODOPTERA EXEMPTA* (WALK.) ON NATURAL DIETS

INTRODUCTION

Rapid and accurate techniques for distinguishing between instars of a given species are required in studies relating to insect biology and ecology, for example in constructing life tables when monitoring population changes and mortality factors (Campbell *et. al.*; 1977; Nebeker, 1977; Podoler, 1974; Varley and Gradwell, 1968). In order to meet this need numerous attempts have been made to relate the increase in linear dimensions or weight of successive insect instars to numerical rules. The most relevant of these to the present work is Dyar's (1890) rule according to which the head capsules of certain lepidopterous larvae follow a regular geometrical progression. This rule should in fact be accredited to Brooks (Crosby, 1973) whose work preceded Dyar's by four years. The

determination of larval instars by measuring head capsule widths is a common practice (Matthee, 1946; Rose, 1975; Tostowaryk, 1971). Other commonly used parameters include the faecal pellet size (Sardesai, 1969) and the distance between the frontal setae on the clypeus of the head capsule (Podoler and Klein, 1978).

Hattingh (1941) observed six larval instars in S. exempta but later it was found that this was the case in the gregareous phase of the laboratory larvae and that most solitary larvae passed through five instars (Matthee, 1946). When reared on maize diet as single larvae, some were found to pass through five and others through six instars (David, et al., 1975). Measurements of head capsule widths of samples of larvae in three successive generations from an outbreak have shown that larvae passed through six instars (Rose, 1975). There was, however, variation in instar sizes between generations and an overlap between instars three to six. Furthermore, the rate of larval development varied with host grass species and habitat. The fast growing larvae showed better synchronisation of the developmental stages.

In insects, moulting and morphogenesis are directly controlled by hormones secreted by the prothoracic glands (PG) and the Corpora allata (CA) both of which are controlled by neurohormonal or neural signals from the brain. The control centres in the brain are in turn influenced by environmental factors either directly or indirectly through altered internal milieu (Wigglesworth, 1954). External factors including temperature and quality and quantity of food can alter the number and the nature of moults. Starvation for instance causes Trogoderma to undergo stationary moults accompanied by a decrease in size (Beck, 1971). Some species of Lepidoptera increase the duration of the intermoult period under food shortage conditions to allow full growth (Skoblo, 1935). In some species reduced food supply leads to precocious pupation (Lower, 1961) or supernumerary larval moults (Kellog and Bell, 1904; Gaines and Campbell, 1935; Beck, 1950).

Grass species vary nutritionally with respect to species, age and part of the plant. They also probably differ with seasons and the geographical location. Little is known, however, concerning the effect of the nutrition of different host plants on growth and development patterns of the larvae of S. exempta.

MATERIALS AND METHODS

In this study the head capsule widths and the distances between the frontal setae on the clypeus of the head capsule measured using a dissecting microscope equipped with a micrometric occular were used in distinguishing instars. Larvae belonging to different instars were preserved in 70% ethanol until they were measured. Older instars were obtained by introducing first larvae into one pound kilner jars in groups of twenty. Each jar was fitted with a top consisting of a filter paper and a metalic or plastic ring. The patterns of development on various host plants were compared by rearing the larvae on maize, Zea mais L.; star grass, Cynodon dactylon (L.) Pers.; Kikuyu grass, Pennisetum clandestinum Chiov.; Panicum maximum Jacq.; Setaria plicatilis (Hochst.) Hack.; and a sedge, Cyperus maranguensis K. Schum.

Larvae were kept under constant conditions of temperature and humidity at 18°C and 80% R.H., 25°C and 70% R.H and 30°C and 60% RH. The first and the last experiments were carried out in temperature and humidity controlled chambers but the other one was carried out in an insectary. In each of the three

treatments there were ten jars for each host plant. The sedge was, however, not included in the study carried out in the insectary.

Fresh food was supplied daily and added whenever necessary. The cut ends of leaves were immersed in water in one ounce transparent plastic vials to maintain the water content of leaves. The faecal pellets were removed from jars daily and the larvae were transferred to clean and sterile jars whenever necessary.

Samples of thirty larvae reared on each of the host plant species in each of the three treatments were collected at the beginning of each instar and measured. In addition large samples of larvae were collected from an infestation at Athi River on 23rd February 1979 and Lukenya in June, 1980. The outbreak sites were about three kilometres apart. At the time of larval infestation, Athi River experienced plenty of rainfall, whereas Lukenya had hardly any for most of the larval duration. The dominant grass species at Athi River and Lukenya were C. dactylon and Pennisetum mezianum respectively. Collected larvae were preserved separately in ethanol until they were measured.

RESULTS

Development patterns at 18°C and 80% R.H.

At 18°C and 80% RH. the number of larval instars varied from six to seven. Larvae reared on *C. dactylon*, *Z. mais* and *P. clandestinum* went through six instars (Tables 49 and 50) while those reared on *P. maximum*, *S. plicatilis* and *C. maranguensis* went through seven instars (Tables 51 and 52). By the fourth instar stage the seven instar group had significantly ($P<0.001$) lower mean head capsule widths than the six instar group. The mean head capsule width of the fifth instar larvae on *C. maranguensis* was equivalent to the mean head capsule width for the fourth instar larvae in the six instar group. Similarly the mean head capsule width for the sixth instar larvae on *P. maximum* and *C. maranguensis* were comparable to the mean head capsule width for the fifth instar larvae on *Z. mais* and *P. clandestinum*.

The mean distances between the frontal setae of second instar larvae reared on *S. plicatilis* and *C. maranguensis* (Table 53) were significantly ($P<0.001$)

TABLE 49

THE MEAN OF HEAD CAPSULES (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SIX INSTARS AT 18°C AND 80% R.H.

HOST PLANT	INSTAR	MEAN S.E.	RATIO
C. dactylon	1	0.354±0.008	1.588
	2	0.562±0.004	1.580
	3	0.888±0.010	1.539
	4	1.367±0.016	1.477
	5	2.019±0.021	1.271
	6	2.597±0.043	
Z. mais	1	0.354±0.008	1.588
	2	0.562±0.004	1.705
	3	0.958±0.012	1.441
	4	1.380±0.012	1.447
	5	1.997±0.017	1.346
	6	2.687±0.038	
P. clandestinum	1	0.354±0.008	1.588
	2	0.562±0.004	1.637
	3	0.920±0.009	1.541
	4	1.418±0.004	1.353
	6	2.520±0.017	

TABLE 50

THE MEAN DISTANCE (mm) BETWEEN THE FRONTAL SETAE STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SIX INSTARS AT 18°C AND 80% R.H.

HOST PLANT	INSTAR	MEAN	S.E.	RATIO
C. dactylon	1	0.048	± 0.0004	1.958
	2	0.094	± 0.001	1.670
	3	0.157	± 0.002	1.312
	4	0.206	± 0.003	1.539
	5	0.317	± 0.005	1.350
	6	0.428	± 0.005	
Z. mais	1	0.048	± 0.0004	1.979
	2	0.095	± 0.001	1.516
	3	0.144	± 0.002	1.479
	4	0.213	± 0.003	1.467
	5	0.313	± 0.005	1.316
	6	0.412	± 0.007	
P. clandestinum	1	0.048	± 0.0004	1.979
	2	0.095	± 0.001	1.568
	3	0.149	± 0.002	1.385
	4	0.206	± 0.003	1.403
	5	0.289	± 0.003	1.405
	6	0.406	± 0.004	

TABLE 51

THE MEAN WIDTHS OF HEAD CAPSULES (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SEVEN INSTARS AT 18°C AND 80% R.H.

HOST PLANT	INSTAR	MEAN	S.E.	RATIO
P. maximum	1	0.354	± 0.008	1.579
	2	0.559	± 0.002	1.496
	3	0.836	± 0.015	1.372
	4	1.147	± 0.014	1.398
	5	1.603	± 0.018	1.215
	6	1.947	± 0.022	1.351
	7	2.630	± 0.021	
C. maranguensis	1	0.354	± 0.008	1.525
	2	0.540	± 0.001	1.548
	3	0.836	± 0.013	1.238
	4	1.035	± 0.042	1.300
	5	1.345	± 0.014	1.452
	6	1.953	± 0.025	1.371
	7	2.677	± 0.029	
S. plicatilis	1	0.354	± 0.088	1.441
	2	0.516	± 0.007	1.631
	3	0.832	± 0.012	1.218
	4	1.013	± 0.026	1.481
	5	1.500	± 0.009	1.253
	6	1.880	± 0.004	1.289
	7	2.424	± 0.080	

TABLE 52

THE MEAN DISTANCE BETWEEN THE FRONTAL SETAL (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SEVEN INSTARS AT 18°C AND 80% R.H.

HOST PLANT	INSTAR	MEAN	S.E.	RATIO
P. maximum	1	0.048	± 0.0004	2.000
	2	0.096	± 0.001	1.385
	3	0.133	± 0.002	1.444
	4	0.192	± 0.002	1.302
	5	0.250	± 0.002	1.160
	6	0.290	± 0.009	1.490
	7	0.432	± 0.008	
C. maranguensis	1	0.048	± 0.004	1.750
	2	0.084	± 0.001	1.500
	3	0.126	± 0.006	1.341
	4	0.169	± 0.003	1.237
	5	0.209	± 0.003	1.426
	6	0.298	± 0.006	1.376
	7	0.410	± 0.006	
S. plicatilis	1	0.048	± 0.0004	1.583
	2	0.076	± 0.001	1.697
	3	0.129	± 0.002	1.318
	4	0.170	± 0.002	1.335
	5	0.227	± 0.0001	1.247
	6	0.283	± 0.002	1.424
	7	0.403	± 0.004	

shorter than those for the group which went through six instars. Differences in mean distances between the frontal setae of the six and seven instar groups were quite large at the beginning of the third instar stage. The means for the fifth instar larvae on S. plicatilis and the C. maranguensis were equivalent to the means for the fourth instar larvae in the subgroup which went through six instars. The means for the sixth instar larvae in the groups which went through seven instars were equivalent to the mean for fifth instar larvae reared on P. clandestinum.

Development patterns at 25°C and 70% R.H.

At 25°C and 70% RH. larvae on C. dactylon, Z. mais and P.. clandestinum went through five instars (Tables 53 and 54). The group of larvae on P. maximum went through six instars while those on S. plicatilis went through seven instars (Table 55 and 56). The mean head capsule width for larvae reared on P. maximum was the smallest at the second instar stage and remained smaller than the means for the corresponding instar means for larvae which went through five instars. The decrease in the mean head capsule width for larvae on

S. plicatilis was pronounced at the third instar stage and for the fourth instar larvae it was equivalent to the mean for the third instar larvae in the five instar group.

When mean distances between the frontal setae were examined, the decrease in size was detectable at the second instar stage in larvae reared on P. maximum and S. plicatilis. At the third instar stage the larvae on S. plicatilis were smaller than the larvae on P. maximum. The mean for the former at the fourth instar stage was equivalent to the mean for the third instar larvae in the subgroup which went through five instars. The mean head capsule widths and the mean distances between the frontal setae are presented in figures 11 and 12.

Development patterns at 30°C and 60% R.H.

Larvae maintained at 30°C and 60% RH. and reared on C. dactylon, Z. mais and P. clandestinum went through five instars (Tables 57 and 58). The samples reared on P. maximum, S. plicatilis and C. maranguensis passed through six instars (Tables 59 and 61). The decrease in the mean head capsule size

TABLE 53

THE MEAN WIDTH OF HEAD CAPSULES (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH FIVE INSTARS AT 25°C AND 70% RH.

HOST PLANT	INSTAR	MEAN S.E.	RATIO
C. dactylon	1	0.354 ± 0.008	1.556
	2	0.551 ± 0.003	1.697
	3	0.935 ± 0.009	1.738
	4	1.625 ± 0.006	1.568
	5	2.548 ± 0.011	
Z. mais	1	0.354 ± 0.008	1.559
	2	0.552 ± 0.004	1.889
	3	1.043 ± 0.014	1.662
	4	1.733 ± 0.013	1.434
	5	2.485 ± 0.014	
P. clandestinum	1	0.354 ± 0.008	1.551
	2	0.549 ± 0.013	1.767
	3	0.970 ± 0.061	1.649
	4	1.600 ± 0.021	1.496
	5	2.396 ± 0.016	

TABLE 54

THE MEAN DISTANCE BETWEEN THE FRONTAL SETAE (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH FIVE INSTARS AT 25°C AND 70% RH.

HOST PLANT	INSTAR	MEAN S.E.	RATIO
C. dactylon	1	0.048 ± 0.0004	1.792
	2	0.086 ± 0.001	1.721
	3	0.148 ± 0.003	1.620
	4	0.240 ± 0.003	1.656
	5	0.397 ± 0.004	
Z. mais	1	0.048 ± 0.004	2.208
	2	0.106 ± 0.002	1.472
	3	0.156 ± 0.002	1.596
	4	0.249 ± 0.002	1.598
	5	0.398 ± 0.003	
P. clandestinum	1	0.048 ± 0.0004	1.938
	2	0.093 ± 0.001	1.613
	3	0.150 ± 0.002	1.547
	4	0.232 ± 0.005	1.672
	5	0.388 ± 0.005	

TABLE 55

THE MEAN WIDTH OF HEAD CAPSULES (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SIX AND SEVEN INSTARS AT 25°C AND 70% RH.

THE SUBGROUP WHICH WENT THROUGH SIX INSTARS

HOST PLANT	INSTAR	MEAN S.E.	RATIO
P. maximum	1	0.354 ± 0.008	1.367
	2	0.484 ± 0.003	1.690
	3	0.818 ± 0.010	1.476
	4	1.207 ± 0.012	1.605
	5	1.937 ± 0.015	1.323
	6	2.563 ± 0.016	

THE SUBGROUP WHICH WENT THROUGH SEVEN INSTARS

HOST PLANT	INSTAR	MEAN S.E.	RATIO
S.. plicatilis	1	0.354 ± 0.008	1.508
	2	0.534 ± 0.078	1.390
	3	0.742 ± 0.018	1.283
	4	0.052 ± 0.004	1.441
	5	1.372 ± 0.015	1.353
	6	1.857 ± 0.019	1.351
	7	2.509 ± 0.023	

TABLE 56

THE MEAN DISTANCE BETWEEN THE FRONTAL SETAE (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SIX AND SEVEN INSTARS AT 25°C AND 70% RH.

HOST PLANT	INSTAR	MEAN	S.E.	RATIO
P. maximum	1	0.048	± 0.0004	1.583
	2	0.076	± 0.001	1.697
	3	0.129	± 0.002	1.403
	4	0.181	± 0.002	1.602
	5	0.290	± 0.003	1.403
	6	0.407	± 0.004	

THE SUBGROUP WHICH WENT THROUGH SEVEN INSTARS

HOST PLANT	INSTAR	MEAN	S.E.	RATIO
S. plicatilis	1	0.048	± 0.0004	1.583
	2	0.076	± 0.001	1.289
	3	0.098	± 0.001	1.480
	4	0.145	± 0.001	1.407
	5	0.204	± 0.005	1.359
	6	0.277	± 0.004	1.412
	7	0.391	± 0.006	

in larvae on S. plicatilis and C. maranguensis was recognisable at the third instar stage but this was not obvious in larvae reared on P. maximum until the fourth instar stage. Fourth instar larvae on C. dactylon, Z. mais and P. clandestinum had only slightly larger mean head capsule widths than the larvae on C. maranguensis, but while the former moulted into the fifth (the last instar) the latter had an extra moult before moulting into the last instar.

The data on the distance between the frontal setae showed a reduction in size at the second instar stage in the sample reared on P. maximum but for the larvae reared on S. plicatilis and C. maranguensis this was recognisable at the third instar stage. As in the case of the head capsule widths the distances between the frontal setae in larvae on C. dactylon, Z. mais, P. clandestinum and C. maranguensis were comparable in size at the fourth instar stage.

Analyses of variance carried out on both the head-capsule widths and the distances between the frontal clypeal setae on the final instar larvae showed significant ($P<0.001$) variations with the number of instars through which the larvae passed. The differences between the means were measured by the Student - Newman -

Keuls test (Sokal and Rohlf, 1969). At the 5% level of significance the mean head capsule widths of the groups which went through five instars were significantly smaller than the means for the samples which went through six and seven instars. The mean head capsule widths for the larvae which went through six instars was slightly smaller than the mean for those which went through seven instars although this was not significant. The mean for the distances between the setae for the subgroup which went through seven instars was significantly greater than the other two means. The latter means were not significantly different from each other although the mean for the subgroup which went through five instars was slightly smaller.

As expected the head capsule widths and the distances between the frontal clypeal setae of successive larval instars increased at geometric rates (Tables 61 and 62) and were highly correlated to the instars as shown by the proportion of their variations (r^2) accounted for by the instars. The rate of increase between instars was greatest in larvae which went through five instars and least in those which went through seven instars. The relation between the logarithms of

TABLE 57

THE MEAN WIDTH OF HEAD CAPSULES (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH FIVE INSTARS 30°C AND 60% RH.

HOST PLANT	INSTAR	MEAN	S.E.	RATIO
C. dactylon	1	0.354	± 0.008	1.630
	2	0.577	± 0.006	1.711
	3	0.987	± 0.012	1.712
	4	1.690	± 0.023	1.449
	5	2.448	± 0.022	
Z. mais	1	0.354	± 0.008	1.644
	2	0.582	± 0.006	1.756
	3	1.022	± 0.011	1.710
	4	1.748	± 0.007	1.410
	5	2.465	± 0.012	
P. clandestinum	1	0.354	± 0.008	1.605
	2	0.568	± 0.008	1.879
	3	1.067	± 0.012	1.623
	4	1.732	± 0.017	1.425
	5	2.468	± 0.012	

TABLE 58

THE MEAN DISTANCE BETWEEN THE FRONTAL SETAE (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH FIVE INSTARS AT 30°C AND 60% RH.

HOST PLANT	INSTAR	MEAN S.E.	RATIO
C. dactylon	1	0.048 ± 0.0004	2.083
	2	0.100 ± 0.002	1.620
	3	0.162 ± 0.014	1.623
	4	0.263 ± 0.025	1.578
	5	0.415 ± 0.004	
Z. mais	1	0.048 ± 0.0004	2.063
	2	0.099 ± 0.004	1.667
	3	0.165 ± 0.002	1.667
	4	0.275 ± 0.002	1.491
	5	0.410 ± 0.005	
P. clandestinum	1	0.048 ± 0.0004	1.958
	2	0.094 ± 0.002	1.830
	3	0.172 ± 0.002	1.547
	4	0.266 ± 0.004	1.459
	5	0.388 ± 0.004	

TABLE 59

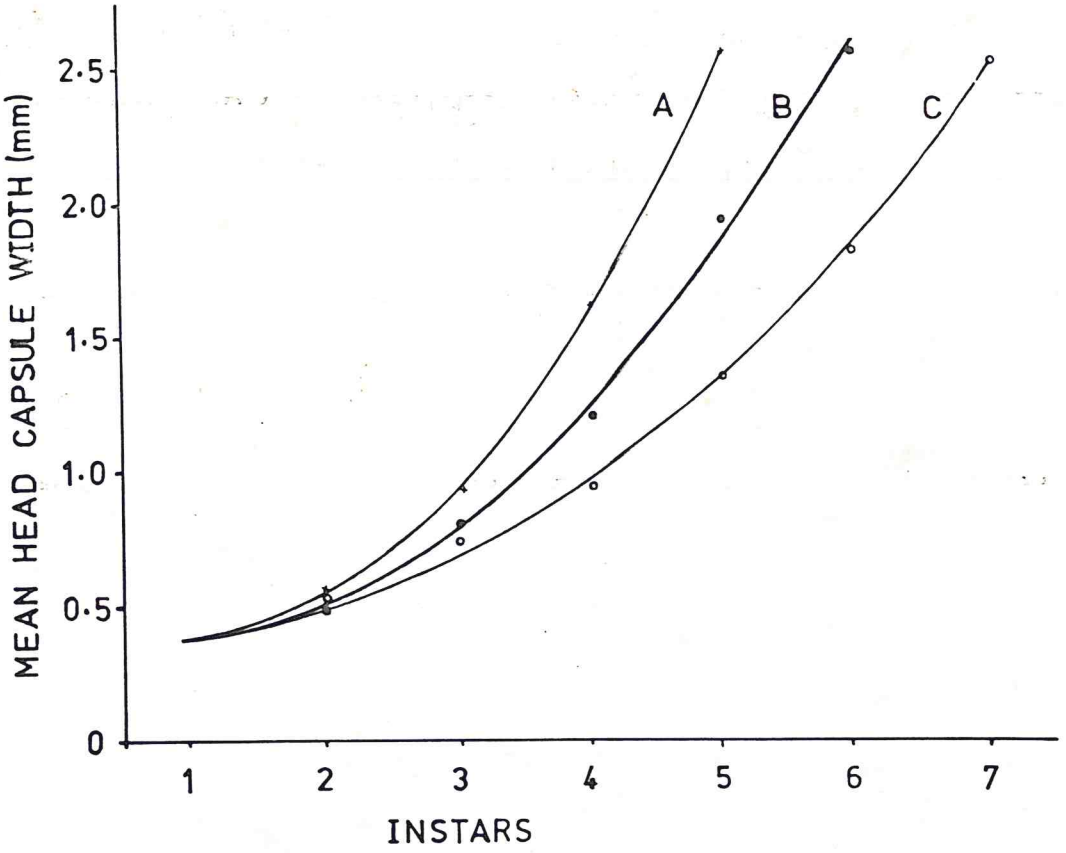
THE MEAN WIDTH OF HEAD CAPSULES (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SIX INSTARS AT 30°C AND 60% RH.

HOST PLANT	INSTAR	MEAN S.E.	RATIO
P. maximum	1	0.354 ± 0.008	1.376
	2	0.487 ± 0.006	1.975
	3	0.962 ± 0.013	1.509
	4	1.452 ± 0.017	1.344
	5	1.952 ± 0.018	1.296
	6	2.530 ± 0.015	
C. maranguensis	1	0.354 ± 0.008	1.619
	2	0.573 ± 0.007	1.523
	3	0.872 ± 0.022	1.844
	4	1.608 ± 0.29	1.361
	5	1.888 ± 0.003	1.128
	6	2.467 ± 0.020	
S. plicatilis	1	0.354 ± 0.008	1.653
	2	0.585 ± 0.007	1.520
	3	0.889 ± 0.009	1.459
	4	1.297 ± 0.017	1.447
	5	1.877 ± 0.021	1.356
	6	5.545 ± 0.016	

TABLE 60

THE MEAN DISTANCE BETWEEN THE FRONTAL SETAE (mm), STANDARD ERRORS AND INSTAR GROWTH RATIOS FOR LARVAE WITH SIX INSTARS AT 30°C AND 60% RH.

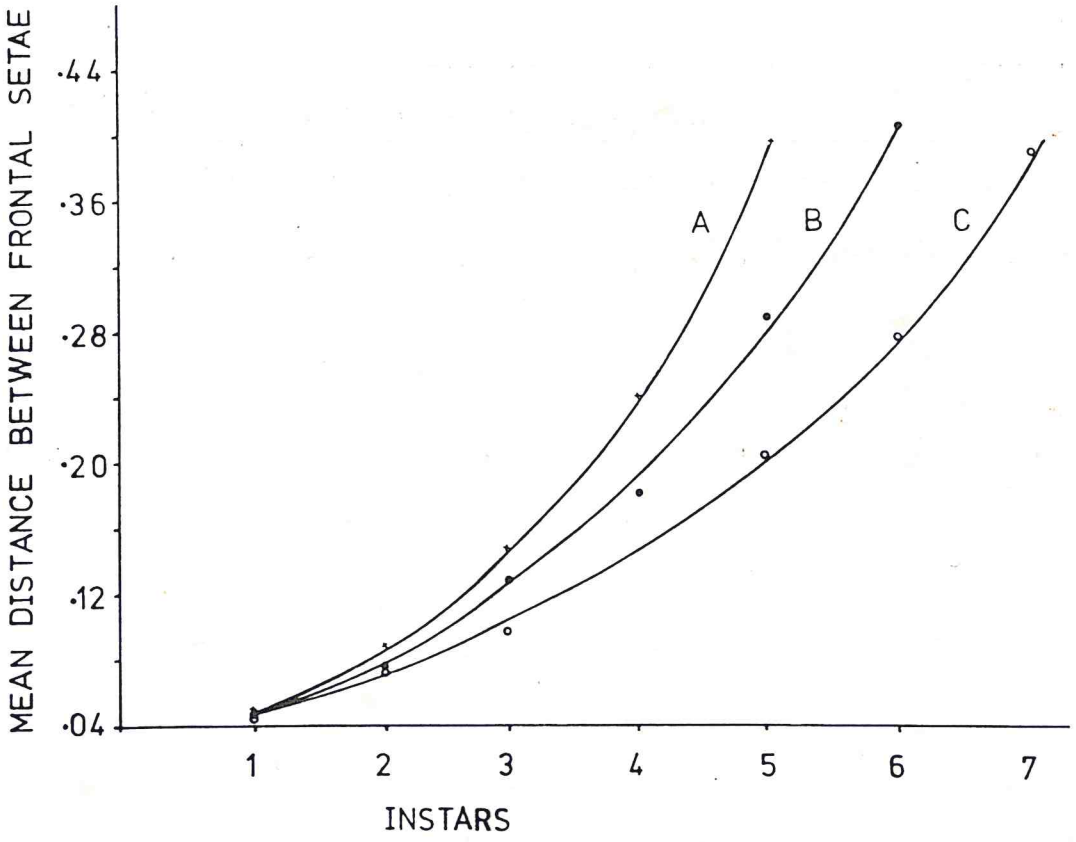
HOST PLANT	INSTAR	MEAN S.E.	RATIO
P. maximum	1	0.048 ± 0.0004	1.771
	2	0.085 ± 0.001	1.741
	3	0.148 ± 0.003	1.439
	4	0.213 ± 0.003	1.347
	5	0.287 ± 0.004	1.449
	6	0.416 ± 0.004	
C. maranguensis	1	0.048 ± 0.0004	2.042
	2	0.098 ± 0.002	1.459
	3	0.143 ± 0.002	1.755
	4	0.251 ± 0.001	1.398
	5	0.351 ± 0.006	1.162
	6	0.408 ± 0.004	
S. plicatilis	1	0.048 ± 0.0004	1.938
	2	0.093 ± 0.002	1.473
	3	0.137 ± 0.002	1.387
	4	0.190 ± 0.004	1.484
	5	0.282 ± 0.004	1.468
	6	0.414 ± 0.005	



A – C.dactylon

B – P.maximum

C – S.plicatilis



A–C·dactylon B–P·maximum C–S·plicatilis

these measurements and instars is illustrated in Figures 13 and 14. The lines are for the pooled data and the points are for the larvae reared at 25°C and 70% RH. The rate of increase depended on the number of instars through which the larvae passed irrespective of the host plant on which they fed, and temperature and humidity conditions under which they were kept.

Figures 15 and 16 present the histograms of head capsule widths and the distances between the frontal clypeal setae of larvae collected from outbreak sites at Athi River and Lukenya. Most of the larvae collected from Athi River were in the final larval instar with only a very small proportion of larvae in the younger instars. On the other hand only about half of the larvae collected from Lukenya were in the final instar stage and the rest represented various younger stages. Thus the Lukenya larvae showed a greater diversity in size than the Athi River sample. These observations suggested that since Athi River received adequate rainfall there was good growth of grass and the larvae had plenty of high quality food, whereas food was inadequate both in quantity and quality at Lukenya due to poor rainfall. There was, thus synchronisation in larval development at Lukenya than at Athi River.

TABLE 61

THE RELATION BETWEEN THE HEAD CAPSULE WIDTH AND INSTARS

(a) THE POPULATION WHICH WENT THROUGH FIVE LARVAL INSTARS

TEMPERATURE AND RH.	HOST PLANT	REGRESSION COEFFICIENT (b)	r^2
25°C 70% RH.	C. dactylon	0.218	0.999
	Z. mais	0.219	0.991
	P. clandestinum	0.213	0.997
30°C 60% RH.	C. dactylon	0.215	0.996
	Z. mais	0.216	0.994
	P. clandestinum	0.218	0.996

(b) THE POPULATION WHICH WENT THROUGH SIX LARVAL INSTARS

TEMPERATURE	HOST PLANT	REGRESSION COEFFICIENT (b)	r^2
18°C 80% RH.	C. dactylon	0.177	0.991
	Z. mais	0.177	0.990
	P. clandestinum	0.173	0.987
25°C 70% RH.	P. maximum	0.179	0.994
30°C 60% RH.	P. maximum	0.179	0.976
	C. maranguensis	0.178	0.969
	S. plicatilis	0.170	0.999

(c) THE POPULATION WHICH WENT THROUGH SEVEL LARVAL INSTARS

TEMPERATURE AND R.H.	HOST PLANT	REGRESSION COEFFICIENT (b)	r^2
18°C80% RH.	P. maximum	0.142	0.986
	C. maranguensis	0.1413	0.991
	S. plicatilis	0.139	0.987
25°C 70% RH.	S. plicatilis	0.139	0.997

(d) THE RELATIONSHIP BETWEEN HEAD CAPSULE WIDTHS AND INSTARS

NUMBER OF LARVAL INSTARS	REGRESSION COEFFICIENT (b)	S.E.	r^2
5	0.216	0.0044	0.995
6	0.178	0.0031	0.986
7	0.140	0.0032	0.990

(e) THE REGRESSION EQUATIONS FOR RELATIONSHIPS

NUMBER OF INSTARS	EQUATIONS
5	$y = 2.335 \pm 0.216x$
6	$y = 2.397 \pm 0.178x$
7	$y = 2.445 \pm 0.140x$

Where y is the $\log_{10}$ of the head capsule width (μ) and x the number of the larval instar.

TABLE 62

THE RELATION BETWEEN THE DISTANCE BETWEEN THE FRONTAL SETAE OF THE CLYPEUS AND INSTARS

(a) THE POPULATION WHICH WENT THROUGH FIVE LARVAL INSTARS

TEMPERATURE AND R.H.	HOST PLANT	REGRESSION COEFFICIENT (b)	r^2
25°C 70% RH.	C. dactylon	0.229	0.990
	Z. mais	0.231	0.989
	P. clandestinum	0.227	0.985
30° 60% RH.	C. dactylon	0.228	0.999
	Z. mais	0.221	0.983
	P. clandestinum	0.221	0.994

(b) THE POPULATION WHICH WENT THROUGH SIX LARVAL INSTARS

TEMPERATURE AND R.H.	HOST PLANT	REGRESSION COEFFICIENT	r^2
18° 80% RH.	C. dactylon	0.184	0.997
	Z. mais	0.182	0.980
	P. clandestinum	0.178	0.977
25°C 70%RH.	P. maximum	0.187	0.996
30°C 60%RH.	P. maximum	0.184	0.982
	C. maranguensis	0.187	0.963
	S. plicatilis	0.179	0.986

(c) THE POPULATION WHICH WENT THROUGH SEVEN INSTARS

TEMPERATURE AND R.H.	HOST PLANT	REGRESSION COEFFICIENT	r^2
18°C 80" RH.	P. maximum	0.146	0.962
	C. maranguensis	0.147	0.982
	S. plicatilis	0.149	0.979
25°C 70" RH.	S. plicatilis	0.149	0.997

(d) THE RELATIONSHIP BETWEEN THE DISTANCE BETWEEN THE FRONTAL CLYPEAL SETAE AND INSTARS

NUMBER OF LARVAL INSTARS	REGRESSION COEFFICIENT	S.E.	r^2
5	0.226	0.0060	0.990
6	0.183	0.0042	0.980
7	0.148	0.0044	0.980

(e) THE REGRESSION EQUATIONS FOR RELATIONSHIPS

NUMBER OF ONSTARS	EQUATIONS
5	$y = 1.500 \pm 0.226x$
6	$y = 1.561 \pm 0.183x$
7	$y = 1.598 \pm 0.148$

where y is the logarithm_{10} of distance between the frontal clypeal setae and x is the larval instar.

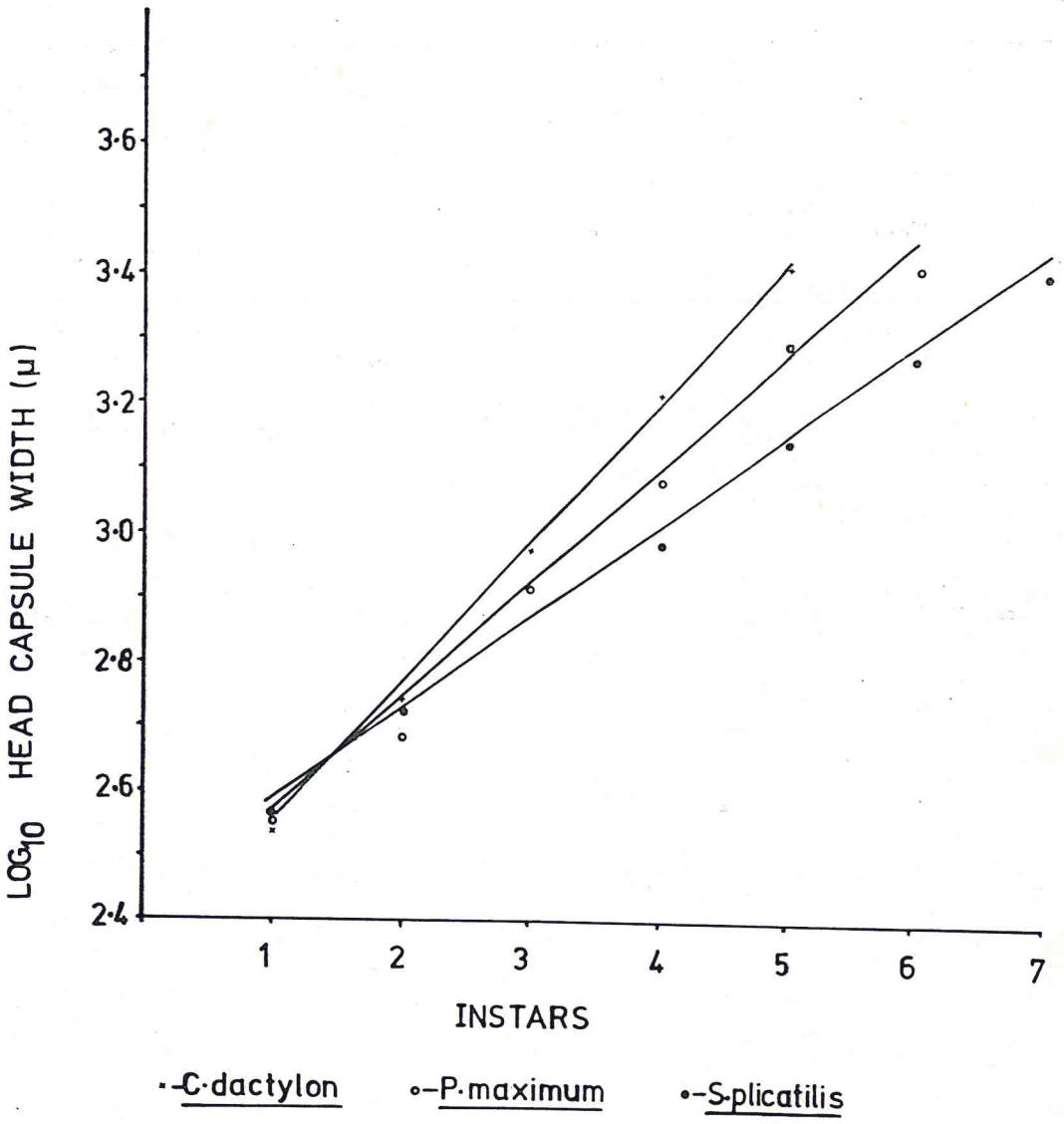
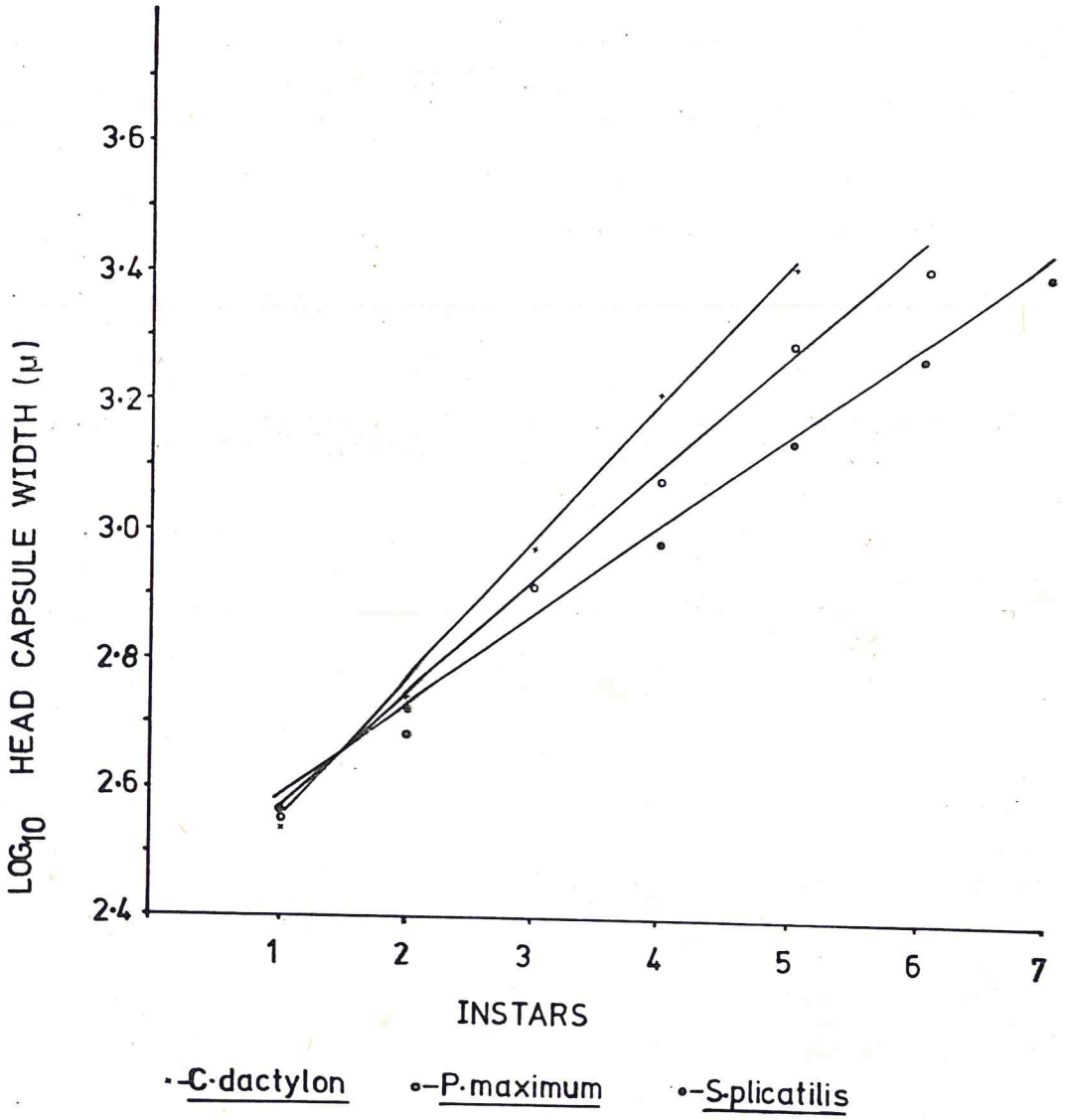
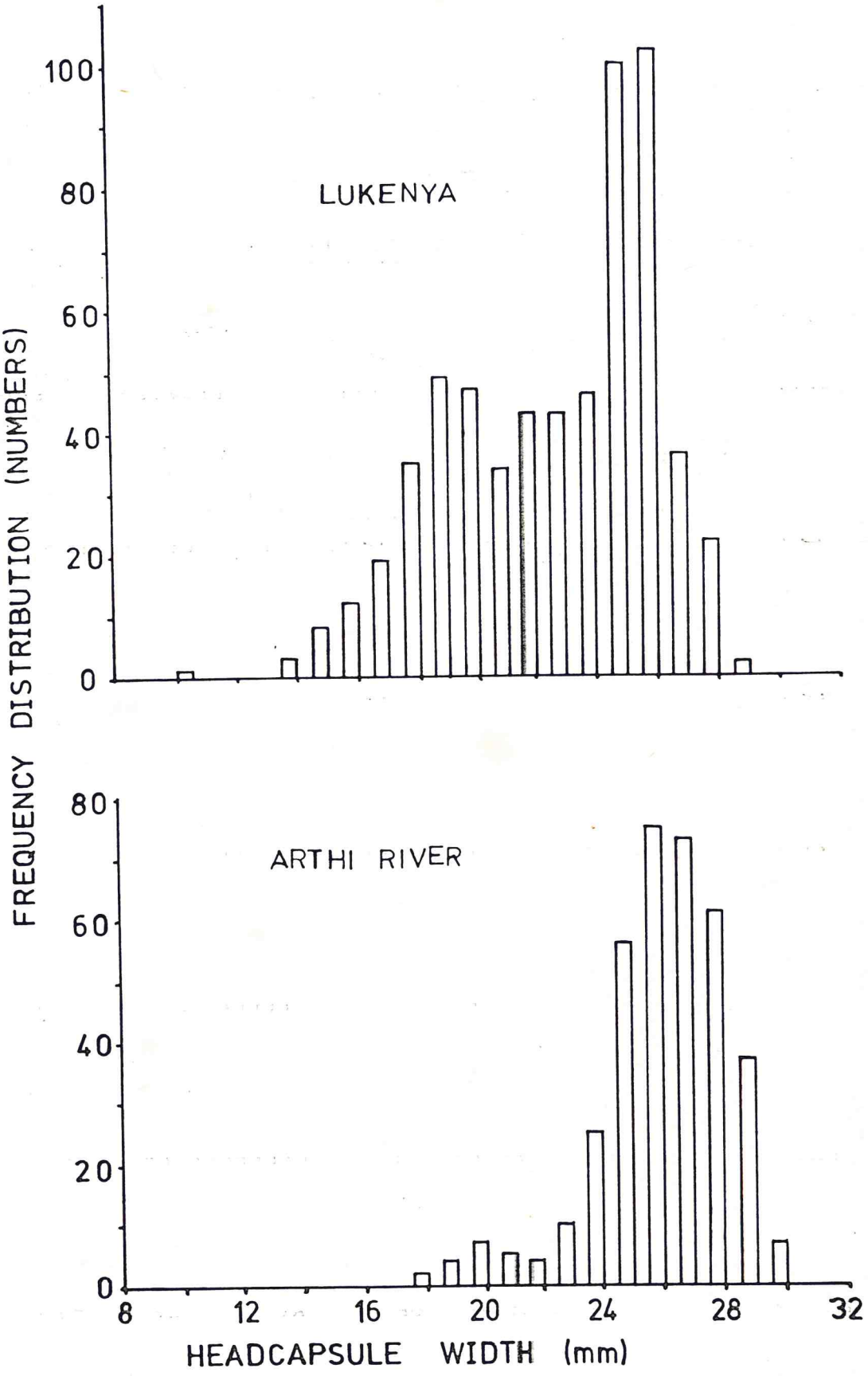
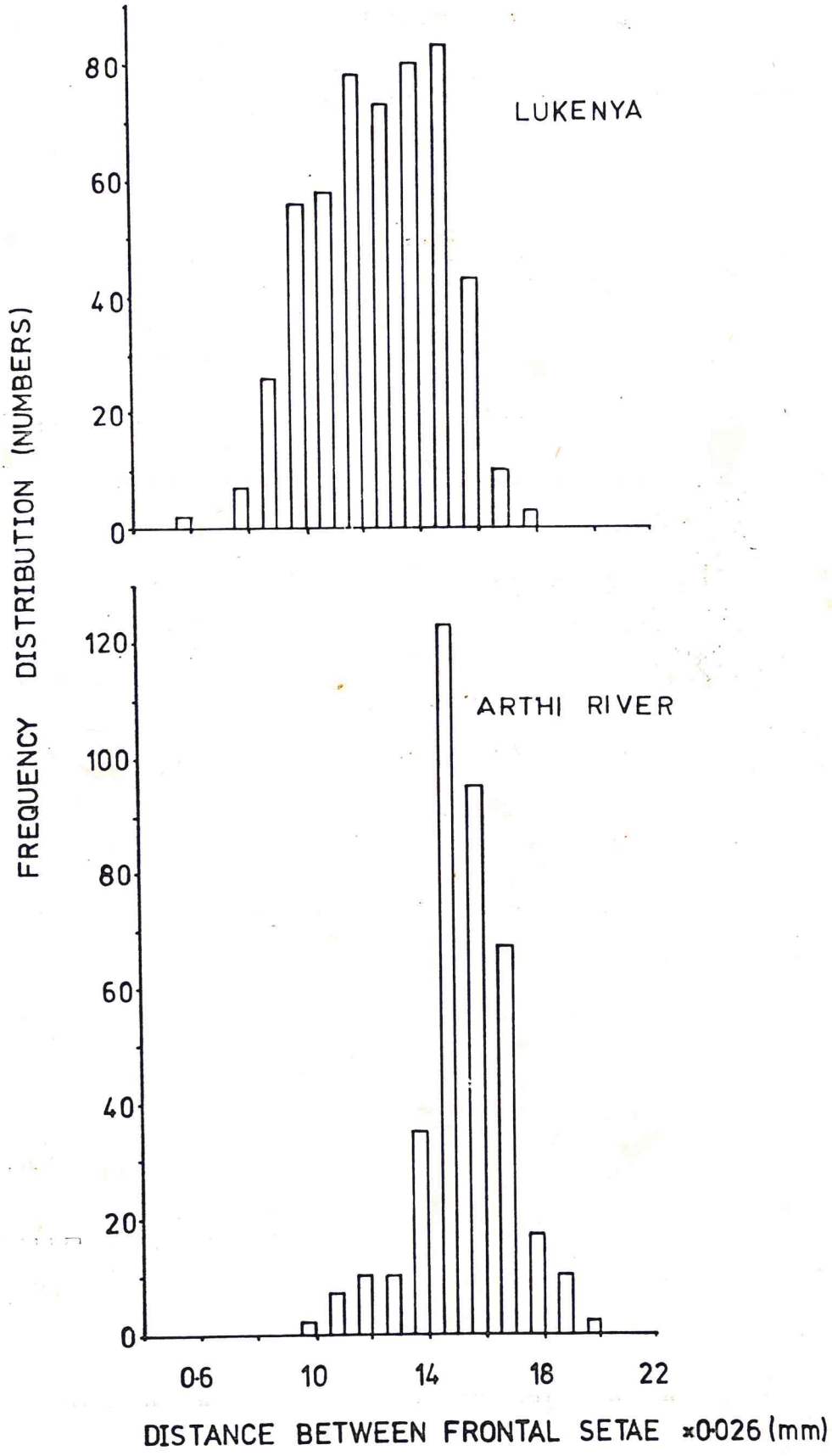

LOG10 HEAD CAPSULE WIDTH (μ)
3·6
3·4
3·2
3·0
2·8
2·6
2·4
1
2
3
4
5
6
7
INSTARS
·–C·dactylon
∘–P·maximum
•–S·plicatilis

FIGURE 14


3·6
3·4
3·2
3·0
2·8
2·6
2·4
LOG10 HEAD CAPSULE WIDTH (μ)
1
2
3
4
5
6
7
INSTARS
·–C·dactylon
o–P·maximum
•–S·plicatilis

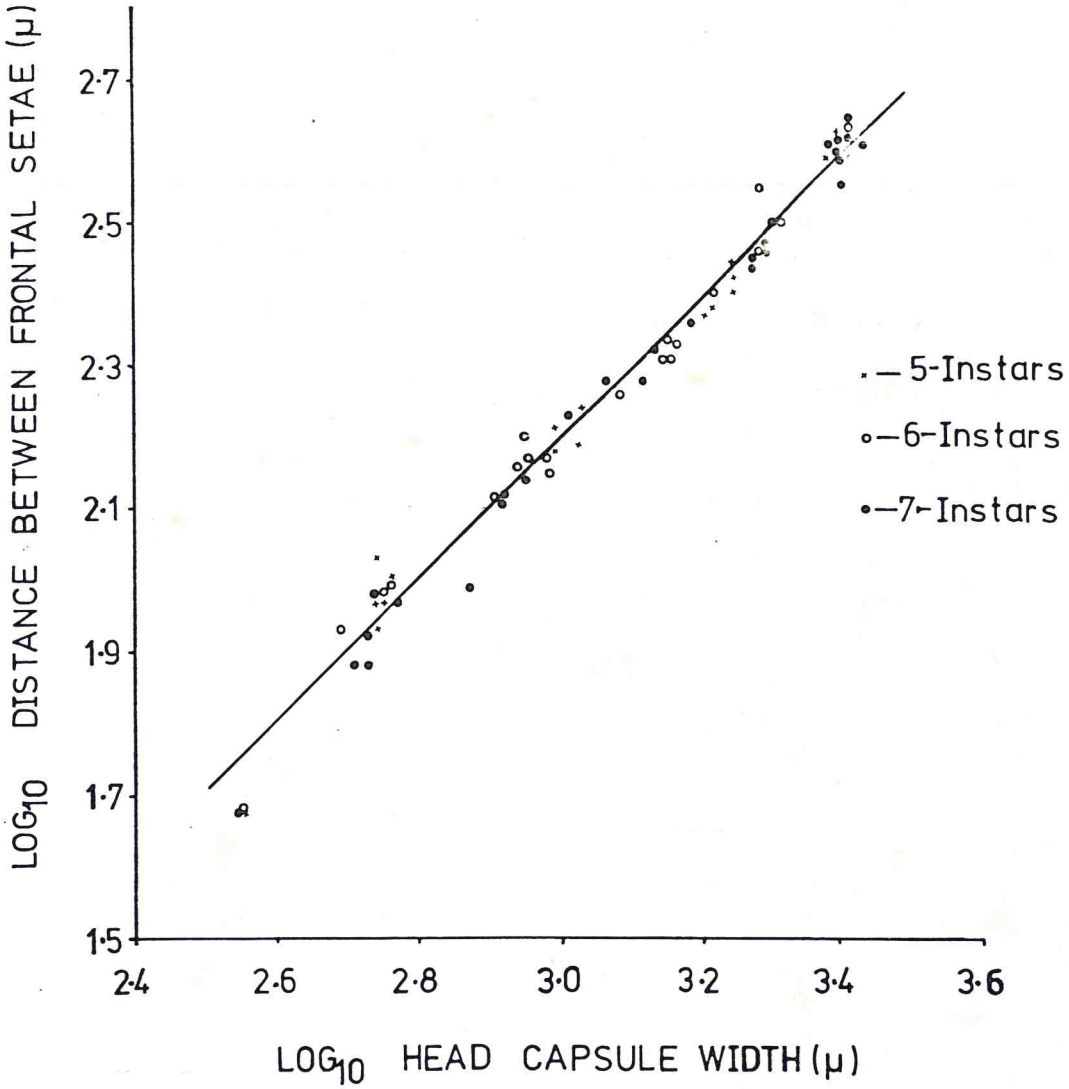

LUKENYA
ARTHI RIVER
FREQUENCY DISTRIBUTION (NUMBERS)
HEADCAPSULE WIDTH (mm)
0
20
40
60
80
100
8
12
16
20
24
28
32


LUKENYA
ARTHI RIVER
FREQUENCY DISTRIBUTION (NUMBERS)
0
20
40
60
80
0
20
40
60
80
100
120
0·6
10
14
18
22
DISTANCE BETWEEN FRONTAL SETAE ×0·026 (mm)

As expected the logarithm_{10} of the distance between the frontal setae is highly correlated to the logarithm_{10} of the head capsule width (Figure 17). The relationship between them can be expressed as

$$y = 0.99x - 0.76$$

where y is the logarithm_{10} of the distance between the frontal setae and x the logarithm_{10} of the head capsule width.


LOG10 DISTANCE BETWEEN FRONTAL SETAE (μ)
2·7
2·5
2·3
2·1
1·9
1·7
1·5
2·4
2·6
2·8
3·0
3·2
3·4
3·6
LOG10 HEAD CAPSULE WIDTH (μ)
5-Instars
6-Instars
7-Instars

DISCUSSION

Larvae fed on C. dactylon, Z. mais and P. clandestinum went through the least number of instars in any given condition of temperature and humidity. S. plicatilis produced larvae which went through the highest number of instars and those fed on P. maximum passed through an intermediate number of instars. C. maranguensis was not included in the experiment at 25°C and 70% RH. and so it was not possible to group it with either S. plicatilis or P. maximum. On the basis of the number of larval moults, C. dactylon, Z. mais and P. clandestinum provided the optimum food requirements. S. plicatilis, P. maximum and C. maranguensis could support larval growth but the larvae required additional moults before reaching the final instar. Larvae reared on the most suitable food plants went through an additional moult at 18°C and 80% RH. and those reared on S. plicatilis, considered most unsuitable, reduced the number of instars by one at 30°C and 60% RH. These observations suggest that temperature and humidity conditions as well as food have an effect on the number of instars.

S. plicatilis was the toughest of the host plant species used although both P. maximum and C. maranguensis were quite tough whereas C. dactylon, Z. mais and P. clandestinum were quite tender. Young C. dactylon had the highest nitrogen level and young Z. mais and P. clandestinum had much higher nitrogen content than S. plicatilis and P. maximum (Chapter 3). Reduced feeding and or less nutrition has been reported to produce supernumerary moults in several lepidopterous larvae (Kellog and Bell, 1904; Decker, 1931; Gaines and Campbell, 1935).

The present results suggest that host plants which are too tough or nutritionally deficient, and sub-optimal temperature effectively reduce the amount of nutritive food consumed per unit time and the larvae are thus effectively under partial starvation. Larvae of Bombyx mori need a minimum time for feeding and reaching the ultimate size before moulting into the next instar (Bouniol, 1938). Since a larva has to ingest a minimum quantity of food for a certain minimum of time to undergo a certain minimum growth before it can moult into the next instar, under continuously harsh conditions the successive instars start undersized and in order to attain the size of the final instar it has

to go through extra moults. If the conditions improve, it could probably make up for the handicap by growing fast and reaching the usual instar size. Intermittent starvation of larvae of Lymantria dispar through the first twenty days of larval life reduces growth but the starved larvae can catch up with the controls if their feeding is not restricted during the subsequent forty days (Kopec, 1924). Starvation of Manduca sexta larvae at weights less than 4.0g leads to formation of larval pupal intermediates whereas starvation at 5.0g and above has no effect on the nature of the moult (Nijhout and Williams, 1974). The starvation of newly ecdysed fifth instars at varying lengths of time prior to feeding induces an extra larval moult (Jones et al., 1980). The occurrence of an additional moult suggests that starvation prevents the normal decrease in hemolymph Juvenile Hormone (J.H.) titre during the final instar (Nijhout and Williams, 1974; Nijhout, 1975b) and that the programme of metamorphosis initiated at the time of ecdysis to the fifth instar (Nijhout, 1975a) can be altered by starvation.. In some species starved insects moult successively several times with specimen getting smaller all the time (Beck, 1971).

In the present study, the mean head capsule width of the fourth instar, S. exempta larvae reared on C. dactylon at 30°C and 60°C RH. was comparable to that for the fourth instar larvae on C. maranguensis (Tables 53 and 59). Those on C. dactylon had slightly smaller head capsule widths than their counterparts on Z. mais and P. clandestinum but they were able to catch up with them at the fifth instar stage. The larvae on C. maranguensis on the other hand, had an additional moult before they attained the size of the last instar larvae in the group which passed through five instars. Thus an undersized instar can be compensated for by the larva growing faster if it is on a suitable host plant. On an unsuitable host plant species which can barely support growth, the small instar size may be compensated for by an increase in the number of instars. The production of additional instars under unfavourable conditions is very common and is known to occur in grasshoppers, Lepidoptera and other insects (Wigglesworth, 1940). Manduca sexta induced to moult at a smaller size, by starvation during part of the fourth instar, produced fifth instars (normally the last) with undersized head capsules, and often formed one or two supernumerary instars with head capsules larger than in the normal fifth instars

(Nijhout, 1975a). Since the larvae reared on S. plicatilis and P. maximum produced smaller pupae (Chapter 1) than the larvae on C. dactylon, Z. mais and P. clandestinum the results suggest that even though the larvae on poorer host plants attain the normal or greater head capsule dimensions by supernumerary moults, they produce smaller pupae.

Outbreaks of African armyworm larvae resulting from moths migrating down the winds which bring rain (Brown et al., 1969), coincide with the new flush of growth of wild grasses and cultivated cereals. The young as well as the subsequent instars therefore feed on abundant quantities of tender and nutritious feed. Under such optimal conditions growth is fast and synchronous and larvae probably go through only five instars. As the season advances or if the subsequent rainfall is too low for good growth, the grass will increasingly become too tough particularly to the early instars resulting in undersized subsequent instars.

Similarly conditions in the habitats differ with respect to host plant species diversity and physical and chemical properties of host plants in different habitats. Different groups of larvae are therefore exposed to food with different qualities and are thus

likely to vary in development patterns. The more variable the environmental conditions are, the more the variation in larval size. This is demonstrated by the larval populations from Athi River and Lukenya. Athi River larvae were exposed to abundant high quality food and showed a much better synchrony in larval growth than the Lukenya larvae which were feeding on inferior food as a result of poor rains.

SUMMARY

The number of moults through which larvae of the African armyworm pass varies with the host plants and temperature. On less nutritious host plants or under sub-optimal temperature conditions larvae may moult into undersized subsequent instars. Such instars may catch up with the normal ones if favourable conditions return, otherwise they have to undergo supernumerary moults. The head capsule size or the distance between the frontal clypeal setae is independent of the temperature and host plant. In an outbreak situation the growth of larvae is more synchronous when plenty of tender grass folliage is available than under drought conditions.

CHAPTER 6

WING SIZE VARIATION IN SPODOPTERA EXEMPTA (WALK.) IN RELATION TO SOME HOST PLANTS AND OUTBREAKS SITES

INTRODUCTION

Moths of the African armyworm, Spodoptera exempta (Walk,) caught in traps placed where there had previously been larval outbreaks and where adult moths were emerging show geographical differences in mean wing lengths of the populations (Aidley and Lubega, 1979). These authors have also reported systematic differences in mean wing lengths of moth populations caught in light traps at stations in East Africa during 1973 - 1974.

A similar study involving populations of four generations at a site in Zimbabwe has also shown that populations vary with regard to their mean forewing lengths (Rose, 1975). The moths found before the beginning of the widespread outbreak of caterpillars in January were smaller than those of any of the three sunsequent generations. Those which emerged in February were larger than those of the second generation produced in March but those of the third generation produced in

April and May were the largest. The size of the locally produced moths ranked in the same order as the sizes of their preceding caterpillars.

The differences observed between populations could not be explained by long standing-geographical variation since a study of allele frequency of six polymorphic isoenzymes (Den Boer, 1978) has concluded that moth populations in East Africa mix between themselves and with those in southern Africa. However, environmental factors during larval development may cause differences in adult size. The rate of larval development, for example, is affected by temperature (Hattingh, 1941) and would possibly affect the adult size as instances of increased temperature resulting in smaller insects are known (Uvarov, 1931).

The size of the final instar of S. exempta is reduced by crowding (Matthee, 1946) which is expected to reduce by crowding (Matthee, 1946) which is expected to reduce the size of the adult similarly. Isolated larvae of S. littoralis produce adults with longer forewings than those from crowded larvae (Hodjat, 1970).

Small size in some insects can also result from insufficient food quantity or quality (Trager, 1953). This has not been investigated in the African armyworm whose outbreaks are so strongly associated with new growth of both cereals and pasture grasses, the quality and quantity of which may differ with species and weather conditions in the outbreak sites. The effect of food on wing size is investigated in this chapter by measuring the wing size of moths developing from larvae which fed on known host plants both in the laboratory and under outbreak conditions.

MATERIALS AND METHODS

Larvae of S. exempta were reared separately on maize, Zea mais L.; stargrass, Cynodon dactylon (L) Pers.; Kikuyu grass, Pennisetum clandestinum Chiov.; Panicum maximum Jacq.; and Setaria plicatilis (Hochst) Hack. until they pupated. First instar larvae were obtained from an insectary culture maintained at 25°C and 70% RH. the larvae of which were reared on Z. mais and adults on 10% solution of sucrose. Larvae were kept in groups of twenty in one pound kilner jars covered with a nine centimetre Whatman filter paper held in position by a plastic or metallic ring. There were

ten jars for each grass species. All the larvae were kept in an insectary under the above mentioned conditions of temperature and humidity. Fresh foliage from an experimental plot was supplied daily. The cut ends of grass leaves were kept under water in one ounce plastic vials stoppered with cotton wool to minimize wilting.

During the armyworm outbreak season of 1979 pupae were collected from Athi River, Kajiado and Taveta. Those dug out from sites on which C. dactylon was the dominant grass species, were kept in the laboratory at ambient temperature and humidity until adults emerged.

Moths produced by both the insectary larvae and the outbreak pupae were weighed within twelve hours of emergence and after producing meconium well formed wings were detached. The scales fringing the tips of wings were removed and the distance between the base and tip of each wing was measured using a vernier steel caliper rule reading to 0.05mm. Each wing was then spread on a glass slide with a small drop of water and placed on the stage of a drawing tube at a magnification

of sixty. Magnified outlines of wings were drawn on graph paper and actual wing areas were worked out from the drawings.

The rainfall figures for Athi River, Taveta and Kajiado were obtained from Warden's camp, Taveta Water Supply Department and Kajiado D.C.'s Office respectively.

RESULTS

The mean forewing lengths of both female and male moths reared in the insectary are presented in Table 63. The analyses of variance were performed separately on the forewings of females and males using the method for unequal sample sizes (Sokal and Rholf, 1969).

At the 5% level of significance, the mean lengths of forewings of male moths reared on Z. mais were significantly longer than that for moths reared on the other host plant species. Those for males reared on C. dactylon and P. clandestinum were in the same order of magnitude although the mean forewing length of males reared on the latter host plant was not significantly

TABLE 63

FOREWING LENGTHS (mm) OF MOTHS REARED IN THE INSECTARY GROUPED ACCORDING TO THE HOST PLANTS

HOST PLANT	MALES		FEMALES		DIFFERENCES BETWEEN SEXES
	n	Mean S.D.	n	Mean S.D.	(P)
Z. mais	92	14.53±0.91	102	15.22±0.91	<0.001
C.dactylon	84	14.12±0.91	69	14.94±1.01	<0.001
P.clandestinum	24	13.83±1.10	32	15.00±1.10	0.001
P. maximum	23	13.51±1.21	16	13.81±0.92	NS
S. plicatilis	39	13.04±1.11	35	13.6±1.12	<0.05

different from the mean forewing lengths for males reared on S. plicatilis and P. maximum. Moths developing from larvae reared on C. dactylon had significantly longer mean forewing length than those developing from larvae on S. plicatilis and P. maximum.

The forewing lengths of females could be grouped into those of moths reared on S. plicatilis and P. maximum on the one hand and those of moths reared on P.clandestinum, C. dactylon and Z. mais on the other. The latter moths had significantly longer mean forewing length than the former. Except for the group reared on P. maximum, the females had significantly longer forewing lengths than males.

The mean hindwing lengths of both females and males fall into two significantly different groups ($P<0.05$) consisting of moths developing from larvae reared on S. plicatilis and P. maximum on the one hand and those developing from larvae reared on Z. mais, C. dactylon and P. clandestinum on the other. The means within each group were not significantly different from each other. The results are presented in Table 64. Females had significantly longer hindwing lengths than males in the groups reared on Z. mais, C. dactylon and P. clandestinum but this was not significant in the groups reared on P. maximum and S. plicatilis.

TABLE 64

HINDWING LENGTHS (mm) OF MOTHS REARED ON DIFFERENT GRASS SPECIES IN THE INSECTARY GROUPED ACCORDING TO THE HOST PLANTS

HOST PLANT	MALES		FEMALES		DIFFERENCES BETWEEN SEXES
	n	MEAN S.D	n	MEAN S.D.	(P)
Z. mais	92	11.21±0.69	102	11.81±1.00	<0.001
C.dactylon	81	11.13±0.61	64	11.59±0.68	<0.001
P.clandestinum	30	11.14±0.68	36	11.58±0.70	<0.01
P. maximum	22	10.60±0.59	15	10.70±0.60	NS
S.plicatilis	39	10.34±0.67	33	10.54±0.65	NS

Two way analyses of variance were performed on fore and hindwing lengths of both sexes of moths that emerged from pupae collected from armyworm outbreak sites. The variation in forewing lengths due to the site of origin of the pupae was highly significant ($P<0.001$) (Table 65). In both sexes the forewings of moths from Athi River were significantly longer than those of moths from Taveta ($P<0.001$). Similar comparisons between Taveta and Kajiado moths showed that the former had significantly longer forewings than the latter ($P<0.001$). The variance between sexes was found to be highly significant ($P<0.001$). In all the three localities females had longer forewings than males.

The variation in hindwing lengths due to sites and sexes were both highly significant ($P<0.001$). The Athi River moths had longer hindwings than Taveta moths ($P<0.05$ for females and $P<0.01$ for males).. The wing-lengths of the latter were longer than those for the moths from Kajiado ($P<0.05$ for females and $P<0.001$ for males). As in the case of forewing lengths, the females had longer hindwings than the males (Table 66).

TABLE 65

THE FOREWING LENGTHS (mm) OF MOTHS FROM PUPAE COLLECTED FROM C. DACTYLON STANDS IN ARMYWORM OUTBREAK SITES

LOCALITY	FEMALES		MALES		DIFFERENCES BETWEEN SEXES
	Mean	S.D.	MEAN	S.D.	(P)
Athi River	16.56	± 0.64	15.91	± 0.63	<0.001
Taveta	15.83	± 0.75	15.20	± 0.58	<0.001
Kajiado	15.22	± 0.70	14.67	± 0.54	<0.01

TABLE 66

THE HINDWING LENGTHS (mm) OF MOTHS FROM PUPAE COLLECTED FROM C. DACTYLON STANDS IN ARMYWORM OUTBREAK SITES

LOCALITY	FEMALES		MALES		DIFFERENCES BETWEEN SEXES
	Mean	S.D.	Mean	S.D.	(P)
Athi River	12.62	± 0.51	12.23	±	<0.01
Taveta	12.25	± 0.66	11.88	±0.33	<0.05
Kajiado	11.80	± 0.73	11.41	± 0.37	<0.05

The forewing areas (Table 67) in both sexes varied with the host plants ($P<0.001$). Males reared on S. plicatilis and P. maximum had smaller forewing areas than moths from larvae reared on the other host plant species ($P<0.05$). Similar results were obtained for females except that the females reared on Z. mais had significantly larger forewing areas than those reared on P. clandestinum.

Significant variations also existed in the hindwing areas ($P<0.01$ for males and $P<0.001$ for females) (Table 68). Males reared on S. plicatilis had the smallest wing areas which differed significantly from the wing areas of males reared on C. dactylon and Z. mais. The wing areas for males reared on P. maximum and P. clandestinum were intermediate and were not significantly different from either group. The results for female wing areas were similar except that the hindwing areas for females reared on P. maximum were significantly smaller than those for females reared on Z. mais.

When total wing areas were considered (Table 69) significant variations were found between the means ($P<0.001$). This was expected, as variations were

detected both in the forewing and the hindwing areas. Male moths from larvae reared on S. plicatilis had the smallest total wing areas but were not significantly different from those of moths developing from larvae reared on P. maximum. The wing areas of the latter moths were also not significantly different from those of moths reared on P. clandestinum. However, moths formed from larvae reared on the latter host plant had significantly larger wing areas than moths reared on S. plicatilis ($P<0.05$). Differences between wing areas of moths from larvae which were fed on P. clandestinum, C. dactylon and Z. mais were not significant. Similar results were obtained for females, except that the wing areas for moths developing from larvae fed on P. maximum were significantly smaller than those of moths developing from larvae fed on P. clandestinum. The wing areas for moths which emerged from outbreak pupae were not worked out.

Differences in wing dimensions between sexes

The differences in wing lengths and areas due to sex were tested using the t-test. The results are presented in Tables 63 to 69 and show that females, had longer and larger wings than males. The differences

TABLE 67

FOREWING AREAS (mm^2) OF INSECTARY REARED MOTHS

HOST PLANT	FEMALES		MALES		DIFFERENCES BETWEEN SEXES
	n	Mean S.D.	n	Mean S.D.	(P)
Z. mais	99	132.70±17.51	90	124.79±19.54	<0.01
C. dactylon	67	125.00±18.74	82	115.26±17.84	<0.01
P.clandestinum	35	125.27±22.30	37	115.82±18.80	<0.05
P. maximum	16	103.25±13.84	23	103.50±19.57	NS
S.plicatilis	34	113.28±20.99	38	99.12±15.84	<0.05

TABLE 68

HINDWING AREAS (mm^2) OF INSECTARY REARED MOTHS

HOST PLANT	FEMALES		MALES		Differences Between Sexes
	n	Mean S.D.	n	Mean S.D.	(P)
Z. mais	100	111.09±20.37	88	98.42±17.17	<0.001
C. dactylon	63	107.56±18.47	81	100.02±20.79	<0.05
P. clandestinum	36	106.71±20.64	31	95.03±17.87	<0.05
P. maximum	15	94.93±19.71	23	92.87±17.36	NS
S. plicatilis	33	90.65±19.82	38	86.16±14.79	NS

TABLE 69

THE TOTAL WING AREAS (mm^2) OF INSECTARY REARED MOTHS

HOST PLANT	FEMALES		MALES		DIFFERENCES BETWEEN SEXES
	n	Mean + S.D.	n	Mean + S.D.	(P)
Z. mais	100	244.67 ± 30.67	94	221.07±34.32	<0.001
C.dactylon	64	232.56 ± 27.52	86	215.86±38.95	<0.01
P.clandestinum	35	231.94 ± 25.62	31	212.55±30.75	<0.01
P. maximum	15	204.00 ± 29.43	23	198.41±34.58	NS
S. plicatilis	33	203.36 ± 37.80	38	184.92±27.49	NS

were more pronounced in the moths developing from larvae reared on P. clandestinum, C. dactylon and Z. mais than in moths developing from larvae reared on P. maximum and S. plicatilis;

The ratio (mg/mm^2) between the emergence weight (mg) and the total wing area (mm^2).

The variations in wing areas and lengths made it desirable to work out the ratios of emergence weight to total wing area (Table 70). The results showed that there were significant differences between the treatments ($P<0.01$ for males and $P<0.001$ for females) due to the smaller ratio for both males and females developing from larvae fed on S. plicatilis. Males fed on this host plant had significantly lower ratio than the moths developing from larvae on C. dactylon and Z. mais ($P<0.05$). Apart from these, the ratios between the emergence weights and wing areas seem to give same values irrespective of the host plant and the differences between sexes are not significant. However, the large wing area standard deviations suggest that the wing area determination is a large source of error.

The relevance of rainfall

The coincidence of the arrival of the rains and moths at an outbreak site (e.g. Brown et al., 1969) is a vital adaptation for the survival of the early stages at the high densities characteristic of this species. The survival and quality of the late instars depends on the sustained growth of nutritious food plants. Thus the success of a larval outbreak is very much related to the rainfall totals and the rainfall distribution over the outbreak period. In the present study the rainfall for January and February 1979 was considered as the larvae in all the three localities had pupated by the end of February. The rainfall totals and the number of rainy days for each of the sites of larval outbreak are presented in Table 71.

The midpoint pupation dates were 22nd, 25th and 27th of February, 1979 for Taveta, Athi River and Kajiado respectively. The dates of pupation and the rainfall pattern for the outbreak sites suggest that the Taveta outbreak began at the end of January whereas both Athi River and Kajiado outbreaks began a few days later at the beginning of February.

TABLE 70

THE EMERGENCE WEIGHT/WING AREA RATIOS (mg/mm^2) FOR INSECTARY MOTHS

HOST PLANT	FEMALES		MALES	
	n	Mean ± S.D.	n	Mean ± S.D.
Z. mais	85	0.39 ± 0.08	84	0.39 ± 0.09
C. dactylon	56	0.39 ± 0.07	75	0.37 ± 0.07
P.clandestinum	31	0.38 ± 0.06	28	0.36 ± 0.07
P. maximum	13	0.34 ± 0.05	18	0.35 ± 0.09
S.plicatilis	29	0.31 ± 0.07	36	0.32 ± 0.05

TABLE 71

THE RAINFALL TOTALS (mm) AND THE NUMBER OF RAINY DAYS DURING THE OUTBREAK PERIOD

LOCALITY	JANUARY		FEBRUARY	
	TOTAL	NUMBER OF DAYS	TOTAL	NUMBER OF DAYS
Kajiado	44	4	56	7
Taveta	20	5	43	8
Athi River	45.8	5	250.2	11

TABLE 72

DAILY RAINFALL (mm) AT KAJIADO, ATHI RIVER AND TAVETA FOR JANUARY AND FEBRUARY, 1979

DATE	KAJIADO		TAVETA		ATHI RIVER	
	JANUARY	FEBRUARY	JANUARY	FEBRUARY	JANUARY	FEBRUARY
1	-	2.6	-	1.5	-	4.8
2	-	2.4	-	1.5	-	30.0
3	-	29.2	-	-	-	2.8
4	-	-	-	10.1	-	3.5
5	-	10.5	-	-	-	-
66	-	-	0.6	18.1	-	-
7	-	-	-	-	-	-
8	-	-	-	-	-	-
9	-	-	-	-	-	65.5
10	-	-	0.6	2.6	-	3.3
11	-	-	-	-	-	-
12	-	7.8		-	-	7.8
13	-	-	-	-	-	-
14	-	-	-	-	-	-
15	-	-	-	-		-
16	11.2	-	-	-		-
17	3.0	-	-	-	-	-
18	-	1 9	-	2.6	-	38.2
19	-	2.2	-	-	-	56.0
20	-	-	-	-	-	-
21	-	-	-	2.6	-	-
22	-	-	-	4.0	-	37.3
23	-	-	-	-	-	-
24	-	-	-	-	1.5	-
25	-	-	5.0	-	1.4	-
26	-	-	-	-	2.9	1.0
27	-	-	0.7	-	-	-
28	-	-	-	-	-	-
29	23.4		14.0		16.0	
30	6.4		-		23.0	
31	-	-	-			

At Kajiado most of the rain fell at the onset of the armyworm outbreak and except on 12th of February there was not much rain for much of the larval outbreak. The total rainfall at Taveta was lower than it was at Kajiado but was better distributed over the period of the larval infestation. The heavy rainfall that fell at Taveta at the end of January stimulated germination of grass whose growth was sustained by the heavy rains which fell on the fourth and fifth of February. The armyworm outbreak at Athi River experienced by far the heaviest and better distributed rainfall which lead to better growth of grasses. The rainfall distribution pattern for January and February, 1979 is presented in Table 72.

DISCUSSION

Wing measurements of both insectary and outbreak moths showed significant variations. The forewing lengths of both female and male moths developing from larvae reared on Z. mais were significantly longer than those for the other moths. Larvae which fed on S. plicatilis developed into moths with the shortest and

the smallest wings. Significant differences in wing size were also found between moths from the three field infestations. Moths from Athi River had the longest while those from Kajiado had the shortest wings although the larvae from which they developed fed mainly on C. dactylon in all the sites.

In S. exempta the size of the final larval instar is known to be reduced by high larval density (Matthee, 1946) which could also result in reduction of the adult size. In the related Spodoptera littoralis isolated larvae develop into adults with longer forewings than those developing from crowded larvae (Long and Zaher, 1958, Long, 1959). In the present study, the larval densities in all the treatments were lowest during the last instar as a result of larval mortality. Since larval mortality was more severe in larvae reared on S. plicatilis and P. maximum (Chapter 1), the densities of the final instar larvae were lower on these grass species than on Z. mais, C. dactylon and P. clandestinum. Consequently larval crowding cannot fully account for the reduction in wing size of the resulting moths.

The rate of larval development is greatly influenced by temperature (Hattingh, 1941), and it is possible that

the size of moths is similarly affected. Since the insectary larvae were reared under constant temperature, this influence can be ruled out but it might have applied to the field outbreak populations examined. Also, genetic differences could not explain the differences in wing size of the insectary moths since the larvae were obtained from the same parents.

Outbreaks of the African armyworm are strongly associated with the beginning of the rain and therefore young growths of host plants (Brown et al., 1969) such that young larvae feed on tender and highly nutritious food. The late instars, however, consume comparatively larger quantities of food which can be available only if good growth of grass is sustained by adequate rainfall. Under poor rainfall conditions, not only will the food quantities be insufficient but the grass leaves will also be too tough for the larvae. The differences found in wing size between populations which fed on C. dactylon in different sites probably resulted from differences in the quality and quantity of the host plant.

Athi River received the heaviest rainfall during the time of larval outbreak but there were also

dry periods which made it ideal for good growth of C. dactylon. There was, therefore, plenty of high quality food for the larvae. Although Taveta received the lowest rainfall, it was more evenly distributed over the period of larval development than at Kajiado where the total rainfall was higher. This could have resulted in a better growth of C. dactylon at Taveta than at Kajiado and consequently in the Taveta larvae developing into larger moths with larger wings than did the Kajiado larvae.

The insectary moths varied in their wing size probably as a result of the differences in nutritional quality of the different grass species; for instance, C. dactylon has the highest nitrogen content (Chapter 3). It is possible that the larvae which fed on foliage with higher nitrogen content and possibly primary plant substances produced larger moths with longer and larger wings. The texture of leaves could also affect the consumption rate of larvae and it may be that S. plicatilis and P. maximum are coarser and less succulent than C. dactylon, P. clandestinum and Z. mais, and are therefore consumed at lower rates.

The emergence weight/wing area ratio was smaller for male moths reared on S. plicatilis than for those reared on Z. mais and C. dactylon but no other differences were detected either between the males or females. The differences between the sexes were not significant indicating little difference in wing loading.

SUMMARY

Larvae reared on Z. mais and C. dactylon produced large moths whereas those reared on S. plicatilis and P. maximum produced small moths. There is little or no differences in wing loading and therefore the wing length and area are related to moth size. The differences in moth size are probably related to the nutritional quality of the host plants as well as their texture.

The wing size of moths developing from field pupae appear to be related to the local rainfall at the time of larval development as this influences the quantity and quality of the food plants.

CHAPTER 7

SIZE INDICES IN THE AFRICAN ARMYWORM, SPODOPTERA EXEMPTA (WALK.)

INTRODUCTION

A last instar larvae of the African armyworm can consume 200 mg. dry mass of leaves of Z. mais in the course of the instar (Brown and Odiyo, 1968) and large outbreaks of larvae can force farmers to replant although the second crop can fail as a result of inadequate rainfall. In order to give farmers an early warning, a forecasting service has been in operation in East Africa since 1969 (Betts et al., 1970; Odiyo, 1979). The weekly forecast uses nightly moth catches from a network of light traps supplimented by pheromone traps (Rose and Odiyo, 1979) together with reports of larval outbreaks and meteorological information. Increasing levels of moth catches in traps have been found to be followed by increased probability of larval infestation occurring two to four weeks later at distances up to 200 km from the traps (Betts and Odiyo 1968). Moths are capable of flying over such distances (Aidley, 1974).

The accuracy of the foresasting system has been improved by mapping the known infestations, recording the age of the larvae and the probable duration of development in each of the affected areas in order to estimate dates of moth emergence (Betts, 1976; Rose. 1975). When these estimates are considered in relation to the moth trap catches, they help in identifying possible links between successive generation (Betts et al., 1969).

The accuracy in identifying those links could be further improved if moths from various infestations can be identified by some characters or qualities. Since in the course of migration moth populations originating from various geographical localities mix not much help is expected from genetic variation (den Boer, 1978). Wing lengths of moth populations, however, vary with the sites and time of infestation (Aidley and Lubega, 1979). The variation in wing size is related to the host plant (Chapter 6) larval density (Matthee, 1946) and the prevailing temperature particularly during the final instar (Hattingh, 1941; Hodjat, 1970).

In this chapter some relationships between the forewing size and pupal weight have been worked out and may be useful in estimating weights at pupation and emergence for samples of [illegible] populations with intact

MATERIALS AND METHODS

First instar larvae obtained from an insectary culture maintained at 25°C and 70% R.H. were reared on maize, Zea mais L.; Star grass, Cynodon dactylon (L.) Pers.; Kikuyu grass, Pennisetum clandestinum Chiov.; Guinea grass, Panicum maximum Jacq. and Setaria plicatilis (Hochst.) Hack. until pupation. They were kept in one pound kilner jars in groups of twenty and ten larvae per jar in five replicates. Each jar was covered with a nine centimetre Whatman filter paper held in position by a plastic or metallic ring and kept in the insectary under the above mentioned conditions. Fresh foliage leaves from an experimental plot were washed in running water and drained were supplied daily in sufficient quantities. The cut ends of leaves were kept under water in one ounce plastic vials which were plugged with cotton wool to minimise wilting. The jars were washed with soap, sterilized in 5% sodium hydroxide and 2% tetramide solution for twelve and six hours respectively, rinsed in running water and heat sterilized at 100°C.

Pupae were sexed and weighed within twelve hours of pupation. The thorax width and the straight line distance medially running on the ventral side of the pupa

from its anterior end to the posterior margin of its thorax were measured using a dissecting microscope equipped with a micrometric occular. Measurements were made on thirty pupae of each sex for each of the five host plants and the products of the measurements were regressed on pupal weights.

Only the perfectly formed moths were killed by chloroform vapour and weighed within twelve hours of emergence and after voiding meconium. Their forewings were detached, tightly held flat between two microscopic slides and their lengths and widths were measured using a dissecting microscope fitted with a micrometric occular. The length was taken at its maximum from the base to the tip excluding the tegula and the fringe whereas width was taken perpendicular to the length axis along a line passing through the area of maximum width. Magnified outlines of wings were then drawn on a square paper with the help of a drawing tube and the actual wing areas were worked out. The products of wing lengths and widths were regressed on the pupal weight and on wing areas.

The results were compared using multiple regression analysis (Snedecor, 1956).

RESULTS

The relation between forewing lengths and pupal weight

The forewing length was found to be linearly related to the pupal weight (Table 73) and in all cases the regressions were highly significant ($P<0.001$). Female moths developing from larvae reared on *C. dactylon*, *Z. mais* and *P. maximum* had slighly greater regressions than males although the differences were not significant and there were no such differences between sexes in moths reared on *P. clandestinum* and *S. plicatilis*. Furthermore, there were no significant differences between moths with regard to the larval host plants. In most cases about 50% of the variation in wing lengths were accounted for by variation in pupal weights as deduced from the coefficients of determination (r^2). The smaller moths reared on *S. plicatilis* had much lower coefficients of determination. Table 74 shows the mean pupal weights; emergence weights and forewing lengths of the moths. Larvae reared on *S. plicatilis* developed into the smallest pupae and moths. The regression for pooled data for each sex were also highly significant ($P<0.001$) and that for

females, though not significant, was slighly greater than that for males. The regression based on the pooled data for both sexes was highly significant ($P<0.001$). Whether sexes are examined individually or together the coefficient of determinations (r^2) lay between 49% and 50%. The relationship between the forewing length and the pupal weight for individuals reared on C. dactylon is presented in Figure 18 and those reared on S. plicatilis in Figure 19.

The regression line for the mean forewing length (y) on the mean pupal weight (x) is

$$y = 0.028x + 9.95 \text{ for all females}$$
$$y = 0.027x + 9.57 \text{ for all males}$$
$$Y = 0.027x + 9.78 \text{ for both sexes}$$

The relation between the product (mm) of maximum forewing length (mm) and the maximum forewing width (mm) and pupal weight (mg)

The product of the maximum forewing length and the maximum wing width was linearly related to the pupal weight . (Table 25). Individual regressions were

TABLE 73

REGRESSION OF FOREWING LENGTH (mm) ON PUPAL WEIGHT (mg)

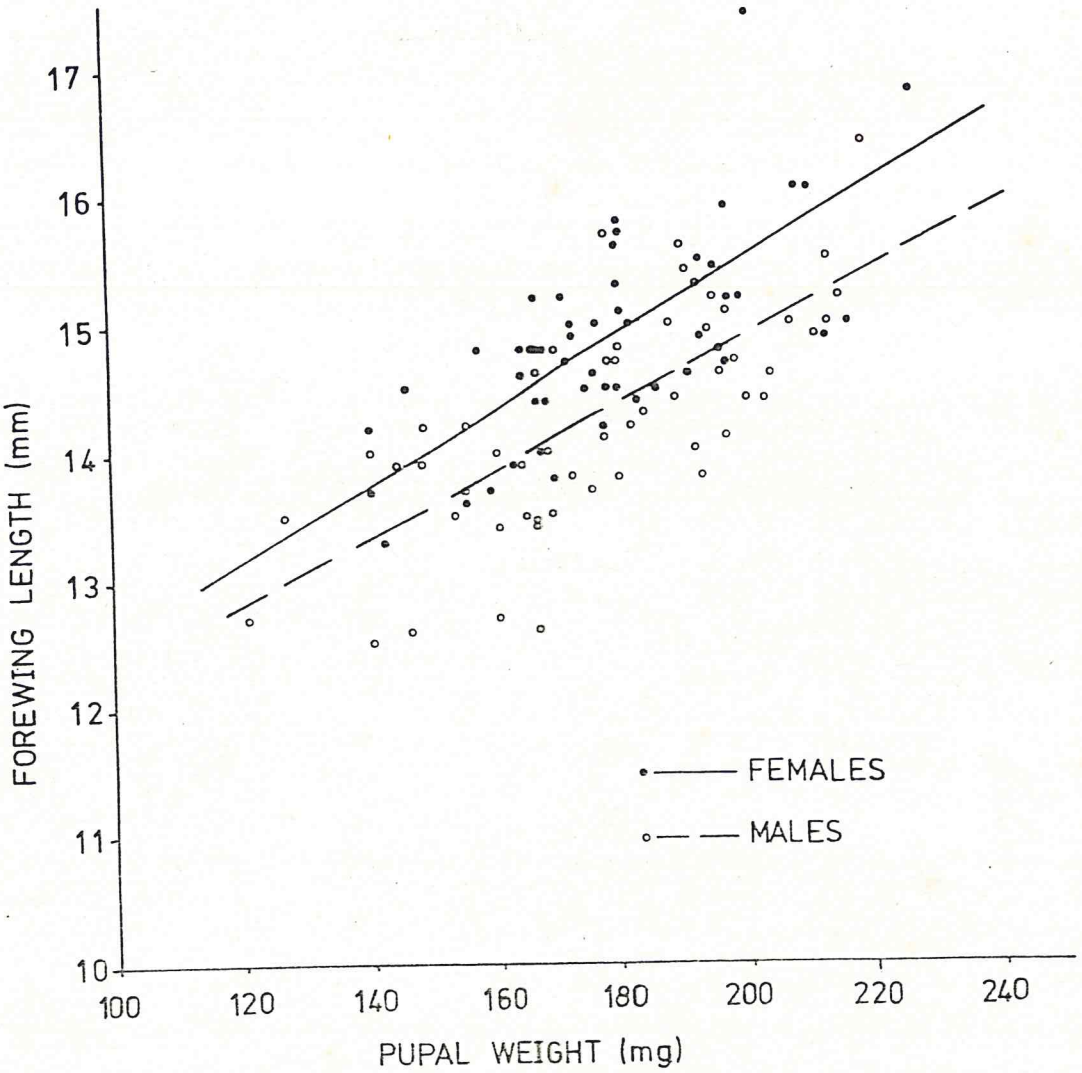
(N = 60 IN EACH CASE)

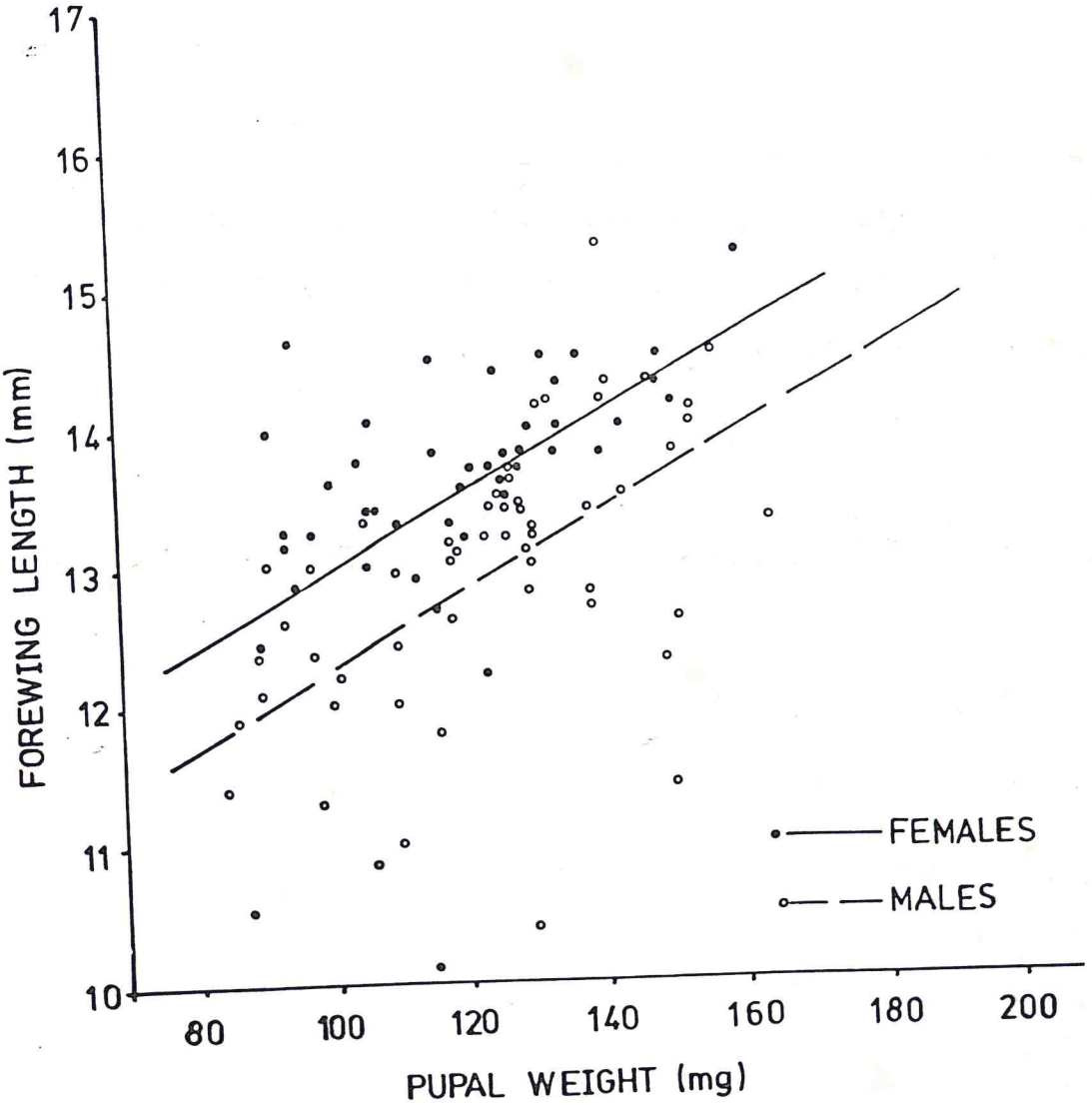
HOST PLANT	SEX	REGRESSION (b ± SE)	r	r^2	a
Z. mais	Females	0.029 ± 0.004	0.70	0.50	9.88
	Males	0.027 ± 0.003	0.74	0.55	9.52
C. dactylon	Females	0.029 ± 0.004	0.73	0.53	9.69
	Males	0.026 ± 0.003	0.72	0.51	9.71
P. clandestinum	Females	0.029 ± 0.004	0.71	0.50	9.60
	Males	0.029 ± 0.003	0.76	0.58	9.45
P. maximum	Females	0.027 ± 0.003	0.78	0.60	10.24
	Males	0.025 ± 0.004	0.69	0.47	9.57
S. plicatilis	Females	0.028 ± 0.004	0.67	0.44	10.20
	Males	0.028 ± 0.006	0.58	0.33	9.49
Pooled data	Females	0.028 ± 0.002	0.71	0.50	9.95
	Males	0.027 ± 0.002	0.69	0.49	9.57
	Both sexes	0.027 ± 0.001	0.70	0.49	9.78

TABLE 74

MEAN PUPAL AND WEIGHTS AT EMERGENCE (mg) AND FOREWING LENGTHS (mm) USED IN REGRESSION OF FOREWING LENGTH AND EMERGENCE WEIGHT ON PUPAL WEIGHT (N = 60 IN EACH CASE

HOST PLANT	SEX	PUPAL WEIGHTS (MEAN ± S.E.)	EMERGENCE WEIGHT (MEAN±S;E.)	FOREWING LENGTH (MEAN ± S.E.)
Z. mais	Females	181.81 ± 1.49	91.67 ± 1.55	15.20 ± 0.10
	Males	172.14 ± 3.14	80.68 + 2.21	14.25 ± 0.12
C. dactylon	Females	178.71 ± 2.44	90.96 ± 1.65	14.92 ± 0.10
	Males	176.35 ± 3.04	84.27 ± 1.79	14.25 ± 0.11
P.clandestinum	Females	185.50 ± 2.94	85.33 ± 1.57	14.91 ± 0.12
	Males	176.94 ± 2.80	77.18 ± 1.70	14.33 ± 0.10
P. maximum	Females	134.93 ± 2.68	67.09 ± 1.81	13.84 ± 0.09
	Males	150.49 ± 3.69	64.12 ± 1.55	13.41 ± 0.14
S. plicatilis	Females	120.75 ± 2.58	57.41 ± 1.36	13.61 ± 0.11
	Males	121.96 ± 2.58	55.44 ± 1.45	12.87 ± 0.13


17
16
15
14
13
12
11
10
FOREWING LENGTH (mm)
100
120
140
160
180
200
220
240
PUPAL WEIGHT (mg)
FEMALES
MALES


17
16
15
14
13
12
11
10
FOREWING LENGTH (mm)
80
100
120
140
160
180
200
PUPAL WEIGHT (mg)
FEMALES
MALES

highly significant ($P<0.001$) with females, except those developing from larvae reared on S. plicatilis, having higher regressions than males though the differences between sexes were not significant. It was also shown that the regressions for samples reared on the five grass species were not significantly different from each other. Pooled data for each sex gave highly significant regressions ($P<0.001$) with the regressions for females being slightly but not significantly higher than the regression for males. Similarly the regression for the pooled data for both sexes was highly significant ($P<0.001$).

The regressions for the smaller moths developing from larvae reared on P. maximum and S. plicatilis had lower coefficients of determination than the regression for the larger moths developing from larvae on Z. mais, C. dactylon and P. clandestinum. Even so, the coefficients of determination obtained by regressing the product of forewing lengths and forewing width on pupal weight were much higher than those obtained by regressing forewing lengths on pupal weight. On this basis the product of forewing length and the forewing width taken at their maximum is a more accurate index of pupal weight than the

TABLE 75

THE REGRESSION OF THE PRODUCT (mm^2) OF THE FOREWING LENGTH (mm) AND THE MAXIMUM WING WIDTH (mm) ON PUPAL WEIGHT (mg) (N = 30 IN EACH CASE)

HOST PLANT	SEX	REGRESSION (b ± S.E.)	r	r^2	a
Z. mais	Females	0.240 ± 0.017	0.094	0.88	40.31
	Males	0.239 ± 0.019	0.92	0.85	35.74
C. dactylon	Females	0.242 ± 0.019	0.92	0.85	39,27
	Males	0.238 ± 0.023	0.89	0.80	36.77
P. clandestinum	Females	0.262 ± 0.020	0.93	0.86	37.28
	Males	0.226 ± 0.019	0.92	0.85	38.38
P. maximum	Females	0.270 ± 0.042	0.77	0.59	31.12
	Males	0.212 ± 0.029	0.91	0.65	40.74
S. plicatilis	Females	0.234 ± 0.037	0.76	0.58	38.71
	Males	0.272 ± 0.036	0.82	0.67	33.27
Pooled Data	Females	0.249 ± 0.010	0.90	0.81	37.28
	Males	0.236 ± 0.011	0.88	0.77	37.16
	Both sexes	0.243 ± 0.007	0.89	0.79	37.13

forewing length alone. The relationship between the product of the forewing length and width and the pupal weight is represented in Figure 20 for C. dactylon and Figure 21 for S. plicatilis.

The mean pupal weights and the mean products of forewing lengths and wing widths are given in Table 77. The pupae produced by larvae reared on Z. mais, C. dactylon and P. clandestinum are characterised by females being much larger than males. The differences between sexes in the smaller pupae produced by larvae reared on P. maximum and S. plicatilis were much smaller.

The regression line for the mean product of the forewing length and width on pupal weight (x)

$y = 0.249x + 37.28$ for all females

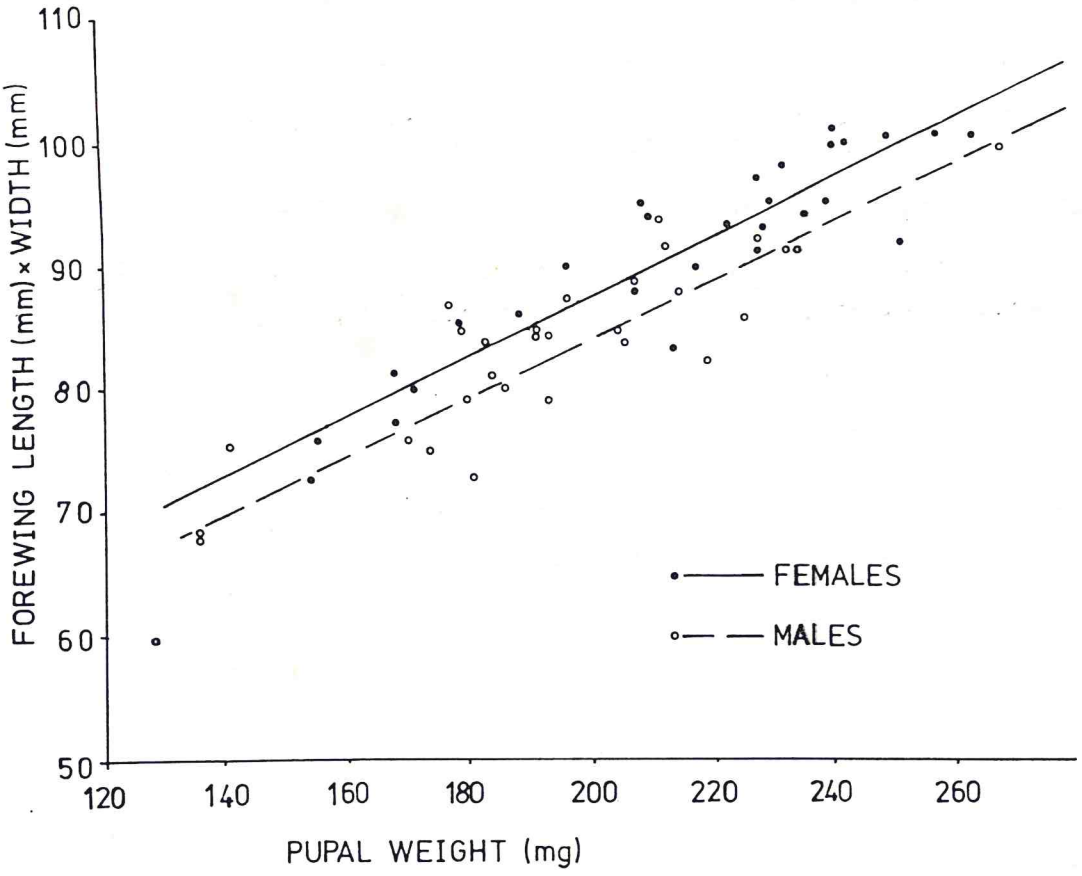
$y = 0.236x + 37.16$ for all males

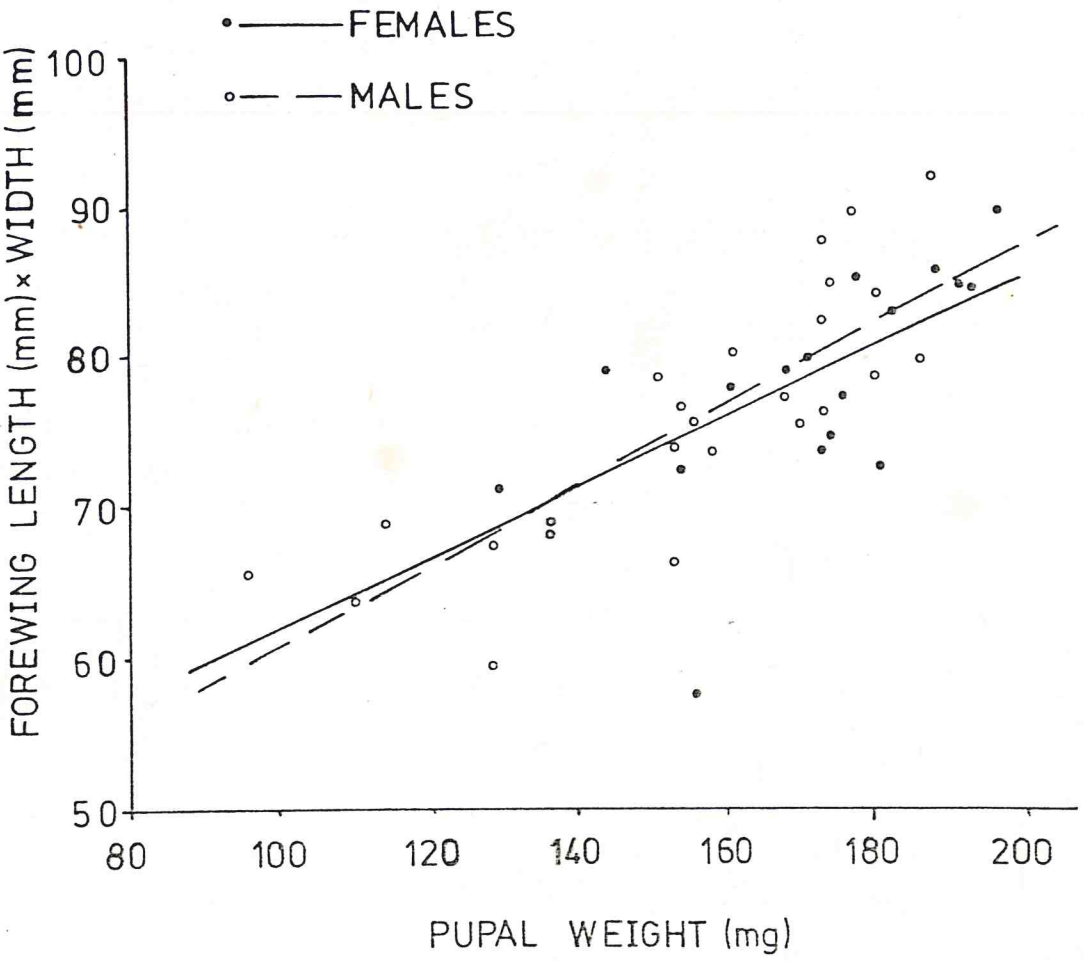
$y = 0.243x + 37.13$ for both sexes

TABLE 76

MEAN PUPAL WEIGHTS (mg) AND PRODUCTS (mm^2) OF THE MAXIMUM FOREWING LENGTHS (mm) AND WIDTHS (mm) (N = 30 IN EACH CASE)

HOST PLANT	SEX	PUPAL WEIGHTS (MEAN ± S.E.)	FOREWING LENGTHS (MEAN ± S.E.)	FOREWING WIDTH (MEAN ± S.E.)	FOREWING LENGTH x WIDTH (MEANS±S.E.)
Z. mais	Females	226.28 ± 7.36	15.53 ± 0.16	6.07 ± 0.07	94.61 ± 1.88
	Males	198.94 ± 4.59	14.18 ± 0.35	5.74 ± 0.05	83.37 ± 1.19
C. dactylon	Females	216.25 ± 5.83	15.53 ± 0.14	5.88 ± 0.05	91.56 ± 1.53
	Males	193.22 ± 5.84	14.52 ± 0.14	5.65 ± 0.07	82.70 ± 1.55
P. clandestinum	Females	206.64 ± 7.26	15.27 ± 0.04	5.96 ± 0.06	91.70 ± 2.05
	Males	182.45 ± 5.89	14.14 ± 0.14	5.58 + 0.07	79.68 ± 1.44
P. maximum	Females	168.38 ± 3.45	14.15 ± 0.13	5.59 ± 0.06	76.57 ± 1.21
	Males	165.02 ± 4.34	13.83 ± 0.12	5.59 ± 0.65	75.71 ± 1.14
S. plicatilis	Females	166.45 ± 2.96	14.11 ± 0.10	5.50 ± 0.04	77.59 ± 0.91
	Males	157.11 ± 4.29	13.78 ± 0.15	5.44 ± 0.07	75.93 ± 1.41


110
100
90
80
70
60
50
FOREWING LENGTH (mm) × WIDTH (mm)
120
140
160
180
200
220
240
260
PUPAL WEIGHT (mg)
FEMALES
MALES


FEMALES
MALES
FOREWING LENGTH (mm) × WIDTH (mm)
100
90
80
70
60
50
80
100
120
140
160
180
200
PUPAL WEIGHT (mg)

The Relation between the product (mm^2) of the maximum forewing length (mm) and width (mm) and the forewing area (mm^2)

The product of the forewing length and the forewing width taken at their maximum is linearly related to the wing area (Table 77). The resulting regressions for both female and male moths reared on C. dactylon were highly significant ($P<0.001$). Though not significant, the regression coefficiant for females were slighly lower than that for the males. The common regression (Figure 22) for each sexes was also highly significant ($P<0.001$) and the coefficients of determination was 95% in each case. Therefore if the width and the length taken at their maximum are known both the pupal weight and the forewing area can be estimated. The regression line for the relationship between the product (y) of the maximum forewing length and width on the forewing area x is

(a) $y = 1.419x - 0.32$ for females

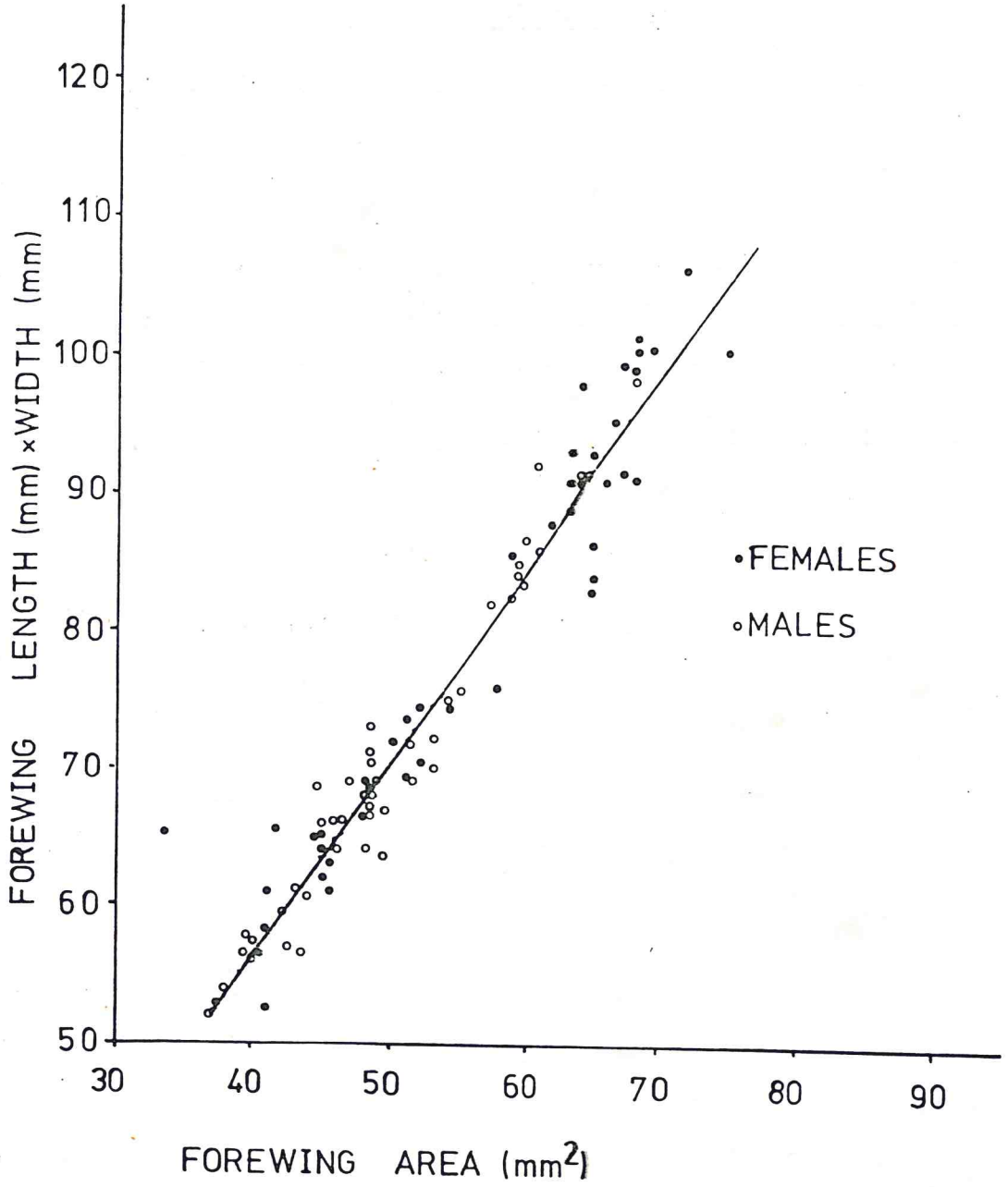
(b) $y = 1.441x - 1.62$ for males

(c) $y = 1.427x - 0.85$ for both sexes.

TABLE 77

THE REGRESSION OF THE PRODUCT (mm^2) OF THE MAXIMUM FOREWING LENGTH (mm) AND WIDTH (mm) ON FOREWING AREA (mm^2) (N = 50 FOR EACH SEX)

SEX	REGRESSION (b ± S.E.)	r	r^2	a
Females	1.419 ± 0.046	0.97	0.95	-0.32
Males	1.441 ± 0.049	0.97	0.95	-1.63
Both	1.427 ± 0.033	0.97	0.95	-0.85


120
110
100
90
80
70
60
50
30
40
50
60
70
80
90
FOREWING LENGTH (mm) × WIDTH (mm)
FOREWING AREA (mm²)
•FEMALES
◦MALES

The raw data for the forewing lengths and widths as well as areas for this relationship are presented in appendix 5.

The relation between the product (mm^2) of the thorax width (mm) and the straight line distance on the ventral side between the anterior pupal end and the posterior margin of the thorax

This product was found to be linearly related to the pupal weight (Table 78) and the regressions were highly significant ($P<0.001$). Figures 23 and 24 are regression lines for moth which developed from larvae reared on C. dactylon and S. plicatilis respectively. Though not significant the regressions for males were slightly higher than those for females. The differences between regressions were found to be insignificant and the regressions for pooled data for each sex were found to be highly significant ($P<0.001$). The regression for males was slightly higher than that for females and the regression for both sexes was also significant ($P<0.001$).

The coefficients of determination were reasonably high and therefore these dimensions can be used in estimating the pupal weight. The mean pupal weights and

TABLE 78

THE REGRESSION OF THE PRODUCT (mm^2) OF PUPAL THORAX WIDTH (mm) AND THE LENGTH (mm) FROM THE ... AL ANTERIOR TIP TO THE POSTERIOR MARGIN OF THE THORAX ON THE PUPAL WEIGHT (mg)

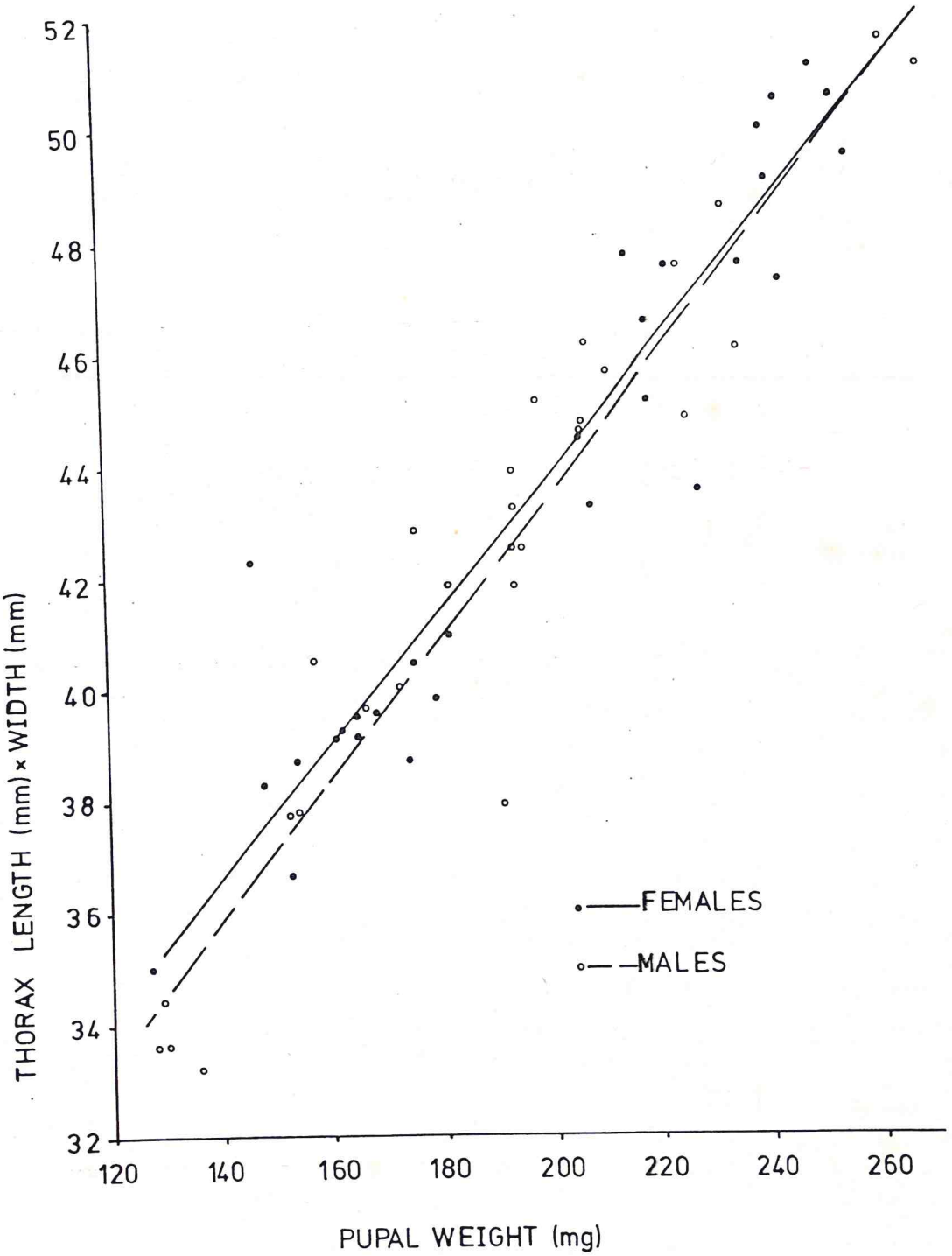
(N = 30 IN EACH CASE)

HOST PLANT	SEX	REGRESSION ± S.E.	r	r^2	a
Z. mais	Females	0.121 ± 0.006	0.96	0.93	19.41
	Males	0.139 ± 0.013	0.90	0.81	15.36
C. dactylon	Females	0.121 ± 0.008	0.94	0.89	19.66
	Males	0.127 ± 0.008	0.95	0.91	18.07
P. clandestinum	Females	0.151 ± 0.012	0.93	0.86	13.28
	Males	0.131 ± 0.016	0.85	0.71	17.82
P. maximum	Females	0.144 ± 0.019	0.82	0.68	15.00
	Males	0.148 ± 0.172	0.85	0.72	14.53
S. plicatilis	Females	0.153 ± 0.019	0.84	0.70	13.36
	Males	0.186 ± 0.016	0.91	0.83	9,30
Pooled data	Females	0.133 ± 0.005	0.92	0.84	16.82
	Males	0.138 ± 0.006	0.89	0.80	15.99
	Both sexes	0.135 ± 0.004	0.91	0.82	16.45

TABLE 79

MEAN PUPAL WEIGHTS (mg) AND PRODUCTS (mm^2) OF THE THORAX DIMENSTIONS USED IN CALCULATING THE REGRESSION IN TABLE 76 (N = 30 IN EACH CASE) ± S.E.

HOST PLANT	SEX	PUPAL WEIGHTS	THORAX LENGTH	THORAX WIDTH	DIMENTIONAL PRODUCT
Z. mais	Females	207.53 ± 7.40	9.12 ± 0.08	4.88 ± 0.06	44.61 ± 0.93
	Males	181.04 ± 5.82	8.88 ± 0.09	4.59 ± 0.005	40.60 ± 0.90
C. dactylon	Females	202.14 ± 6.76	9.09 ± 0.10	4.87 ± 0.06	44.17 ± 0.87
	Males	189.98 ± 6.56	9.01 ± 0.09	4.68 ± 0.06	42.27 ± 0.89
P. clandestinum	Females	195.95 ± 6.82	8.93 ± 0.12	4.79 ± 0.07	42.91 ± 2.22
	Males	180.69 ± 4.81	0.95 ± 0.09	4.63 ± 0.05	41.55 ± 0.75
P. maximum	Females	159 82 ± 3.64	8.52 ± 0.06	4.45 ± 0.05	38.00 ± 0.67
	Males	150.11 ± 3.96	8.46 ± 0.07	4.33 ± 0.05	36.67 ± 0.69
S. plicatilis	Females	141.87 ± 2.97	8.22 ± 0.06	4.26 ± 0.04	35.07 ± 0.54
	Males	130.95 ± 2.85	8.13 ± 0.06	4.12 ± 0.04	33.59 ± 0.58


52
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160
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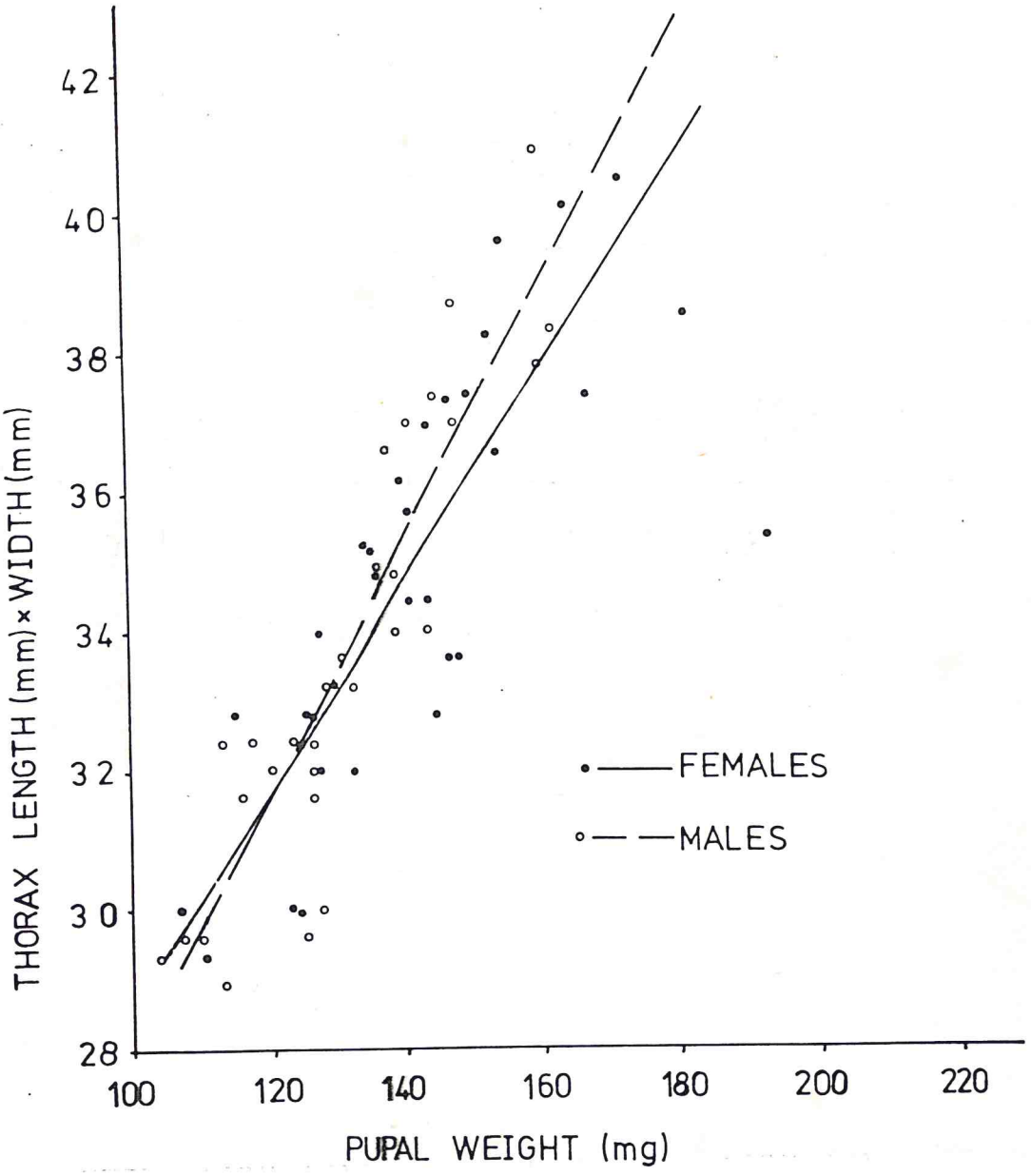
220
240
260
THORAX LENGTH (mm) × WIDTH (mm)
PUPAL WEIGHT (mg)
FEMALES
MALES


42
40
38
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32
30
28
100
120
140
160
180
200
220
THORAX LENGTH (mm) × WIDTH (mm)
PUPAL WEIGHT (mg)
FEMALES
MALES

the mean products of the pupal dimenstions are presented in Table 79 and the raw data in appendix 6.

The regression line for the mean product (y) of the thorax width and the straight line distance on the ventral side between the anterior pupal end and the posterior margin of the thorax on the pupal weight (x) is

(a) $y = 0.133x + 16.82$ for all the females

(b) $y = 0.138x + 15.99$ for all the males

(c) $y = 0.135x + 16.45$ for both sexes.

The relation between the emergence weight and the pupal weight

Weights at emergence are linearly related to the pupal weights (Table 80) and the regressions were all highly significant ($P<0.001$). Exeept for the sample reared on Z. mais the regressions for females were slightly higher than those for males although neither the differences between sexes nor samples reared on the

different grass species were significant. The pooled data for each sex gave a significant ($P<0.001$) regression and again the regression for females was slightly but not significantly higher than that for males. The regression for both sexes was also highly significant ($P<0.001$) and the regressions for moths developing from larvae reared on C. dactylon and S. plicatilis are presented on Figure 25 and 26 respectively. The relationship between the moth emergence weight (y) and the pupal weight (x) is given by

(a) $y = 0.486x + 0.11$ for females

(b) $y = 0.474x - 2.53$ for males

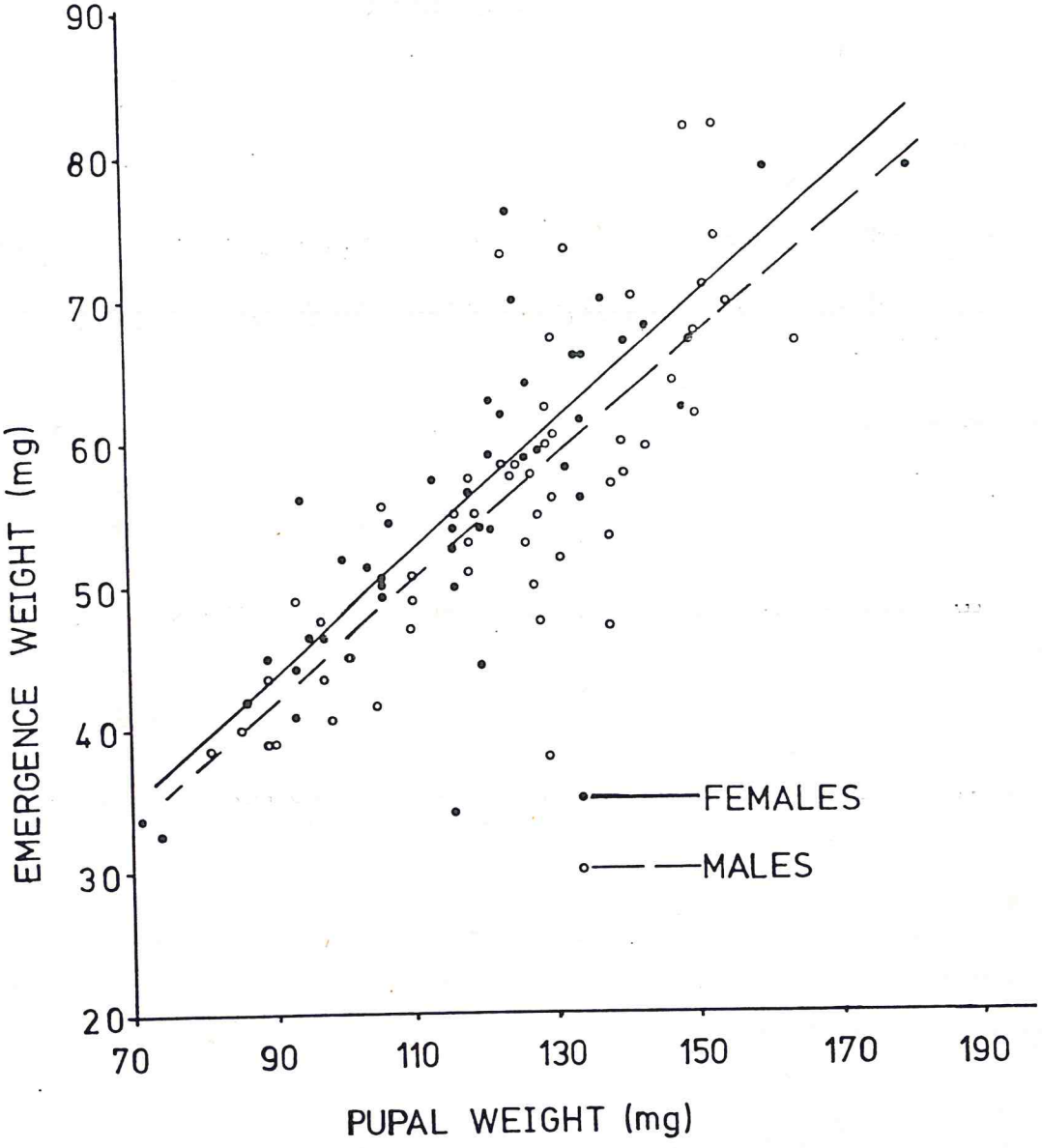
(c) $y = 0.479x - 1.03$ for both sexes.

The coefficients of determination were in all cases above 60% and therefore the weight at emergence can be estimated from the pupal weight. Since the weight at emergence and the pupal weight are related the use of relationships between length or the product of the forewing length and the forewing width and the pupal weight can reasonably be used in estimating the moth size.

TABLE 80

THE REGRESSION OF WEIGHT AT EMERGENCE ON PUPAL WEIGHT (N = 30 IN EACH CASE)

HOST PLANT	SEX	REGRESSION (b ± S.E.)	r	r^2	a
Z. mais	Females	0.504±0.047	.81	.66	-0.05
	Males	0.518±0.042	.85	.72	-7.66
C. dactylon	Females	0.549±0.052	.81	.66	-7.14
	Males	0.502±0.042	.84	.71	-4.32
E. clandestinum	Females	0.485±0.44	.82	.68	-4.72
	Males	0.476±0.049	.79	.62	-7.11
P. maximum	Females	0.463±0.045	.81	.64	2.31
	Males	0.448±0.026	.91	.83	-0.37
S. plicatilis	Females	0.438±0.038	.83	.69	4.52
	Males	0.423±0.043	.78	.61	3.88
Pooled data	Females	0.438±0.038	.81	.66	0.11
	Males	0.474±0.018	.84	.71	-2.53
	Both sexes	0.479±0.013	.83	.69	-1.03


90
80
70
60
50
40
30
20
EMERGENCE WEIGHT (mg)
70
90
110
130
150
170
190
PUPAL WEIGHT (mg)
FEMALES
MALES

The foregoing results have shown that the product of the forewing length and width is related linearly to both the pupal weight and the wing area. The relationships are expressed as

$$(1)\quad y = 0.243x + 37.13 \qquad \text{(Table 75)}$$

where y is the product of the wing dimensions and x the pupal weight and

$$(2)\quad y = 1.427x - 0.85 \qquad \text{(Table 77)}$$

where y is the same as above but x is the wing area. If x is substituted by w and a in equation one and two, then

$$y = 0.243w + 37.13$$

and

$$y = 1.427a - 0.85$$

Since for a given individual or sample y is constant

$$0.243w + 37.13 = 1.427a - 0.85$$

and

$$w = \frac{1.427a - 0.85 - 37.13}{0.243}$$

$$w = 5.87a - 156.30$$

Therefore if the forewing area a can be determined accurately, the pupal weight w can be estimated from the above equation.

DISCUSSION

The forewing length can be used in estimating the pupal weight within twelve hours of pupation and theoretically this is reasonable since length is the principal dimension of the wing area, a variable basic to wing loading. The coefficients of determination (r^2) were, however, low and varied between 33% to 60% with the samples reared on S. plicatilis giving the lowest values. However, the product of the forewing length and the maximum width was found to be highly correlated to the forewing area. It was also found to be highly correlated to the pupal weight and is a better size index than the forewing length alone. The coefficients of determination were again lower for the moth samples reared on S. plicatilis and P. maximum than in the other samples.

The products of the length and width of the thorax of pupae can also be used in estimating the pupal weights with fairly high accuracy. The coefficients of determination in this case were all above 68%.

The coefficients of determination for individuals reared on Z. mais, C. dactylon and P. clandestinum were much larger than those for moths reared on S. plicatilis and P. maximum in the regressions for forewing and thorax dimenstions on the pupal weight. Similar results were obtained for the relationship between the pupal weight and winglength except females reared on P. maximum had a higher coefficient of determination.

The regression coefficients for females were slightly higher than those for males when the forewing length and the product of the forewing length and width were regressed on pupal weight although these differences were not significant. In some lepidopterans the fresh weight wing area ratio is greater in females than in males (Long, 1959) and for a given wing length the females have a greater biomass than males (Miller, 1977).

Moths used in these investigations were well fed but still there were differences in size of pupae and moths resulting from differences in host plants the larvae fed on. In outbreak situation the food quality and quantity is expected to decline with the season but even at the beginning of the season high densities of larvae can

lead to insufficient food during the last instars. Low rainfall may also result in suboptimal quantity and quality of food. Instances are known when insufficient food quantity and quality produce smaller insects (Tragger, 1953). High larval density of S. exempta during the last instar by itself is known to reduce the insect size (Matthee, 1946). Furthermore, in some insects high temperature can also reduce size substantially (Uvarov, 1931).

The effect of these influences singly or collectively on these relationships are not known. It may well be that the decrease in the weight under harsh environment constraints are not accompanied by an equivalent decrease in the wing size. However, knowledge of these relationships can be valuable in ecological and physiological work. In many cases outbreaks are visited when the larvae have already pupated and moths are caught after they have been flying over long distances. It is likely that weights change with time after pupation and emergence so that direct weighing of moths or pupae can not possibly give useful weight estimates.

SUMMARY

Pupal weights of S. exempta can be estimated from the forewing length but greater accuracy can be achieved by using the product of the maximum forewing length and width which is highly correlated to forewing area. While still in pupal stage, the product of the thorax width and the straight line between the anterior tip of the pupa and the posterior margin of the thorax can be used in estimating the pupal weight. The larger the pupae the higher the correlation. In field situations food quality and quantity, larval density and temperature may affect the size of the final instar and would be expected to affect the size of pupae and adults. These investigations have not established how these factors affect these relationships.

CONCLUDING DISCUSSION

The rate of development of S. exempta larvae was highest on Z. mais but C. dactylon was a far more suitable host plant than the other wild grass species tested and was comparable to Z. mais. The larvae fed on

these host plants and P. clandestinum produced the largest pupae although the adults which emerged from the pupae formed by the larvae reared on the latter host plant were smaller than expected from their pupal weights. This could have resulted from the water content of the pupae being high as a result of the high water content of the host plant. The larvae transferred from C. dactylon to P. maximum and S. plicatilis at various stages produced smaller pupae than those left on C. dactylon and the differences between them were negligible. This suggests that the pupal weight is affected by the grass species fed on during the last instar. Consumption rates, digestibility and respiratory costs were not determined but P. maximum and S. plicatilis have lower nitrogen content than C. dactylon and this could have contributed to the lower pupal weights. In some insects the growth of larvae is affected by nitrogen levels of the leaves of the host plants (Cibula et al., 1967; Taylor and Bardner, 1968; Slansky and Feeny, 1977).

In C. dactylon nitrogen level declines with leaf age and the larvae fed on the youngest leaves would have been expected to form the largest pupae and moths. This, however, is not so because the survival of larvae on

the younger grass leaves was higher so that the larval density during the last instar was highest. High larval density during the the larval life is known to reduce the size of the final instar (Matthee, 1946) and would be expected to affect the size of the pupae and adults similarly.

Although availability and nutritional quality of the host plants are to factors that affect the distribution and population dynamics of phytophagous insects (Andrewatha and Birch, 1954), temperature is also an important factor in development rate of immature stages of S. exempta under laboratory conditions (Hattingh, 1941) and this has been confirmed by field cage results from three Kenyan localities (Persson, 1981). The present results have shown that the rate of development of larvae and pupae is much higher during the warmer months than during the colder months. In field situation, however, not only is the temperature varying but the larvae also encounter leaves of different age and nutritional quality. It is therefore possible that the rate of larval development is lower in the field than in the field cage where the larvae were reared on tender leaves from experimental plots and temperature was the main variable.

Moths which emerged from pupae produced by larvae reared on Z. mais and C. dactylon had longer and larger wings than those developing from larvae reared on P. maximum and S. plicatilis. Wings of moths which emerged from pupae collected from outbreak localities varied in size with the prevailing rainfall. Forewing lengths and forewing areas of intact wings can be used in estimating the pupal weights. The product of the pupal thorax width and the length from pupal anterior tip to the posterior margin of the thorax can also be used in estimating the pupal weight. The estimation of pupal weights from forewing length, forewing area and thorax dimensions is useful because weights unlike these parameters change with time.

Although some of the larval mortality was probably due to bacteria and fungus these results suggest that at least under laboratory conditions the nuclear polyhedrosis virus is the single most important mortality factor. In the field situation predators and parasites probably play an important role in controlling armyworm populations but this may be counterbalanced by the migratory behaviour and extremely high fecundity of the

insect. As mortality due to virus is negatively correlated to the amount of sunshine and positively correlated to the amount of cloud cover (Persson, 1981) the success of an outbreak probably depends on the availability of food as well as the duration of sunshine.

The growth indices (Pant and Dang, 1969; Howe, 1971) and net reprodctive rate R_o and the capacity for increase r_c (Southwood, 1966) were higher for the groups reared on C. dactylon and Z. mais and lowest for the groups on S. plicatilis and P. maximum. The laboratory results may not be representative of what is happening in the field because predation, parasitism and some pathogens are excluded. At the beginning of the outbreak season, however, tender grass is abundant and temperature is high and therefore the conditions are favourable for rapid growth. Furthermore, such outbreaks occur in areas where there had been no previous outbreaks or resident populations and it is unlikely that parasites and predators are abundant enough as to cause a substantial decrease in size of the usually high density populations of outbreak larvae.

Z. mais is mainly a seasonal crop and it may only be important in building the population of the African armyworm at the beginning of the outbreak season when it is germinating. C. dactylon on the other hand, may be important both during the outbreak and off-season.

Field surveys in the Kenya uplands have shown that armyworm moths and caterpillars are present during the off-season particularly on C. dactylon pastures where the grasses remain green (Rose, personal communication).

The higher survival and the larger size of pupae and adults obtained when S. exempta larvae are reared on C. dactylon suggest that this host plant is nutritionally superior to other wild grass species tested. Surveys of outbreaks have shown that larvae were more abundant on C. dactylon than on the other grass species. This could have been due to better survival of larvae on or movement of larvae from other grass species to C. dactylon. It is also known that within the general area of wind convergence, outbreaks are localised partly to topography (Rose, personal communication) and that in field cages females prefer C. dactylon to Z. mais for oviposition (Persson, unpublished results). S. exempta moths are probably capable of discriminating between host plants using their eyes which are highly sensitive (Langer et al., 1979).

The preference for C. dactylon has been confirmed in choice experiments both in the laboratory

and field cage. This is not suprising because C. dactylon is high in nitrogen which is known to have a significant influence on the growth of lepidopterous larvae (Slansky and Feeny, 1977). However, C. dactylon is highly cyanogenic and Cyanogensis is an effective plant defence mechanism against attack by a variety of animals including insects (Jones, 1962; Parsson and Rothschild, 1964; Rehr et al., 1973; Blaue et al., 1978). It can be suggested that S. exempta is fully adapted to cyanogenesis. The basis of this tolerance is not known but S. eradania possess an extremely high microsomal mixed function oxidase activity which could be involved in detoxifying naturally encountered food plants (Krieger et al., 1971; Brattsen, 1977). Low concentrations of cyanogenic glycosides in combination with glucose elicit strong biting response in the Mexican bean beetle Epilachna varivestis (Nayar and Fraenkel, 1963). S. exempta larvae under certain conditions can feed on cassava, Manihot esculenta (Ma, 1976) which is cyanogenic and it may be that both C. dactylon and M. esculenta contain cyanogenic sugars which by themselves or in the presence of other sugars elicit strong feeding or biting response of S. exempta larvae.

The number of instars of S. exempta larvae varies from five to seven. Under any given temperature the larvae reared on C. dactylon, Z. mais and P. clandestinum go through the lowest number of instars. Tough nutritionally deficient host plants and suboptimal temperatures reduce the rate of food consumption and the larvae are under partial starvation. Reduced feeding is known to produce supernumerary moults in several lepidopterous larvae (Kellog and Bell, 1904; Decker, 1931; Gaines and Campbell, 1935) because the decrease in hemolymph Juvenile Hormone (JH) is prevented (Nijhout and Williams, 1974; Nijhout, 1975b). The programme of metamorphosis can therefore be altered by starvation (Nijhout, 1975a) and it will not be surprising if it is found that in the field the larvae go through fewer instars at the start of the outbreak season when tender grass is abundant and temperatures are high than later on during the season when leaves are olde and temperatures are lower. Similar variations may be expected with localities experiencing different rainfall as this directly determines the quality and quantity of food available to larvae.

SUMMARY

The development of the African armyworm S. exempta was more rapid on Z. mais and C. dactylon than on P. maximum, S. plicatilis and P. clandestinum. Survival, pupal weights and weights at emergence were highest in the groups reared on Z. mais and C. dactylon. Although females were variable in the number of egg they laid, those on C. dactylon and Z. mais oviposited the highest numbers of eggs. As a result of these the groups of insects reared on these host plants had the highest growth indices, net reproductive rate and capacity for increase. On depletion of the preferred host plants or young foliage, older larvae can feed on the less preferred grass species and older leaves. Late instars survive better on less suitable grass species than early instars but their pupal weights are lower than those for individuals which remain on C. dactylon as controls. The rate of development of immature stages of S. exempta is influenced by the prevailing temperature.

The most important mortality factor of the African armyworm under laboratory conditions is a nuclear polyhedrosis virus which is more effective on larvae on unsuitable host plants and at high density

particularly during the last instar. Other mortality factors are bacteria and a fungus. Mortality during the egg and pupal stages is very low.

Larvae of the African armyworm go through five, six or seven instars depending on the host plant and the prevailing temperature. This suggests that larvae feeding on the unsuitable host plants or which are kept under low temperature regimes are effectively under partial starvation and their metamorphosis programmes change depending on the extent of starvation.

AREAS FOR FUTURE WORK

The preference for C. dactylon in choice experiments in the laboratory and in mixed pastures in the field suggests that it is the natural habitat for low density populations of armyworm caterpillars. It is highly cyanogenic grass species. Cyanogenesis is an effective defence mechanism of plants against animals and insects. Since the caterpillars do not only tolerate but prefer feeding on C. dactylon, they must have evolved a counter adaption against cyanogenesis. The mechanisms

by which C. dactylon is detoxified need to be investigated and so does the basis for the preference for C. dactylon.

The leaves of C. dactylon particularly at younger stages have higher nitrogen content than the leaves of the other grass species tested. This may be important in understanding the common occurrence and success of outbreaks of the African armyworm on new flush of grasses which are high in nitrogen content and raises speculation about the consequences of applying nitrogenous fertilizers on levels and success of infestation in cereal crops.

Field surveys have shown that armyworm moths and catepillars are present in the C. dactylon pastures in the highlands of Kenya when there are virtually no outbreaks of caterpillars. This is probably due to the presence of green grasses in the uplands but the presence of these populations gives an opportunity to study and measure their abundance and distribution so as to asses their significance in relation to the first outbreaks of caterpillars. Outbreak populations grow and spread fast and are difficult and expensive to control. Studies on the habitats of the off-season populations could suggest control strategies of the low

off-season populations and or to the first outbreak population in order to prevent large scale outbreaks. This will minimise the crop loss, the overall cost of control and the use of environmentally dangerous pesticides.

In the laboratory the differences between pupal durations are very small. The outbreak caterpillars are exposed to tender and nutritions food and favourable temperature and the growth of the caterpillars is therefore synchronised resulting in the caterpillars pupating at approximately the same time. Since the pupal duration depends on temperature, approximate dates of emergence can be known and if moths can be concentrated using baits soon after emergence, it may be possible to apply control measures directly on them and subsequent outbreaks can be contained. This is not practiced presently but moths from previous outbreak areas cause more and larger outbreaks if they are not controllled.

C. dactylon is preferred to the other grass species examined, it would be useful to investigate the selective ability of females for oviposition sites.

This could be tackled by estimating the densities of egg batches on the different grass species in the field. It would also be useful to investigate the basis for the selection.

The African armyworm as a pest of grasslands and cereals must have benefitted from human activities including deforestation, cultivation of cerel monocultures, overgrazing and burning because these activities tend to stimulate new growth of grass at the beginning of the season. The understanding of man's part in boosting the population of such an insect could be useful in range management and agricultural practices.

The nuclear polyhedrosis virus is the single most important larval mortality factor of S. exempta particularly during the first and the last instars under the laboratory conditions and in field cage experiments. These findings raise the need for studying the ecology of the virus in outbreak and low density populations of S. exempta and for assessing its potential in biological control of the African armyworm.