OVIPOSITION PREFERENCE, LARVAL FEEDING PREFERENCE AND LARVAL FOOD QUALITY OF *HELIOTHIS ARMIGERA*

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ABSTRACT

Relationships between tomato fruitworm(Heliothis armigera conferta Walker) and four host plants(lucerne, tomato, aster, sweetcorn) were studied in field, greenhouse and controlled laboratory conditions at Palmerston North, New Zealand during 1984-1986. The objective of the field trials was to investigate seasonal development, population growth and feeding behaviour of larvae on the four host plants. In the laboratory, oviposition preference within and between plant species, effects of larval foods on development, parameters of larval food quality, feeding preference and induction of feeding preference by different foods were investigated.

In the field very few (male) moths were caught by pheromone traps before January, numbers reached a peak in March and had declined to zero by late April. Individual meteorological parameters (minimum night temperature, maximum day temperature and rainfall) showed no significant correlation with moth catches. On mature stages of the four plants larvae fed preferentially on tomato fruits, sweetcorn cobs and aster flowers over plant leaves but were hardly observed at all on lucerne.

Glasshouse experiments showed that female moths preferred to oviposit on the upper half of plants, leaves were preferred over other plant parts and upper leaf surfaces were preferred over lower leaf surfaces. Oviposition preference was however affected by the flowering stage of the plants. At the pre-flowering stage lucerne was the most preferred but at flowering aster was the most preferred. Odour played a significant role in plant selection for oviposition.

Different larval foods gave significant differences in growth and

development of the insect as measured by several biological parameters. When larval period, mortality, percent pupation, pupal weight, adult fecundity and life span were combined into an overall fitness index reproductive parts of all plants(flowers, fruits and cobs) gave better performance than leaves.

Dry matter content (and its reciprocal water content) and nitrogen content of foods, considered alone or combination, did not provide an adequate measure of food quality for larvae. Larval growth rate on a particular food was clearly influenced by rate of ingestion of that food and larvae tended to consume less of those foods that were more readily digested and assimilated. The nitrogen requirement of H.armigera larvae for adequate growth and development appeared to be low at about 1.9% of dry matter which was approximately the nitrogen level found in the reproductive parts of the plants.

Newly hatched larvae expressed clear preferences for particular plant species in the order lucerne leaves > tomato leaves > aster leaves > sweetcorn leaves. However, these preferences could be modified in later larvae by early feeding experience but artificial diet (based on kidney bean) had little effect on food preference. Feeding preference for reproductive parts of plants was more strongly expressed than for leaves and reproductive parts evoked greater induction of preference.

CHAPTER 1

INTRODUCTION

Tomato fruitworm, Heliothis armigera(Hubner) is a major pest throughout the tropics and subtropics and, to a lesser extent, temperate regions. Many common names have been applied to the larvae of this species including bean pod borer, bollworm, climbing cutworm, common bollworm, cotton bollworm, gram podborer, flower caterpillar, lucerne budworm, tobacco budworm and tomato worm or grub, which refer to the crop attacked and feeding habit of larvae, and aptly allude to the more important injury caused (Broadley,1977; Zalucki et al.,1986).

H.armigera has been recorded throughout Africa, Asia, Australasia, Europe and South Pacific Islands but not in North or South America. In the New World Heliothis is represented by the species,H.zea and the closely related H.virescens. High populations of H.armigera appear in areas where host plants and alternative host plants are available throughout the year especially in tropical and subtropical regions. The highest number of annual generations, and more overlapping of generations, occur in these areas while in temperate regions only 2 or 3 generations are usually found due to overwintering and diapausing pupae(Atanasov,1964; Wangboonkong,1975).

Moths of H.armigera cause no plant damage as they merely feed on nectar. However, the larvae, as the list of the common names implies, have been known for many years as serious pests of wild and cultivated plants throughout the world. Two plant families, Leguminosae and Solanaceae, figure most prominently as hosts for larvae although genera from a great number of plant families are listed as hosts. These two

plant families, Leguminosae and Solanaceae, are considered as primary hosts for the species(Hardwick,1965; Kirkpatrick,1961b).

In New Zealand, H.armigera conferta(Walker) occurs on a wide range of wild and cultivated plants, and is known as tomato fruitworm or corn earworm because it is recorded as a major pest on tomatoes, sweetcorn and maize(Helson,1972; Scott,1984). The species is found throughout New Zealand but especially in the North Island. Its southerly distribution is probably maintained by spring and summer migrants. Adults emerge with the warmer spring weather, beginning about October in northern areas and later in southern areas (Gaskin, 1970a; Valentine,1975). There generally are 3 generations a year and more overlapping of generations occurs in the more northerly regions. Highest populations are usually recorded from the lowland areas of the warmer North Island. Heaviest infestations of crops by larvae are in late summer between January and March (Cameron and Valentine, 1985; Davies,1973; Fox,1970a). Overwintering (and diapausing) pupae are usually present from April to September.

The important pest status of H.armigera and of the Heliothis complex in general has been reported from many countries. The wide host range of most species causes a range of economic effects resulting from larval feeding and costs of control measures have in some instances been estimated. For example, the damage by H.zea to various crops in the United States has been estimated to be in hundreds of millions of dollars(Hyslop,1927). Wilson(1982) in Australia estimated the cost of Heliothis control in 1980 to be about A$ 23.5 million. In Thailand, H.armigera has been considered as the single most important pest of cotton which almost completely destroyed the crop in 1975 (Wangboonkong,1975,1981). In India, Lal et al.(1985) estimated monetary

loss from chickpea infestation by H.armigera at about Rs 450 million per year.

Up to the present, most effort has been directed towards chemical control and recommendations for insecticide use on various crops. Microbiological control agents such as Bacillus thuringiensis and nuclear polyhedrosis virus and botanically based insecticides such as pyrethroids have been used commercially (Daoust and Roome,1974; Forrester,1985). The widespread use of insecticides not only may create residue problems in the environment but can also induce the development of insect resistance. Resistance has occurred most notably to DDT(Twine and Kay,1973; Wilson,1974) but resistance to synthetic pyrethroids has recently been detected in Australia(Gunning et al.,1984) and in Thailand (Collins,1986; McCaffery et al.,1986).

Many attempts have been made to manipulate pest populations so as to maintain them below the economic threshold and integrated pest management programmes have been discussed and applied to some pest species. Zalucki et al.(1986) have proposed potential tactics for Heliothis management for regional schemes that would include destruction and/or management of alternative hosts, disruption of mating behaviour by pheromones and release of sterile males. These potential tactics may not be successful unless the fundamental ecology and biology of the local populations are well understood. Thus amongst other things lists of hosts and alternative hosts in an area, seasonal development of pest populations and relationships between the insect and its host plants in terms of oviposition and feeding preference are needed.

Despite the considerable economic importance of H.armigera and need for its management in New Zealand, work on host-plant relationships is limited. Thus studies were initiated in the field, greenhouse and

under controlled laboratory conditions at Palmerston North, New Zealand the main objectives of which were:

1. To investigate seasonal development and population growth of H.armigera on four host plants in field plots.

2. To investigate the preference of larvae between four plant species and to observe larval feeding behaviour.

3. To determine oviposition preference within and between four plant species.

4. To study the effects of larval foods(plant species, plant parts and artificial diet) on development.

5. To define parameters of larval food quality

6. To investigate feeding preference of larvae and induction of feeding preference by different foods.

CHAPTER 2

LITERATURE REVIEW

This literature review considers first the genus Heliothis broadly then deals specifically with Heliothis armigera with which the experimental work reported in this thesis was concerned.

Species of the genus Heliothis are major pests throughout the tropics and subtropics and, to a lesser extent, in temperate regions. The New World species, Heliothis zea (Boddie) and the closely related Old World species, Heliothis armigera (Hubner), are in each hemisphere major agricultural pests. Associated with them in different parts of the world are other closely related species such as H.virescens (Fabricius) in the United States of America and H.punctigera (Wallengren) in Australia (Hardwick,1965; Common,1953). The genus Heliothis and its complex of species constitute a morphological and biological relatively homogeneous group and the information reviewed in this chapter reflects these common characteristics.

BIOLOGY OF THE GENUS HELIOTHIS

Many common names have been applied to the larvae of the genus Heliothis. Those most commonly encountered are corn earworm, tomato fruitworm, tobacco budworm, cotton bollworm, lucerne budworm, gram podborer and flower caterpillar, which refer to the crop attacked, and aptly allude to the most important injury caused by the larvae (Broadley,1977; Zalucki et al.,1986). Identification to species often causes some difficulty because of the close similarity in external

appearance of adults and immature stages and the slight difference of eggs. The main features used to distinguish Heliothis species are wing scales of newly emerged moths, genitalia and the cremaster of pupae (Kirkpatrick,1961a).

The following discussion of Heliothis life history and habits is centred on H.armigera but the same basic pattern is found in other species.

First,the four life stages-adult,egg,larva and pupa are considered separately.

1.Adult

The stout-bodied moths are of typical Noctuid appearance, vary considerably in colour, but are generally dull yellow or olive-grey to brown with a series of dark, irregular, transverse lines across the forewing. The wing span is about 35 to 40 mm. There are two circular spots on each forewing. The large spot is about half-way between the base and apex of the wing, and the smaller one near the base. The hindwing is pale, with strongly marked veins and a broad, dark apical border with two lighter spots in it (Kirkpatrick,1961a; Zalucki et al., 1986). Moths are nocturnal in habit, flying, mating and laying eggs at dusk and often rest on crop plants during daylight hours (Grichanov, 1983; Roome,1975). However, particularly in higher latitudes, adults of H.zea may be observed feeding and ovipositing in great numbers during the late afternoon and evening. This may be partially in response to low night-time temperatures which inhibit normal Noctuid activity (Hardwick,1965). Moths usually feed on flower nectar and an ample supply of nectar substantially increases egg production. Nectar availability may partially explain why oviposition co-incides with

flowering of host plants (Broadley,1977; Roome,1975). However, Lukefahr and Martin(1964) demonstrated that H.zea in the United States was able to mate and oviposit without having fed but about a 50% increase in both fecundity and longevity resulted when adults fed on a sucrose solution. Kravchenko(1984) reported that there were three active periods per 24 hours of H.armigera moths in cages and in cotton fields, the morning and the evening periods being related to feeding and the night one to mating. Moreover, Patil et al.(1981) showed that females of H.armigera were more active pre-midnight and males were active in the post-midnight period. Moths usually copulate 2 to 4 days after emergence. One mating is sufficient for production of fertile eggs though females are able to mate 6 to 7 times. Most eggs are laid within the first five days(Coaker, 1960). The number of eggs laid and duration of adult life are affected by food available to adults, but there is no significant effect on the fertility of eggs. Although oviposition occurs even if only water is provided to adults, the number of eggs laid is reduced (Mourikis and Vassilaina-Alexopoulou,1970). Adult life span is betwen 6 and 15 days and there is no difference between the sexes. However, adult life span is highly affected by food available to adults and to larvae (Abul Nasr et al.,1976; Ayad,1977; Pretorius,1976).

Although the number of plant species on which Heliothis will oviposit seems almost limitless, each species seems to prefer certain host plants in different geographical areas(Alvarado-Rodriguez et al., 1982; Doss,1979; Farrar and Broadley,1985; Mabbett and Nachapong, 1984). Eggs are usually deposited on the upper half of the plant and on both surfaces of the plant parts such as terminal growth, leaves and flowers. In India and Thailand, H.armigera prefers laying eggs on

cotton to other host plants, particularly on leaf terminals and bracts and most eggs are found on the first three leaves from the top of the stem (Mabbett and Nachapong,1984; Patel et al.,1974). Atanasov (1964) showed that H.armigera laid eggs on all parts of maize plants but preferentially on leaves. In the United States, Widstrom et al.(1977) stated that H.zea preferred to oviposit on the adaxial surface of young leaves on the middle portion of the leaves of corn and Alvarado-Rodriguez et al.(1982) reported that H.zea moths demonstrated a highly significant preference for oviposition on leaves of tomato rather than on bloom, fruits or stems. The latter also reported that no preference was shown for dorsal vs ventral leaf surfaces. In Australia, Firempong(1986) studied oviposition of H.armigera on 9 host plants and demonstrated that there were significant differences between certain plants with insects from some populations but not from others. He also found no correlation between adult oviposition and larval feeding preferences.

2.Egg

An individual moth has been known to lay over 3000 eggs, but the average is about 1000. Eggs are deposited singly on selected parts of the host plants(Broadley,1977). A Heliothis egg is typically sub-spherical, being shorter than wide. Eggs of different species of Heliothis are remarkably uniform in size, varying from a mean height of 0.42 mm in H.virescens to 0.59 mm in H.zea. The chorion is marked with 28 to 35 vertical ribs, most ribs being entire but some branched. The micropyle is in the middle of the summit and is surrounded by a smooth ribless area. The eggs of different species can usually be identified by a variation in the reticular pattern in the micropylar area. Only in

H.hawaiiensis, are the cells of the first, second and third series and the cross-walls of the rib cells consistently well defined. In the other species, these are often weakly or only partially defined. When deposited, the egg is yellowish-white and glistening, except for the egg of H.rubrescens which is dark yellow. About 24 hours before hatching the colour changes to light-grey or dark brown as the larva matures within the chorion (Hardwick, 1965; Kirkpatrick,1961a; Pearson,1958).

3.Larva

The larva leaves the egg by chewing an exit hole in the upper part of the confining egg shell. Hatching takes about 30 minutes and newly hatched larvae usually consume their egg shells (Wangboonkong,1975). The newly emerged larva is about 1 mm in length, with a yellowish-white to reddish-brown body and black head capsule without prominent markings. In the second instar, the head is similar in colour to, or paler than, that of the first instar. The trunk becomes darker as the larva increases in size, and is often marked dorsally with orange-brown or brown. In the third instar, two colour phases often become evident. They vary from green to brown and are marked by numerous, fine, longitudinal lines of white or cream. These two colour phases are maintained through the fifth instar. The pattern from the third to the fifth instar becomes more sharply defined but the essential features remain unchanged (Hardwick,1965; Pearson,1958). Large larvae are more strongly coloured than small ones and have distinct, longitudinal stripes suffused with variable coloured markings. Overall pigmentation of larvae may be either green, fawn, pink, yellow or brown, only the claws and spiracles remaining black. The skin has a characteristic granular appearance and can be seen under magnification to be rough.

The surface consists of close-set, minute tubercles. In addition to 3 pairs of true legs at the fore end each larva possesses 4 pairs of false legs in the middle and 1 pair of false legs at the hind end of the body. This arrangement allows the larvae to move in an undulating fashion. There are normally 5 to 6 instars,but exceptionally 7 instars are found during cold conditions when larval development is prolonged (Hardwick,1965; Helson,1972; Kirkpatrick,1961a).

Feeding begins shortly after emergence from the egg, and continues until the larva is fully grown. Larvae are cannibalistic and usually only one full-grown larva is found in a confined space, for instance, the tip of a corn cob (Joyner and Gould,1985; Metcalf and Flint,1951; Twine,1971).

4.Pupa

The fully grown larva moves off the host plant and transforms into the pupa in a specially constructed chamber in the soil. Broadley (1977), Hardwick(1965) and Kirkpatrick(1961a) have described the pupa of the genus Heliothis. It possesses the following characters:

When first formed, the pupa is light-green or yellow-brown, smooth-surfaced, rounded both anteriorly and posteriorly, and soft-bodied. Three or four days after pupation, the pupal case rapidly hardens and the colour slowly changes to dark-brown or mahogany-brown. Three dark spots appear in an oblique line in the eye. At the posterior end, the cremaster consists of two spines borne directly on the rounded terminus of the tenth abdominal segment, or on an apical prolongation of that segment. The distance between the outer edge of these cremaster spines at the junction with the cremaster differs between species and has been used for identification within the genus(Kirkpatrick, 1961a).

Duration of the pupal stage is usually 12 to 20 days. However, when conditions are unsuitable, for example during winter, several months may be required before development is completed(Akkawi and Scott, 1984; Kay,1982a; Lopez et al.,1984; Wilson,1983).

The total life span of Heliothis varies, depending on species, food and environmental condition. Life history data shown in Table 2.1 is that of Singh et al.(1982) for H.armigera in New Zealand on artificial diet under laboratory conditions at 25°C and 18:6(L/D) photoperiod.

The average generation time from egg to egg was about 38 days and the sex ratio was 1:1. There were 6 or 7 larval instars. Details are shown in the Table 2.1.

Table 2.1 Development of Heliothis armigera conferta on an artificial diet at 25±1°C and 18:6 (L/D) photoperiod. (data of Singh et al., 1982)

Feature	Mean ± S.E.
Larval period (days)	17.3 ± 0.2
Prepupal period (days)	3.9 ± 0.1
Pupal period (days)	13.7 ± 0.3
Total survival to pupa (%) (includes diapausing pupae)	99
Pupal weight (mg) : Male	407.5 ± 8.5
: Female	392.4 ± 7.8
Survival to adult (%)	99.5
Adult life span (days) : Male	12.0 ± 1.6
: Female	11.9 ± 0.8
Pre-oviposition period (days)	2.7 ± 0.2
Fecundity (eggs/female)	973.0 ± 121
Pupal diapause (%)	36.9
Diapause duration (days)	129.7 ± 6.2

DISTRIBUTION

The genus Heliothis is widely distributed in tropical and temperate regions of the world as shown in Table 2.2. The New World species, H.zea is found in North America and South America from Canada to Uruguay. In South America Heliothis is represented by the endemic group of species consisting of H.atacamae, H.bracteae, H.gelotopoeon and H.titicacae. H.virescens, closely related to H.zea, is common in the United States and has been reported as an important pest of cotton in Peru(Pearson,1958). In Europe, H.armigera is the main species and occurs in the south of the region, especially along the Mediterranean coast, where H.peltigera also is recorded occasionally (Pedgley,1985; Pietanza,1968). The Old World species, H.armigera is also an important pest throughout Africa. It is abundant in eastern Africa, including Madagascar. Other species which are occasionally reported from Africa are H.assulta, H.dipsacea, H.fletcheri, H.peltigera and H.toddi, and H.helenae on St.Helena Island. In Asia, the genus is represented by the widely distributed H.armigera, and geographically restricted H.tibetensis (Coaker,1960; Hardwick,1965). The four main species found in Australia are H.armigera, H.punctigera, H.assulta and H.rubrescens and the new species, H.prepodes (Common, 1953,1985; Kirkpatrick,1961a). Of those only the first two species have been recorded in New Zealand and H.punctigera only as an occasional immigrant. On the islands of the Pacific Ocean, Heliothis is variously represented by H.armigera, H.assulta, H.pacificta, H.confusa, H.pallida, H.hawaiiensis and H.zea. The last two species are commonly found in Hawaii (Gaskin, 1970b; Kirkpatrick, 1961b; Pearson, 1958; Valentine, 1975).

Table 2.2 Distribution of Heliothis species in the world. (summarized from Ba-Angood,1984;Barber,1937;Coaker,1960;Common,1953;Dugdale,1973; Hardwick,1965;Kravchenko,1984;Neunzig,1963;Pearson,1958;Pedgley, 1985;Wangboonkong,1975 and Yuan et al, 1965)

Species	North America	South America	Africa	Asia	Europe	Australia	New Zealand	Pacific Islands
armigera (Hubn.)			*	*	*	*	*	*
assulta (Guen.)			*	*		*		*
atacamae (Hard.)		*						
bracteae (Hard.)		*						
confusa (Hard.)								*
dipsacea (Linn.)			*		*			
fletcheri (Hard.)			*					
gelotopoeon (Dyar)		*						
hawiiensis (Quai.)								*
helenae (Hard.)			*					
minuta (Hard.)								*
molochitina (Berg.)	*	*						
pacificta (Hard.)								*
pallida (Hard.)								*
peltigera (Schi.)			*		*			
phloxiphaga (Grot.)	*							
prepodes sp.n.						*		

Table 2.2 (continued)

Species	North America	South America	Africa	Asia	Europe	Australia	New Zealand	Pacific Islands
punctigera (Wall.)						*	(*)	
rubrescens (Walk.)						*		
toddi (Hard.)			*					
tibetensis (Hard.)				*				
titicacae (Hard.)		*						
virescens (Fabr.)	*	*						
viriplaca				*	*			
zea (Bodd.)	*	*						*

(*) = occasional immigrant

ECONOMIC IMPORTANCE

Heliothis moths cause no plant damage as they merely feed on nectar. The larvae of several species however have been known for many years as serious pests of wild plants and cultivated crops throughout the world. The wide host range of most species results in a range of economic effects from larval feeding. According to Hyslop(1927), H.zea is the third most destructive insect pest in the United States after codling moth and cutworms. Monetary losses in the United States resulting from the damage by H.zea to various crops have been estimated in the hundreds of million of dollars. In North America, the most attacked food plant of H.zea is undoubtedly maize followed by cotton (Barber,1937; Liapis et al.,1984). In the Old World, H.armigera similarly feeds on a wide variety of crops and the damage from larval feeding causes economic losses in many areas. It has been reported that H.armigera is the worst pest of maize in Queensland,Australia and on Guam (Hardwick,1965). In Thailand, this species has been recognised as the most important pest of cotton which was almost completely destroyed in 1975(Wangboonkong,1975, 1981). In India, Lal et al.(1985), Singh and Sidhu(1980) and Tewari and Moorthy(1984) assessed monetary loss from chick pea infestation by H.armigera at around Rs 450 million per year, 33% of cotton squares were destroyed and 49.7% of tomato fruits were damaged each year. H.punctigera, the endemic Australian species, evidently has as wide a host range as H.armigera and H.zea and has been serious pest of cotton and lucerne along the East Coast of Australia (Broadley,1977; Kirkpatrick,1961b). In Africa, H.armigera occurs wherever cotton is grown and is regarded as a major pest, as well as of citrus and market-garden crops in East and South Africa. Species of

Heliothis have also been known as minor pests in North and West Africa, with H.armigera sometimes becoming troblesome in these areas where outbreaks result in crop destruction (Abul Nasr et al.,1976; Coaker, 1957; Daramola,1986; Khalid et al.,1981).

CROP SPECIES AFFECTED

Larvae of the genus Heliothis feed upon many species of plants. H.armigera, H.gelotopoeon and H.punctigera are regarded as omnivorous, or at least polyphagous. In contrast species such as,H.assulta and H.hawaiiensis are more restricted in feeding habit. Although a number of graminaceous plants besides maize and a few malvaceous plants besides cotton are consumed by H.armigera and H.zea, the two plant families that seem to figure most prominently as hosts for Heliothis species are the Leguminosae and the Solanaceae. These two plant families are considered by some authors as primary hosts for the genus (Hardwick,1965; Kirkpatrick,1961b; Neunzig,1963). Although Heliothis larvae feed predominantly on herbaceous and low woody plants, they are by no mean confined to them. Damage to fruit trees, for example mango,has been recorded for a number of species(Siddappaji,1972). Even conifers cannot be excluded from host plant lists,because larvae of H.armigera have been found attacking the soft parts of young radiata pine (Pinus radiata) in the North Island of New Zealand (Alma,1977).

The enumeration of food plants of Heliothis species summarized from many reports is shown in Appendix 1.

SEASONAL DEVELOPMENT

Heliothis species have been shown to develop continuously in tropical areas but with increasing latitude to become more dependent on pupal diapause to survive the winter. Larval development is highly affected by climatic conditions, but also by food availability, natural enemies and to a lesser extent by competition between species. In most parts of the world larvae can be found on suitable host plants throughout the growing season and sometimes even during winter (Broadley,1977). In tropical zones, under most conditions, populations seem to be relatively stable even though preferred host plants may be limited because larvae can survive and feed on many alternative hosts. Wangboonkong (1975) reported that populations of H.armigera in Thailand were still constant after harvesting maize and cotton as larvae were then usually found on various solanaceous and malvaceous plants. Environmental conditions play a major role in variation of populations from year to year. Coaker(1960) and Zhang(1984) showed that the most important factors of the environment in Uganda and China which affected H.armigera populations were temperature and rainfall. Populations were low during the dry season and at low temperatures. Populations generally build up with the development of the crops, oviposition starting a few days before flowering and increasing to a maximum that coincides with the flowering peak of cultivated crops. In temperate areas, populations reach a peak in summer then gradually decline to spend the winter in pupal diapause.

Under relatively unfavourable climatic conditions, for example in temperate areas with a cold winter period, Heliothis species generally have only 2 or 3 generations a year and most of the time is spent as pupae overwintering or in pupal diapause. Atanasov(1964), Twine(1978) and Yuan et al.(1965) reported that H.armigera usually has 2 generations

a year and overlapping of generations is common. Pupal diapause is rarely found in hot climatic regions (Bilapate et al.,1984; Coaker, 1960; Wangboonkong,1975). The incidence of pupal diapause and diapause duration depend on climatic conditions and may vary with the species. Kay(1982a) for example stated that H.armigera in Southern Queensland,Australia, formed about 80% diapause pupae between late-April and August. However, Singh et al.(1982) showed that the same species reared on artificial diet at 25°C and 18:6(L/D) photoperiod in Auckland, New Zealand formed only 20 to 40% diapause pupae. Diapause lasted in this instance about 130 days.

Besides environmental conditions and the food supply, one of the major factors which regulates Heliothis populations is natural enemies-parasites, predators and pathogens. Natural enemies play a very important role in controlling Heliothis populations in all life stages even in diapause pupae. Wilson(1983) reported that parasitism by 4 species of Hymenoptera and 2 species of tachinids(Diptera) caused heavily mortality of diapausing pupae of H.armigera in Australia. Kay(1982b) showed that 3 parasites of H.armigera; Heteropelma scaposum, Carcelia sp., and Microgaster sp. overwintered in host pupae and emerged mainly at the same time as their hosts. Among those natural enemies which cause mortality in Heliothis, egg-and larval parasitism by tachinids, ichneumonids and braconids are the most important. Trichogramma spp. are the main egg-parasite of Heliothis species (Gupta et al.,1984; Kfir,1982; Li,1984). There are many reports which show the efficacy of various larval parasites such as Microgaster sp., Chaetopthalmus sp., Heteropelena scaposum, etc. on Heliothis larvae in different parts of the world (Broadley,1984; Hill et al.,1985; Mani and Krishnamoorthy, 1983). Widely used pathogens in controlling larvae are Bacillus thuringiensis and baculoviruses. It is also reported that fungi, such as Paecilomyces farinosus cause pupal mortality of

H.armigera in New Zealand (Alma,1975a; Ignoffo et al.,1983; Odak et al.,1984; Sidor,1977). Chen et al.(1984) and Pawar and Jadhav(1983) recorded that red spider (Allothrombium sp.) and hunting wasps (Delta spp.) were predators of Heliothis larvae.

HELIOTHIS ARMIGERA (HUBNER)

1.Distribution and host plants

As shown in Table 2.2 and Figure 2.1, H.armigera is world wide in distribution. The species has been reported in Asia, Africa, Europe, Australia and the islands of the Pacific Ocean; also exceptionally in North and South America. In Asia, the species occurs from Siberia(USSR) through the Middle East, and from the northern part of China through Indonesia (Ba-Angood,1984; Bai et al.,1979; Hardwick,1965). In Asian countries, outbreaks of H.armigera generally occur in areas where cotton, maize and legumes are extensively cultivated such as India, China, Pakistan and Thailand (Keerthisinghe,1982; Lal et al.,1985; Singh and Sidhu,1980). In Africa, H.armigera has been recorded throughout the continent, although it is considered to be a serious pest of cotton and legumes only on the east coast of Africa and on Madagascar. In the northern and the western parts of Africa, it is known as a relatively minor pest of cultivated crops (Aboul-Nasr et al.,1981; Nyiira,1970; Reed,1965). In Europe, H.armigera is probably indigeneous along the Mediterranean coast and occurs only as a migrant in many other parts of Europe(Pedgley,1985). In Australia, H.armigera has been recorded mainly on the east coast ,especially in Queensland and New South Wales. It is also found in New Zealand,Fiji,Cook Islands,Niue Island and some other South Pacific Islands (Common,1953; Dugdale, 1973; Kirkpatrick,1961b).

The important host plants of H.armigera are included in Appendix1.

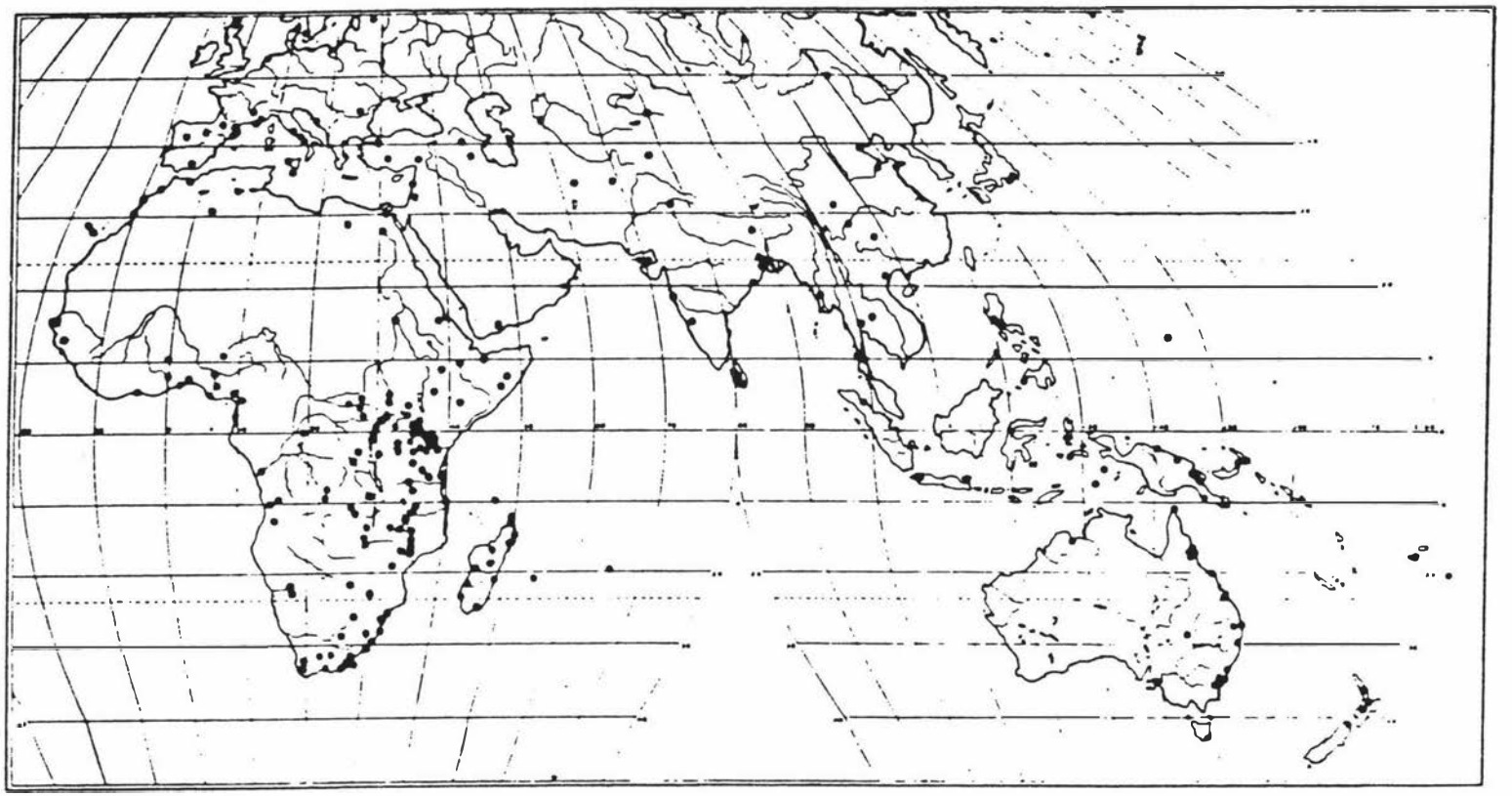

Figure 2.1 World distribution of Heliothis armigera.(From Hardwick,1965)

2.Occurrence in Australasia

In recent years an enormous volume of literature has appeared on the biology, taxonomy, ecology and control of Heliothis species in Australia. According to Common(1953,1985) and Kirkpatrick(1961a), there are 5 species in Australia-H.armigera, H.assulta, H.prepodes, H.punctigera and H.rubrescens. Two are serious pests: H.armigera, which is cosmopolitan and H.punctigera which is endemic to Australia and occurs in New Zealand as an occasional migrant. Based on the structure of the genitalia, Hardwick(1965) classified H.armigera and H.punctigera in two different subgenera and considered the former as the most primitive species in the genus. Controversially, Daly and Gregg(1985) demonstrated the low genetic differentiation between these two species and suggested that H.punctigera was derived from H.armigera. However, further study may help to clarify these concepts.

There has evidently been confusion between these two species in Australia. It was previosly recorded that H.armigera occurred throughout the country but after morphological and genitalia studies it is clear that two distinct species have been confused under this name. It has now been concluded that H.armigera is largely confined to coastal and subcoastal Queensland and New South Wales, and that H.punctigera occurs throughout Australia though still concentrated in the same areas as H.armigera (Common,1953; Kirkpatrick,1961a; Zalucki et al.,1986).

Noctuidae recorded in New Zealand prior to 1871 were listed by Fereday(1874) and all species named by Taylor(1855), included many species known to occur in Australia such as Helicoverpa armigera conferta(= Heliothis armigera conferta Walker) (cited by Fox,1978). There are several reports to show that many insect species found in New Zealand,including Heliothis,have migrated from Autralia. There are numerous records of H.armigera and H.punctigera from New Zealand in the past three decades. In late-October, 1968, 5 males and 6 females of

H.punctigera were caught by light trap at Massey University,Palmerston North (Gaskin,1970b), and in November of the same year they were also caught by M/V light trap in Ruakura,Hamilton(Dugdale,1969). In the same season (February), larvae of this species were found on tobacco and peach in Opouri Valley,Marlborough Sounds; Ngatimoti and Motueka Valley, Nelson by Dugdale(1969), and in March,1969 adults were recorded at Lake Hawea, Otago and at Wellington but they were not found the next summer.They seem unable to survive the winter in New Zealand (Fox,1970b).

Whilst 1956 and 1968 were noted for the large immigrations of the blue moon butterfly (Hypolimnas bolinanerina) and the painted lady butterfly (Cynthia kershawi) respectively, 1971 was noted for the crimson speckled footman (Utetheisa puchelloides). Also in 1971 and after, numbers of H.armigera and H.punctigera have been recorded. After a week of strong north-westerly winds in October,1971, adults of H.punctigera were recorded in Nelson; Manaia,Hamilton; Opunake, Taranaki; Ngunguru,Whangarei; Helensville,Auckland and North Auckland. It is believed that all moths caught were migrants from the east coast of Australia. Most such migrants are found on the west coast of both North and South Islands of New Zealand (Fox,1973a, 1973b, 1975, 1976, 1978).

Although H.armigera is a very common pest in New Zealand, it has been recorded from light traps less frequently than H.punctigera. The species is also found in Fiji, Cook Islands, Kermadec Islands, Niue and other south-west Pacific Islands (Dugdale,1973). In New Zealand, H.armigera is mostly confined to the North Island, especially in the warmer lowland areas. However, Gaskin(1970a) set a light trap at Massey University, Palmerston North between October 1966 and December,1968 and reported that few moths were caught in October, November and December and a great number of moths were caught in February and March.

Fox(1970a) also recorded one moth in the Egmont National Park at South Egmont elevation 3000 feet, in January,1970. Moths of this species were also recorded in Hastings, Napier and Ashburton,Christchurch during summer (Davies,1973; Wood, 1973). Because of its wide range of food plants and capability of surviving through the New Zealand winter, H.armigera is more important as a pest and occurs in higher populations than H.punctigera (Gaskin,1966).

The question may be asked as to how migrant Heliothis get to New Zealand? In the months of September,October,November and December,1968 an unusually large number of records of migrant Lepidoptera stimulated a number of papers (Davies,1973; Dugdale,1969, 1973; Fox,1970a, 1970b, 1973a, 1973b, 1975, 1976; Gaskin,1970a; etc.). Most of the moths were caught along the west coast of both Islands of New Zealand and their occurrence seems to be associated with the following phenomena:

1. Strong and prolonged westerly winds.

2. Northwest winds associated with the northern edge of a depression.

3. Cold fronts.

4. The presence of large bushfires in Australia.

When one, two or all factors occur together migrant insects are often recorded soon after in New Zealand. Unless specimens are marked in Australia and recaptured in New Zealand, it is of course impossible to state categorically that an unusual moth found in New Zealand is in fact an immigrant specimen. Australian species of moths have been known to breed in New Zealand from time to time, and some of them like H.armigera have established breeding populations. This makes it very difficult if not impossible to decide whether a given specimen of an Australian species has in fact just arrived in New Zealand or whether it is has been bred there.

Taranaki seems to be the favoured place for migrant Heliothis.

This may be, because of location with respect to the East Coast of Australia, warm climate and a wide range of suitable host plants. Fox(1978) showed that migrant insects recorded in Taranaki have probably come from Australia between Newcastle and Brisbane with a mean travelling speed of 48 km/h. Of these only about half are able to breed when they arrive. The possibility of survival of migrant moths in New Zealand and production of offspring depends primarily on climate and food plants. Climatic factors are obviously important for Heliothis because the winter in New Zealand is too cold for the active stages and host plants are also restricted at this time. Polyphagous species such as H.armigera have a far greater chance of survival than those which are host-specific. Furthermore, H.armigera is well adapted to the winter as its diapause pupae can survive unfavourable conditions and moths emerge when the conditions are more suitable. Populations of this species are thus established and augmented by summer breeding in New Zealand.

INSECT-PLANT RELATIONSHIPS

Co-evolution between insects and plants apparently began in the early Cretaceous, about 125 million years ago when the Angiosperms underwent explosive evolution, largely displacing the pre-existing flora over most of the world. This provided a major impetus for the evolution of phytophagous insects. Furthermore, the diversification of flowering plants has often been attributed to their use of insects for pollination. This need to attract insects implies a partial reduction in repellency which may have enabled the first insect herbivores to develop. It is interesting to note that flowering plants are generally much more palatable to insects than the more primitive plants such as conifers and ferns which do not require insects for pollination (Edwards and Wratten,1980; Hodkinson and Hughes,1982; Jones and Coaker,1978).

Insects, however have not evolved solely with respect to plants any more than have plants with respect to insects but the plant is probably more critical to the insect than vice versa. Plants serve not only as food but also as microhabitat, shelter and protection (Dethier,1970; Southwood,1972).

Differences in the damage caused by an insect species to different plants in a locality during a given period reflect their relative susceptibility or resistance and are determined by factors which influence the establishment of a population of an insect on the plants (Saxena,1969). From information presented in the reviews of Bordner et al.(1983), Dethier(1976), Harborne(1977), Jermy(1966), Kennedy(1965), Renwick(1983) and Thorsteinson(1960), it is apparent that the behaviour of insects in selecting a host plant for food and shelter is affected by a wide array of physical and chemical stimuli. The preference or non-preference of insects for different plants may be observed in respect of their orientational, feeding and/or ovipositional responses. Simultaneously, environmental factors may influence the ability of the plant to combat insect attack, and chemical constituents of the plant may have indirect effects on the success or failure of its attackers. Fraenkel(1969) and Schoonhoven(1968) suggested that secondary substances in plants are directly involved in the feeding behaviour of insects. Major classes of secondary substances involved in insect-plant interactions are nitrogen compounds(alkaloids, amines, non-protein amino acids, cyanogenic glycosides, glucosinolates); terpenoids (monoterpenes, sesquiterpene lactones, diterpenoids, saponins, limonoids, cucurbitacins, cardenolides, caratenoids); and phenolics (simple phenols,flavonoids including tannins and quinones) (Bernays,1981; Edwards and Wratten,1980; Harborne,1977). Secondary substances may act as both feeding stimulants and deterrents depending on the adaptation of the insect to them. The presence of secondary

substances therefore may offer protection from one insect but may increase the risk of invasion by others.

From the insect's point of view all chemical innovations of plants are relevant regardless of the reason for their appearance. Insects can adapt biochemically at different stages in the processes of digestion and assimilation or alternatively insects can learn new feeding habits and move away in search of more suitable food. Metabolic modifications, especially the development of specific enzymes and detoxification mechanisms, have greater relevance and are probably the most common and important modifications for herbivory. Detoxification usually involves oxidations, reductions, hyrolyses or conjugations of molecules, and a group of enzymes called mixed-function oxidases in insect guts are probably the most important detoxification system in insects (Blum,1983; Brattsten et al.,1977). Krieger et al.(1971) surveyed the activity of midgut microsomal oxidase enzymes in larvae of 35 species of Lepidoptera and showed that the mean oxidase activity in polyphagous species was nearly 15 times greater than in monophagous species. Moreover, instead of detoxifying plant toxins,insects can also deal with them by sequestering them. Polyphenols, alkaloids, terpenoids, among other chemical substances, are sequestered by a wide range of insects and in some cases may be used in the insect's defense (Blum,1983; Duffey,1980).

Lepidoptera are thought to have evolved subsequent to the Angiosperm explosion in the early Tertiary, about 60 million years ago and they seem to be the last of the major orders of herbivorous insects to have evolved to their host plants(Hodkinson and Hughes,1982). Lepidopterous insects have since undergone a long and varied period of co-evolution and adaptation with their host plants. Thus,it is not surprising that different species of Lepidoptera have developed different patterns of host-plant relationship coupled with different

life cycle strategies and feeding mechanisms for exploitation of their hosts. In general, groups of closely related host-specific insect species often feed on groups of closely related plant species, indicating a close evolutionary relationship between the two groups. However, this is not always the case and in some more recent groups,including Lepidoptera, the evidence suggests that host-plant switching on to distantly related plant groups has frequently occurred (Mulkren,1967; Powell,1980).

1.Relationships between Heliothis species and their food plants

Plant tissues consist mainly of water and relative indigestible compounds such as cellulose and lignin. This makes them a good potential source of water for phytophagous insects, but in many cases an unpromising source of energy and nutrients. The fresh weight of leaves may therefore be more than 90% water and only 1 to 3% protein with most of the residue carbohydrate. Most leaf material thus has a lower energy content than insect tissue. On a dry weight basis, most plant tissues contain at most 3 to 4% nitrogen while insect tissues contain 7 to 14% (DeFoliart,1975; Gorham and Sanger,1967; Hughes,1971; Mattson,1980). In terms of gross composition therefore most plant tissue is fairly low grade food for insects. Thus to acquire the quantities of energy, nitrogen and often phosphorus they need, herbivorous insects have to consume disproportionately large quantities of plant for each unit of insect growth. However, some plant tissues provide a better food source than others in terms of energy, nitrogen content and water soluble B-vitamins. Thus, seeds, pollen and active meristems have a relatively high protein content which may be expressed as high energy and/or nitrogen level. Numerous studies though, such as Al-Zubaidi and Capinera(1984), Hughes(1971), McNeill(1973), Morrow and Fox(1980) and Parry(1976), have indicated that total energy content and total nitrogen

are at best fairly crude indicators of the potential food resource available to a herbivore.

Many investigators have demonstrated larval feeding preference of Heliothis for different parts of host plants. Although Heliothis larvae do feed on almost all parts of host plants, they feed preferentially on reproductive parts such as fruits,flowers, flower buds, pods and seeds i.e.those plant parts of higher nutritional value. Burkett et al. (1983),Farrar and Bradley(1985) and McMillian et al.(1966) showed that H.zea in the United States of America preferred tomato fruits,tomato flowers, corn kernels,corn seeds and cotton flowers and bolls to tomato leaves, corn leaves and cotton leaves. They also reported that larvae fed on preferred food had the highest mean survival. Wilson and Waite(1982) also showed that H.armigera and H.punctigera larvae in Australia fed selectively on fruits, terminals, squares and bolls of cotton. For H.armigera, a number of workers have investigated larval feeding behaviour on various plant parts in different areas of the world. On cotton, larvae feed preferentially on cotton buds, flowers, fruits, terminal shoots, squares and bolls, although a significant amount of leaf-feeding is also exhibited. (Mabbett et al.,1979; Pretorius, 1976; Singh and Sidhu,1980). On tomato where almost all parts are consumed, larvae still prefer fruits and flowers, especially young fruits during the flowering stage(Tewari and Moorthy,1984). Besides cotton and tomato,flowers and immature fruits of kenaf (Hibiscus cannabinus), inflorescences of mango and of ornamental plants such as carnation, rose, gerbera and gladiolus are preferred to their leaves (Kishore and Misra,1985; Pietanza,1968; Singh,1985).

However, not all potential host plants provide food for Heliothis. Some plant organs may possess structures which repel,injur or kill insects landing on them but the most intensively studied barriers between Heliothis and potential plant food are the secondary metabolites

especially alkaloids. These are heterocyclic nitrogen compounds that exist as water soluble cations such as nicotine, cocaine, quinine, morphine and caffeine. Fery and Cuthbert (1975) reported varying degrees of antibiosis among excised foliage of tomato species and further showed that an ethanolic extract from tomato leaves was responsible for reducing survival rates of H.zea larvae. The most effective growth inhibitor in tomato to all tomato fruitworm species is α-tomatine which is isolated mainly from tomato leaves. Other growth inhibitors which have been found in leaves of Heliothis host plants,especially in tomato leaves, are chlorogenic acid,rutin and 2-tridecanone (Campbell and Duffey,1981; Elliger et al.,1981; Farrar and Kennedy,1987; Isman and Duffey,1982; Williams et al.,1980).

2.Oviposition of Heliothis species on plants

The theory of larval memory,also known as Hopkins'host selection principle,postulates that the females of phytophagous insects prefer to oviposit upon the same plant species as that upon which they themselves had fed as larvae (for review see Dethier,1954). This principle has stimulated a number of papers and has been tested on a great number of insect species. Most reports have concluded that there is no correlation between larval feeding preferences and oviposition preferences (Firempong, 1986; Jackson et al.,1983; Rausher,1979; Wiklund,1974) i.e.that Hopkins'host selection principle is not valid.

Several investigators have reported that chemical cues in the form of odours emanating from rapidly growing plants attract noctuid moths and stimulate oviposition (Fletcher,1941; Jones et al.,1973). Selection of a suitable oviposition site may also be influenced by the surface texture of the substrate(Callahan,1957). Available adult food for consumption before or during oviposition also enhances the attractiveness of the plant to the moth (Nuttycombe,1930). However,

Farrar and Bradley(1985), Firempong(1986), Hillhouse and Pitre(1976), Jackson et al.,(1983) and Snodderly and Lambdin(1982) pointed out that moths do not always oviposit on the same plants or parts of plants on which they feed or their larvae feed.

In general,moths of Heliothis species select for oviposition host plants in the flowering stages over other phenological stages (Firempong, 1986; Hardwick,1965; Neunzig,1969).These authors also pointed out the co-incidence of availability of nectar for adult moths. Adult food evidently has an important effect on adult longevity and egg production. Callahan(1961, 1962) for example, never observed mating when adults of H.zea were unfed, and mated ovipositing females fed more often and for longer periods than did unmated ones.However,Lukefahr and Martin(1964) found that H.zea was able to mate and oviposit without having fed but about a 50% increase in both fecundity and longevity resulted when adults were fed on a sucrose solution. Mourikis and Vassilaina-Alexopoulou (1970) also reported that H.armigera can lay eggs only when water is provided for adults.

Heliothis species tend to lay eggs on all parts of host plants (Atanasov,1964; Barber,1943; Johnson et al.,1975; Mabbett and Nachapong,1984). However,the oviposition preferences of Heliothis species have been investigated in 3 major respects; (1)reproductive parts such as fruits, flowers and flower buds vs vegetative parts such as leaves,stems leaflets: (2)upper vs lower part of plant: (3)lower vs upper surface of substrates. Broadley(1977), Hardwick(1965), Johnson et al.(1975), Lingren et al.(1977) and Neunzig(1969) stated that H.armigera, H.punctigera, H.virescens and H.zea preferred to oviposit on flowers and flower buds over leaves.In contrast, a great number of papers such as of Alvarado-Rodriguez et al.(1982), Farrar and Bradley(1985), Hillhouse and Pitre(1976), Jackson et al.(1983), Mabbett and Nachapong(1984), Patel et al.(1974), Snodderly and Lambdin(1982) and

Widstrom et al.(1979) reported that the same four species demonstrated highly significant preferences for oviposition on flat plant parts such as leaves and leaflets rather than on fruits,flowers and flower buds. Alvarado-Rodriguez et al.(1982), Hillhouse and Pitre(1976), Mabbett and Nachapong(1984), Patel et al.(1974) and Widstrom et al.(1979) showed that most eggs of H.armigera, H.virescens and H.zea were laid on the upper half of host plants such as tomato,cotton, and tobacco. Alvarado-Rodriguez et al.(1982) and Neunzig(1969) reported that no preference was found for upper or lower leaf surface of tobacco and tomato by H.virescens and H.zea but Jackson et al.(1983) showed that over 87% of eggs were found on the upper five leaves and 79% on the lower surface of tobacco leaves. Hillhouse and Pitre(1976) and Snodderly and Lambdin (1982) also reported that oviposition preferences of other Heliothis species were on the lower surface of host plant leaves. However,Patel et al.(1974) and Reed(1965) found that oviposition of H.armigera on cotton in India and in Tanganyika was primarily on the upper surface of leaves.

It is clear from this literature review that H.armigera, together with several other species of Heliothis, is highly polyphagous but that within plant species larval feeding tends to be concentrated on reproductive plant parts. Factors involved in host plant selection and larval food quality have so far been little studied.

CHAPTER 3

FIELD OBSERVATIONS OF POPULATION DEVELOPMENT ON FOUR HOST PLANTS AND SEASONAL DEVELOPMENT OF *HELIOTHIS ARMIGERA* IN THE MANAWATU

INTRODUCTION

Heliothis armigera conferta Walker occurs on a wide range of wild and cultivated plants in New Zealand, and is known as tomato fruitworm or corn earworm because it is recorded as a major pest on tomatoes and sweetcorn (Helson,1972; Scott,1984). It is of minor importance on capsicums, peas, pumpkins, legume seed crops, beans, lupin, conifer seedlings, marrow, clover, lucerne, peanuts, linen flax, tobacco, strawberry, oats, carrot, onion(flowers), citrus(blossoms) and a great number of ornamental herbaceous plants (Gaskin, 1966; Valentine,1975). On tomatoes the damage is easily recognized by holes eaten in the leaves and fruits. Larvae usually move to tomato fruits as they grow older(Cameron and Valentine,1985; Helson, 1972). Cameron and Valentine (1985) found that large *H.armigera* larvae caused 18-21% fruit damage in 24 hours in a glasshouse experiment. On maize and sweetcorn, larvae prefer corn cobs to leaves. On these plants larvae may reduce yields by desiccating silks during fertilization, or by eating kernels on the formed cobs. Damage is indicated by feeding on silks and the presence of insect frass at the tip of cobs(Helson, 1972; Watson, 1977). Besides these two main crops, *H.armigera* also damages radiata pine in the central North Island of New Zealand. Attack on pine is more severe in the second generation of caterpillars in February and March. Larvae

may also destroy yellow lupin before pine establishment(Alma, 1975b, 1977; Zondag,1982).

H.armigera moths lay their eggs preferentially on host-plant foliage such as tomato and corn leaves, although eggs are occasionally found on silks and corn cobs(Cameron and Valentine,1985; Watson,1977). Newly hatched larvae usually feed on host plant parts where eggs are deposited. The larger larvae then move to preferred plant parts where feeding continues until larvae are fully grown. There are 5 or 6 instars (Singh et al.,1982). Pupae are formed in the soil and most are diapausing pupae. In New Zealand over 60% of pupae of the first generation and 90% of pupae of the second generation enter diapause and overwinter (Alma,1977). In the central North Island of New Zealand, approximately 50% of overwintering pupae are infected with a parasitic fungus, Paecilomyces farinosus and only 1% are attacked by the parasite Pterocormus promissorius (Hymenoptera:Ichneumonidae) (Alma, 1975a, 1977). Adults emerge with the warmer spring weather, beginning about October in northern areas and later in southern areas (Gaskin, 1970a; Spitzer,1970; Valentine,1975). However, Alma(1977) reported that in the central North Island, adults first appear in November and December, with a second brood in February and March. There generally are 2 generations a year and more overlapping generations may be expected in the more northerly regions of New Zealand. Adults from the second generation produce a partial third generation of caterpillars before winter which mostly succumb to cold weather in April. Although some H.armigera moths are usually recorded in spring, the peak of moth numbers occurs between January and March. Highest populations usually occur in the lowland areas of the warmer North Island. Heaviest infestation of crops by H.armigera larvae occurs in late summer between

January and March (Alma,1975b; Cameron and Valentine,1985; Davies, 1973; Fox,1970a; Wood,1973).

H.armigera is found throughout New Zealand especially the North Island, and its southerly distribution is probably maintained by summer migrants. Migration of moths is highly affected by environmental conditions. Temperature plays an important role in migration of moths as they prefer warm conditions. Wind appears to operate as an inhibiting factor for flight. Rain is not regarded as an important factor inhibiting flight but cold rain, even without much wind, is nearly always a sign that very few moths will fly (Gaskin, 1964, 1970a).

FIELD TRIALS

To investigate the preference of H.armigera between four plant species and to observe larval feeding behaviour and seasonal development a small plot field trial was conducted over two seasons at Palmerston North, Manawatu (southern North Island of New Zealand).

MATERIALS AND METHODS

1.Field study area

The trial was conducted in a field area of Massey University land during two spring and summer seasons,1984-85 and 1985-86. The area had previously been used to grow sweetcorn and pumpkin and infestation of these crops by H.armigera had been reported. The area was ploughed twice in spring (September) followed by rotovating to provide a suitable tilth. To assist with weed control paraquat was applied pre-planting to plots to be planted with tomato and aster (For detail see Table 3.1). Soil was sampled and nutrient status tested by the Ministry of

Agriculture and Fisheries. The recommended fertilizers used on the trial site were a mixture of 40 g sulphate of ammonia, 100 g superphosphate and 25 g sulphate of potash per square metre. Each plot measured 5 x 5 m and there were four replications in a Latin square design as shown below and in Plate 3.1.

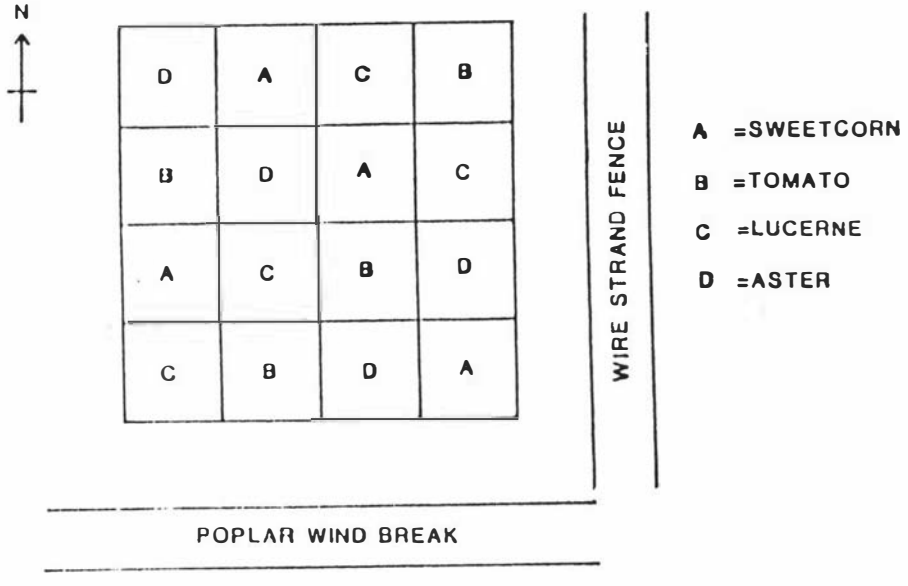

Plate 3.1 General view of experimental area.

(4 November 1984)

2.Plants

Plots (5x5 m) of the four host plants selected from four different plant families were established in spring of each year. The four host plants were sweetcorn(Zea mays) (NK 51036), tomato(Lycopersicon esculentum) (Castlehy 1204), lucerne(Medicago sativa) (Goatid WL 318), and aster (Callistephus chinensis) (Powder Puffs MXD 87).

Lucerne seed was sown directly into the plots at a rate of 20 kg/ha in early October 1984.

Sweetcorn seed was also sown directly into plots in early October with 2 seeds per hole, 15 cm between holes and 25 cm between rows.

Tomato seed was sown in small plastic trays in a glasshouse in late October. When tomato seedlings were about 4 cm high (2 weeks) they were transplanted into plastic pots with one seedling per pot. When plants were about 15 cm high (4 weeks) they were planted into the field plots with 50 cm spacing within and between rows.

Aster seedlings were raised in a similar manner to tomato seedlings but were planted in the field when 5 weeks old with 30 cm spacing within and between rows.

Sweetcorn, tomato and aster were re-established each year on the same plots. Plots were irrigated twice a week as required. Details of pre-plant and early post-emergence herbicide applications are given in Table 3.1. Later weed control was by hand. Populations of H.armigera were allowed to establish naturally.

Table 3.1 Herbicides, rates and application times to field plots.

Plant	Herbicide	Rate	Application time
Tomato	Paraquat	3 l/ha	Pre-planting
Aster	Paraquat	3 l/ha	Pre-planting
Sweetcorn	Atrazine 5A	3 l/ha	First true-leaf
Lucerne	2,4-DB	3 l/ha	2-5 true-leaf

3. Seasonal occurrence of H.armigera larvae on host plants in relation to plant phenology.

Field observations were made between November and March in each season. Starting in November, plants were carefully checked every other day. When the first larva was found observations were made every 3 days. It had been planned to determine sites of egg deposition on plants but this proved impossible in the field situation. Because of low numbers of larvae through into December and January, larvae were directly counted on particular parts of the plants i.e. tomato leaves, tomato flowers, tomato fruits, aster leaves, aster flowers, sweetcorn leaves, sweetcorn cobs, lucerne leaves and lucerne flowers. Counts of larvae were made between 2 and 3 pm because of their activity during this period.

Each plant species required a different method of assessing larval populations and thus no absolute scale of population density could be devised. However, valid comparison could be made between numbers of larvae on different parts of plants for each plant species. Thus the means of numbers of larvae observed over two growing seasons were used to calculate percent of larvae on different parts of each plant species.

4.Damage to tomato fruits by larvae of H.armigera

At harvest tomato fruits were grouped into 4 categories by weight. These were 1-10 g, 10.01-20 g, 20.01-40 g, and over 40 g. Twenty fruits of each weight category were sampled from each plot, giving a total of 80 fruits of each category for each sampling date over the 4 replications. Sampling was undertaken on February 4, 11, 18, 25, and March 4,1985. Each fruit was put into a small plastic bag and all bags returned to the laboratory where each fruit was weighed and the presence of larvae recorded. All holes in fruits were checked but only fresh holes were considered as damage.

Differences in amount of damage and numbers of larvae between fruit size categories were subjected to T-test and correlation analysis.

5.Infestation of aster flowers by larvae of H.armigera

When aster plants (variety Powder Puffs MXD 87) bloomed in February,1985 they produced 5 different colours; white, pink, mauve, purple and red. From February 4, no larvae were observed on aster leaves and all were found on flowers generally one larvae to one flower. Total larvae and total aster flowers were counted every 3 days and numbers of larvae on the different colours of flowers were also recorded.

Correlation coefficient, multiple regression and T-test were used for data analysis.

6. Infestation of sweetcorn cobs by larvae of H.armigera

In February, 1985 the sweetcorn was maturing and observations were carried out every 3 days between February 4, and March 2. Total sweetcorn cobs were counted and the number of cobs damage by H.armigera larvae was recorded. As most larvae on cobs cannot be seen because of their concealed habit, corn cobs were checked for presence of frass at the tips and destruction of silks. Actual presence of larvae was also checked.

Results are expressed as percentage infestation of cobs.

7. Pheromone trapping of H.armigera at Palmerston North

Four pheromone traps were operated from December 25, 1985 to April 30, 1986 in the trial area. Each trap was made of cylindrical plastic drain pipe, 30 cm long and 15 cm diameter supported by 2 stakes approximately 1 m above ground level and tightened by wire. One trap was set in each corner of the field trial area. To avoid any bias of wind direction, 2 traps were orientated N-S and the other two E-W. The pheromone laminates were purchased from SIRATAC Ltd., New South Wales, Australia. One pheromone laminate was hung centrally inside each trap by a thin wire. Each trap tube was lined inside with insect trapping grease (Tanglefoot supplied by DSIR, Auckland) spread on a polythene film liner which was renewed every 3 days. Pheromone laminates were replaced every 3 weeks. Moths caught were removed daily, identified to species and the numbers recorded.

Some factors affecting the numbers of moths caught by traps are peak responsive period of moths, wind velocity, temperature, atmospheric pressure, rain, light intensity, air currents, fog and nocturnal skylight (Hartstack et al.,1979; Kehat et al.,1980). Environmental factors considered in interpreting the present trap catches were maximum

day temperature, minimum night temperature, wind velocity, and rainfall. These data were obtained from the DSIR meteorological station, Palmerston North which was situated less than 1 km from the trial area.

Statistical values calculated were correlation coefficients between numbers of moths caught and environmental factors (based on daily weather and 3 days trap data) and analysis of variance to test the significance of differences.

RESULTS

1. Seasonal occurrence of H.armigera larvae on host plants in relation to plant phenology

As the method of assessment was not constant across plant species, comparisons between species are only approximate and should be interpreted with caution. In December all host plants were immature (no flowers) and negligible numbers of larvae were found. The first larva was found on aster leaves on January 2, 1985 in the first season and on tomato leaves on December 27, 1985 in the second season. After these dates more larvae occurred on aster and tomato leaves but none on sweetcorn leaves. In January, plants of all four species were flowering and larvae were found on both leaves and flowers of tomatoes and asters. On lucerne, totals of only 4 and 5 larvae were found on leaves in January of each season respectively and none was found at any time on lucerne flowers. On sweetcorn, larvae were first found on both leaves and the tips of cobs on the same day in late January. Soon after tomatoes produced fruits, aster bloomed, and sweetcorn cobs formed seeds, most larvae moved onto these plant parts. This was associated with a decline in the numbers of larvae on leaves of all plants until by February hardly any were found on foliage.

Thus by late January and in February most larvae were feeding on

tomato fruits and aster flowers with some on sweetcorn cobs. When tomato fruits started to ripen in February the total number of larvae on these plants decreased. This continued progressively up to harvest.

The numbers of larvae in each season on different plant parts are shown in Figures 3.1 for tomatoes, 3.2 for aster, and 3.3 for sweetcorn. Figure 3.4 shows mean numbers of larvae over two seasons on all plant parts. From these results it could be concluded that the relative preference of feeding sites of H.armigera larvae on each plant species were:

Tomato : fruits > leaves > flowers

Aster : flowers > leaves

Sweetcorn : cobs > leaves

Lucerne : hardly preferred at all compared to other species

2.Damage to tomato fruits by larvae of H.armigera

Damage to tomato fruits by H.armigera between February 4, and March 4, 1985 is shown in Table 3.2. There was no significant difference in damage between fruit of category 1 and 2, and 3 and 4. Differences were significant between category 1 and 3 (P=0.001), 1 and 4 (P=0.013), 2 and 3 (P=0.01), and 2 and 4 (P=0.017). This showed that damage to tomato fruits by H.armigera larvae was higher in smaller fruits (1-20 g) than in larger ones (above 20 g). The percentages of tomato fruits which possessed larvae on them were 6.7, 6.5, 5.5, and 4.2 % for size categories 1 to 4 respectively. Smaller fruits (1-20 g) thus had significantly more larvae than larger fruits (above 20 g) (P=0.011).

3.Infestation of aster flowers by larvae of H.armigera

Infestation of aster flowers by larvae of H.armigera in the field at Palmerston North between February 4, and March 2,1985 is shown in Table 3.3 and Figure 3.5. Mean numbers of white, mauve, pink, red and

purple asters were 200.6, 242.9, 284.2, 302.9 and 458.3 respectively. Differences between these values were significant except between pink and red. Mean numbers of larvae per 10 flowers on white, mauve, pink, red and purple flowers were 1.37, 0.29, 0.45, 0.15 and 0.04 respectively. These figures show highly significant differences. It may be concluded that many more H.armigera larvae were found on white than on purple flowers, although this aster variety produced many more purple than white flowers. Thus the results showed that;

Number of aster flowers : white < mauve < pink = red < purple but number of larvae on flowers : white > mauve > pink > red > purple.

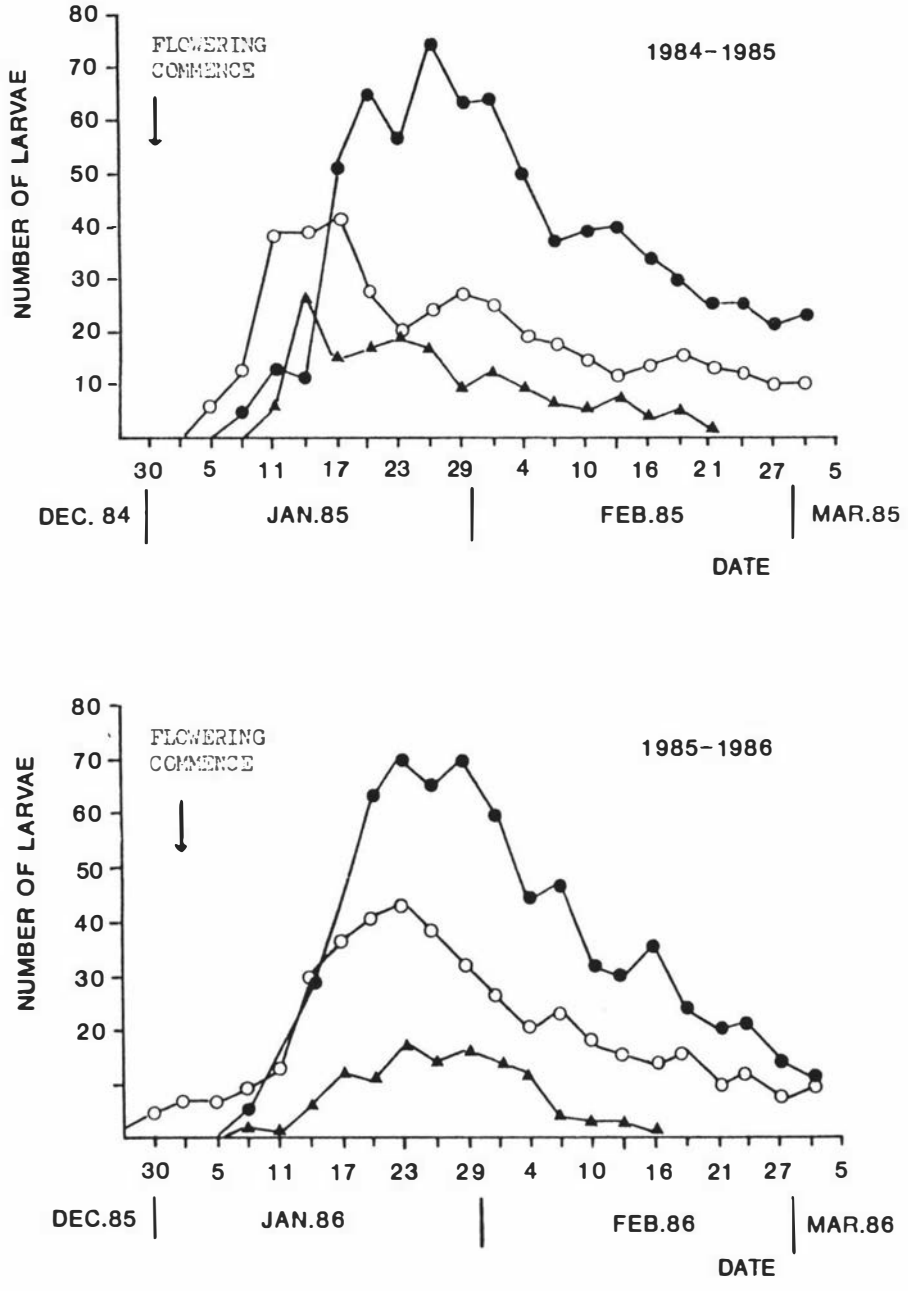

Figure 3.1 Numbers of H.armigera larvae observed every 3 days from December 27, to March 2, 1984-1985 and 1985-1986 on tomato plants.
(O) on leaves, (▲) on flowers, (●) on fruits

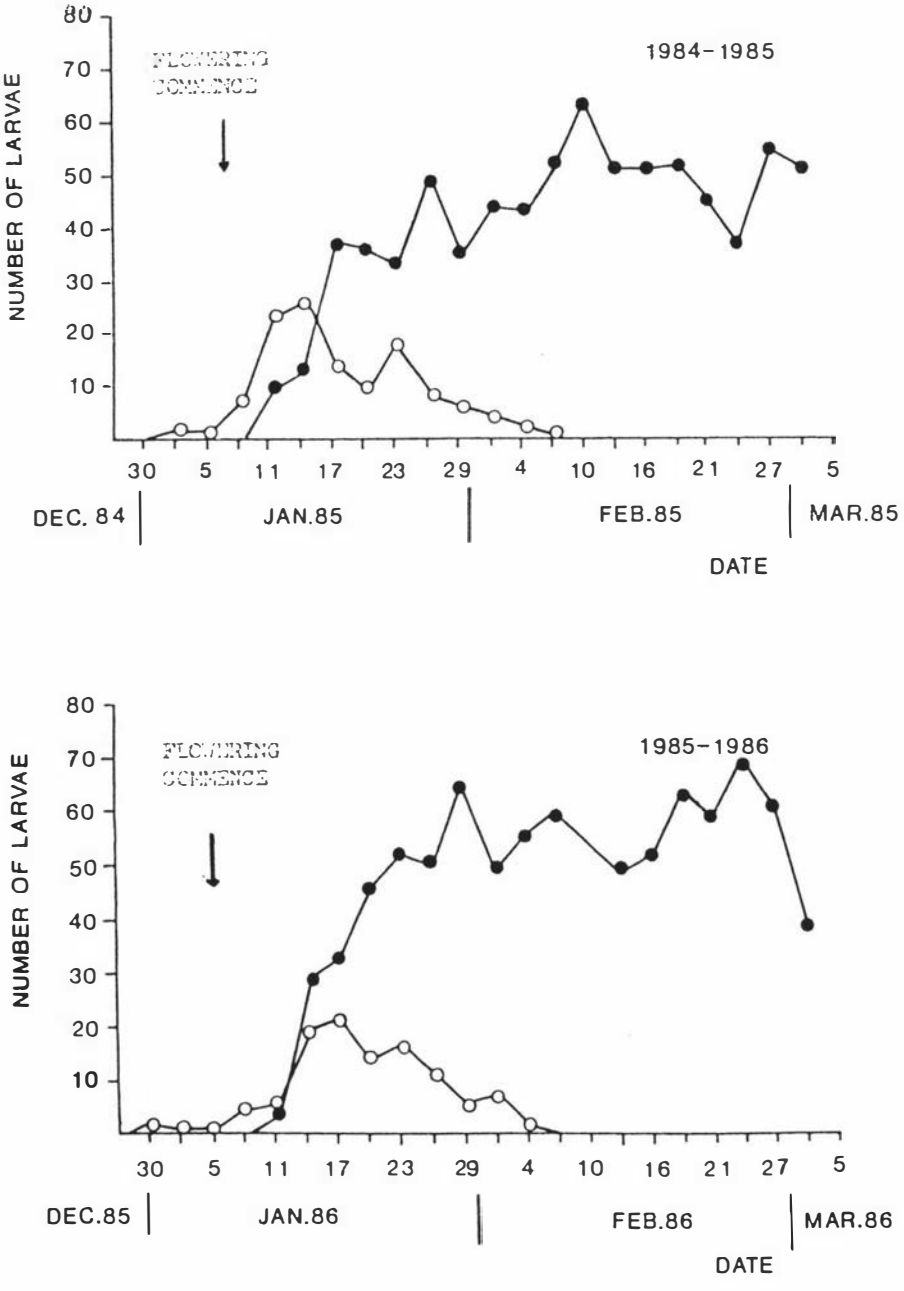

Figure 3.2 Numbers of H.armigera larvae observed every 3 days from December 27, to March 2, 1984-1985 and 1985-1986 on aster plants.
(O) on leaves, (●) on flowers

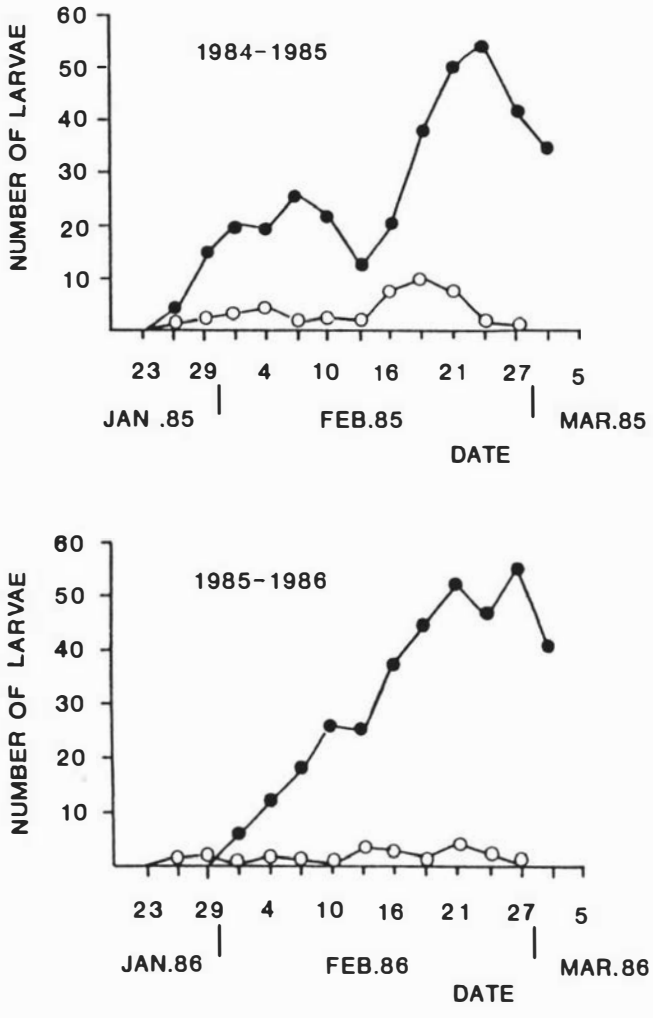

Figure 3.3 Numbers of H.armigera larvae observed every 3 days from December 27, to March 2, 1984-1985 and 1985-1986 on sweetcorn plants.
(O) on leaves, (●) on cobs

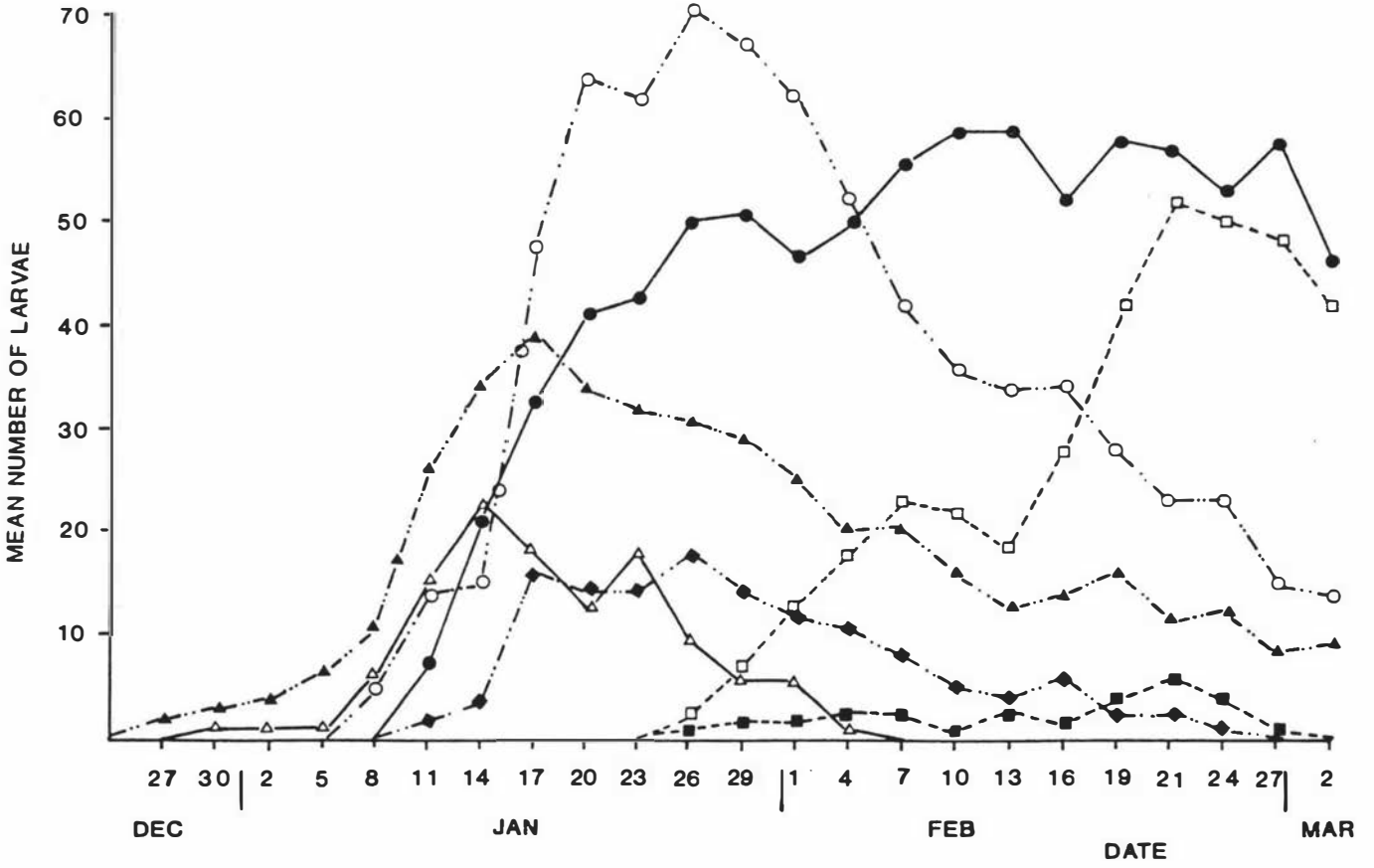

Figure 3.4 Mean numbers of H.armigera larvae on different plant parts observed every 3 days from December 27, to March 2, average over the two seasons, 1984-1985 and 1985-1986.
(▲) on tomato leaves, (◆) on tomato flowers, (○) on tomato fruits, (△) on aster leaves, (●) on aster flowers, (■) on sweetcorn leaves, (□) on sweetcorn cobs

Table 3.2 Damage to each size category of tomato fruits by H.armigera larvae between February 4, and March 4, 1985.
(For statistical analysis and differences see page 45)

Sampling date	Category 1		Category 2		Category 3		Category 4	
	No.fruit damaged per 80	No.larvae on fruits	No.fruit damaged per 80	No.larvae on fruits	No.fruit damaged per 80	No.larvae on fruits	No.fruit damaged per 80	No.larvae on fruits
4/2	38	3	50	6	28	5	32	2
11/2	41	6	51	4	32	4	24	4
18/2	36	7	34	5	30	4	32	4
25/2	40	6	45	6	33	5	30	5
4/3	39	5	47	5	27	4	29	2
Total	194	27	227	26	150	22	147	17
%	48.50	6.70	56.75	6.50	37.50	5.50	36.75	4.20

Table 3.3 Mean total numbers of aster flowers and mean numbers of *H.armigera* larvae per 10 flowers observed between February 4, and March 2,1985.
(All colours of flowers flowered at the same time)

	Aster flowers (mean ± S.E.)	Larvae per 10 flowers (mean ± S.E.)
White	200.6 ± 20.36	1.37 ± 0.12
Mauve	242.9 ± 13.83	0.29 ± 0.03
Pink	284.2 ± 19.86	0.45 ± 0.05
Red	302.9 ± 25.71	0.15 ± 0.02
Purple	458.3 ± 21.31	0.04 ± 0.02

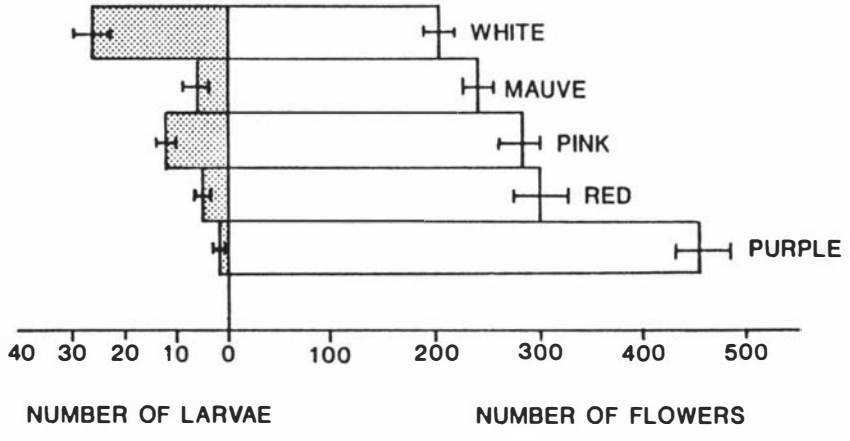

Figure 3.5 Mean total numbers of H.armigera larvae observed every 3 days between February 4, and March 2, 1985 on different colours of aster flowers.

4.Infestation of sweetcorn cobs by larvae of H.armigera

In February, 1985 the sweetcorn cobs were severely damaged (Table 3.4). The overall mean percentage was 23.6 % and percent of cobs with H.armigera larvae 11.2. The percentage of cobs damaged increased from 18.2 % on February 4 to 29.5 % on March 2. There was a close correlation between numbers of cobs and numbers of larvae present.

Table 3.4 Infestation of sweetcorn cobs by larvae of H.armigera between February 4, and March 2, 1985.

Date	Total cobs sampled	No.of cobs damaged	%of cobs damaged	No.of larvae on cobs	%of cobs with larvae
4/2	230	42	18.3	19	8.3
7/2	239	51	21.3	26	10.9
10/2	255	54	21.2	17	6.7
13/2	255	57	22.3	12	4.7
16/2	283	60	21.2	20	7.1
19/2	283	66	23.3	37	13.1
21/2	283	72	25.4	50	17.7
24/2	291	75	25.8	54	18.6
27/2	291	80	27.5	41	14.1
2/3	302	89	29.5	34	11.3
Means	271.2	64.6	23.6	31	11.2

5.Pheromone trapping of H.armigera at Palmerston North.

Between December 25, 1985 and April 30, 1986, 306 Heliothis moths were caught by the 4 pheromone traps; all were H.armigera males. The first moth was caught on December 29, 1985 and the last on April 25, 1986. The percentage of moths caught from December to April was 1.3, 14.1, 24.5, 44.1 and 16.0 for each month respectively with a clear peak in March (Table 3.5). There was no difference in the numbers of moths caught from pheromone traps orientated E-W compared to N-S. The mean values of moths caught per night, daytime maximum temperature, night time minimum temperature, wind velocity and rainfall during the trapping period were 2.4, 21.9°C, 12.6°C, 10.7 km/h and 2.9 mm/day respectively. Minimum temperature at night showed the most effect on numbers of moths caught ($r=0.1247$, $P=0.082$) and maximum temperature in daytime showed the least effect ($r=-0.0304$, $P=0.368$) but no environmental factor showed significant correlation with moth catches (Table 3.6). The relationships between numbers of moths caught and maximum temperature, minimum temperature, wind velocity and rainfall are shown in Figure 3.6.

It may be concluded that at Palmerston North between December 1985 and April 1986, numbers of moths caught was highest in March but that for individual days there was no significant effect of temperature, wind velocity or rainfall on trap catches.

Table 3.5 Pheromone traps catches of H.armigera moths in experimental plot area between December 1985 and April 1986.

Period	Numbers of moths caught		Total	%of total
	Trap orientation			for period
	E-W	N-S		
December 1985	1	3	4	1.3
January 1986	23	20	43	14.1
February 1986	40	35	75	24.5
March 1986	57	78	135	44.1
April 1986	28	21	49	16.0
Total	149	157	306	
%	48.7	51.3		100

Table 3.6 Correlation coefficients(r) and probability(P) between environmental factors and pheromone trap catches of H.armigera.

	Moths caught per night	Maximum day T(°C)	Minimun night T(°C)	Wind velocity (km/h)	Rainfall
Moths caught per night		-0.0304 (P=0.368)	0.1247 (P=0.082)	0.1211 (P=0.088)	-0.1154 (P=0.099)
Mean	2.4	21.9	12.6	10.7	2.9
SD	1.759	2.903	3.8	4.962	7.311

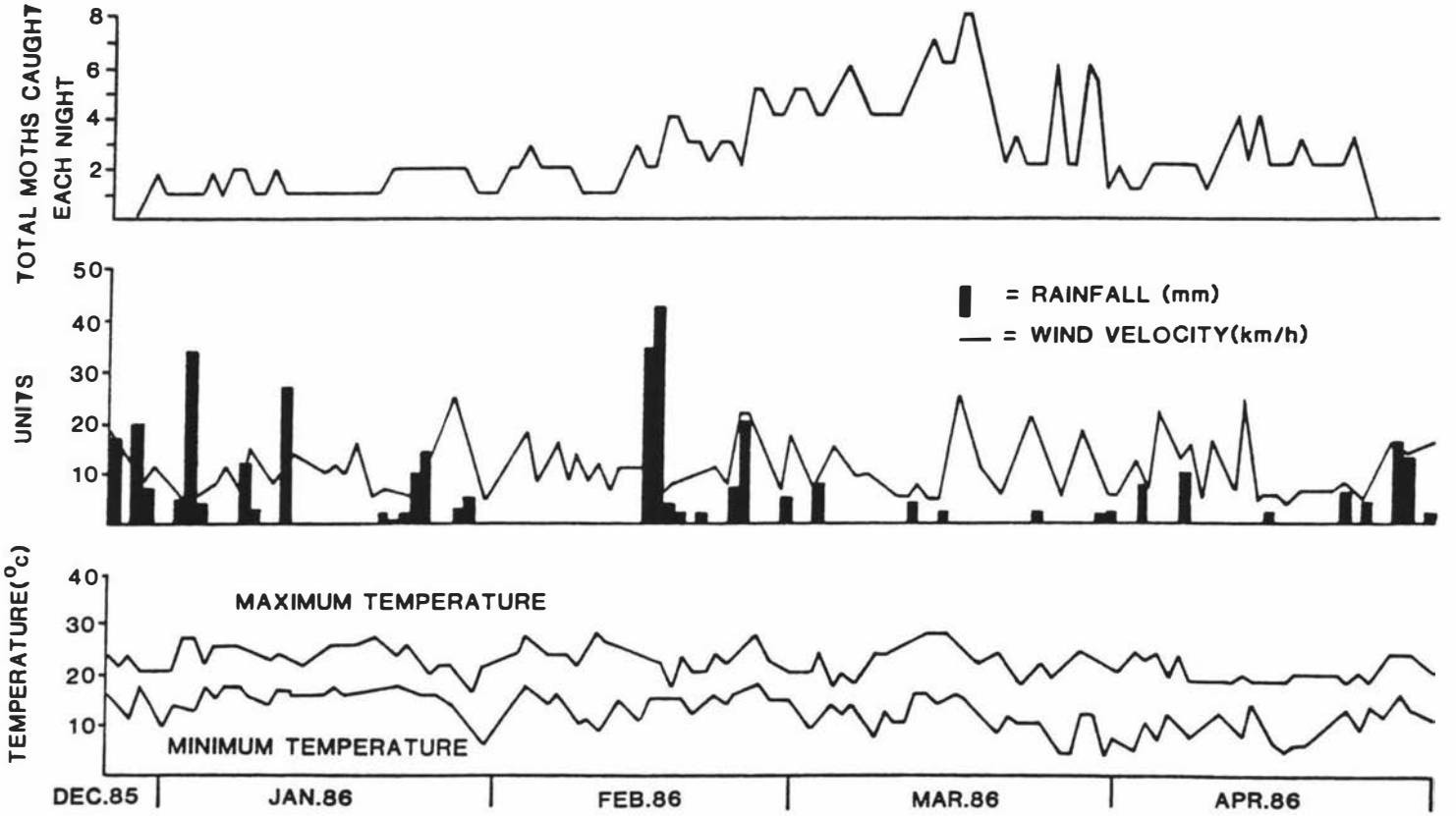

Figure 3.6 Relationship between numbers of H.armigera moths caught in pheromone traps and temperature, wind velocity and rainfall at Palmerston North between December 25,1985 and April 30,1986.

DISCUSSION

1. Seasonal occurrence of H.armigera larvae on host plants and infestations in relation to plant phenology.

In early stages of plant growth (no flowers) before February in both seasons, larvae were found feeding on host plant leaves especially on tomato and aster leaves. This pattern occurred until plants were flowering and then the numbers of larvae on leaves decreased. It may be concluded that, as in this period only leaves were available, H.armigera larvae had no choice of other food sources. Most eggs are probably deposited on plant leaves and stems and newly hatched larvae start feeding where eggs are laid. Burkett et al.,(1983) showed that first instar larvae of H.zea fed initially on the plant parts on which they were placed. Pencoe and Lynch (1982) also reported that first instar larvae of H.zea exhibited a distinct preference for terminals of peanuts as feeding sites which were also the main oviposition sites. Atanasov(1964), Barber(1943) and Johnson et al.(1975) reported that Heliothis species lay eggs on all parts of host plants, although oviposition preferences are often for plant leaves (Alvarado-Rodriguez et al.,1982; Farrar and Bradley,1985; Hillhouse and Pitre, 1976; Mabbett and Nachapong,1984). However, some investigators, for example, Broadley(1977), Johnson et al.(1975), Lingren et al.(1977) and Neunzig(1969) showed that Heliothis species preferred to lay eggs on flowers and flower buds. In the present field trial only leaves and stems were available early in the season for oviposition and for larval

food. Thus newly hatched larvae fed initially on leaves whether they were preferred food or not. From the data it cannot be concluded that lucerne, tomato and aster leaves were preferred food to sweetcorn leaves simply by the numbers of larvae on them. It is probably because more eggs were laid on lucerne, tomato and aster leaves than on sweetcorn leaves. Further experiments are needed to investigate this.

On tomato and aster plants, the first larva was found on leaves in both seasons and later the numbers of larvae increased on flowers and fruits (Figures 3.1, 3.2, 3.3 and 3.4). This result is supported by the finding of Burkett et al. (1983) and Cameron and Valentine (1985). When larvae grow bigger they tend to move off from where they initially fed (such as leaves and terminals) and search for more preferred plant parts. Burkett et al.,(1983), Farrar and Bradley (1985) reported that larvae of H.zea preferred tomato and cotton flowers and fruits to leaves and also that larvae fed on flowers had the highest mean survival. Eger et al.(1982), Pietanza(1968) and Raina et al.(1986) also reported that aster and carnation flowers were preferred by Heliothis species over leaves. On sweetcorn, in the present work larvae were found on the same date on leaves and on cobs. This may be because in this case eggs were laid on both silks and leaves and that newly hatched larvae fed initially on them. Gross et al.(1975), Harrison(1960) reported that H.zea laid eggs preferentially on corn silks and leaves and that newly hatched larvae started feeding where eggs were deposited. Sweetcorn leaves seem to be the least preferred food for H.armigera larvae (Figures 3.3 and 3.4). McMillian et al.(1966) demonstrated that H.zea

utilized corn kernels, tomato fruits, corn silks and corn seed rather than tomato leaves, corn leaves and many other host plant leaves.

One interesting result was the infestation of larvae on aster flowers in relation to flower colour. Although the numbers of purple asters were highest compared to other colours, the numbers of larvae found on them were lowest. The reverse occurred with white aster flowers. No evidence is available to explain this but it could be due to differences in attractiveness of flower pigments or to some other biochemical differences between flowers causing differential oviposition.

2. Pheromone trapping of H.armigera at Palmerston North

The pattern of pheromone trap catches with few moths in December and rising to a peak in March was similar to the results from light traps run at Massey University in 1966-1969 (Gaskin, 1970a; Spitzer, 1970). These authors reported that few moths(<10) were caught before January, although the first moth appeared in October. Gaskin(1970a) also showed variation of catches between two seasons (October to September). In 1966-67, five moths were caught during October to December but only one moth was caught in 1967-68 in the same period. Gaskin's data show that most moths were caught in February and March but none were caught during May to September in either season. Cumber(1951) also ran a light trap in Nelson (north- western South Island) from July 1949 to July 1950 but caught only 3, 3 and 7 H.armigera in January, February and March respectively.

In the present study it can be suggested that the very few moths(4) caught in December may have emerged from overwintering pupae. The number during this period may be low because of diapausing pupae from the previous season and/or pupal parasitism by the fungus, Paecilomyces farinosus (Alma, 1975a, 1977; Valentine,1975). The large number of moths caught in February and March must be mostly progeny from the first seasonal generation of larvae but may be supplemented by late emerging diapausing pupae. Other factors affecting the high trap catches in this period could be 1) optimum temperatures for moth activity, 2) the availability of food for adults in the form of suitable flowers, and 3) the various host plants providing attractive oviposition sites. Moths appearing in April may be from a second generation which mature and then produce a partial third generation of larvae many of which succumb to cold weather in late April and May. This pattern agrees with published descriptions of seasonal development in New Zealand (Valentine,1975).

Mean daily maximum temperature, minimum night temperature, wind velocity and rainfall during the observation period were 21.9°C, 12.6°C, 10.68 km/h and 2.9 mm/day respectively (Table 3.6). Although individual meteorological parameters showed no significant correlation with catches of moths (see Table 3.6), more moths were caught when the minimum night temperature was greater than 10°C, wind velocity was less than 20 km/h and there was less than 8 mm rainfall (Figure 3.6). Gaskin(1964) set a light trap in Wellington during two summer seasons of 1962-64 and reported that factors affecting the flight of Noctuid moths in general

were temperature, wind speed and rain. Other studies have shown that the flight of moths after dark is more dependent on temperature than on other factors. Gaskin(1964) concluded that strong wind appears to operate as an inhibiting factor, but cold rain even without much wind is nearly always a sign that very few moths will be flying. Hartstack et al.(1979) also showed that low temperature at night (<12.8°C) inhibits overall Heliothis moth activity including the courtship response and flight of male moths to pheromone traps. He considered that rain had little direct effect upon trap function, although heavy rain at night may hinder moth flight and thus decrease trap catches.

CONCLUSIONS

In Manawatu, New Zealand during the two growing seasons of 1984-1986, H.armigera moths were first caught by pheromone traps in December and the numbers reached a peak in March and were absent by late April.

In field crops, leaves(tomato and aster) were the first feeding site observed and soon after host plants produced flowers and fruits larvae moved on to these plant parts. On mature stages of plants larvae fed preferentially on fruits(tomato), cobs(sweetcorn) and flowers(aster) over plant leaves. Larvae were hardly observed at all on lucerne plants. The heaviest infestation of plants occurred in February and March.

CHAPTER 4

OVIPOSITION PREFERENCE OF HELIOTHIS ARMIGERA ON DIFFERENT PLANTS

INTRODUCTION

There is limited information on oviposition preference by the tomato fruitworm, H.armigera on different host plants. However, many studies have been conducted within plant species to determine factors influencing oviposition preference and oviposition site for several Heliothis species. Some investigators have suggested that initiation of oviposition response is due to host plant odours which emanate from rapidly growing plants and succulent tissues (Fletcher,1941; Jackson et al.,1984; Johnson et al.,1975). Surface texture of substrate (Callahan,1957; Lukefahr et al.,1965; McColloch, 1920), particular stages of plant growth and development (Mabbett and Nachapong,1983) and the availability of nectar for female moths (Alvarado-Rodriguez et al., 1982; Coaker, 1960) are all known to influence oviposition and egg production. In general, Heliothis spp. moths prefer to lay eggs on host plants in the flowering stage over other phenological stages (Coaker,1960; Firempong,1986; Hardwick, 1965; Neunzig,1969). Working with cotton, Mabbett and Nachapong(1983) found that H.armigera moths preferred to oviposit on healthy plants which were unusually tall. However, Broadley(1978) demonstrated that egg-laying of Heliothis spp. on tobacco in Queensland, Australia did not vary with plant size.

Heliothis moths are known to lay eggs on all parts of host plants (Atanasov,1964; Barber,1943; Mabbett and Nachapong,1984). Hillhouse

and Pitre(1976), Jackson et al.(1983), Patel et al. (1974) reported that Heliothis oviposited preferentially on the "upper half" of host plants. Broadley(1977) and Hardwick(1965) in review papers stated that H.armigera preferred to oviposit on flowers and flower buds over leaves. This is supported by the findings of Johnson et al.(1975), Lingren et al.(1977) and Neunzig(1969) on H.virescens and H.zea. In contrast, Mabbett and Nachapong(1984) and Patel et al.(1974) demonstrated that H.armigera laid eggs preferentially on flat parts of plants such as leaves, leaflets and terminal buds. This result is supported by a great number of publications such as those of Alvarado-Rodriguez et al.(1982), Farrar and Bradley(1985), Hillhouse and Pitre(1976), Jackson et al. (1983) and Snodderly and Lambdin(1982) which were mostly concerned with H.virescens and H.zea. Alvarado-Rodriguez et al.(1982), Broadley (1978) and Neunzig(1969) reported that no preference was found for upper and lower leaf surface of host plant in H.virescens and H.zea. However, Patel et al.(1974) and Reed(1965) found that oviposition of H.armigera on cotton was primarily on the upper surface of leaves. McColloch(1920) also showed that H.zea preferred to lay eggs on the upper leaf surfaces of corn compared to lower leaf surfaces. In contrast, Jackson et al.(1983), Hillhouse and Pitre(1976) and Snodderly and Lambdin (1982) reported that H.virescens and H.zea laid eggs preferentially on the lower leaf surfaces of cotton, tobacco and tomato.

The evidence for distinct preferences for plant parts or developmental stages for oviposition by Heliothis spp. is thus confusing and in some cases conflicting.

In the present work a series of experiments was undertaken to investigate for H.armigera oviposition preference between plant parts, and plant species according to phenological stage of development. The

possible role of plant odour in selection between plant species was also briefly examined.

MATERIALS AND METHODS

Larvae were reared on artificial diet as described in Chapter 5. Fully grown larvae were placed into pupation containers with vermiculite. Newly emerged moths were transferred to mating containers as described in Chapter 5 and provided with 10% honey pollen solution. The mating containers were kept in a controlled temperature room (20 °C) for 3 days before moths were used for experiments because it had been shown that most eggs were laid on the 4th, 5th and 6th days after emergence (Figure 4.1).

Lucerne, tomato, aster and sweetcorn plants were raised individually in plastic planting bags in a greenhouse. No pesticides were applied to these plants.

1. Oviposition preference of H.armigera for plant parts within plant species(mature flowering plants).

Within a greenhouse, one mature flowering plant was placed in a nylon mesh cage (1.5x1x0.5 m) into which 4 male-female pairs of pre-mated moths were released. Plants in the cages were replaced daily and moths were replaced every 2 days over a period of 12 days. There were six separate cages of each plant species. The numbers of eggs laid on each plant were counted in the following categories:

a) All plants: upper and lower half of each plant.

b) All plants: upper and lower surface of leaves.

c) Lucerne plants: flowers, stems and leaves.

d) Tomato plants: flowers, fruits, stems and leaves.

e) Aster plants: flowers, flower buds, stems and leaves(including calices)

f) Sweetcorn plants: tassels, ears, stems and leaves(including leaf sheaths).

Counts for each assessment were converted to percentages and then subjected to angular or arcsine transformation (Little and Hills, 1975).

2. Oviposition preference of H.armigera between four host plants(immature non-flowering plants).

Within a greenhouse, one immature plant each of lucerne, tomato, aster and sweetcorn were placed together in a nylon mesh cage (2x2x1.8 m). Plants were not identical in age but all were expected to flower in approximately 2 weeks time. According to Firempong(1986), the height of host plants strongly influences oviposition preference so all plants in this experiment were adjusted to the same height. Plants were spaced approximately 1 m apart. Five male-female pairs of pre-mated moths were released into the cage and allowed to lay eggs on the plants over 2 days when they were replaced by fresh moths. The process was repeated after 4 days. Moths in the cage were provided with 10% pollen honey solution from a centrally placed cotton wick dispenser. Plants were replaced daily and positions of plant species re-randomised. Numbers of eggs laid on each plant were recorded over 6 consecutive days.

3. Oviposition preference of H.armigera between four host plants (mature flowering plants).

This experiment was conducted in the same manner as experiment 2 but plants used were mature flowering plants. Lucerne and aster were

about 2-weeks into flowering, tomato plants were about 2-weeks into fruiting and sweetcorn plants were about 2-weeks into the cob stage. As availability of nectar from the test plants was considered to be a factor that might influence oviposition preference no pollen honey solution was provided for the moths in this experiment. Numbers of eggs laid on each plant were recorded over 6 consecutive days.

4. Effect of plant odour on oviposition preference of H.armigera (mature flowering plants).

This experiment was conducted in the same manner as experiment 3 but all plants(mature flowering) were covered with 2 layers of white muslin cloth. This was done to eliminate physical and contact chemical factors that could influence egg laying preference such as adult food source, plant surface texture, morphology, surface chemistry and colour leaving plant odour as the only determinant of choice of oviposition site. Moths were provided with 10% pollen honey solution. Numbers of eggs laid on the muslin cloth covering of each plant were counted daily. There were 4 replicates.

RESULTS

1. Oviposition preference of H.armigera for plant parts within plant species (mature flowering plants).

Mean percentages of eggs laid by H.armigera on various parts of lucerne, tomato, aster and sweetcorn plants are presented in Tables 4.1, 4.2, 4.3, 4.4 and Figures 4.2, 4.3 and 4.4. Percentages for each day for each plant are shown in Appendices 3, 4, 5 and 6.

On lucerne, 81.6% of eggs were laid on the plants and 18.4% on

surrounding substrates such as nylon mesh of the cage. Of eggs laid on the plants, 85.4% were laid on the upper half and 14.6% on the lower half. Most eggs were laid on leaves(82%) followed by flowers(13.2%) and stems(4.8%). Of those eggs laid on leaves, 76.6% were on the upper surface and 23.4% on the lower surface (Table 4.1 and Appendix 3)

On tomato, 76.4% of eggs were laid on the plants and 23.6% on other substrates. Of eggs laid on the plants, 79% were laid on the upper half and 21% on the lower half. Most eggs were laid on leaves (75.9%) followed by flowers(16.7%), fruits(5%) and stems(2.4%). Of those eggs laid on leaves, 76.3% were on the upper surface and 23.7% on the lower surface (Table 4.2 and Appendix 4).

On aster, 75.3% of eggs were laid on plants and 24.7% on other substrates. Of eggs laid on the plants, 73.4% were laid on the upper half and 26.6% on lower half. Most eggs were laid on leaves and calices(54%) followed by stems(29.5%), flower buds(10.3%) and flowers(6.2%). Of eggs laid on leaves, there was no significant difference between upper and lower surface, although slightly more eggs were laid on the upper surface(55.6%) than on the lower surface (44.4%) (Table 4.3 and Appendix 5).

On sweetcorn, 85.1% of eggs were laid on plants and 14.9% on other substrates. Of eggs laid on the plants, 75.4% were laid on the upper half and 24.6% on the lower half. Most eggs were laid on leaves(including leaf sheaths)(70.4%) followed by cobs(16.6%), tassels(10.4%) and stems(2.6%). Of those eggs laid on leaves, 72.5% were on the upper surface and 27.5% on the lower surface (Table 4.4 and Appendix 6).

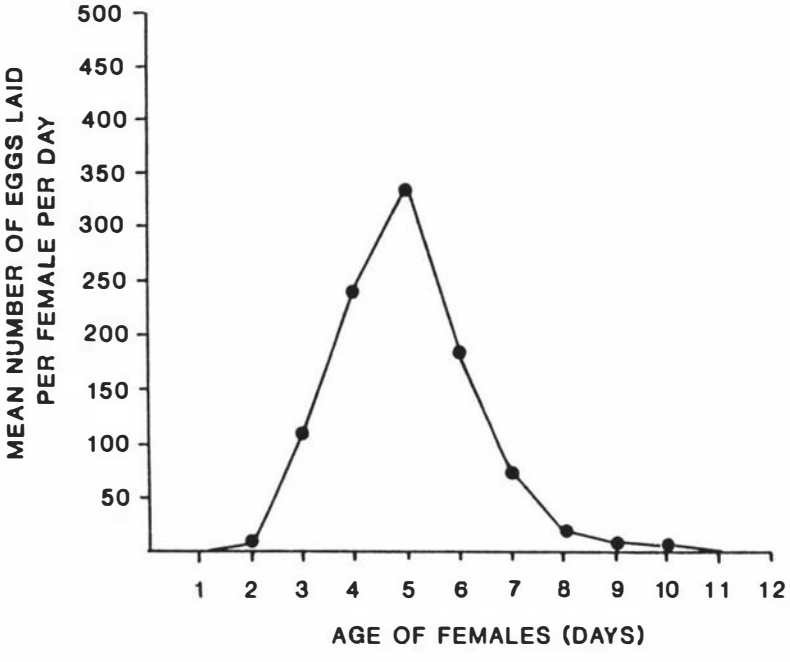

Figure 4.1 Mean numbers of eggs laid per female per day by H.armigera at 20±2°C and 16:8 (L/D) photoperiod.

Table 4.1 Percentages of eggs laid of H.armigera on different parts of mature flowering lucerne plants.

Plant parts	Percent of eggs laid
Flowers	13.2 a
Stems	4.8 b
Leaves	82.0 c
Upper half of plant	85.4 a
Lower half of plant	14.6 b
Upper surface of leaves	76.6 a
Lower surface of leaves	23.4 b

Means within groups in the column, not followed by the same letter are significantly different(P=0.05).

Table 4.2 Percentages of eggs laid of H.armigera on different parts of mature flowering tomato plants.

Plant parts	Percent of eggs laid
Flowers	16.7 a
Fruits	5.0 b
Stems	2.4 c
Leaves	75.9 d
Upper half of plant	79.0 a
Lower half of plant	21.0 b
Upper surface of leaves	76.3 a
Lower surface of leaves	23.7 b

Means within groups in the column, not followed by the same letter are significantly different(P=0.05).

Table 4.3 Percentages of eggs laid of H.armigera on different parts of mature flowering aster plants.

Plant parts	Percent of eggs laid
Flowers	6.2 a
Flower buds	10.3 b
Stems	29.5 c
Leaves and calices	54.0 d
Upper hlaf of plant	73.4 a
Lower half of plant	26.6 b
Lower surface of leaves and calices	55.6 a
Upper surface of leaves and calices	44.4 a

Means within groups in the column, not followed by the same letter are significantly different(P=0.05).

Table 4.4 Percentages of eggs laid of H.armigera on different parts of mature flowering sweetcorn plants.

Plant parts	Percent of eggs laid
Tassels	10.4 a
Cobs	16.6 b
Stems	2.6 c
Leaves and leaf sheaths	70.4 d
Upper half of plant	75.4 a
Lower half of plant	24.6 b
Upper surface of leaves	72.5 a
Lower surface of leaves	27.5 b

Means within groups in the column, not followed by the same letter are significantly different(P=0.05).

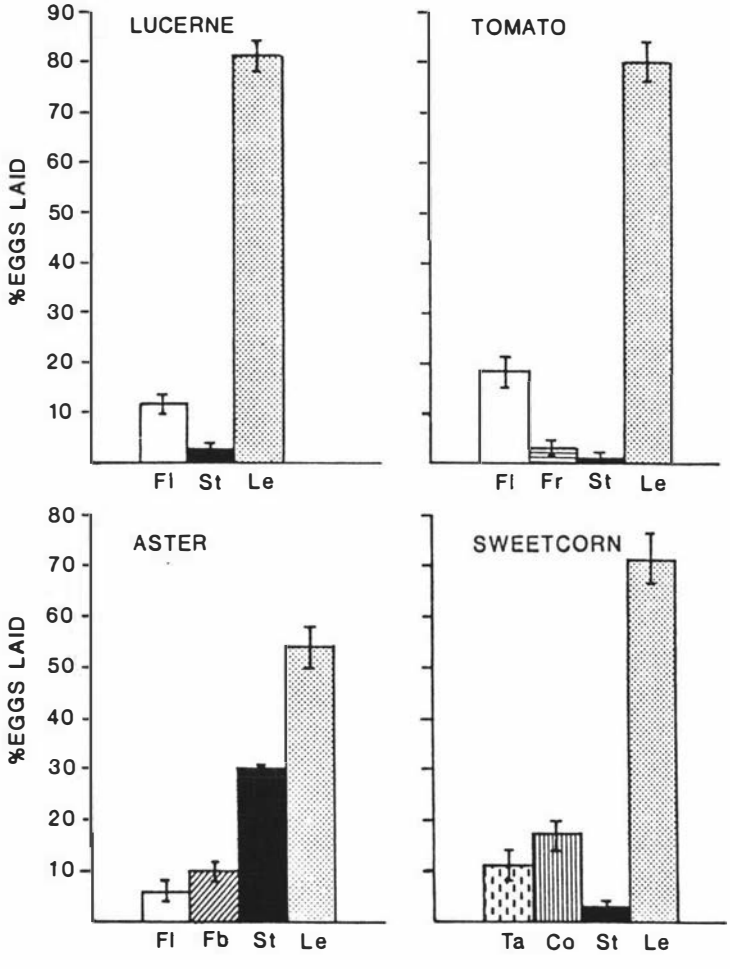

Figure 4.2 Distribution of eggs on different plant parts within plant species. The bars at the top of the columns in Figures 4.2 to 4.5 signify the standard errors.

Abbreviations Co=corn cobs, Fb=flower buds, Fl=flowers, Fr=fruits, Le=leaves(including calices for for aster, leaf sheaths for sweetcorn), St=stems

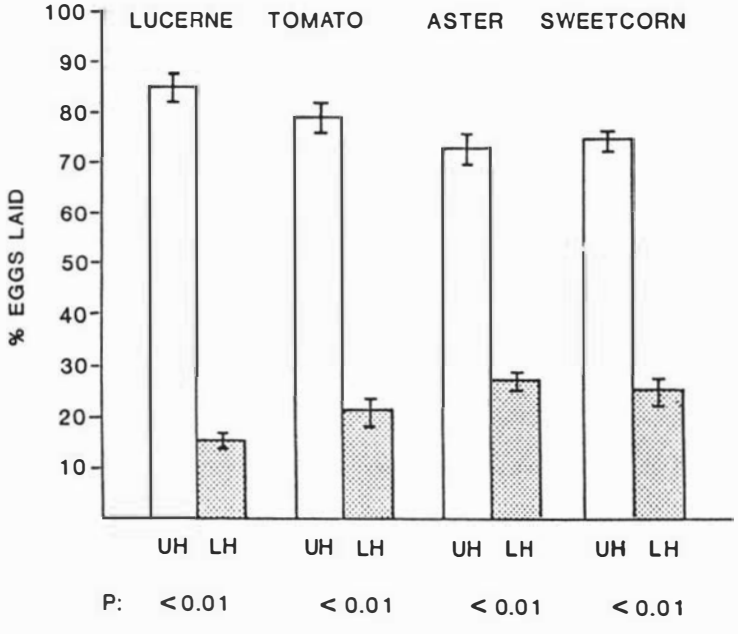

Figure 4.3 Distribution of eggs between upper halves and lower halves of plants.

Abbreviations UH=upper half, LH=lower half, P=probability

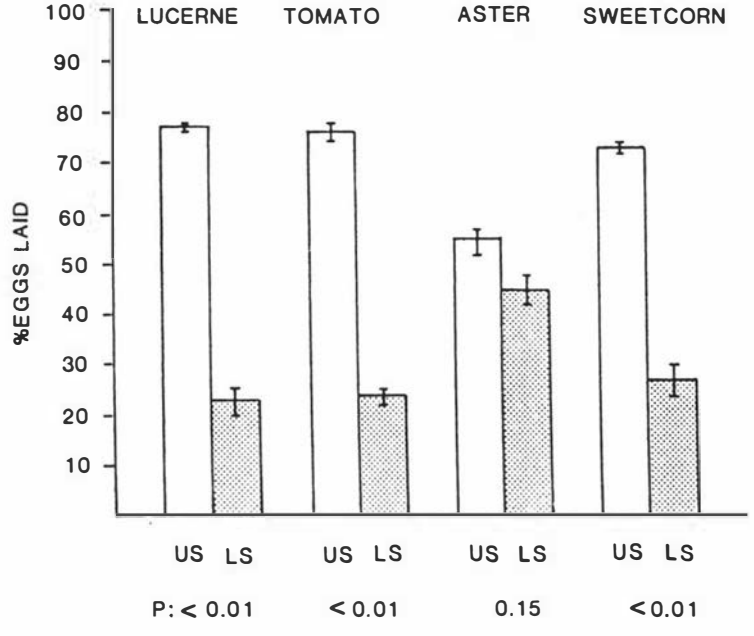

Figure 4.4 Distribution of eggs between upper surfaces and lower surfaces of leaves.

Abbreviations US=upper surface, LS=lower surface, P=probability

2.Oviposition preference of H.armigera between four host plants(immature non-flowering plants).

Mean percentages of eggs laid by H.armigera on immature lucerne, tomato, aster and sweetcorn plants are shown in the first sections of Table 4.5 and Figure 4.5 and are detailed in Appendix 7. On immature non-flowering plants most eggs were laid on lucerne(46%) followed by tomato(25.9%) and aster (20.1%) (not significantly different) and sweetcorn(8%).

3.Oviposition preference of H.armigera between four host plants(mature flowering plants).

Mean percentages of eggs laid by H.armigera on mature lucerne, tomato, aster and sweetcorn plants are shown in the centre sections of Table 4.5 and Figure 4.5 and are detailed in Appendix 7. Most eggs in this case were laid on aster(42.3%) followed by sweetcorn (30.9%), tomato(17.4%) and lucerne(9.4%). All differences were statistically significant.

4.Effect of plant odour on oviposition preference of H.armigera (mature flowering plants).

Mean percentages of eggs laid on white muslin cloth covering the four host plants are shown in final sections of Table 4.5, Figure 4.5 and are detailed in Appendix 7. The order of preference was identical to uncovered mature flowering plants with most eggs being laid on aster(42.4%) followed by sweetcorn(28.6%), tomato(16.6%) and lucerne (12.4%). The difference between tomato and lucerne was not statistically significant.

Table 4.5 Oviposition preference of H.armigera between four host plants.

Host plants	Mean percent of eggs laid		
	Immature plants	Mature plants	Covered mature plants
Lucerne	46.0 a	9.4 a	12.4 a
Tomato	25.9 b	17.4 b	16.6 a
Aster	20.1 b	42.3 c	42.4 b
Sweetcorn	8.0 c	30.9 d	28.6 c

Values in the same column, not followed by the same letter are significantly different(P=0.05).

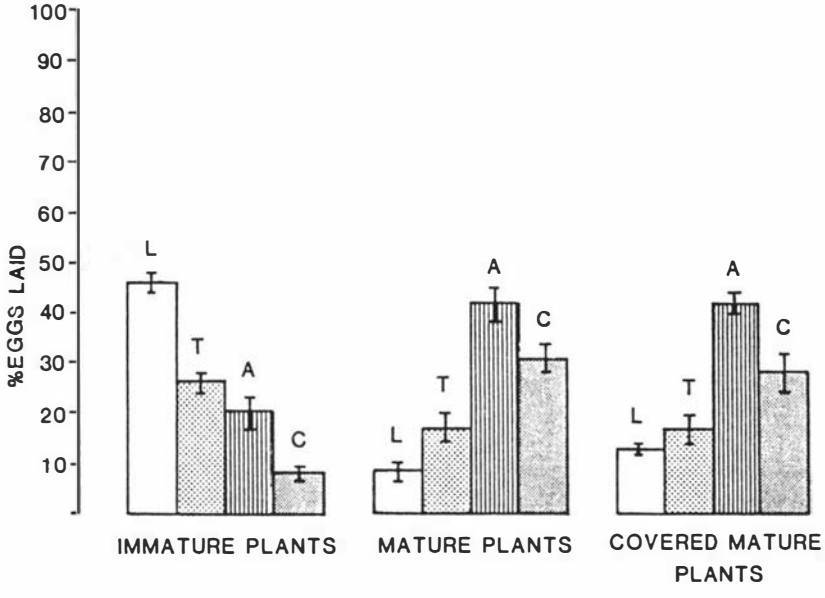

Figure 4.5 Mean percentages of eggs laid on different plants.

Abbreviations A=aster, C=sweetcorn, L=lucerne, T=tomato

DICUSSION

In the experiments described H.armigera females laid some eggs on all available substrates, although most eggs were laid on the test plants. Percentages of eggs laid on non-living substrates (nylon mesh, cage frames, plastic planting bags, soil media, pollen honey containers) ranged from 18.4 to 24.7%. Strong significant preference was shown for oviposition on upper halves of all test plants (range of 73-85%). This result is supported by the finding of Patel et al.(1974) who showed that H.armigera oviposited preferentially on the upper half of cotton plants. Similarly, Hillhouse and Pitre(1976) showed that oviposition by H.virescens and H.zea on soybean occurred in the upper two-thirds of the plant, and in cotton in the upper one-third of the plant. Jackson et al. (1983) also reported that H.virescens laid over 87% of eggs on the upper five leaves of tobacco.

For the four plant species evaluated oviposition preferences for plant parts were as follows:

Lucerne: leaves > flowers > stems

Tomato: leaves > flowers > fruits > stems

Aster: leaves and calices > stems >flower buds > flowers

Sweetcorn: leaves and leaf sheath > cobs > tassels > stems

Significant preference was shown for leaves of all four host plants as an oviposition site as has also been reported by several other investigators. Mabbett and Nachapong (1984) and Patel et al. (1974) reported that H.armigera preferred to lay eggs on flat parts of plants such as leaves, leaflets and terminal buds. Alvarado-Rodriguez et al.(1982), Farrar and Bradley (1985), Hillhouse and Pitre (1976), Jackson et al.(1983), Pencoe and Lynch(1982) and Snodderly and Lambdin(1982) all reported that H.virescens and H.zea laid eggs

preferentially on plant leaves. McColloch(1920) showed that H.zea laid more eggs on corn leaves with rough and hairy surfaces than on leaves with relatively smooth surfaces. However, Broadley(1977) and Hardwick(1965) in their reviews concluded that H.armigera preferred to lay eggs on flowers and flower buds over host plant leaves. Johnson et al.(1975), Lingren et al. (1977) and Neunzig(1969) also found that H.virescens and H.zea moths preferred to lay eggs on flowers compared to leaves.

Percentages of eggs laid on plant stems were very low except on aster. Aster stems possess numerous soft long hairs which could form a suitable oviposition substrate(Plate 1). On the other hand, lucerne and sweetcorn stems are smooth and tomato stems have fewer and sharper hairs which could render them unsuitable. Callahan(1957) demonstrated that villous surfaces were best suited to H.zea moths for maintaining a foothold and Lukefahr et al.(1965) also showed that non-preferred oviposition substrates for H.zea were glabrous such as tomato fruits.

Flowering of host plants affected oviposition preference of H.armigera between plant species. On immature plants (no flowers), moths preferred to lay eggs on lucerne compared to tomato, aster and sweetcorn but on mature plants (with flowers, fruits and cobs) moths preferred aster to sweetcorn corn, tomato and lucerne plants(Table 4.5 and Figure 4.5). This may be because of the adult food available from flowers both before and during oviposition. Although the number of flowers on each each plant was not quantified, it was observed that aster plants had the highest amount of flowers and lucerne the lowest. Alvarado-Rodriguez et al.(1982), Coaker(1960) and Nuttycombe (1930) reported that the availability of nectar for female moths influenced oviposition of H.armigera and H.zea. Coaker(1960), Firempong(1986), Hardwick(1965) and Neunzig(1969) also found that Heliothis moths

preferred to oviposit on host plants in the flowering stage compared to other phenological stages.

When mature host plants were covered with white muslin cloth to eliminate physical, contact chemosensory, and visual stimuli and adult food availability the only remaining influence was odour emanating from plants. Under such conditions the order of preference was unchanged and moths laid more eggs on aster than on sweetcorn, tomato or lucerne plants. This indicates that odour from aster was more attractive for oviposition than odours from the other host plants. Sweetcorn plants were the second most attractive possibly because of odours emanating from silks and developing seed. There was no significant difference in this instance between tomato and lucerne though actual numbers of eggs were greater on cloth covered tomato plants than on similar plants of lucerne. Lack of significance may have been due to the fact that there were only 4 replicates for this comparison. Fletcher(1941) and Hillhouse and Pitre(1976) have previously reported that odours emanating from plants attract H.zea moths and stimulate oviposition. Akkawi and Scott(1984) and Harrison(1960) also demonstrated that corn silks induced oviposition and acted as oviposition sites of H.zea.

It is apparent from these results that change in ovipositional preference between immature and mature plants may be due to differences in odour between mature and immature plants (whether emanating from flowers or not) more than availability of floral nectar.

CONCLUSIONS

From these experiments it can be concluded that oviposition preference by H.armigera on different plants are as follow;

1.Upper half of plants was strongly preferred over lower half.

2.Leaves were preferred over other plant parts and upper leaf surface was preferred over lower leaf surface.

3.Preference between plant species was modified by flowering condition.

On immature plants:Lucerne was most preferred.

On flowering plants:Aster was most preferred.

4.Odour played a significant role in plant selection.

Plate 4.1 Stems of aster showing soft long hair and H.armigera eggs

CHAPTER 5

EFFECTS OF DIFFERENT LARVAL FOODS ON DEVELOPMENT OF *HELIOTHIS ARMIGERA*

INTRODUCTION

The effects of various larval and adult diets on development of *Heliothis* species have been reported by many investigators. Lukefahr and Martin(1964) reported that larvae of *H.virescens* and *H.zea*, fed on artificial medium, corn ears and cotton bolls, produced different pupal weights and that adult longevity and fecundity were influenced by different adult diets. Burkett *et al.*(1983), Farrar and Bradley(1985) and McMillian *et al.*(1966) similarly demonstrated that larvae of *H.zea* reared on cotton flowers, cotton bolls and tomato flowers developed faster, grew longer and heavier and had higher mean survival than those reared on cotton squares and host plant leaves. Pupal weight of *Heliothis* is highly affected by larval food. Doss(1979) found that *H.armigera* larvae fed on soybean pods produced higher pupal weights than those fed on cotton bolls, corn ears and tomato fruits. Reed(1965) also reported that *H.armigera* larvae reared on maize produced higher pupal weight than cotton. Pretorious (1976) found that longevity and fecundity of *Heliothis* adults were also influenced by larval and adult diets and Abul Nasr *et al.* (1976) also showed that *H.armigera* larvae reared on corn ears had longer adult life span and higher numbers of eggs laid than those reared on cotton bolls. Broadley and Butler(1983) showed that longevity of *H.armigera* adults was increased by providing water or honey solutions.

The objective of this study was to determine the biological fitness in terms of growth and development, survival, and adult fecundity of H.armigera when larvae fed on 8 different foods.

MATERIALS AND METHODS

Larvae of H.armigera, collected from infested field crops in Manawatu, North Island of New Zealand were reared on artificial diet in controlled laboratory conditions at 25±2°C and 16:8 (L/D) photoperiod. The composition of the formulated diet is shown in Appendix 2. Eggs obtained from generations 3 to approximately 15 were used for production of larvae to avoid natural parasitism from the field.

Lucerne, tomato, aster and sweetcorn plants were raised in a greenhouse. No pesticides were sprayed on these plants.

In controlled laboratory conditions at 25±2°C and 16:8 (L/D) photoperiod, healthy newly hatched larvae were placed singly into clear plastic containers(312 cm^3) with ventilated lids using a fine camel hair brush. An excess of artificial diet, lucerne leaves, tomato leaves, tomato fruits, aster leaves, aster flowers, sweetcorn leaves and sweetcorn cobs were provided and replaced daily. There were 50 individual larvae for each food. Moulting dates of each larvae were determined by checking the exuviae and the shed head capsules daily. When fully grown larvae stopped feeding and became shortened in length they were transferred to fresh plastic containers with a layer of vermiculite for pupation. After a short period(6-8 hrs), pupae were weighed and sexed by viewing the last abdominal segment through a stereomicroscope (see details in Kirkpatrick,1961a and Mourikis and Vassilaina-Alexopoulou, 1970). Sex of adult moths was confirmed after

emergence from pupae. Numbers of moults, percent mortality prior to pupation, larval duration, percent pupation, prepupal period and pupal period (excluding diapausing pupae) were recorded.

Single pairs of male-female newly-emerged moths from each food source were released into clear plastic oviposition containers(5079 cm^3). The bottom of the containers was completely covered with a white filter paper which acted as an oviposition site and also absorbed excess moisture. The top of the containers was covered with white muslin cloth on which was placed a moist black filter paper. This also acted as an oviposition site. A ventilated lid was used. Moths were provided with 10% pollen honey solution through an absorbent cotton wick held in a small plastic cup on the bottom of the oviposition container. A water saturated cotton wick was also placed in each container to maintain high humidity which was crucial for oviposition. The oviposition containers were placed in an room at 20±2°C and 16:8 (L/D) photoperiod and exposed to natural light.

Eggs were collected daily by changing the muslin cloth and filter papers. Eggs were counted and then placed in clear plastic boxes (18x11x10 cm) which were lined on the bottom with moist tissue paper to provide high humidity for hatching. Four replicates each of one pair of moths from each food source were recorded. Pre-oviposition period, oviposition period, numbers of eggs laid and percent hatchability, and post-oviposition period, were assessed.

As high mortality of larvae occurred when fed solely on tomato leaves, aster leaves and sweetcorn leaves (see Table 5.1) an additional experiment was undertaken in which these larvae were shifted when part grown to more suitable food. Thus fifty newly-hatched larvae were provided with tomato leaves, aster leaves and sweetcorn leaves up to the

third moulting, then shifted to tomato fruits, aster flowers and sweetcorn cobs respectively and retained on these foods until pupation. All procedures were otherwise the same as in the previous experiment.

RESULTS

1 Effects of different foods on larval development.

Numbers of moults, duration a larval life and percentage pupation for the seven natural foods and artificial diet are shown in Table 5.2. On most foods larvae moulted 4 to 6 times but the duration of the larval period varied considerably with different foods. Larvae fed on lucerne leaves had the shortest larval period, 17.5 days, whilst larvae fed on sweetcorn leaves had the longest period, 26.3 days. Those fed on artificial diet, tomato leaves, tomato fruits, aster leaves, aster flowers and sweetcorn cobs had 18.9, 20.6, 18.4, 22.8, 17.9 and 17.9 days respectively. Differences between larval periods for lucerne leaves, artificial diet, tomato fruits, aster flowers and sweetcorn cobs were not significant. Artificial diet and tomato fruits gave the highest percent pupation (each 96%) while tomato leaves gave the lowest at 24% (Table 5.2).

Results for larvae which were shifted from one food to another after the third moult are shown in Table 5.3. For all three plants (tomato, aster and sweetcorn) larval developmental periods and percentage pupation were intermediate between those for larvae fed solely on leaves and those on fruits (tomato), flowers(aster) or cobs(sweetcorn).

Table 5.1 Cumulative percent mortality of each instar of H.armigera larvae through to pupation when larvae were reared on different plant parts in controlled laboratory conditions. (n=50)

Food	Cumulative percent mortality of instars						
	1st	2nd	3rd	4th	5th	6th	Pupation*
Lucerne leaves	10	16	22	26	30	34	44 a
Tomato leaves	12	24	36	44	52	68	76 b
Tomato fruits	4	4	4	4	4	4	4 c
Aster leaves	8	14	18	24	28	32	46 a
Aster flowers	8	12	14	14	14	14	16 d
Sweetcorn leaves	14	22	30	36	48	56	62 e
Sweetcorn cobs	8	10	12	12	12	12	12 f

* Total percent mortality from newly hatched larvae to pupation. Values in the last column, not followed by the same letter are significantly different. (P=0.05)

Table 5.2 Effects of different foods on larval development through to pupation. (n=50)

Food	No.of moults	Larval period (days±S.E.)	Percent pupation
Artificial diet	4-6	18.9 ± 0.14	96 a
Lucerne leaves	4-5	17.5 ± 0.34	56 b
Tomato leaves	4-6	20.6 ± 0.41	24 c
Tomato fruits	4-6	18.4 ± 0.33	96 a
Aster leaves	4-6	22.8 ± 0.28	54 b
Aster flowers	4-6	17.9 ± 0.14	84 d
Sweetcorn leaves	4-5	26.3 ± 0.43	38 e
Sweetcorn cobs	4-5	17.9 ± 0.29	88 d

Values in the last column, not followed by the same letter are significantly different. (P=0.05)

Table 5.3 Effects of shifting larvae from poor to higher quality food after the third moult on larval development and pupation. (n=50)

Food	No. of moults	Larval duration (days±S.E.)	Percent pupation
Tomato leaves shifted to tomato fruits	4-6	19.0 ± 0.18	64 a
Aster leaves shifted to aster flowers	4-6	17.9 ± 0.21	76 b
Sweetcorn leaves shifted to sweetcorn cobs	4-6	22.2 ± 0.28	58 c

Values in the last column, not followed by the same letter are significantly different. (P=0.05)

2 Effects of different larval foods on pupal weight, pupal period and sex ratio

Results are summarized in Tables 5.4 and 5.5. Large differences in pupal weight occurred when larvae fed on different foods. Artificial diet gave the highest mean weight of 416.9 mg followed by 339.5 mg for tomato fruits. Weights of pupae for other foods were 288.6, 225, 316.5, 326.2, 275.6 and 332.1 mg for lucerne leaves, tomato leaves, aster leaves, aster flowers, sweetcorn leaves and sweetcorn cobs respectively. The sex ratio was close to 1:1 in all cases and differences between weights of male and female pupae were not significant for any food. The shortest pupal period was 12.3 days for larvae reared on aster leaves and the longest 18.1 days for artificial diet.

Results for pupae arising from larvae which were shifted from one food to another during larval development are shown in Table 5.5. For all three plants shifting larvae to reproductive plant parts resulted in higher pupal weights than larvae fed exclusively on leaves and in the case of tomato and aster pupal weights were actually greater than those for larvae fed on tomato fruits and aster flowers respectively throughout their life.

Table 5.4 Effects of different larval foods on the pupal stage of H.armigera

Food	Pupal weight (mg±S.E)			Sex ratio (Female:Male)	Pupal period (days ± S.E.)
	Overall mean	Female	Male		
Artificial diet	416.9± 5.56	411.5± 7.90	420.5± 7.66	1:0.9	18.1± 1.28
Lucerne leaves	288.6± 8.31	287.3±11.35	289.8±12.41	1:1.1	17.4± 0.47
Tomato leaves	225.0±17.40	219.3±17.88	230.7±31.61	1:1	14.6± 0.82
Tomato fruits	339.5± 5.60	335.6± 9.78	342.5± 6.48	1:1.3	14.0± 0.26
Aster leaves	316.5± 8.90	317.0±12.75	312.1±12.03	1:1.1	12.3± 0.41
Aster flowers	326.2± 5.07	325.7± 6.40	328.2± 8.41	1:0.8	13.2± 0.29
Seeetcorn leaves	275.6±14.81	281.4±19.70	265.6±23.23	1:0.8	13.1± 0.52
Sweetcorn cobs	332.1± 6.45	345.1± 9.41	317.9± 7.89	1:0.9	14.1± 0.23

Table 5.5 Effects of shifting larvae from poor to higher quality food after the third moult on the pupal stage of *H.armigera*.

Food	Pupal weight (mg ± S.E.)			Sex ratio (Female:Male)	Pupal period (days ± S.E.)
	Overall mean	Female	Male		
Tomato leaves shifted to tomato fruits	372.2 ± 8.46	382.1 ± 13.92	356.7 ± 9.65	1:1	15.4 ± 0.42
Aster leaves shifted to aster flowers	341.8 ± 7.29	340.8 ± 8.43	343.2 ± 12.82	1.0.8	13.3 ± 0.25
Sweetcorn leaves shifted to sweetcorn cobs	308.4 ± 10.12	315.9 ± 13.11	291.7 ± 14.74	1:0.9	16.1 ± 0.31

3 Effects of different larval foods on adult life span and fecundity

Results are shown in Table 5.6. Female moths arising from larvae fed on all foods started laying eggs after an average period of 2.7 to 3.7 days. There were no significant differences between these pre-oviposition periods except for that from larvae fed on tomato leaves which produced the longest period (3.7 days).

Oviposition periods, post-oviposition periods, female life spans, male life spans, numbers of eggs laid and percent hatchability were highly affected by larval food. Analysis of the data by Duncan multiple range test showed significant differences at the 5% level which enabled foods to be grouped as follows.

Oviposition period(days)

1. Artificial diet(5.5) and tomato fruits(5.2)
2. Aster flowers(4.5) and sweetcorn cobs(4.5)
3. Lucerne leaves(3.5), tomato leaves(3.5) and aster leaves(2.7)
4. Sweetcorn leaves(2.2)

Post-oviposition period(days)

1. Artificial diet(6.5) and tomato fruits(5.5)
2. Aster flowers(4.5) and sweetcorn cobs(4.7)
3. Lucerne leaves(4),tomato leaves(2.7),aster leaves(3.2) and sweetcorn leaves(3.5)

Female life span(days)

1. Artificial diet(14.7) and tomato fruits(13.7)
2. Aster flowers(11.5) and sweetcorn cobs(11.7)
3. Lucerne leaves(10.2) and tomato leaves(10)
4. Aster leaves and sweetcorn leaves(8.5)

Male life span(days)

1. Artificial diet(13.5)
2. Tomato fruits(11.5),aster flowers(11.2) and sweetcorn cobs(11)
3. Lucerne leaves(9.2),tomato leaves(9.2),aster leaves(9.7) and
4. Sweetcorn leaves(7.7)

Numbers of eggs laid(per female)

1. Artificial diet(845.3) and tomato fruits(733.3)
2. Aster flowers(512.8) and Sweetcorn cobs(605.8)
3. Lucerne leaves(332.8),tomato leaves(221.8) and aster leaves(336)
4. Sweetcorn leaves(160.8)

Hatchability of eggs(%)

1. Artificial diet(89.5),tomato fruits(88.5),aster flowers(86.1) and sweetcorn cobs(91.3)
2. Lucerne leaves(79.9) and aster leaves(77.7)
3. Tomato leaves(72.1) and sweetcorn leaves(69.5)

Results of shifting larvae from poor to higher quality foods on the adult stage and fecundity are shown in Table 5.7. Oviposition periods, post-oviposition periods, female life spans and male life spans were longer and numbers of eggs laid were higher than for larvae fed on host plant leaves alone for all these plants.

Table 5.6 Effects of different larval foods on adult stage and fecundity of H.armigera. (n=6)

Food	Pre-oviposition period (days±S.E.)	Oviposition period (days±S.E.)	Post-oviposition period (days±S.E.)
Artificial diet	2.7±0.25	5.5±0.29	6.5±1.04
Lucerne leaves	2.7±0.25	3.5±0.29	4.0±0.41
Tomato leaves	3.7±0.25	3.5±0.29	2.7±0.48
Tomato fruits	2.7±0.25	5.2±0.25	5.5±0.65
Aster leaves	3.0±0.25	2.7±0.25	3.2±0.48
Aster flowers	2.7±0.25	4.2±0.25	4.5±0.25
Sweetcorn leaves	2.7±0.25	2.2±0.25	3.5±0.29
Sweetcorn cobs	2.7±0.25	4.5±0.29	4.7±0.25

Table 5.6 (continued)

Food	Female life spans (days±S.E.)	Male life spans (days±S.E.)	No.of eggs laid per female (mean±S.E)	Hatch-ability (%)
Artificial diet	14.7±1.03	13.5±0.65	845.3±21.33	89.5
Lucerne leaves	10.2±0.48	9.2±0.48	332.8±34.97	79.9
Tomato leaves	10.0±0.58	9.2±0.48	221.8±46.71	72.1
Tomato fruits	13.7±0.63	11.5±0.96	733.3±88.06	88.5
Aster leaves	9.2±0.75	9.7±0.25	336.0±39.89	77.7
Aster flowers	11.5±0.48	11.2±0.48	512.8±70.91	86.1
Sweetcorn leaves	8.5±0.50	7.7±0.49	160.8±25.52	69.5
Sweetcorn cobs	11.7±0.25	11.0±0.41	608.5±73.99	91.3

Table 5.7 Effects of shifting larvae from poor to higher quality food on the adult stage and fecundity of H.armigera. (n=6)

Food	Pre-oviposition period (days±S.E.)	Oviposition period (days±S.E.)	Post-oviposition period (days±S.E.)
Tomato leaves shifted to tomato fruits	3.2±0.25	4.2±0.25	3.7±0.25
Aster leaves shifted to aster flowers	3.5±0.29	3.7±0.25	3.5±0.29
Sweetcorn leaves shifted to sweetcorn cobs	3.0±0.25	4.2±0.25	4.2±0.25

Table 5.7 (continued)

Food	Female life span (days±S.E.)	Male life span (days±S.E.)	No.of eggs laid per female (mean±S.E.)	Hatch-ability (%)
Tomato leaves shifted to tomato fruits	12.2±0.75	10.5±0.29	299.5±51.31	75.1
Aster leaves shifted to aster flowers	10.7±0.48	10.2±0.25	399.0±17.18	78.8
Sweetcorn leaves shifted to sweetcorn cobs	12.0±0.25	9.7±0.25	314.5±14.05	77.1

DICUSSION

The individual parameters of larval food quality evaluated in this study (larval period, percentage pupation, pupal weight, etc.) are discussed first, then how well they correlate one with another and finally how they may be combined into an overall index of food quality.

1.Larval period.

Larvae fed on lucerne leaves had the shortest development period (mean of 17.5 days) while those fed on sweetcorn leaves had the longest (mean of 26.3 days). However, differences in development period of larvae reared on lucerne leaves, artificial diet, tomato fruits, aster flowers and sweetcorn cobs were not significant and all these larval foods were satisfactory in terms of duration of larval development. Within plant species, larval development periods on reproductive parts such as fruits(tomato), flowers(aster) and cobs (sweetcorn) were shorter than those on plant leaves.

The result for lucerne is similar to that reported by Bilapate et al.(1977) who found that the maximum larval period of H.armigera reared on lucerne leaves in India at a constant temperature of 26±1°C was 18 days. However, under similar conditions and on the same food in South Africa, Pretorius(1976) found that the larval period was 25.1 days. Abul Nasr et al.(1976) reared H.armigera on different diets at 16-22°C and 50-60%R.H. and reported that larval periods obtained from corn ears, artificial diet(based on kidney bean) and tomato fruits were 12.3, 13 and 16.4 days respectively. Doss(1979) showed that H.armigera reared on corn ears and tomato fruits at 27±1°C and 60.5%R.H. had larval periods of 19 and 23 days and Pretorius(1976) also reported that larval

periods of H.armigera reared on maize cobs and tomato leaves were 17.4 and 23.3 days respectively. Although it is clear from the results reported here and from other published information that duration of larval period varies with diet Habib and Patel(1977) working with H.zea did not consider that duration of the larval stage was an adequate indicator of host-plant suitability, presumably because it did not correlate well with other parameters.

2.Percent pupation.

Mortality of larvae was high on some foods in the present study thus resulting in low percent pupation e.g. tomato leaves gave only 24%. In contrast, tomato fruits and artificial diet gave 96% pupation. Firempong(1986), Pretorius(1976) and Singh et al.(1982) all found that percent pupation of H.armigera was relatively high when larvae were reared on "high quality" food especially artificial diet.

3.Pupal period.

Larval food had a major influence on pupal period of H.armigera in the present study (see Table 5.4) but pupal period was not closely correlated with other biological parameters (see Table 5.8 and later discussion). Mean pupal period varied from 12.3 days obtained from larvae fed on aster leaves to 18.1 days on artificial diet. From a population increase point of view, insects with the shortest pupal period should be the most successful other factors being equal.

The results show some anomalies in pupal periods with respect to larval development on the same food. For example aster leaves and sweetcorn leaves gave shorter pupal periods than aster flowers and sweetcorn cobs, whereas larval periods on these foods were the reverse.

There was thus little correlation between larval period and pupal period for individual foods. This result is supported by the findings of Abul Nasr et al.(1976), Doss(1979), Firempong(1986), Pretorius(1976) and Reed(1965). For example, Doss(1979) reported that larval periods of H.armigera larvae fed on corn ears and tomato fruits were 19 and 23.9 days but pupal periods were 12.3 and 11.6 days respectively. Pretorius(1976) also showed that H.armigera reared on maize cobs, tomato leaves and lucerne leaves had mean larval periods of 17.4, 23.3 and 25.1 days while pupal periods were 11.9, 10.7 and 14.4 days respectively.

4.Pupal weight.

Pupal weight was also highly influenced by larval food. Artificial diet gave the highest pupal weight(mean of 416.9 mg) and tomato leaves gave the lowest of 225 mg. Within plant species all reproductive parts i.e. tomato fruits, aster flowers and sweetcorn cobs produced heavier pupae than leaves of these plants though the difference for aster was not statistically significant. Firempong(1986) reared H.armigera larvae on 9 different foods and also reported that artificial diet gave the heaviest pupae(428.6 mg) followed by maize cobs(336.5 mg). Lucerne leaves gave the lightest(180.3 mg), considerably less than the present figure of 288.6 mg. Pretorius (1976) found that H.armigera larvae reared on diet, maize cobs, lucerne leaves and tomato leaves had mean pupal weights of 380, 260, 220 and 200 mg respectively. Doss(1979) reported that larvae of H.armigera reared on corn ears and tomato fruits had pupal weights of 336.9 and 322.2 mg respectively, close to the present values.

5.Adult fecundity, life span, oviposition period and egg hatchability.

Adult longevity and fecundity of H.armigera were also highly influenced by larval food. Female life spans, male life spans, oviposition periods, numbers of eggs laid and percent hatchability of eggs obtained from larvae fed on reproductive parts of plants (tomato fruits, aster flowers and sweetcorn cobs) were all greater than on leaves of these plants or on lucerne leaves.

Larvae fed on artificial diet gave the longest female and male life spans, the longest oviposition period, the highest number of eggs laid and the second highest percent hatchability of eggs. On the other hand, sweetcorn leaves produced the lowest values for these biological parameters. Abul Nasr et al.(1976) reported that H.armigera larvae fed on tomato fruits and corn ears had the same male and female life span but oviposition period obtained from larvae fed on corn ears (5.9 days) was longer than from tomato fruits(3.1 days) and numbers of eggs laid were 507.6 and 263.4 respectively. The present work showed that the number of eggs laid was positively correlated with oviposition period and female life span ($P < 0.05$) which was similar to the results of Abul Nasr et al.(1976) and Doss(1979). In contrast, Pretorius(1976) reported that there was no correlation between adult lifespan, oviposition period, number of eggs laid and percent hatchability of eggs when larvae of H.armigera were reared on different diets.

When larvae were reared on leaves of tomato, aster and sweetcorn up to the third instar and then shifted to tomato fruits, aster flowers and sweetcorn cobs respectively larval periods, percent pupation, pupal weights, adult longevity, oviposition periods, numbers of eggs laid and percent hatchability of eggs were all intermediate between those for larvae fed solely on leaves and those solely on reproductive parts of

these plants. It may be concluded that leaves of these plants were the poorer foods for larvae of H.armigera compared to their fruits, flowers or cobs.

These effects of different larval diets on growth and development of H.armigera are similar to those known to occur with other Heliothis species. For example, larvae of H.zea fed on flowers and bolls of cotton developed faster and grew larger than those fed on leaves and terminals (Farrar and Bradley, 1985). Lukefahr and Martin (1964) also showed that larval foods influenced pupal weight, longevity and fecundity of H.zea and H.virescens.

6.Ranking and correlation between parameters of larval food quality.

The results from Tables 5.2, 5.4 and 5.6 may be summarized by ranking the foods for each biological parameter as in Table 5.8. It will be noted that the rank values of the different biological parameters are with few exceptions within three rank points of each other for all foods. The main exceptions are lucerne leaves and artificial diet for larval period; and artificial diet, aster leaves and sweetcorn leaves for pupal period.

The consistency of rank values, and thus good correlation between the different parameters for individual foods, indicates that almost any of the biological parameters measured, with the exception of pupal period, could be used as an indicator of food quality. Artificial diet ranked 1 or 2 for all parameters with the exception of larval period and pupal period which gave anomalous rankings.

In the final two columns of Table 5.8 overall ranking of food has been derived by summing the individual rank values for each biological

parameter (column 10) and arranging these in final rank order in column 11. On this basis the foods may be ranked for quality as:

artificial diet > tomato fruits > sweetcorn cobs > aster flowers > lucerne leaves > aster leaves > tomato leaves > sweetcorn leaves

Such treatment of the data enables one to rank food for overall "quality" but gives no indication of relative quantitative differences.

In terms of potential for population increase over several generations the important parameters of food quality are duration of larval development, percentage pupation and fecundity of adults as cited by Firempong(1986) (attributed to Birch,1948) in proposing a "fitness index" :-

$$\text{fitness index (rI)} = \frac{lx\ mx}{T}$$

where lx = percent pupation

mx = pupal weight(gm)

(as a measure of fecundity)

T = duration of larval development(days)

Fitness indices calculated on this basis from the present data are shown in the second column of table 5.9.

Birch's fitness index is clearly designed to express the capability of an insect population to increase (over one or more complete generations) and could be improved by adding values for pupal period and hatchability of eggs and by substituting actual eggs laid for pupal weight.

The new expression would then be:

$$\frac{lx\ ex\ hx}{1000 - Tl - Tp}$$

where lx = percent pupation

ex = number of eggs laid(per female)

hx = percent hatch of eggs

Tl = duration of larval development(days)

Tp = duration of pupal development(days)

1000 has been added to the lower part of the expression to reduced the numerical value of the derived index to a reasonable figure (the expression has no meaning in absolute terms)

Two other biological parameters that could affect rate of population growth are adult sex ratio and duration of the egg stage and values for these factors should perhaps be included in the revised biological fitness index. However, as the sex ratio in the present study was consistently close to 1:1 it was considered unnecessary to include it in the expression. Duration of the egg stage was not specifically determined but observations indicated that it did not differ markedly according to larval diet.

The values of the new expression for the different food in the present study have been calculated and are presented in the right hand side of Table 5.9.

Table 5.8 Ranking of different foods according to biological parameters. (1 represents the best and 8 represents the poorest performance) Abbreviations: LP = larval period, %P = percent pupation, PW = pupal weight, PP = pupal period, OP = oviposition period, FL = female life span, ML = male life span, EL = number of eggs laid per female, HT = percent hatchability of eggs.

Food	LP	%P	PW	PP	OP	FL	ML	EL	HT	Sum of ranking	Overall ranking
Artificial diet	5	1	1	8	1	1	1	1	2	21	1
Lucerne leaves	1	5	6	7	5	5	6	6	5	46	5
Tomato leaves	6	8	8	6	5	6	6	7	7	59	7
Tomato fruits	4	1	2	4	2	2	2	2	3	22	2
Aster leaves	7	6	5	1	7	7	5	5	6	49	6
Aster flowers	2	4	4	3	4	4	3	4	4	32	4
Sweetcorn leaves	8	7	7	2	8	8	8	8	8	64	8
Sweetcorn cobs	2	3	3	5	3	3	4	3	1	25	3

Table 5.9 Fitness indices for different larval foods.

Food	Fitness index	Rank	Value relative to artif. diet=1.00	"Improved" fitness index	Rank	Value relative to artif. diet=1.00
Artificial diet	2.12	(1)	1.00	21.23	(2)	1.00
Lucerne leaves	1.09	(5)	0.51	5.76	(5)	0.27
Tomato leaves	0.26	(8)	0.12	1.28	(7)	0.06
Tomato fruits	1.78	(2)	0.84	24.18	(1)	1.14
Aster leaves	0.75	(6)	0.35	5.07	(6)	0.24
Aster flowers	1.53	(4)	0.72	15.69	(4)	0.74
Sweetcorn leaves	0.40	(7)	0.19	1.23	(8)	0.06
Sweetcorn cobs	1.63	(3)	0.77	19.37	(3)	0.91

On the basis of the first described fitness index there is a slight change in the ranking order of close pairs (7-8) compared to the ranking presented in Table 5.8. There are also minor differences in ranking order based on the new expression when larval and pupal periods, actual number of eggs laid and percent hatch of eggs are added (Table5.9). Whichever fitness index is used therefore makes very little difference to the ranking order of the foods evaluated. It may be noted that in both schemes reproductive parts of the plants (flowers, fruits and sweetcorn cobs) rank high whereas leaves of all plants rank low. These differences are emphasised when the fitness indices are examined relative to artificial diet (columns 4 and 7 of Table 5.9). The "improved" fitness index further exaggerates these differences between reproductive and vegetative plant parts. Thus tomato leaves drop from 0.12 (relative to 1.00 for artificial diet) according to Birch's index to 0.06 on the "improved" index whereas tomato fruits rise from 0.84 to 1.14. Similarly, sweetcorn leaves drop from 0.19 on the old index to 0.06 while sweetcorn cobs rise from 0.77 to 0.91. There are similar less marked changes for aster leaves and flowers, and lucerne foliage drops from 0.51 to 0.27.

The normal habit of H.armigera larvae (and other Heliothis spp.) in the field is to feed on flowers, fruits and seeds of plants as soon as these are available rather than foliage. From these results this can be clearly interpreted as a tendency to feed on the much more nutritionally valuable parts of the plants. Of the natural foods used in this experiment, on the basis of the "improved" fitness index, only tomato fruits exceed artificial diet in value, and sweetcorn cobs are close behind. For all four plants foliage rated very poorly.

It may be concluded that although several biological parameters could be used as indicators of host-plant quality, the combination of

several parameters into a broad based index is more meaningful. Further investigations into the reasons for these differences in food quality are needed and this is the subject of the next chapter.

CONCLUSIONS

There are significant differences between the quality of larval foods for *H.armigera* as measured by different biological parameters such as duration of larval period, percent pupation, pupal weight, fecundity and adult life span. Reproductive parts of plants (flowers, fruits, seeds) have higher quality than leaves.

Ranking of food quality varies somewhat with the biological parameter used. When a wide range of biological parameters are combined into an overall "fitness index" the larval foods evaluated could be ranked in the following order of decreasing value:

1. Artificial diet
2. Tomato fruits
3. Sweetcorn cobs
4. Aster flowers
5. Lucerne leaves
6. Aster leaves
7. Tomato leaves
8. Sweetcorn leaves.

CHAPTER 6

FACTORS DETERMINING FOOD QUALITY FOR DEVELOPMENT OF *HELIOTHIS ARMIGERA*

INTRODUCTION

In chapter 5 it was shown that the eight larval foods evaluated (including artificial diet) differed considerably in quality as defined by a biological fitness index. In this chapter work is described which attempted to elucidate reasons for these differences.

Growth, development and reproduction of insects are highly dependent on the quantity and quality of food ingested. Furthermore, ingestion of food depends upon its being found and accepted. Besides being available, acceptable, digestible, assimilable and able to provide all nutrients required for energy production and biomass increase, food must also provide chemicals other than nutrients that influence the necessary behaviour of insects, whether directly involved in alimentation or as effectors of functions distinct from alimentation (Hagen *et al.*,1984; Scriber and Slansky,1981). Food quality is an extremely complex and elusive thing to measure, compounded by how much nutrient the insect can obtain per unit weight of food ingested, the accessibility of the nutrients and the concentrations of chemical attractants, phagostimulants, repellents and toxins (Crawley, 1983). It is difficult, therefore, to prescribe a general index of food quality. If a nutrient is defined as a compound required for normal growth, maintenance and reproduction, then that which is a nutrient for one phytophagous species may not be a nutrient for another species.

Factors which determine larval food quality for development of H.armigera have not previously been investigated. However, studies on other herbivores have been conducted for the past several decades and it is now recognized that the broad qualitative nutrient requirements of insects are basically similar as those of animals in general. One of the most important nutrients is nitrogen. Nitrogen plays a central role in all metabolic processes and in genetic coding (Ito and Mukaiyama,1964; Mattson,1980). Current hypotheses suggest that insects feeding on protein-rich plants will be more successful than insects that consume plant material of lower protein value (Al-Zubaidi and Capinera, 1984; Baker,1975; Mattson,1980). The minimum nitrogen content of food that will keep body nitrogen level stable is known for a few insect species. For example, butterfly larvae and grasshopper nymphs need at least 3% nitrogen in dry matter of food (Mattson,1980) but the specialist Eucalyptus leaf beetle, Paropsis sp. can survive with only 1% (Fox and Macauley,1977). However, some studies have, to the contrary, reported that elevation of plant foliage nitrogen does not result in increased performance of insect populations (Broadway and Duffey,1986; Faeth et al.,1981; Schroeder,1976; Stiling et al.,1982).

Although nitrogen content seems likely to be a primary growth limiting factor for many phytophagous insects, water content of food may be even more fundamental (Scriber,1977,1978). Usually, insects ingest water with their food and the content can vary from 1 to more than 90%. Many phytophagous insects require a high moisture intake (Waldbauer, 1968). Scriber and Slansky (1981) calculated nutritional values for last instar foliage-chewing larvae to be significatly greater on leaves of 75-95% water content than on leaves of lower water content. Scriber and Feeny (1979) also showed that larvae of 20 species of Lepidoptera

grew faster and more efficiently on herbaceous plants whose water contents ranged from 70 to 91% than on the foliage of shrubs and trees with water contents of 51 to 74%. However, it should be remembered that high water content of food means correspondingly low dry matter content and to compensate, higher rates of ingestion are required. It is possible that this could be a limiting factor for some insect species and for any particular insect there is likely to be an optimum water content of food which may differ from species to species. The highest quality food is of no use unless it is ingested and thus any study of comparative food quality for an insect species must include assessment of food consumed.

The objective of this study was to investigate quality of the 8 larval foods in terms of relative rates of ingestion, dry matter content and nitrogen content.

MATERIALS AND METHODS

H.armigera larvae and food materials were raised in the same manner as in the work reported in Chapter 5.

1.Amount of food eaten and larval weight gain

Portions of all foods (fresh artificial diet, lucerne leaves, tomato leaves, tomato fruits, aster leaves, aster flowers, sweetcorn leaves and sweetcorn cobs) were weighed and then each divided into two halves. The first half of each food was dried in an oven at 100°C for 24 h and then reweighed to determine the dry matter content. The second half was placed into a clear plastic container (312 cm^3) with a ventilated lid and lined on the bottom with a moist filter paper to keep

the food material fresh. One healthy newly hatched larva was placed in each container. Each larva was then transferred daily to another container with fresh known-weight food material until pupation. Each day unconsumed food was dried in an oven at 100°C for 24 h. The dry weight of unconsumed food was summed through to pupation and then converted to unconsumed fresh weight. The total amount of food eaten, expressed as fresh weight, was calculated from initial fresh weight minus fresh weight of unconsumed food. When each mature larva stopped feeding it was weighed to determine weight gained. Final weight of larvae was assumed to be the total weight gained because the weight of newly hatched larvae was negligible (less than 0.5mg) and could be ignored. There were 30 replications of individual larvae for each food.

2.Dry matter content of food

From the fresh weights and oven dry weights of each food, percent dry matter content was calculated as follows:

$$\text{Percent dry matter content} = \frac{\text{Dry weight}}{\text{Fresh weight}} \times 100$$

3.Total nitrogen content of food

After weighing to determine dry matter content the dried half of each food material was ground and then dried again at 100°C for 24 hr. Total nitrogen was measured from 20-replicate samples by the micro-Kjeldahl technique of McKenzie and Wallace(1954) and Bremner and Mulvaney(1982).

4.Parameters of food utilization

From the data the following parameters of larval growth and feeding efficiency were calculated (Evans,1939 ; Waldbauer,1968).

Consumption index(C.I)

$$C.I. = \frac{W}{\bar{T}\bar{A}}$$

where W = fresh (or dry) weight of food eaten

T = duration of feeding period(days)

A = mean fresh weight of larva during feeding period

The relative growth rate(R.G.R.)

$$R.G.R. = \frac{G}{\bar{T}\bar{A}}$$

where G = fresh weight gained by larva during feeding period

T = duration of feeding period(days)

A = mean fresh weight of larva during feeding period

The efficiency of conversion of ingested food(E.C.I.)

$$E.C.I. = \frac{\text{weight gained}}{\text{weight of food ingested}} \times 100$$

RESULTS

1. Amount of food eaten and larval weight gain

Results of amount of food eaten and larval weight gained are summarized in Table 6.1. The highest amount of fresh food eaten by far was tomato fruits (29660.8 mg) followed by artificial diet, aster leaves, sweetcorn cobs, tomato leaves, sweetcorn leaves, aster flowers (all 5700-7000 mg) and lucerne leaves the least (2783.5 mg). Significant differences between amounts of food eaten are given in Table 6.1. Tomato fruits also gave the highest dry weight consumption (1957.6 mg) and lucerne leaves the least (527.8 mg). Total larval weight gained (i.e final weight of larvae) differed considerably on the different foods. Artificial diet, tomato fruits, aster leaves, aster flowers and sweetcorn cobs produced heavy larvae with similar weights ranging from 510.6 to 530.3 mg. These were followed by tomato leaves and sweetcorn leaves (393.6 and 395.1 mg). The lowest weight gain was for larvae fed on lucerne leaves (352.2 mg).

Table 6.1 Amount of food eaten and total weight gained by *H.armigera* larvae when fed on 8 different foods.

Food	Amount of food eaten(mg/larva±S.E.)		Total larval weight gained
	Fresh weight	Dry weight	(mg±S.E.)
Artificial diet	7033.9± 290.8 b	1195.8± 49.5 b	530.3±10.5 a
Lucerne leaves	2783.5± 134.1 e	527.8± 25.4 e	352.2± 8.6 c
Tomato leaves	5788.9± 300.6 d	875.3± 48.5 c	393.6± 9.8 b
Tomato fruits	29660.8±1622.1 a	1957.6±107.1 a	517.1±10.4 a
Aster leaves	6530.2± 198.9 bc	1187.8± 36.2 b	510.6±12.9 a
Aster flowers	5690.9± 133.3 d	1173.5± 27.5 b	533.0±10.9 a
Sweetcorn leaves	5728.6± 137.9 d	829.5± 19.9 d	395.1± 8.2 b
Sweetcorn cobs	6311.6± 59.9 cd	1232.7± 11.7 b	530.0± 6.9 a

Means in columns of the table, not followed by the same letter, are significantly different at the 5% level (P=0.05).

2.Dry matter content of food

There were significant differences in percent dry matter content of foods (Table 6.2). Aster flowers had the highest dry matter content (20.62%) followed by sweetcorn cobs, lucerne leaves, aster leaves, artificial diet, tomato leaves and sweetcorn leaves. Tomato fruits had the lowest at 6.60%. Thus tomato fruits had the highest water content (93.40%) and aster flowers the lowest (79.38%). Details of dry matter contents (and water contents) of each food are given in Table 6.2.

3.Nitrogen content of food

Nitrogen contents of dried foods are shown in the final column of Table 6.2. The foods fall into 5 significantly different groups (P=0.05). Artificial diet had the highest nitrogen content (4.59%) followed by tomato leaves(4.51%) and lucerne leaves(4.18%). Aster leaves and sweetcorn leaves had lower and closely similar contents (3.18% and 3.11%). The group with the lowest nitrogen content were tomato fruits (1.87%), aster flowers(1.86%) and sweetcorn cobs(1.89%). Perhaps unexpectedly all plants had higher nitrogen content in their leaves than in their reproductive parts(fruits, flowers and cobs).

Table 6.2 Dry matter content, water content and nitrogen content of each food.

Food	%Dry matter content (mean±S.E.)	%Water content	%Nitrogen content (mean±S.E.)
Artificial diet	17.00±0.03	83.00	4.59±0.02 a
Lucerne leaves	18.96±0.20	81.04	4.18±0.03 c
Tomato leaves	15.12±0.13	84.88	4.51±0.03 b
Tomato fruits	6.60±0.08	93.40	1.87±0.04 e
Aster leaves	18.19±0.35	81.81	3.18±0.02 d
Aster flowers	20.62±0.21	79.38	1.86±0.02 e
Sweetcorn leaves	14.48±0.21	85.52	3.11±0.05 d
Sweetcorn cobs	19.53±0.19	80.47	1.89±0.03 e

Means in the column of the table, not followed by the same letter, are significantly different at the 5% level(P=0.05)

4.Parameters of food utilization

Parameters of food utilization by larvae are shown in Table 6.3. On fresh weight basis of food, tomato fruits gave the highest consumption index(C.I) followed by tomato leaves, artificial diet, sweetcorn cobs, aster flowers, aster leaves, sweetcorn leaves and lucerne leaves which were 6.23, 1.43, 1.40, 1.33, 1.19, 1.12, 1.10 and 0.90 respectively. On dry weight basis, tomato fruits also gave the highest C.I. followed by sweetcorn cobs, aster flowers, artificial diet, tomato leaves, aster leaves, lucerne leaves and sweetcorn leaves which were 0.41, 0.26, 0.25, 0.24, 0.23, 0.20, 0.17 and 0.16 respectively.

The efficiency of conversion of ingested food (E.C.I.) varied considerably. Lucerne leaves gave the highest E.C.I.(12.65) followed by aster flowers(9.37), sweetcorn cobs(8.40), aster leaves(7.82), artificial diet (7.54), sweetcorn leaves(6.90), tomato leaves(6.80) and tomato fruits(1.74).

There was a strong negative correlation between C.I. and E.C.I. ($r=-0.825$, $P=0.006$) indicating that larvae ate less of those foods that were readily digested and assimilated.

The relative growth rate(R.G.R.) did not follow any particular pattern or correlate well with any other parameter. Larvae reared on lucerne leaves had the highest R.G.R. followed by aster flowers and sweetcorn cobs, tomato fruits, artificial diet, tomato leaves, aster leaves and sweetcorn leaves which were 0.114, 0.112, 0.112, 0.109, 0.106, 0.097, 0.088 and 0.076 respectively.

Table 6.3 Parameters of food utilization; C.I.=consumption index, E.C.I.=efficiency of conversion of ingested food, R.G.G.=relative growth rate.

Food	C.I.[a]	C.I.[b]	E.C.I.[a]	E.C.I.[b]	R.G.R.
Artificial diet	1.40	0.24	7.54	44.32	0.106
Lucerne leaves	0.90	0.17	12.65	66.73	0.114
Tomato leaves	1.43	0.23	6.80	44.97	0.097
Tomato fruits	6.23	0.41	1.71	26.41	0.109
Aster leaves	1.12	0.20	7.82	43.01	0.088
Aster flowers	1.19	0.25	9.37	45.42	0.112
Sweetcorn leaves	1.10	0.16	6.90	47.63	0.076
Sweetcorn cobs	1.33	0.26	8.40	42.99	0.112

a) calculated from fresh weight of food and fresh weight of larvae.

b) calculated from dry weight of food and fresh weight of larvae.

DISCUSSION

One food(tomato fruits) had considerably higher water content (93.40%) than all other foods which ranged 79-85% (Table 6.2). On fresh weight basis, larvae consumed vastly more tomato fruit than any other food; more than 4 times the next highest (artificial diet). This greatly increased intake more than compensated for lower dry matter content of tomato fruits compared to other foods. Thus dry matter ingested was also highest for tomato fruits and about 50% higher than the next highest (sweetcorn cobs). Lowest fresh weight consumption was of lucerne leaves being about 50% of the next lowest, aster flowers. Water content of lucerne leaves was relatively low, at 81%, but even so lucerne leaves also had lowest dry matter intake.

These data on relative consumption rates suggest that tomato fruits may contain a feeding stimulant and that lucerne leaves may contain a feeding deterrent though this was not investigated further in the present work. One possible explanation is simply that the very high water content of tomato fruits stimulates feeding of larvae. Overall the best biological performance and average ranking was in fact obtained from larvae fed on tomato fruits (with the highest water content) though the lowest overall ranking was for larvae fed on sweetcorn leaves which had the second highest water content but gave only a modest dry matter intake (Tables 5.7 and 6.2).

Scriber and Feeny(1979) studied larvae of 9 species of swallowtail butterflies, 10 species of bombycoid moths and southern armyworm and postulated that one leaf characteristic responsible for high larval growth was water content because larvae grew faster and more efficiently

on herbaceous plants (70-91% water content) than on the foliage of shrubs and trees (51-74% water content). Scriber(1977) showed that Hyalophora cecropia (Lepidoptera; Saturniidae) fed on low-water content leaves grew more slowly and was less efficient at utilizing plant biomass, energy and nitrogen than larvae fed leaves which were fully supplemented with water. Scriber and Slansky (1981) concluded that biological performances of certain foliage-chewing insects were significantly greater on leaves with water contents in the range of 75-95% than those on less water contents. In the present work there was no apparent association of biological performance with water content of food with the exception of tomato fruits.

Efficiency of conversion of ingested food to body weight(E.C.I.) was much higher for lucerne leaves(the highest) than for tomato fruits (the lowest). This to a large extent compensated for low ingestion of lucerne leaves so that relative growth rates(R.G.R.) on these two foods were not very different.

The range of values for E.C.I. based on fresh weight of food was 7.4 times (ratio of highest to lowest). On the basis of dry weight of food (perhaps more meaningful) the ratio was only 2.53 times. On dry weight basis all foods gave E.C.I.s of 43-47 except for tomato fruits(26.4) and lucerne leaves(66.7).

A surprising feature was that nitrogen contents were lower in the reproductive parts (fruits, flowers and cobs) than in leaves of all three plants in which comparison was made. In all cases, in contrast, the biological fitness index of reproductive parts was much higher than leaves (Table 5.8). If nitrogen is a limiting factor for growth and development of H.armigera this raises two questions. 1) What is the minimum nitrogen requirement for this species and 2) why are the fitness

indices and biological performances relatively low on leaves with high nitrogen contents?

The present work does not answer the first question precisely but it is evident that H.armigera requires only very low nitrogen content of food to keep body nitrogen level stable. It is clear from the performance of larvae fed tomato fruits, aster flowers and sweetcorn cobs that only about 1.9% nitrogen is sufficient for growth and development of this insect.

However, if this conclusion is valid then fitness indices and biological performances of larvae fed on leaves should be better than in Tables 5.7 and 5.8 because all leaves contain relatively high nitrogen contents (range of 3.1-4.5%). A possible explanation is that leaves of all 4 plants tested contain harmful allelochemics and/or undesirable physical properties such as toughness and high fibre content that limit digestion and assimilation. Artificial diet, which is well-balanced in nutrients and without allelochemicals or high fibre content but with the same nitrogen content as leaves(4.6%), showed the highest biological fitness index (or second highest to tomato fruits on the "improved" index).

The minimum requirement of nitrogen content in food is known for relatively few insects. Mattson(1980) reported that butterfly larvae and grasshopper nymphs needed at least 3% nitrogen in dry matter of food while Fox and Macauley(1977) showed that growth performance of Paropsis leaf beetles on Australian Eucalyptus tree was correlated with small differences in nitrogen content(range of 0.5-1.9%). Broadway and Duffey(1986) demonstrated that larvae of H.zea grew best on artificial diet containing 1.2% casein (a dietary protein). At concentrations of casein greater or less than 1.2%, H.zea were delayed in larval

development, suggesting that there is a low optimum value. Al-Zubaidi and Capinera(1984) reported that larvae of beet armyworm (Spodoptera exigua) fed on foliage with high nitrogen levels (2%) gave shorter larval development, higher larval weight, higher egg production, lower mortality but no difference in pupal development than those fed on foliage with low nitrogen levels(0.5 and 1%). However, Broadway and Duffey(1986), Faeth et al.(1981), Schroeder(1976), Stiling et al.(1982) all argued that elevation of nitrogen in food did not result in increased performance of insects.

The results presented in this chapter shed little light on the reasons for differences in biological fitness indices of foods as evaluated in Chapter 5. In fact they do not even adequately explain relative growth rates of larvae or final weights of pupae on the different foods. However, larval weight gain is one parameter which correlates well with overall ranking and with pupal weight ($r=0.731$, $P=0.02$).

It can only be concluded that the nutritional factors in the various foods are much more complex than simply dry matter content (and its reciprocal water content) and nitrogen levels. Amounts of cellulose may vary between plant tissues and this could be a further factor affecting the insect's ability to digest different diets. Cellulose contents however were not determined in the present study.

CONCLUSIONS

Dry matter content (and its reciprocal water content) and nitrogen content of foods, either considered alone or in combination, do not provide an adequate measure of food quality for larvae of H.armigera.

However, rate of ingestion of food differed greatly and this must be a major factor influencing larval growth rate on a particular food.

Efficiency of conversion of ingested food to body weight also differed widely between foods and larvae tended to consume less of these foods that were more readily digested and assimilated (lucerne leaves especially).

The nitrogen requirement of H.armigera appears to be low (about 1.9% of dry matter). Nitrogen level of flowers(aster), fruits(tomato) and cobs(sweetcorn) were surprisingly low(less than 2%) but larvae grew well on these foods.

CHAPTER 7

FOOD SELECTION AND INDUCTION OF FEEDING PREFERENCE IN LARVAE OF HELIOTHIS ARMIGERA

INTRODUCTION

Feeding preferences of particular phytophagous insects are commonly characterised by those plant species that are acceptable or preferred by them. However, though the feeding preferences of newly hatched insects must be primarily genetically determined it is known that such preferences (for some insects at least) may be modified by early feeding experience i.e. preference may be induced rather than inherited. Any investigation of feeding preference for a particular species must therefore consider both newly hatched "naive" insects and those that have already fed on a particular food for a period of time.

Induction of feeding preference has been demonstrated for several species of lepidopterous larvae on different foods by various investigators. Working with the oligophagous tobacco hornworm (Manduca sexta) which normally feeds on solanaceous plant species, de Boer and Hanson (1984), Jermy et al. (1968), Saxena and Schoonhoven (1978), Schoohoven(1967) and Yamamoto(1974) demonstrated that feeding preferences (among solanaceous plants) could be modified depending on plant species on which the larvae had beed reared. An increased preference was found for the rearing plant species relative to other plant species. Similar induction has been reported in numerous other lepidopterous species (eg. Barbosa et al., 1979; Greenblatt et al., 1978; Hanson, 1976; Jermy et al., 1968; Wiklund,1973) and in a few

non-lepidopterous insects; Caurausius morosus(Phasmida) by Cassidy(1978) and Haltica lythri (Coleoptera) by Phillips(1977). However, induction of feeding preference does not seem to occur in all herbivores as failure to induce change has been reported. For example, the butterfly Limenitis rubidus did not induce on two plant species but did on four other species (Hanson,1976) and two Pieris species did not induce on four food plants(Chew, 1980).

Induction of food preference in H.armigera larvae has not been reported. However, Jermy et al.(1968) studied H.zea larvae and reported that modification of feeding preference during the larval period could be induced by plants within the insect's innate host range but could not be induced by plants outside this range. The modified behaviour induced by a short exposure (during only one instar) was retained through the moult and after the gut had been purged of possible previous food. Jermy et al.(1968) concluded that the information serving as a basis for the induced habit was stored in the central nervous system.

The present study was designed to examine the feeding preference of newly hatched and of fourth instar larvae of H.armigera when reared on artificial diet and to investigate induction of feeding preferences after rearing larvae on other specific foods.

MATERIAL AND METHODS

Larvae of H.armigera were reared on artificial diet in controlled laboratory conditions at ca 25°C and 16:8(L/D) photoperiod. The composition of the formulated diet is shown in Appendix 1. Eggs obtained from this colony were used for production of test larvae.

Lucerne, tomato, aster and sweetcorn plants were grown and maintained under nearly identical growing conditions in a greenhouse. No pesticides were sprayed on these plants.

The assay chamber for feeding preference tests consisted of a clear plastic cup (312 cm^3) with a ventilated lid and a 1 cm thick paraffin wax layer on the bottom (8 cm in diameter). For humidity control, which was necessary to reduce larval and food desiccation, a moist filter paper was placed on the paraffin layer. Test foods (portions of foliage or reproductive parts of plants) were arranged in ABAB fashion around the edge of the floor of the cup and supported by pins. The test procedure was based on that used by Jermy et al.(1968) and Phillips(1977).

A single larva was placed individually in the centre of each assay chamber at approximately the same distances from each food sample. All tests were conducted under continuous light in controlled laboratory conditions over a 12-hour period. The assay chamber is illustrated in Figure 7.1.

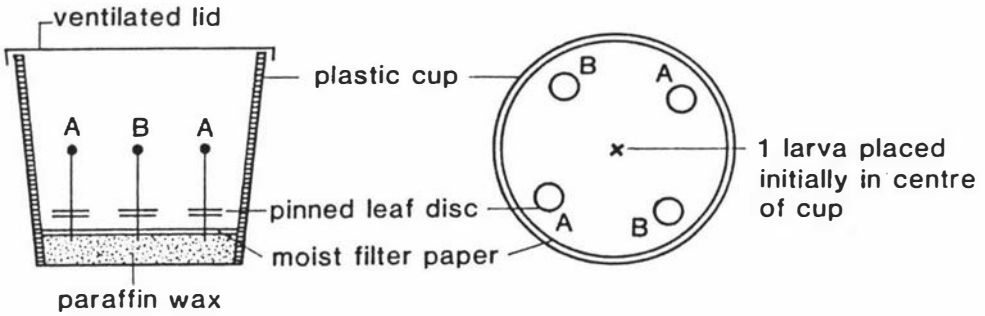

Figure 7.1 Arrangement for preference tests. A and B are leaf discs of two different plant species mounted on pins.

1. Preference of newly hatched larvae for different foods

1.1 Preference tests using leaf discs

Using a cork borer, leaf discs 11 mm in diameter were punched from fresh leaves of each plant species to be examined. Two leaf discs from two different plant species were placed in each chamber (ABAB arrangement). Comparisons were made between leaf discs of the following pairs; lucerne vs tomato, lucerne vs aster, lucerne vs sweetcorn, tomato vs aster, tomato vs sweetcorn and aster vs sweetcorn. Each leaf disc was fixed on a pin and stood horizontally about 5 mm above the surface of moist filter paper (see Figure 7.1). One healthy newly hatched larva was placed singly in the centre of each assay chamber using a fine brush. There were 30 replicates of each comparison.

As the amount of leaf disc eaten by newly hatched larvae was so small and impractical to measure, the positions of larvae were recorded at the 1st, 3rd, 6th and 12th hour after initiating a test.

1.2 Preference for reproductive parts of plants

For evaluation of preference for reproductive parts of plants, fresh green tomato fruits, aster flowers and sweetcorn cobs (cut to approximately the same size) were placed in assay chambers without supporting pins. The trial procedure was otherwise the same as for leaf discs.

2. Induction of feeding preference by rearing on a specific food

2.1 Rearing on artificial diet and plant leaves

Larvae of *H.armigera* were reared on artificial diet, lucerne leaves, tomato leaves, aster leaves and sweetcorn leaves until the third moult. After moulting, larvae were held individually in small

containers and starved for 12 hours. Larvae were then tested individually under continuous light for 12 hours. All tests were multichoice between discs of lucerne, tomato, aster and sweetcorn leaves offered simultaneously. Two leaf discs of each plant species 13 mm in diameter (given a total area of 265.6 mm^2) were used in each test. At the end of 12-hour period the area of leaf discs remaining was estimated by placing transparent graph paper over them. Leaf area consumed was calculated from the initial area minus that remaining. A correction factor for leaf thickness was considered unnecessary as de Boer and Hanson(1984) found no effect of leaf weight differences upon food choice. Assay chambers in which leaf discs of one plant species were completely consumed were ignored because the leaf discs of another plant species might then have been consumed without choice.

Mean preference values were calculated after Cassidy(1978) as follow:

$$PV = \frac{CA-CB}{\overline{CA}+\overline{CB}}$$

where PV = Mean preference value

CA = Area of leaf A consumed

CB = Area of leaf B consumed

CA+CB = Total area consumed

2.2 Rearing on artificial diet and reproductive parts of plants

Larvae of H.armigera were reared on artificial diet, tomato fruits, aster flowers and sweetcorn cobs until the third moult. After moulting, larvae were held individually in empty containers and starved for 12 hours. Larvae were then tested individually under continuous light for 12 hours. All choice tests were between pairs of tomato fruits, aster flowers and sweetcorn cobs. Portions of these were cut to

approximately the same size. At the end of the 12-hour test period the positions of larvae were recorded and percentages of larvae on each food calculated. Binomial distribution of Snedecor and Cochran(1967) were applied to calculate significant differences.

RESULTS

1. Preference of newly hatched larvae for different foods

1.1 Preference tests using leaf discs

Results of preference tests of newly hatched larvae for leaf discs of the four different plant species are summarized in Table 7.1 and illustrated in Figure 7.2.

In dual tests of lucerne leaves vs sweetcorn leaves, tomato leaves vs sweetcorn leaves and aster leaves vs sweetcorn leaves larvae tended to wander around the assay chambers for the first 3 hours and at that time more larvae were found elsewhere than on leaf discs (Figure 7.2(c), (e) and (f)). By the 6th hour in all comparisons most larvae had moved to and started feeding on leaf discs. By the 12th hour preference for leaf discs of one plant or the other were clearly expressed. It can be concluded from the 12th hour figures that preferences were in the order:

Lucerne leaves > tomato leaves > aster leaves > sweetcorn leaves

1.2 Preference for reproductive parts of plants

Results of preference tests of newly hatched larvae for reproductive parts of plants are summarized in Table 7.2 and in Figure 7.3.

In contrast to tests with leaf discs most larvae showed strong preference for reproductive parts of plants by moving to them within the

1st hour in all tests. In the paired comparison of tomato fruits vs aster flowers {Figure 7.3(a)} all larvae were on the test foods after 1 hour and in the worst situation (tomato fruits vs sweetcorn cobs) after 3 hours only 13% of larvae were not on the test samples.

It can be concluded that preferences of newly hatched larvae for reproductive parts of plants were in the order:

Tomato fruits $\rangle$ sweetcorn cobs $\rangle$ aster flowers

Table 7.1 Percentages of newly hatched larvae of H.armigera on leaf discs of four host plants. (n=30)

Position of larvae	Elapsed time(hours)				P
	1	3	6	12	
Lucerne leaves	46.6	56.7	70.0	80.0	0.01
Tomato leaves	36.7	20.0	26.7	20.0	
Elsewhere	16.7	23.3	3.3	0	
Lucerne leaves	30.0	50.0	53.3	66.7	0.01
Aster leaves	43.3	30.0	30.0	30.0	
Elsewhere	26.7	20.0	16.7	3.3	
Lucerne leaves	40.0	23.3	53.5	70.0	0.01
Sweetcorn leaves	6.7	6.7	13.3	10.0	
Elsewhere	53.3	70.0	33.3	20.0	
Tomato leaves	63.3	63.3	60.0	66.7	0.01
Aster leaves	10.0	6.7	6.7	26.7	
Elsewhere	26.7	30.0	33.3	6.6	

Table 7.1 (continued)

Position of larvae	Elapsed time(hour)				P
	1	3	6	12	
Tomato leaves	26.7	26.7	40.0	43.3	0.05
Sweetcorn leaves	13.3	10.0	26.7	26.7	
Elsewhere	60.0	63.3	33.3	30.0	
Aster leaves	20.0	63.3	86.7	93.3	0.01
Sweetcorn leaves	13.3	13.3	3.3	3.3	
Elsewhere	66.7	23.3	10.0	3.3	

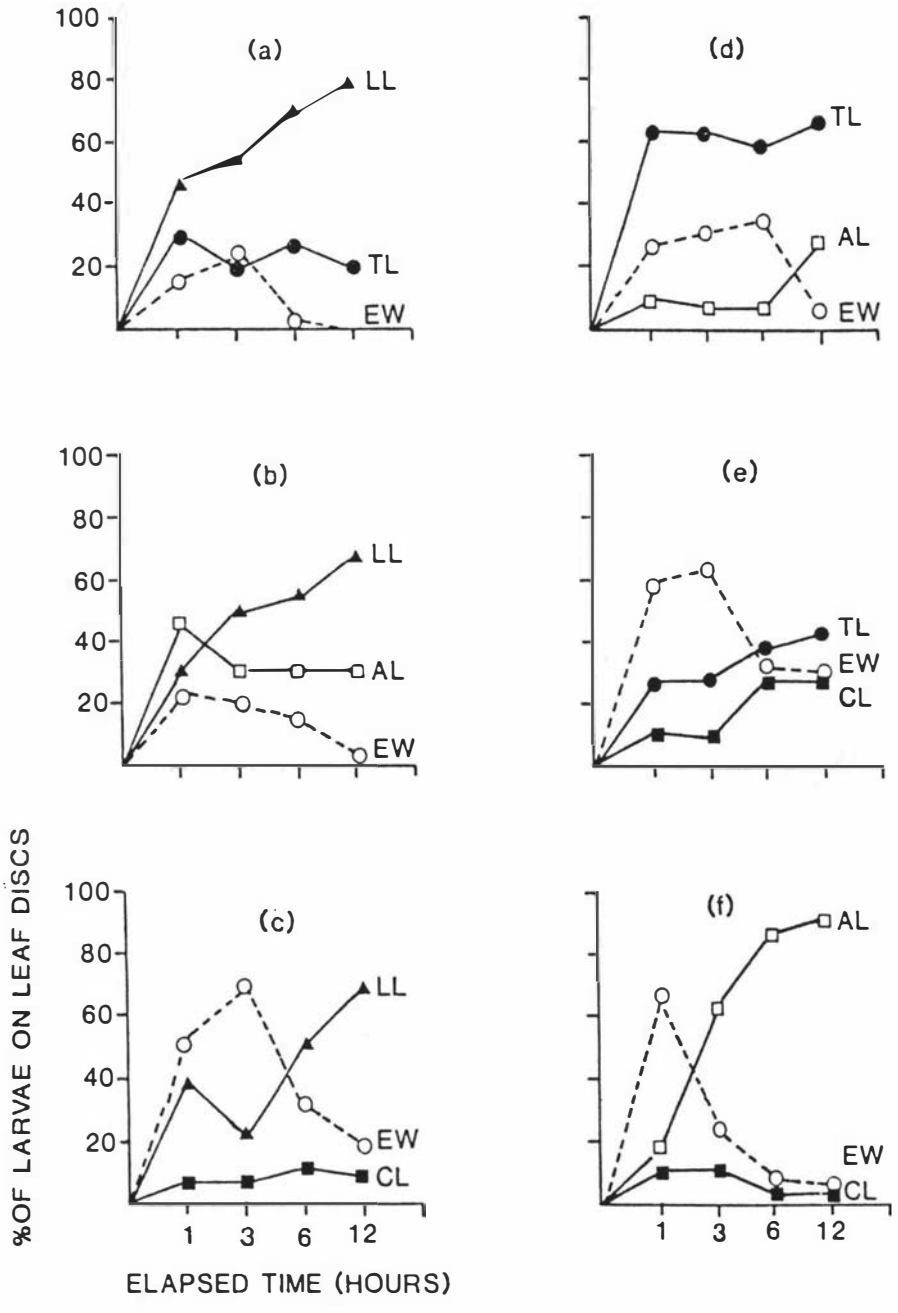

Figure 7.2 Percentages of newly hatched larvae of H.armigera on leaf discs of four host plants.

Abbreviations AL=aster leaves, CL=sweetcorn leaves, EW=elsewhere, LL=lucerne leaves, TL=tomato leaves

Table 7.2 Percentages of newly hatched larvae of H.armigera on reproductive parts of host plants. (n=30)

Position of larvae	Elasped time(hours)				P
	1	3	6	12	
Tomato fruits	66.7	56.7	56.7	53.3	0.05
Sweetcorn cobs	26.7	30.0	43.3	46.7	
Elsewhere	6.6	13.3	0	0	
Tomato fruits	80.0	86.7	76.7	73.3	0.01
Aster flowers	20.0	13.3	23.3	26.7	
Elsewhere	0	0	0	0	
Sweetcorn cobs	70.0	63.3	76.7	73.3	0.01
Aster flowers	20.0	33.3	20.0	23.3	
Elsewhere	10.0	3.3	3.3	3.3	

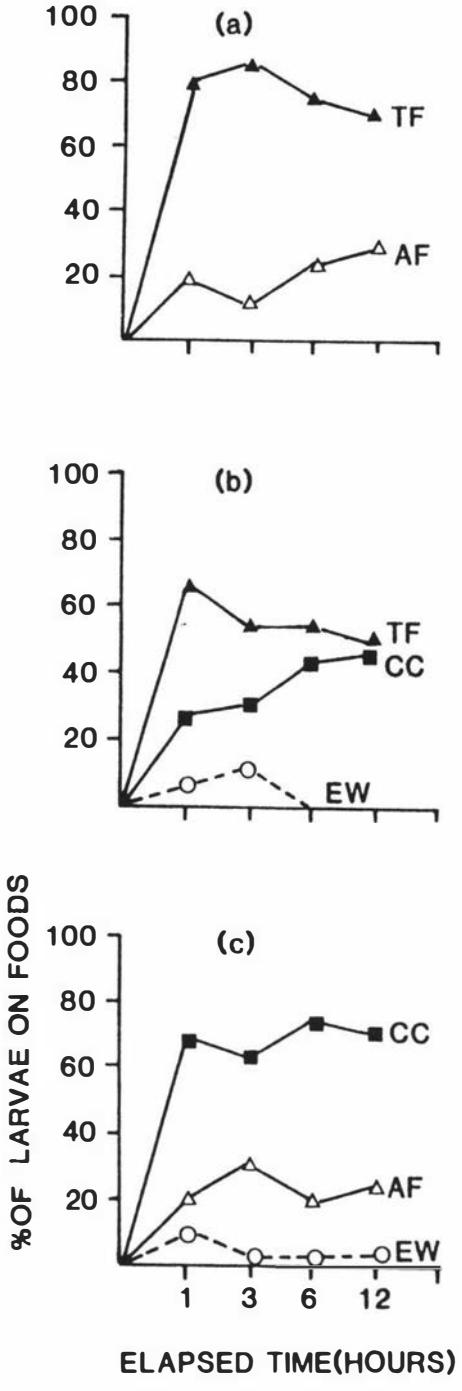

Figure 7.3 Percentages of newly hatched larvae of H.armigera on reproductive parts of plants.

Abbreviations AF=aster flowers, CC=sweetcorn cobs, EW=elsewhere, TF=tomato fruits

2. Induction of feeding preference by rearing on a specific food

2.1 Rearing on artificial diet and plant leaves

Fourth instar larvae raised on artificial diet preferred lucerne leaves over aster leaves (PV=0.72, P=0.01), tomato leaves (PV=0.90, P=0.01) and sweetcorn leaves(PV=0.86, P=0.01). Aster leaves were preferred over tomato leaves (PV=0.43, P=0.01) and sweetcorn leaves (PV=0.23, P=0.05) and tomato leaves were preferred over sweetcorn leaves (PV=0.31, P=0.05) (Table 7.3 and Figure 7.4). It can be concluded that larvae reared on artificial diet and then fed on plant leaves preferred them in the order;

Lucerne leaves〉aster leaves〉tomato leaves〉sweetcorn leaves

This preference heirarchy is the same as that for newly hatched first instar larvae except that the order of aster and tomato leaves is reversed.

Similarly fourth instar larvae raised on lucerne leaves showed strong preference for lucerne leaves over aster leaves (PV=0.84, P=0.01), tomato leaves (PV=0.80, P=0.01) and sweetcorn leaves (PV=0.83, P=0.01) (Table 7.4 and Figure 7.5).

However, fourth instar larvae raised on aster leaves preferred aster leaves over lucerne leaves (PV=0.74, P=0.01), tomato leaves (PV=0.88, P=0.01) and sweetcorn leaves (PV=0.80, P=0.01) (Table 7.4 and Figure 7.5).

Similary fourth instar larvae raised on tomato leaves preferred tomato leaves over lucerne leaves (PV=0.23, P=0.05), aster leaves (PV=0.76, P=0.01) and sweetcorn leaves (PV=0.82, P=0.01) (Table 7.4 and Figure 7.6).

Fourth instar larvae raised on sweetcorn leaves showed significant preference only for sweetcorn compared to tomato (PV=0.88, P=0.01) and

no preference compared to aster leaves (PV=0.01, P=0.8). The strong preference for lucerne leaves was not affected by raising larvae on sweetcorn leaves (PV=0.65,P=0.01) (Table 7.4 and Figure 7.6). Feeding on sweetcorn leaves therefore induced preference only with respect to tomato leaves which only ranked third (next to sweetcorn leaves) in uninduced larvae.

Table 7.3 Feeding preference of fourth instar larvae reared on artificial diet. Numbers in parentheses are percentages of food consumed. (n=30)

Test choice	Leaf area consumed (mm^2)	Mean preference value(PV)	P
Lucerne leaves	204.97 (86.2)	0.72	0.01
Aster leaves	32.90 (13.8)		
Lucerne leaves	219.43 (94.8)	0.90	0.01
Tomato leaves	12.00 (5.2)		
Lucerne leaves	198.93 (93.0)	0.86	0.01
Sweetcorn leaves	15.03 (7.0)		
Aster leaves	158.34 (71.8)	0.43	0.01
Tomato leaves	62.11 (28.2)		
Aster leaves	145.90 (61.5)	0.23	0.05
Sweetcorn leaves	91.17 (38.5)		
Tomato leaves	123.52 (65.6)	0.31	0.05
Sweetcorn leaves	64.80 (34.4)		

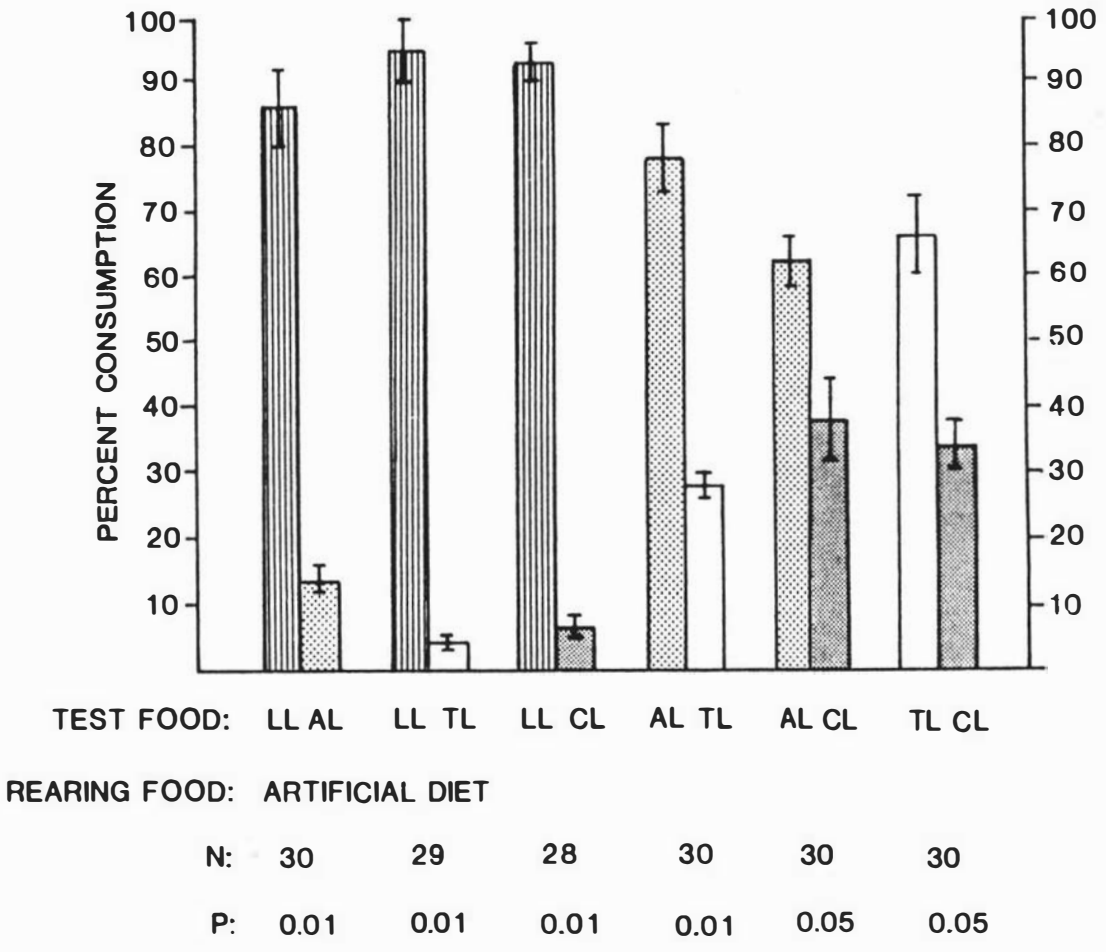

Figure 7.4 Feeding preference on plant leaves of fourth instar larvae of H.armigera reared on artificial diet. The bars at the top of the columns signify standard errors.

Abbreviations In Figures 7.4 to 7.6 :-

AL=aster leaves, CL=sweetcorn leaves,

LL=lucerne leaves, TL=tomato leaves,

N=number of replicates, P=probability

Table 7.4 Feeding preference of fourth instar larvae reared on specific foods. Numbers in parentheses are percentages of food consumed. (n=30)

Raised food	Test choice	Leaf area consumed(mm^2)	Mean preference value(PV)	P
Lucerne leaves	Lucerne leaves	240.73 (92.2)	0.84	0.01
	Aster leaves	20.37 (7.8)		
	Lucerne leaves	214.13 (89.8)	0.80	0.01
	Tomato leaves	24.37 (10.2)		
	Lucerne leaves	246.60 (91.5)	0.83	0.01
	Sweetcorn leaves	23.00 (8.5)		
Aster leaves	Aster leaves	233.40 (87.5)	0.74	0.01
	Lucerne leaves	33.37 (12.5)		
	Aster leaves	246.53 (94.0)	0.88	0.01
	Tomato leaves	15.83 (6.0)		
	Aster leaves	257.77 (90.1)	0.80	0.01
	Sweetcorn leaves	28.30 (9.9)		

Table 7.4 (continued)

Raised food	Test choice	Leaf area consumed(mm^2)	Mean preference value(PV)	p
Tomato leaves	Tomato leaves	170.40 (61.4)	0.23	0.05
	Lucerne leaves	107.30 (38.6)		
	Tomato leaves	213.77 (88.9)	0.76	0.01
	Aster leaves	26.80 (11.1)		
	Tomato leaves	192.27 (90.9)	0.82	0.01
	Sweetcorn leaves	19.20 (9.1)		
Sweetcorn leaves	Sweetcorn leaves	42.53 (17.7)		
	Lucerne leaves	197.33 (82.3)	0.65	0.01
	Sweetcorn leaves	109.60 (49.3)		
	Aster leaves	112.80 (50.7)	0.01	0. 8
	Sweetcorn leaves	212.93 (94.1)	0.88	0.01
	Tomato leaves	13.43 (5.9)		

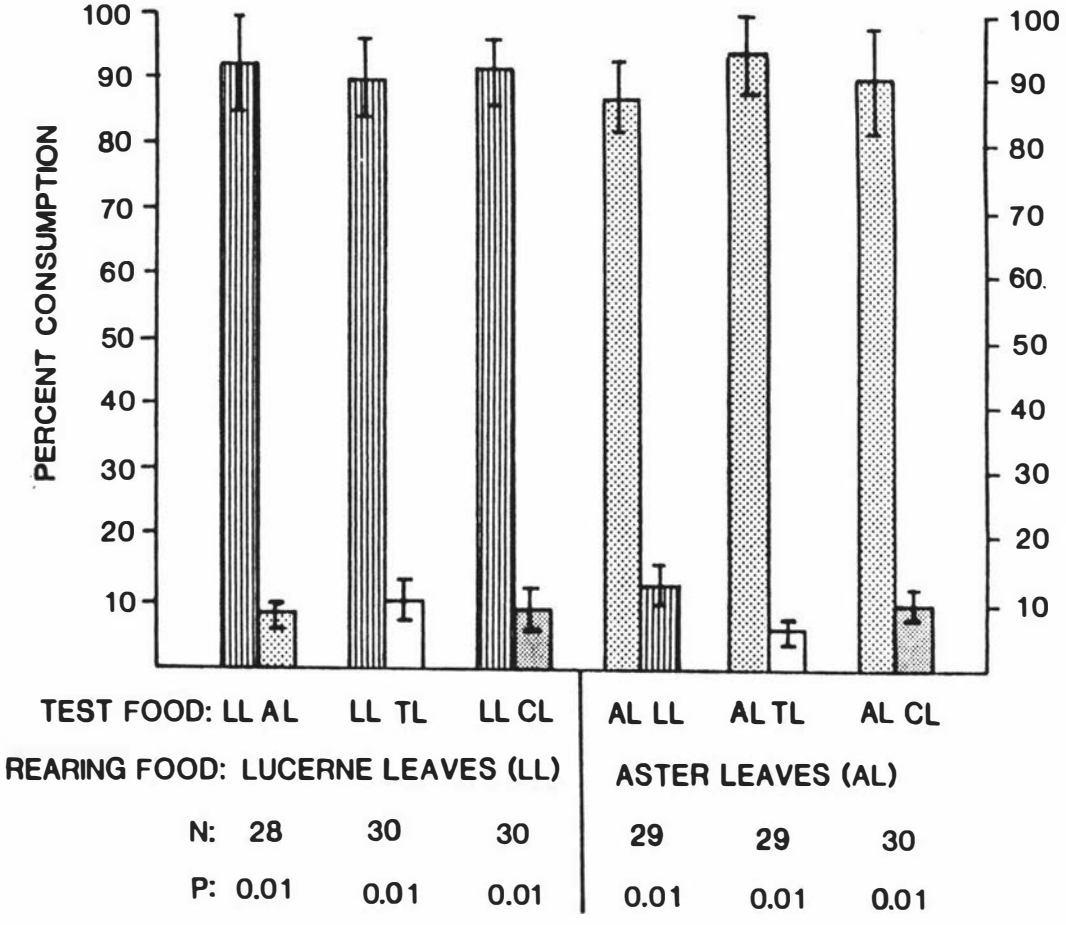

Figure 7.5 Feeding preference on plant leaves of fourth instar larvae of H.armigera reared on lucerne and aster leaves.

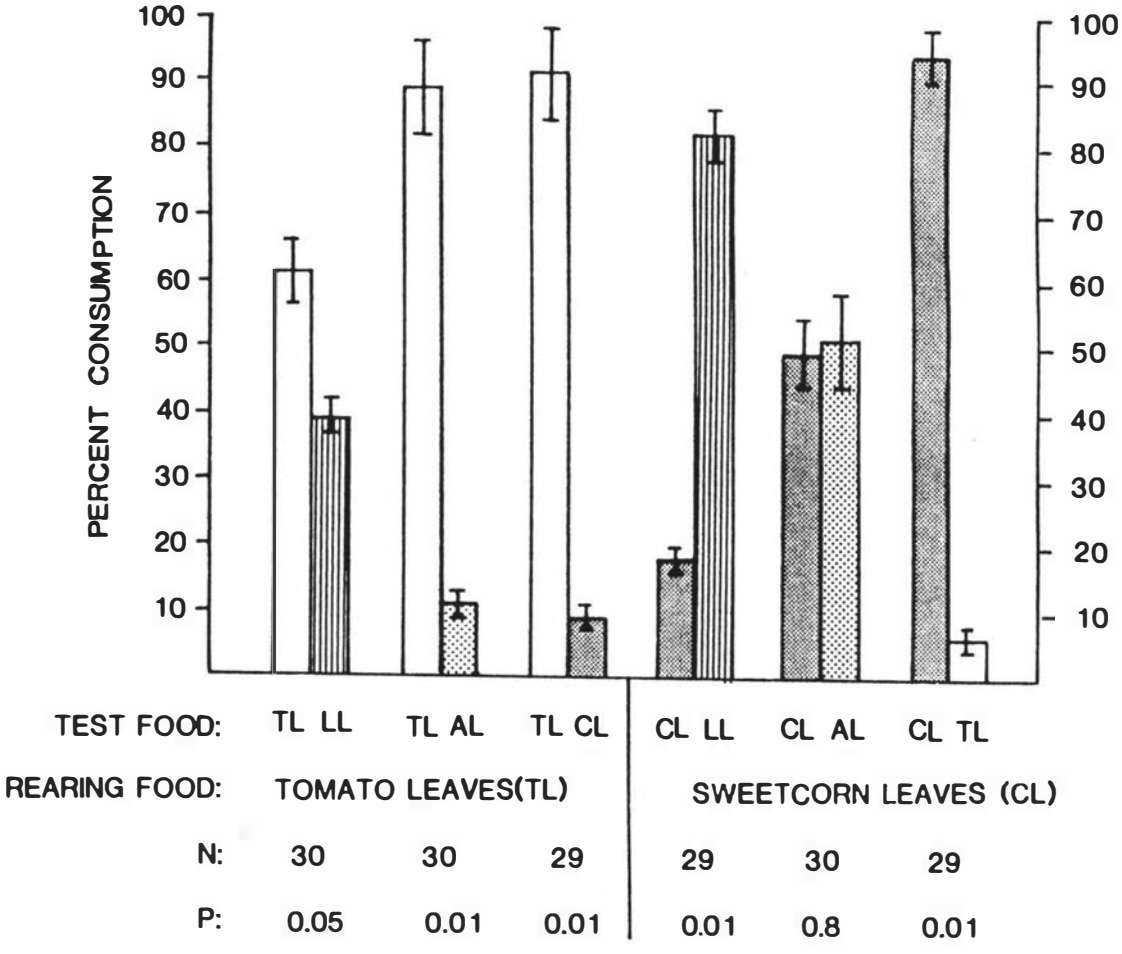

Figure 7.6 Feeding preference on plant leaves of fourth instar larvae of H.armigera reared on tomato and sweetcorn leaves.

2.2 Rearing on artificial diet and reproductive parts of plants

Fourth instar larvae raised on artificial diet preferred tomato fruits over sweetcorn cobs (P=0.05) and aster flowers (P=0.01). Sweetcorn cobs were preferred over aster flowers (P=0.05) (Table 7.5 and Figure 7.7). It can be concluded that feeding preferences of fourth instar larvae raised on artificial diet were in the order;

Tomato fruits > sweetcorn cobs > aster flowers

This was the same order of preference as shown by newly hatched first instar larvae (see Table 7.2).

Larvae raised on reproductive parts of plants to fourth instar showed highly significant preference for the plants on which they were raised (Table 7.6 and Figure 7.8). Thus fourth instar larvae raised on tomato fruits preferred tomato fruits over sweetcorn cobs (P=0.01) and aster flowers (P=0.10). Larvae raised on sweetcorn cobs preferred sweetcorn cobs over tomato fruits (P=0.01) and aster flowers (P=0.01) and larvae raised on aster flowers preferred aster flowers over tomato fruits (P=0.05) and sweetcorn cobs (P=0.05).

Table 7.5 Feeding preference of fourth instar larvae raised on artificial diet then offered reproductive parts of plants. (n=30, P=probability)

Test choice	%Larvae feeding on food at 12th hour	P
Tomato fruits	70.0	0.05
Sweetcorn cobs	30.0	
Tomato fruits	80.0	0.01
Aster flowers	20.0	
Sweetcorn cobs	70.0	0.05
Aster flowers	30.0	

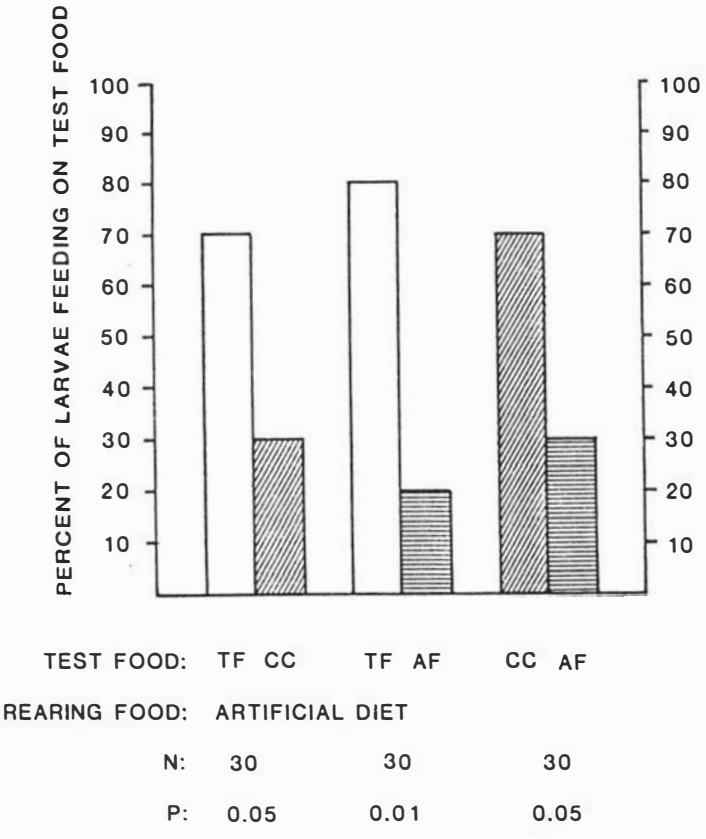

Figure 7.7 Feeding preference on reproductive parts of plants of fourth instar larvae of H.armigera reared on artificial diet.

Abbreviation In Figures 7.7 and 7.8 :-

AF=aster flowers, CC=sweetcorn cobs, TF=tomato fruits, N=number of replicates, P=probability

Table 7.6 Induction of food preference by fourth instar larvae raised on reproductive parts of plants. (n=30, P=probability)

Raised on	Test chioce	%Larvae feeding on food at 12th hour	P
Tomato fruits	Tomato fruits	80.0	0.01
	Sweetcorn cobs	20.0	
	Tomato fruits	86.7	0.01
	Aster flowers	13.3	
Sweetcorn cobs	Sweetcorn cobs	93.3	0.01
	Tomato fruits	6.7	
	Sweetcorn cobs	96.7	0.01
	Aster flowers	3.3	
Aster flowers	Aster flowers	70.0	0.05
	Tomato fruits	30.0	
	Aster flowers	73.3	0.05
	Sweetcorn cobs	26.7	

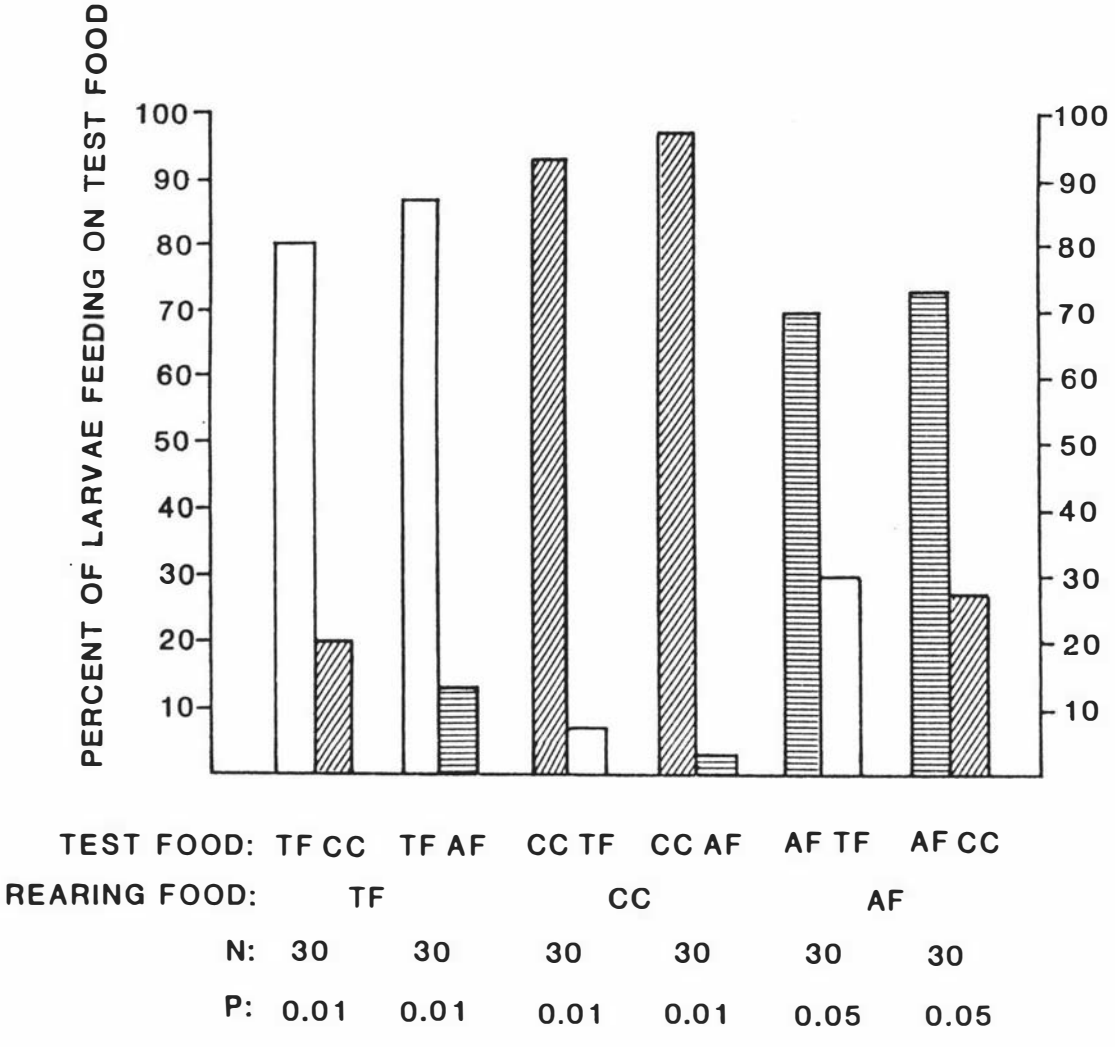

Figure 7.8 Feeding preference on reproductive parts of plants of fourth instar larvae of H.armigera reared on a specific food.

DISCUSSION

1. Preference of newly hatched larvae for different foods.

Newly hatched larvae did not generally immediately approach plant leaf discs. In all paired tests more larvae wandered around the assay chambers for the first 3 hours than occupied leaf discs(Figure 7.2). This may be because leaf discs of all four plants do not contain sufficiently strong attractants or feeding stimulants or perhaps because larvae had lost strong hostplant preference after the colony had been reared on artificial diet for several generations. However, by the 6th hour in all paired tests most larvae had moved to and started feeding on leaf discs of one test plant or the other. By 12th hour larvae showed stronger preference for lucerne leaves over leaves of the other three plants. Sweetcorn leaves were consistently the least preferred of all. Lucerne leaves may therefore possess more potent attractants than the other three plants.

The above experience parallels that of Schoonhoven(1967) who, working with the oligophagous tobacco hornworm(M.sexta), reported that after rearing larvae on artificial diet, they lost their hostplant specificity. Although acceptable hosts were provided, larvae spent some time in restless wandering and performing test bites. Hostplant specificity gradually reappeared when larvae were reared on their original host plants. Yamamoto(1974) also reported that newly hatched larvae of tobacco hornworm raised on artificial diet showed a polyphagous habit and would feed on many kinds of non-host plants (in addition to normal host plants) although they were not able to grow on them. Saxena and Schoonhoven(1982) found that newly emerged first-instar larvae of M.sexta showed equally strong orientational and

feeding responses to host tomato, non-host radish and an artificial diet but suggested that the naive first instar larvae cannot be considered polyphagous. Unlike the oligophagous tobacco hornworm, H.armigera is polyphagous and in current tests showed strong preference for lucerne leaves although most larvae spent the first 3 hours wandering around assay chambers.

In contrast, first instar H.armigera larvae showed rapid response to reproductive parts of plants within the first hour in all tests. Tomato fruits were much more preferred than sweetcorn cobs and aster flowers(Figure 7.3) and thus may contain stronger attractants and feeding stimulants. However, in all tests a few larvae still wandered around the assay chambers for some time and most of these were on the lids of the test chambers. This may be due to the effect of overhead light provided during the experiments as in rearing of H.armigera it was observed that newly hatched larvae tend to move towards to the light.

2.Induction of feeding preference by rearing on a specific food.

Fourth instar larvae raised on artificial diet exhibited the same feeding preferences as newly hatched larvae on both leaves and reproductive parts of plants with the minor exception of reversal of preference for tomato and aster leaves. These larvae showed strong preference for lucerne leaves over other leaves. This may be because lucerne leaves contain stronger feeding stimulants than other leaves but the results may also be influenced by the fact that the larvae were raised on artificial diet based on kidney beans which are in the same plant family as lucerne (Leguminosae). However, such artificial diet raised larvae when offered reproductive parts of plants preferred tomato fruits to sweetcorn cobs and aster flowers. These test foods are not in

the same plant family as kidney beans. Stadler and Hanson(1978) reported that M.sexta raised on artificial diet were not behaviourally "naive" with respect to its constituents but were induced to feed preferentially by them. They did not agree with Jermy et al. (1968), Schoonhoven(1967) and Yamamoto(1974) who suggested that artificial diets were neutral in effect. It seems unwise to generalise about the likely effects of artificial diets without taking into account their specific constituents.

In the present work the strong induction of feeding preferences found with the four different plant species and plant parts (Tables 7.4, 7.6 and Figures 7.5 to 7.8) extends to H.armigera the results of earlier induction experiments with many insects, for example Lepidoptera-H.zea(Jermy et al.,1968), M.sexta(Hanson and Dethier,1973; Jermy et al.,1968; Stadler and Hanson,1978; Saxena and Schoonhoven,1978,1982; Yamamoto,1974), Lymantria dispar(Barbosa et al.,1979), Pieris spp.(Chew, 1980), Callosomia promethea and Polygonia interrogationis (Hanson,1976), Hyphantria cunea (Greenblatt et al.,1978) and non-Lepidoptera- Caurausius morosus (Phasmidae)(Cassidy,1978) and Haltica lythri (Coleoptera)(Phillips, 1977).

Leaves of lucerne, aster and tomato gave the strongest induction of feeding preference. Larvae reared on sweetcorn leaves(the least preferred by newly hatched and diet reared larvae) showed significant preference for sweetcorn leaves only when compared to tomato leaves, and not compared to aster or lucerne leaves. Moreover, the strong preference for lucerne leaves was not affected by raising larvae on sweetcorn leaves, though leaf area of sweetcorn leaves consumed was greater than for larvae raised on artificial diet. Jermy et al.(1968) raised larvae of H.zea on artificial diet to the early sixth instar and

then allowed them to feed on geranium or dandelion or cauliflower leaves for 48 hours. The larvae then showed strong preference to these foods in choice tests and the authors concluded that preference in this insect species could be induced in only 2 days. The present results with H.armigera do not support this conclusion because even raising larvae to fourth instar (over approximately 10 days) did not induce preference to all foods.

This suggests that for H.armigera larvae, although feeding preference can be modified by food which has previously been consumed, the strength of induction for each food is different and the least preferred food cannot overcome innate preference for the much more strongly preferred ones.

Reproductive parts of plants induced greater preference than leaves and larvae raised on tomato fruits, sweetcorn cobs or aster flowers showed very strong preferences to that food. This, together with the rapid orientation of first instar larvae to these plant parts, suggests that they contain more potent attractants and/or feeding stimulants than leaves.

CONCLUSIONS

These results show that although newly hatched "naive" larvae of *H.armigera* express clear preferences for particular plant species, these preferences may be modified by early feeding experience i.e. induction of feeding preference was readily achieved. Artificial diet included some plant materials(kidney beans) but had little effect on food preference.

Preference for reproductive parts of plants was more strongly expressed than for leaves and reproductive parts evoked greater induction.

CHAPTER 8

GENERAL DISCUSSION

In this chapter discussion concentrates on interrelationships between results reported in earlier experimental chapters and their significance in relation to the overall ecology of Heliothis armigera. However, for convenience, discussion is organised under five headings:

1) Seasonal development
2) Feeding sites of larvae in the field
3) Larval food quality
4) Larval feeding preference
5) Oviposition preference

1. SEASONAL DEVELOPMENT

In cool temperate climates with a distinct winter, such as Manawatu, North Island, New Zealand, all activity of H.armigera ceases over the winter months and the population is present as diapausing pupae in the soil. In terms of initiation of a new season's generation it is important to know when adult moths start emerging from overwintering pupae or fly into the area from outside. Although data were obtained on male moth activity from pheromone traps operated over the 1985-86 season the results do not enable firm conclusions to be drawn as to dates of first emergence or immigration.

Pheromone traps were operated from December 25,1985 to April 30,1986. The first moth was caught on December 29,1985 and the last on April 25,1986 Emergence of moths could have started before traps were

set in 1985. However, numbers of moths caught before January are very low then gradually increase to reach a peak in March (Table 3.5). This pattern is similar to the results from light traps run at Massey University, Palmerston North in 1966-69 (Gaskin,1970a; Spitzer,1970). These authors also found that few moths(<10) were caught before January, although the first moth appeared in October. From October 28,1986 to April 24,1987 two pheromone traps were operated in the same area by Dr.P.G.Fenemore and only one moth was caught before January (unpublished data). The few moths caught before January in both years may well have originated from overwintering pupae and the numbers may be low because diapausing pupae vary in time of emergence (Singh et al., 1982). Also numbers of pupae surviving the winter may be reduced due to parasitism by the fungus, Paecilomyces farinosus (Alma,1975a, 1977; Valentine,1975). The large numbers of moths caught in February and March must be mostly progeny from the first summer generation of larvae but may be supplemented by late emerging diapausing pupae.

Pheromone trap catches may also be influenced by prevailing weather conditions and thus may not necessarily reflect moth abundance. Although individual meteorological parameters (maximum day temperature, minimum night temperature, wind velocity and rainfall) show no significant correlation with catches of moths, more moths were caught when minimum temperature was greater than 10°C, wind velocity was less than 20 km/h and there was less than 8 mm rainfall. Hartstack et al. (1979) reported that low temperatures at night (<12.8°C) inhibit overall Heliothis moth activity including the courtship response and flight of male moths to pheromone traps. These results therefore suggest that the greater numbers of moths caught in February and March compared to other months may be due to in part to the warmer weather at this time. The

availability of food for adults in the form of nectar from flowers, host plants providing attractive oviposition sites and the availability of larval food plants may also be contributing factors to attracting moths to the trial area and hence boosting trap catches in late summer.

Although H.armigera conferta moths have not been recorded in winter in New Zealand, a number of other Noctuid moths have been caught by light traps (Spitzer, 1970). The closely related sub species, H.armigera occurs throughout the year in Autralia but temperatures are undoubtedly higher than in New Zealand. Persson(1976) operated light traps continuously for one and a half years in south coastal Queensland and reported that H.armigera moths occurred throughout the year, although numbers were low in winter. In eastern coastal Australia there are two peaks of moth populations, the bigger peak occurs in November-December and a smaller one in March-April (Wilson,1983).

It had been planned to record dates of occurrence of eggs and to investigate sites of egg deposition on plants in field plots but this proved impossible in the field situation. Initially the number of moths during the early growing season (before January) was very low as discussed and hence numbers of eggs must also have been very low at this time. The peak of moth activity (February and March) must have resulted in heavy oviposition as it was soon followed by heavy infestation of the plants but no quantitative data on egg numbers was obtained. Results of oviposition behaviour studies in the glasshouse are discussed later.

Small larvae when disturbed usually drop from the plant and hang suspended on silk threads and thus are difficult to observe. As the feild plots were observed daily it should have been possible to determine exactly when the first larva appeared. However, in both seasons (early January in the first season and late December in the

second) the first larva recorded was already in the third instar. Besides low numbers of eggs laid other possible factors responsible for low larval populations early in the season are inclement weather and insufficiency of high quality food as reproductive parts of plants had not developed at this stage. Between late January and March the numbers of larvae increased rapidly associated with flowering and fruit production of plants.

Movement of Heliothis larvae within plant species has been investigated by some workers (eg. Burkett et al.,1983; Farrar and Bradley,1985; Pencoe and Lynch,1982; Snodderly and Lambdin,1982). In general, movement seems to be influenced by host plant phenology, availability of suitable food, and sometimes competition with other larvae. In current field observations, larvae were first found on host plant leaves and the numbers gradually increased as overall larval populations increased (Figure 3.4). After tomatoes produced fruits and asters and lucerne flowered some larvae were found on fruits of tomato and flowers of aster but not on lucerne flowers. These larvae probably moved from nearby leaves. On sweetcorn plants, larvae were found on both leaves and cobs on the same date but the numbers on leaves were consistently low. No larvae were found on lucerne plants in late season which may have been due to migration from lucerne to the more suitable foods (tomato fruits, aster flowers and sweetcorn cobs) on adjacent plots. Laboratory studies (Chapter 5) showed that these foods were of much higher quality than lucerne foliage in ability to support larval growth.

As host plants matured larval population on reproductive parts (flowers, fruits and cobs) progressively increased associated with decline in numbers on all host plant leaves. Broadley(1978) reported

that in Australia although eggs of Heliothis species were found on leaves of all stages of pre-flowering tobacco, larvae tended later to move up the plant towards the reproductive structures.

After February in both seasons, larval populations decreased on most plant parts but remained high on aster flowers and sweetcorn cobs. The decline of larval populations at this time may be because host plants were approaching senescence resulting in insufficient suitable food, and/or the effects of natural enemies. Cameron and Valentine(1985) reported that larvae of H.armigera were heavily parasitised by Cotesia kazak (Braconidae) in tomatoes and soybeans at Pukekohe(northern North Island) in February and March, but parasitism was not evident in the current study.

2.FEEDING SITES OF LARVAE IN THE FIELD

Larvae were found feeding on tomato and aster leaves early in both growing seasons and later a few occurred on lucerne leaves. However, it cannot be concluded that tomato, aster and lucerne leaves are necessarily the preferred feeding sites to other plant parts simply because of the numbers of larvae on them. It is more likely that such distribution reflects oviposition preference and that newly hatched larvae started feeding where eggs were deposited. In any case, during this period only leaves were available and larvae had no other choice of food. Burkett et al.(1983) reported that first instar larvae of H.zea fed initially on plant parts on which they were placed. Pencoe and Lynch(1982) found that first instar larvae of H.zea exhibited a distinct preference for terminal leaves of peanuts as feeding sites but these were also the main oviposition sites. However, it can be safely

concluded that sweetcorn leaves were least preferred for oviposition or feeding compared to the other plant species because no larvae were found on them until late January each year when the plants had started forming cobs.

From late January to March all four host plants were maturing and a choice of food sources was available. Most larvae were then found feeding on reproductive parts of plants (flowers, fruits and cobs). On tomatoes, fruits were the main feeding sites especially young fruits (Table 3.2). Although actual numbers of larvae on fruits were quite low (about 6 larvae per 80 fruits), damage to fruits was relatively severe (about 45%). Small larvae in particular tended to move from one fruit to another, usually without consuming each completely. Larger larvae tended to remain on particular fruits. This could be because the mouthparts of larger larvae enable them to deal with the tough outer surface of fruits and/or their stronger preference for fruits. On aster plants, where flowers were preferred feeding sites to leaves, many more larvae occurred on light coloured flowers (white and pink) than on dark colour (red and purple). No evidence is available to explain this but it could be due simply to differences in attractiveness or visual contrast of the colours for ovipositing moths or to other biochemical differences such as odour between the different coloured flowers. On sweetcorn, larvae strongly preferred cobs to leaves and numbers of larvae on leaves were very low at all times. Larvae were never observed feeding on stems of any host plants in either season. The results showed clearly that for tomato, aster and sweetcorn, fruits, flowers and cobs respectively are the preferred feeding sites over other plant parts. Numbers of larvae recorded from lucerne were too low to reach firm conclusions.

Larval feeding site preferences of Heliothis species have been investigated by many workers. On tomato, Snodderly and Lambdin(1982) observed relatively large amounts of feeding on fruits(40-60%) throughout larval development of H.zea and increases in leaf feeding early and late. However, Burkett et al.(1983) observed a significant preference for flowers of tomato and larvae fed on flowers had the highest mean survival. Flowers, bolls and fruits of cotton have been recorded as preferred feeding sites for larvae of Heliothis species (Broadley, 1978; Farrar and Bradley,1985; Slosser et al.,1978; Wilson and Waite,1982). Wardhaugh et al.(1980) also reported that larvae preferred to feed on the heads of sunflowers.

In early December 1985, before larvae were found on host plants in the field plots, a small number of early instar H.armigera larvae were found feeding on leaves of the annual weed Amaranthus sp. adjacent to the plots. Even though Amaranthus spp. may not be suitable hosts, larvae may nevertheless feed on them if eggs are laid on their leaves. Once host plants started to mature (late January) very few larvae were found on Amaranthus. Amaranthus spp. have been recorded as host plants of Heliothis species by Kareem et al.(1970). They can perhaps therefore be considered as possible alternative wild host plants in the Manawatu.

3. LARVAL FOOD QUALITY

The effects of larval foods on the biological performance of H.armigera in terms of larval period, mortality of larvae, percent pupation, pupal weight, pupal period, fecundity and adult life span have been discussed in Chapter 5.

Of the natural foods, tomato fruits gave the best biological performance as expressed by the biological fitness index, followed by sweetcorn cobs, aster flowers, lucerne leaves, aster leaves, tomato leaves and sweetcorn leaves. Birch's fitness index, designed to express the capability of an insect population to increase, was improved by adding values for pupal period and hatchability of eggs and by substituting actual eggs laid for pupal weight (see discussion in Chapter 5). The "improved" fitness indices for tomato fruits(24.18), sweetcorn cobs(19.37) and aster flowers(15.69) are much higher than for leaves of all plants evaluated (range of 1.23-5.76) (Table 5.9) thus confirming that reproductive parts of plants (flowers, fruits and cobs) are of much higher quality than leaves in terms of potential for population increase.

Among plant leaves, lucerne and aster gave higher "improved" fitness indices(about 5) than tomato and sweetcorn(about 1). Tomato leaves and sweetcorn leaves also gave the highest larval mortality and poorest growth. These leaves may contain chemical feeding deterrents or toxins and/or high fibre content which is difficult for larvae to ingest. Fery and Cuthbert (1975) showed that ethanolic extract of tomato leaves reduced survival of H.zea larvae. Farrar and Kennedy(1987) also reported that 2-undecanone, a constituent of the glandular trichomes of tomato, when combined with 2-tridecanone

increased larvae mortality and caused deformity and mortality of pupae of H.zea, but not alone. More recently α-tomatine, chlorogenic acid, rutin and a new caffeyl derivative of an aldaric acid are major allelochemics isolated from tomato leaves that affect larval development of H.zea (Elliger et al.,1981). Moreover, Campbell and Duffey(1981) reported that α-tomatine caused prolonged larval development, disruption or prevention of pupal eclosion, deformation of genital structures and reduction in adult weight and longevity of the parasitoid Hyposoter exiguae when α-tomatine-fed H.zea larvae were parasitised.

Major nutritional requirements for insects are nitrogen, vitamins, phospholipids and free sugars present universally in leaf tissues (Harborne, 1977). Scriber and Slansky(1981) suggested that leaf water and nitrogen (or correlated factors) determine upper limits of larval performance. However, maximum performance may not be attained because other factors such as the presence of allelochemicals. Nitrogen plays a central role in all metabolic processes and in genetic coding (Ito and Mukaiyama, 1964; Mattson,1980). However, the minimum nitrogen content of food that will keep body nitrogen level stable is known for only a few insect species for example some butterfly larvae and grasshopper nymphs(Mattson, 1980) and a beetle, Paropsis sp.(Fox and Macauley, 1977).

The effects of various host plants on development of H.armigera and other Heliothis species have been reported by many workers. Most publications concentrate on the effects of foods on a particular stage such as larval development, pupal weight and pupal period, fecundity and adult life span (eg. Abul Nasr et al.,1976; Ayad,1977; Doss,1978; Lukefahr and Martin,1964; Pretorius,1976; Reed,1965). Unfortunately none have attempted to determine the bases of food quality and optimum

requirements of nutritional ingredients for Heliothis species have not been reported. Thus the present work attempted to investigate the significance of nitrogen content, dry matter content (and its reciprocal water content) and to measure amounts of food consumed (consumption index,C.I.), efficiency of conversion of ingested food(E.C.I.), and relative growth rate(R.G.R.) in relation to different foods.

Unfortunately the results do little to explain food quality for growth and development of H.armigera. When the individual nutrients are considered, tomato fruits, sweetcorn cobs and aster flowers had lower nitrogen content (about 1.9%) than leaves (range of 3.1-4.5%) but fruits, cobs and flowers gave much higher biological fitness indices than leaves. On the other hand, artificial diet of 4.6% nitrogen content gave the highest biological fitness index (close to that of tomato fruits). There is also no apparent association of biological performance with water content of food with the possible exception of tomato fruits which had higher water content and better performance than all other natural foods. Consumption indices and efficiency of conversion of ingested food to body weight varied considerably between foods and these parameters also do not adequately explain relative growth rates of larvae or weights of pupae on the different foods (see detail in the discussion of Chapter 6).

It is therefore evident that nutritional factors in the various foods influencing insect growth and development are much more complex than simply nitrogen content and dry matter content (and its reciprocal water content). Further investigation of nutritional factors is needed and should include 1) major nutrients required for growth and development 2) minimum requirement for each nutrient 3) feeding stimulants and deterrents affecting intake and 4) secondary substances

affecting development.

4. LARVAL FEEDING PREFERENCE

Newly hatched first instar larvae from a colony maintained on artificial diet showed strong orientational and feeding response for leaf discs from lucerne over those from tomato, aster and sweetcorn but preference was not clearly expressed until the 12th hour. Similar preferences were shown for reproductive parts of plants (flowers, fruits and cobs) but in contrast, were exhibited within the 1st hour. Fourth instar larvae raised on artificial diet showed the same or closely similar feeding preferences as newly hatched larvae on both leaves and reproductive parts of plants.

These results show that larval feeding preference was inherited and was closely correlated with the quality of foods as expressed by a biological fitness index. Thus among plant leaves, lucerne gave the best biological performance and was the most preferred while sweetcorn gave the poorest performance and was least preferred. Tomato fruits were preferred to sweetcorn cobs and these to aster flowers. Fitness indices were in the same order. It is apparent therefore that larvae are able to respond to some properties of the more suitable foods. This behaviour could be evoked by stronger attractants and feeding stimulants of food which is of higher quality for insect development.

There has been much discussion in the past whether preferential feeding behaviour of insects is determined solely by nutritional requirements or by response to hostile chemicals in plants. It is now generally agreed that both nutritional and non-nutritional chemical factors may guide insect selection of plants. The main taste response

of insects is to sweetness (free sugars), nitrogen (protein or free amino acids), vitamins, phospholipids and sterols (Harborne,1977; House,1961). Other chemical plant constituents known as "secondary plant substances" may also be important in regulating feeding behaviour (Fraenkel,1969; Schoonhoven,1968). These substances may act as feeding attractants or deterrents to particular insects depending on how the insect adapts biochemically and anatomically to the digestion and assimilation of plant tissue. The major classes of secondary plant substances involved in insect-plant interaction have been summarised by Harborne(1977).

The present results showed that larvae of H.armigera preferred to feed on tomato fruits compared to sweetcorn cobs and sweetcorn cobs compared to aster flowers. The biological fitness indices of these foods was in the same order. Tomato fruits therefore not only meet the nutritional requirements of this insect but also clearly contain secondary plant substances which act as attractants and/or feeding stimulants. In contrast, aster, tomato and sweetcorn leaves were least preferred and were nutritionally poor. This suggests the presence of feeding deterrents and/or digestive suppresants in these leaves. No evidence was obtained from the present work to indicate the chemical nature of these substances but alkaloids (eg. tomatine, demissine), phenolics (eg. tannins) and amines which occur universally in leaves of angiosperms, especially tomatoes (Elliger et al.,1981; Harborne,1977: Farrar and Kennedy,1987) could be involved.

It has been shown that feeding preference of larvae of H.armigera can be modified by food previously consumed. The strength of induction for each food is different and the least preferred food cannot overcome innate preference for the more strongly preferred ones. Induction of

feeding preference was found with the four different plant species and plant parts. Thus leaves of lucerne, aster and tomato gave strong induction of preference while sweetcorn leaves induced preference only in relation to tomato leaves which ranked close to them in both food quality and initial feeding preference. However, feeding preference was strongly induced by reproductive parts of all plants (flowers, fruits and cobs).

These results may help to explain why more larvae were found feeding on tomato fruits, sweetcorn cobs and aster flowers than on leaves of these plants in field plots. Most newly hatched larvae probably feed initially on host plant leaves as a consequence of oviposition preference. When larvae are larger they tend to wander and take test bites from other plant parts. If they find more suitable food by chance or through the action of attractants and feeding stimulants, after a short period feeding preference may be induced to the new food (flowers, fruits and cobs). The very low numbers of larvae recorded from sweetcorn leaves in the field may be because sweetcorn leaves are of poor quality resulting in high mortality of larvae feeding on them and/or they are unable to induce feeding preference compared to other plant parts.

Further information on secondary plant substances from host plant species and plant parts which may act as feeding stimulants and attractants and feeding deterrents is needed to clarify factors regulating feeding behaviour of H.armigera. A practical benefit from such findings would be to assist plant breeders in developing new plant varieties which possess resistant properties.

5. OVIPOSITION PREFERENCE

Under caged greenhouse conditions H.armigera moths laid eggs on all parts of plants and on non-living substrates surrounding the plants but showed strong preference for the upper halves of all test plants (73-85% of eggs laid). Patel et al.(1974) recorded similar results on cotton plants. Hillhouse and Pitre(1976) and Jackson et al.(1983) also found that H.virescens and H.zea oviposited preferentially on the upper halves of cotton, soybean and tobacco plants.

This preference for the upper parts of plants may be influenced by food availability for moths, as they feed on floral nectar, but could also be affected simply by plant height. Firempong(1986) demonstrated that the height of host plants had a strong influence on oviposition by H.armigera as most eggs were laid on plants that were artificially elevated than on lower ones. Preference for the upper parts of plants may also be due to the flying behaviour and settling habit of moths themselves because it was observed that moths usually rested near the tops of plants and sometimes on the upper parts of experimental cages. As with plants, more eggs were observed on the upper parts of non-living substrates than on the lower parts. It seems therefore that these factors may be more important than any plant characteristics.

Leaves of all four host plants tested were preferred oviposition sites compared to other plant parts and stems were least preferred except for aster. These results are similar to those of Mabbett and Nachapong(1984) and Patel et al.(1974) for H.armigera and for H.virescens and H.zea (Alvarado-Rodriguez et al.,1982; Farrar and Bradley, 1985; Hillhouse and Pitre(1976); Jackson et al.,1983; Pencoe and Lynch,1982; Snodderly and Lambdin,1982). However, Broadley(1977), Hardwick (1965), Johnson et al.(1975), Lingren et al.(1977) and Neunzig

(1969) reported that H.armigera, H.virescens and H.zea preferred to lay eggs on flowers rather than leaves.

Surface texture of substrates may play an important role in oviposition preference of Heliothis species. Hairy or rough-textured surfaces i.e. leaves of all four test plants and aster stems attract more oviposition but smooth surfaces such as tomato fruits, tomato and sweetcorn stems were not suitable oviposition sites. Callahan(1957) suggested that villous surfaces were the best suited to H.zea moths for maintaining a foothold. Hassan(1985) also reported that hairy surfaces attracted more oviposition by H.armigera. General morphology of plant parts may also influence oviposition preference. Flat parts, for example leaves, flowers and flower buds of aster seem to be preferred. Mabbett and Nachapong(1984) also showed that H.armigera laid eggs preferentially on the flat parts of cotton plants such as leaves and leaflets.

The flowering state of plants may also affect oviposition preference of H.armigera. On immature plants(no flowers), moths preferred to oviposit on lucerne rather than tomato, aster and sweetcorn plants but on mature plants(with flowers, fruits and cobs) moths preferred aster to sweetcorn, tomato and lucerne plants. This may be because of adult food available from flowers both before and during oviposition.

This aspect of oviposition behaviour of Heliothis has been widely investigated and many workers have commented on the coincidence of peak oviposition with peak flowering, nectar production and silk formation in maize (Alvarado-Rodriguez et al.,1982; Coaker,1965; Firempong,1986; Hardwick,1965; Neunzig,1969; Nuttycombe,1930). The presence of extra-floral nectar in cotton is closely correlated with oviposition preference and oviposition site selection (Wilson,1983; Zalucki et

al.,1986). However, oviposition occurs on pre-flowering stages of soybeans, cotton and tobacco and at any stage of sunflowers, tomatoes and lucerne (Broadley,1978; Wardhaugh et al.,1980).

Odours of host plants also affect oviposition preference of H.armigera as muslin covered mature plants gave the same order of preference as uncovered plants with aster the most attractive and lucerne the least. No evidence was obtained to indicate the sources of odours from each plant or their nature. Fletcher(1941) and Hillhouse and Pitre(1976) have previously reported that odours emanating from plants attract H.zea moths and stimulate oviposition. Cullen(1969), however concluded that chemicals cues, the availability of adult food and humidity were not important for H.punctigera in selecting an oviposition site and suggested that surface texture was the principal cue.

It may be suggested from the results reported here and from Zalucki et al.(1986) that on both flowering and pre-flowering plants oviposition preference is influenced primarily by the following factors 1) surface texture of substrates 2) availability of food(nectar) for adults and 3) chemical cues (especially odours) whether emanating from reproductive parts or leaves of host plants. It is also clear that the main oviposition sites are not necessarily the main feeding sites for larvae. A comparison of oviposition sites and feeding preferences of H.armigera on different plants is given in Table 8.1 and shows that oviposition preference is not associated with quality of the larval food.

Table 8.1 Oviposition preference and feeding preference by *H.armigera* larvae on four host plants.

Plant	Oviposition preference (in greenhouse)	Feeding site preference (in field plot)	Feeding preference (in laboratory)
Lucerne	Leaves	Hardly observed	Not available
Tomato	Leaves	Fruits	Fruits
Aster	Leaves	Flowers	Flowers
Sweetcorn	Leaves	Cobs	Cobs

However, as larvae are able to select food of higher quality this implies that larval feeding preference and adult oviposition preference are determined by two separate gene complexes. A practical benefit of the study is that examination of plants in the field to determine egg populations should be concentrated on those parts of plants where eggs prefer to be laid rather than where larvae are found.

6.CONCLUDING REMARKS

It has been clearly demonstrated in this thesis that host plants species and plant parts vary considerably in larval food quality as measured by larval growth rate, percentage survival and adult fecundity. Such differences in food quality must affect the ability of field populations to develop on different plants as expressed in a biological

fitness index.

However, oviposition preference of adults for particular plant species and plant parts was not always closely correlated with larval food quality. This suggests that in the field other additional factors may be involved such as activity and effectiveness of natural enemies which were excluded from laboratory experimentation.

The ease of induction of larval feeding preference in H.armigera suggests that larval feeding behaviour may be to some extent flexible. Whether larvae could develop the ability to utilise less suitable foods more effectively given time remains to be determined.

Knowledge of oviposition preference between crop species and larval food quality as determined here for tomato, lucerne, aster and sweetcorn could assist in the formulation of total population management strategies for Heliothis.

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APPENDICES

Appendix 1 Food plants of Heliothis species.

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Botanical name	Common name	Heliothis spp.	References
Acanthaceae			
Crossandra infundibuliformis	crossandra	armigera	27
Ruellia runyonii	monkey plant	armigera	9
		virescens	9
		zea	9
Aizoaceae			
Trianthema pilosa	pigweed	punctigera	13
Trianthema portulacastrum	black pigweed	armigera	13

		punctigera	13
Zaleya galericulata	hogweed	punctigera	30
Amaranthaceae			
Amaranthus gangeticus	amaranth	armigera	12
Amaranthus interruptus	amaranth	punctigera	13
Amaranthus paniculatus	amaranth	armigera	12
Amaranthus polygamus	amaranth	armigera	12
Amaranthus spp.	amaranth	zea	17
Amaranthus thunbergii	amaranth	armigera	12
Amaranthus tristis	amaranth	armigera	12
Amaranthus viridus	amaranth	armigera	12
Gomphrena globosa	globe amaranth	punctigera	30
Anacardiaceae			
Mangifera indica	mango	armigera	23
Balsaminaceae			
Impatiens balsamina	balsam	punctigera	30
Bignoniaceae			
Tecomaria capensis	cape honeysuckle	armigera	30
Boraginaceae			
Echium plantagineum	Paterson's curse	armigera	30
		punctigera	30

Cannaceae			
Canna indica	canna	punctigera	30
Capparidaceae			
Cleome viscosa	tickweed	punctigera	30
Caricaceae			
Carica papaya	pawpaw	armigera	
Caryophyllaceae			
Dianthus caryophyllus	carnation	armigera	13
		punctigera	4
Chenopodiaceae			
Beta vulgaris	beetroot	armigera	30
		punctigera	30
Chenopodium album	fat hen	armigera	30
Chenopodium polygonoides	saltweed	Heliothis spp.	30
Chenopodium triangulare	fishweed	Heliothis spp.	30
Rhagodia hastata	berry saltbush	Heliothis spp.	30
Salsola kali	soft roly-poly	Heliothis spp.	30
Compositae			
Arctotheca calendula	capeweed	punctigera	30
Bidens pilosa	cobbler's pegs	Heliothis spp.	30
Calendula sp.	marigold	punctigera	4
Callistephus chinensis	aster	Heliothis spp.	30
Calotis lappulaceae	daisy burr	Heliothis spp.	30
Carthamus lanatus	saffron thistle	armigera	30
Carthamus tinctorius	safflower	armigera	13
		punctigera	13

Conyza canadensis	fleabane	Heliothis spp.	30
Dahlia pinnata	dahlia	armigera	30
Eupatorium adenophorum	hemp agrimony	Heliothis spp.	30
Galinsoga ciliata	galinsoga weed	armigera	21
Galinsoga parviflora	potato-weed	armigera	21
Gerbera jamesonii	gerbera	armigera	13
Gnaphalium japonicum	cudweed	Heliothis spp.	30
Guizotia abyssinica	Niger seed	punctigera	30
Helianthus annus	sunflower	armigera	30
		punctigera	13
		viriplaca	18
Helianthus sp.	sunflower	zea	9
Helichrysum spp.	everlastings	punctigera	30
Lactuca sativa	lettuce	armigera	13
Lactuca serriola	prickly lettuce	Heliothis spp.	30
Ratibida columnaris	coneflower	virescens	9
Sigesbeckia orientalis	indian weed	rubrescens	13
Sonchus oleraceus	sow thistle	armigera	19
Tridax procumbens	tridax daisy	armigera	19
Xanthium pinnata	noogoora burr	punctigera	13
Xanthium spinosa	bathurst burr	Heliothis spp.	30
Zinnia elegans	common zinnia	punctigera	30

Convolvulaceae

Ipomoea aquatica	potato vine	punctigera	30
Ipomoea cordofana	morning glory	armigera	13
Ipomoea purpurea	morning glory	virescens	17
Operculina turpethum	onion vine	punctigera	30

Cruciferae

Brassica campestris	brown sarson	punctigera	30
Brassica juncea	indian mustard	punctigera	30
Brassica napus	rape	armigera	30
		punctigera	30
Brassica nigra	black mustard	armigera	30
		punctigera	30
Brassica oleracea	cabbage	armigera	13
		punctigera	13
	cauliflower	punctigera	30
	broccoli	armigera	30
Brassica rapa	turnip	armigera	30
Brassica sp.	choisim	punctigera	30
Capsella bursa-pastoris	Shepherd's purse	Heliothis spp.	30
Lepidium hyssopiforium	pepper cress	Heliothis spp.	30
Mathiola incana	gillyflower	punctigera	30

Cucurbitaceae

Citrullus lantanus	melon	armigera	30
		punctigera	30
Citrullus lanatus	watermelon	punctigera	13
Citrullus vulgaris	watermelon	armigera	24
		punctigera	13
Cucumis melo	rock melon	punctigera	30
Cucumis sativa	cucumber	punctigera	30
Cucurbita moschata	pumpkin	armigera	12
	squash	punctigera	30
Cucurbita pepo	pumpkin	armigera	8
		punctigera	30
	marrow	punctigera	30

Lagenaria siceraria	bottle gourd	armigera	24
Trichosanthes anguina	snake gourd	armigera	12
Euphorbiaceae			
Acalypha hispida	chenille plant	armigera	30
		punctigera	30
Acalypha wilensia	copper-leaf	armigera	30
		punctigera	30
Leptopus decaisnei		punctigera	30
Ricinus communis	castor bean	armigera	30
Fabaceae			
Schrankia latidens	morongia	virescens	9
Geraniaceae			
Geranium dissectum	cranesbill	virescens	26
		zea	26
Pelagonium rodneyanum	geranium	punctigera	30
Gramineae			
Avena sativa	oat	armigera	4
Eleusine coracana	ragi	armigera	21
Hordeum vulgare	barley	armigera	30
Oryza sativa	rice	punctigera	30
Panicum miliaceum	French millet	armigera	13
Pennisetum americanum	pearl millet	armigera	25
Sorghum spp.	sorghum	armigera	13
		virescens	9
		zea	9
Triticum aestivum	wheat	armigera	30

		punctigera	30
Zea mays	maize,	armigera	13
	sweetcorn	punctigera	13
		viriplaca	18
		zea	29
Hypericaceae			
Hypericum perforatum	St John's wort	punctigera	4
Iridaceae			
Gladiolus sp.	gladiolus	armigera	13
		punctigera	13
Juglandaceae			
Juglans sp.	walnut	armigera	31
Laminaceae			
Lamium amplexicaule	deadnettle	punctigera	30
Origanum vulgare	wild marjoram	armigera	30
Salvia reflexa	mintweed	punctigera	30
Stachys sp.	stachys	punctigera	30
Leguminosae			
Alysicarpus vaginalis	alyce clover	punctigera	30
Arachis hypogaea	peanut	armigera	30
		zea	20
Atylosia scarabaeoides	wild pigeon pea	armigera	22
Cajanus cajan	pigeon pea,	armigera	13
	gram	virescens	15
		zea	15

Centrosema pubescens	centro	armigera	30
Cicer arietinum	chick pea	armigera	13
Dalea pogonathera	prairie clover	virescens	9
Desmodium sp.	tick clover	virescens	17
		zea	17
Dolichos lablab	lablab, lubia	armigera	6
Glycine max	soybean	armigera	26
		punctigera	13
		virescens	10
		viriplaca	18
		zea	10
Lathyrus odoratus	sweet pea	viriplaca	18
Lathyrus sativus	khessari	armigera	13
Lupinus angustifolius	blue lupin	punctigera	30
Lupinus arborea	yellow lupin	armigera	1
Lupinus texensis	Texas-	virescens	7
	bluebonnet	zea	7
Macroptilium lathyroides	phasey bean	armigera	30
		punctigera	30
Medicago denticulata	burr, medic	armigera	13
Medicago sativa	lucerne	armigera	16
		punctigera	4
		viriplaca	
Phaseolus vulgaris	kidney bean	armigera	30
		viriplaca	18
Pisum sativum	garden pea	armigera	13
		punctigera	13
Sesbania campylocarpa	sesbans	punctigera	30
Sesbania cannabina	sesbania pea	armigera	30
		punctigera	30

Sesbania erubescens	sesbans	punctigera	30
Stizolobium deeringianum	velvet bean	punctigera	30
Stylosanthes humilis	Townsville-lucerne	punctigera	30
Trifolium repens	white clover	armigera	16
		viriplaca	13
Trifolium pratense	red clover	armigera	28
Vicia benghalensis	purple vetch	punctigera	30
Vicia sativa	common vetch	punctigera	30
Vicia villosa	Russian vetch	punctigera	30
Vigna radiata	mung bean	armigera	3
Vigna sesquipedales	snake bean	punctigera	30
Vigna unguiculata	cowpea	armigera	30
Liliaceae			
Allium fistulosum	onion	armigera	24
Asparagus officinalis	asparagus	punctigera	30
Sanseviera sp.	hemp	armigera	19
Linaceae			
Linum usitatissimum	linseed, linenflax	armigera	5
		punctigera	4
		viriplaca	18
Linaria canadensis	toadflax	virescens	17
Malvaceae			
Abelmoschus esculentus	okra	armigera	13
		punctigera	13
Abelmoschus ficulneus	native rosella	punctigera	30
Abutilon indicum	Indian latern		

	flower	punctigera	30
Abutilon otocarpum	desert Chinese latern	punctigera	30
Abutilon oxycarpum	flannel weed	punctigera	30
Abutilon trisulcatum	flowering maple	virescens	9
		zea	9
Althaea officinalis	marsh mallow	punctigera	30
Gossypium hirsutum	cotton	armigera	13
		dipsasea	19
		peltigera	19
		punctigera	13
		virescens	14
		zea	14
Hibiscus cannabinus	kenaf	armigera	30
Hibiscus esculentus	okra	armigera	13
Hibiscus rosa-sinensis	hibiscus	punctigera	13
Hibiscus sabdariffa	rosella	armigera	30
Hibiscus trionum	bladder ketmia	armigera	30
Malva parviflora	mallow	zea	9
Malvastrum tricuspidatum	false mallow	armigera	19
Malvaviscus drummondii	achania	virescens	9
Sida cordifolia	flannel weed	armigera	30
Sida retusa	paddy's lucerne	Heliothis spp.	30
Sida rhombifolia	sida	assulta	17
		virescens	17
Sida spinosa	spiny sida	punctigera	30
Martyniaceae			
Ibicella parodii	yellow-flower	molochitina	2

Melastomaceae			
Rhexia alifanus	deergrass	virescens	17
Rhexia marianus	deergrass	virescens	17
Rhexia nashii	deergrass	virescens	17
Meliaceae			
Owenia acidula	emu apple	punctigera	30
Mimosaceae			
Neptunia monosperma	native sensitive plant	punctigera	30
Moraceae			
Ficus platypoda	fig	punctigera	30
Musaceae			
Musa acuminata	cavendish banana	armigera	13
Musa paradisiaca	banana	punctigera	30
Musa sp.	banana	armigera	30
Myoporaceae			
Eremophila gilesii	green turkey bush	punctigera	30
Eremophila longifolia	berrigan	punctigera	30
Myrtaceae			
Eucalyptus spp.	eucalyptus	armigera	8
Melaleuca incana	teatree	armigera	30
Nyctaginaceae			

Boerhavia diffusa	tarvine	punctigera	30
Onagraceae			
Gaura parviflora	clock-weed	virescens	9
Jussiaea decurrens	primrose-willow	zea	17
Oxalidaceae			
Oxalis pes-caprae	soursob	punctigera	30
Papaveraceae			
Papaver nudicaule	Iceland poppy	punctigera	30
Papaver somniferum	opium poppy	armigera	30
		punctigera	30
Passifloraceae			
Passiflora edulis	passion fruit	armigera	30
Passiflora foetida	passion-flower	virescens	9
Pedaliaceae			
Josephina eugeniae	Josephina burr	punctigera	30
Sesamum indicum	sesame	armigera	12
		punctigera	30
Pinaceae			
Pinus radiata	radiata pine	armigera	1
Polygonaceae			
Rumex sp.	dock	punctigera	30
Portulacaceae			
Portulaca grandiflora	rose-moss	punctigera	30

Portulaca filifolia	pigweed	*armigera*	30
		punctigera	30
Portulaca oleracea	pigweed	*armigera*	19
Portulaca tuberosa	pigweed	*punctigera*	30
Portulaca sp.	pigweed	*punctigera*	30
Proteaceae			
Macadamia integrifolia	macadamia nut	*armigera*	30
Macadamia tetraphylla	Queensland nut	*armigera*	30
		punctigera	30
Resedaceae			
Reseda luteola	wild mignonette	*armigera*	30
Rosaceae			
Ameniaca vulgaris	apricot	*punctigera*	4
Fragaria sp.	strawberry	*armigera*	13
		punctigera	13
Malus domestica	apple	*armigera*	5
		punctigera	4
Malus sylvestris	crab apple	*punctigera*	30
Prunus domestica	plum	*punctigera*	30
Prunus persica	peach	*armigera*	30
		punctigera	30
Rosa sp.	rose	*armigera*	30
		punctigera	30
Rutaceae			
Citrus limon	lemon	*armigera*	30
Citrus sinensis	orange	*armigera*	13
Xanthoxylum americanum	prickly ash	*armigera*	31

Scrophulariaceae

Antirrhinum majus	snapdragon	armigera	30
		punctigera	30
Castilleja indivisa	Texas-	virescens	7
	paintbrush	zea	7
		phloxiphaga	7
Verbascum virgatum	mullein	armigera	30

Solanaceae

Capsicum frutescens	capsicum	punctigera	30
Datura leichhardtii	thornapple	punctigera	30
Datura metel	thornapple	armigera	12
Lycopersicon esculentum	tomato	armigera	13
		assulta	13
		punctigera	13
		zea	19
Nicandra physaloides	apple of Peru	armigera	19
Nicotiana noctiflora	tobacco	molochitina	2
Nicotiana repanda	wild tobocco	virescens	9
		zea	9
Nicotiana tabacum	tobacco	armigera	13
		assulta	4
		punctigera	13
		virescens	11
Petunia x hybrida	petunia	armigera	30
		punctigera	30
Physalis minima	wild gooseberry	assulta	13
Physalis peruviana	cape gooseberry	assulta	4
Physalis virginiana	ground cherry	Heliothis spp.	30

Solanun echinatum	—	punctigera	30
Solanum elaeagnifolium	night shade	virescens	9
		zea	9
Solanum melongena	eggplant	punctigera	30
Solanum tuberosum	potato	armigera	30
		punctigera	30
Tiliaceae			
Corchorus olitorius	jute	punctigera	30
Urticaceae			
Urtica sp.	stinging nettle	punctigera	30
Verbenaceae			
Verbena bipinnatifida	vervian	virescens	9
		zea	9
Verbena bonariensis	purpletop	Heliothis spp.	30
Verbena neomexicana	verbena	virescens	9
		zea	9
Verbena officinalis	common verbena	Heliothis spp.	30
Vitaceae			
Vitis vinifera	grape	armigera	13
Zingiberaceae			
Zingiber officinale	ginger	armigera	30
Zygophyllaceae			
Kallstroemia tribuloides	caltrop	molochitina	2
Tribulus terrestris	puncture vine	molochitina	2

	caltrop	Heliothis spp.	30
Zygophyllum sp.	twinleaf	Heliothis spp.	30

Appendix 2 The composition of the formulated diet for H.armigera.

soaked kidney bean	2133	g
dried brewery yeast	320	g
ascorbic acid	20	g
methyl p-hydroxybenzoate	10	g
formaldehyde	20	ml
agar	126	g
cholesterol	0.5	g
distilled water	6400	ml

Appendix 3. Percent of eggs laid by *H. armigera* on lucerne.

Days	Flowers	Leaves	Stems	Plants		Leaf surfaces	
				Upper half	Lower half	Upper	Lower
1	29.4	66.7	3.9	90.5	9.5	72.4	27.6
2	12.7	84.9	2.4	82.7	17.3	66.9	33.1
3	4.8	90.0	5.2	79.8	20.2	79.5	20.5
4	12.0	71.6	16.5	86.6	13.4	89.1	10.9
5	20.4	77.5	2.1	79.0	21.0	90.4	9.6
6	10.7	88.4	0.9	94.0	6.0	85.5	14.5
7	9.3	82.9	7.8	88.6	11.4	82.5	17.5
8	7.0	91.5	1.5	87.6	12.4	86.1	13.9
9	10.6	82.5	6.9	82.4	17.6	79.9	20.1
10	6.8	92.0	1.2	71.4	28.6	64.3	35.7
11	18.4	74.9	6.7	90.4	9.6	63.4	36.6
12	16.8	80.7	2.5	91.5	8.5	59.4	40.6
Mean	13.2	82.0	4.8	85.4	14.6	76.6	23.4

Appendix 4. Percent of eggs laid by *H. armigera* on tomato.

Days	Flowers	Fruits	Stems	Leaves	Plants		Leaf surfaces	
					Upper half	Lower half	Upper	Lower
1	21.4	3.8	0.5	73.3	68.5	31.5	74.3	25.7
2	11.6	4.7	1.2	82.5	78.0	22.0	68.6	30.4
3	31.4	6.5	2.3	59.8	80.1	19.9	79.4	20.6
4	14.3	1.4	3.7	80.6	90.1	9.9	84.5	15.5
5	18.3	3.6	2.2	75.9	73.5	26.5	88.0	12.0
6	23.0	2.3	5.4	69.3	83.7	16.3	71.6	28.4
7	18.8	4.7	3.7	72.8	80.4	19.6	80.4	19.6
8	16.9	5.0	1.1	77.0	81.3	18.7	75.5	24.5
9	9.6	4.7	2.4	83.3	91.3	8.7	60.4	39.6
10	15.9	9.7	3.4	71.0	63.5	36.5	71.1	28.9
11	11.2	8.4	1.1	79.3	69.9	30.1	90.0	10.0
12	8.1	5.3	1.9	84.7	88.3	11.7	72.5	27.5
Mean	16.7	5.0	2.4	75.9	79.1	20.9	76.3	23.7

Appendix 5. Percent of eggs laid by *H. armigera* on aster.

Days	Flowers	Flower buds	Stems	Leaves and calices	Plants		Leaf surfaces	
					Upper half	Lower half	Upper	Lower
1	5.4	18.3	28.0	48.4	74.6	25.4	66.2	37.8
2	1.5	5.1	39.7	53.7	61.5	38.5	61.6	38.4
3	1.5	6.2	50.7	41.6	61.2	38.8	41.4	58.6
4	14.7	2.9	41.2	41.2	79.4	20.6	83.9	16.1
5	5.1	8.5	27.1	59.3	71.2	28.8	65.7	34.3
6	6.0	15.9	22.3	55.8	67.3	32.7	50.0	50.0
7	0.6	7.8	28.3	63.3	64.3	35.7	52.9	47.1
8	3.7	6.3	24.5	65.5	77.3	22.7	48.3	51.7
9	5.1	22.8	14.0	58.1	72.8	27.2	59.5	40.5
10	18.0	13.9	16.2	51.9	84.0	16.0	57.9	42.1
11	3.4	8.0	31.6	57.0	80.4	19.6	46.2	53.8
12	9.1	8.2	30.0	52.7	87.0	13.0	38.1	61.9
Mean	6.2	10.3	29.5	54.0	73.4	26.6	55.6	44.4

Appendix 6. Percent of eggs laid by *H. armigera* on sweetcorn.

Days	Ears	Tassels	Stems	Leaves and leaf sheaths	Plants		Leaf surfaces	
					Upper half	Lower Half	Upper	Lower
1	11.6	8.4	2.6	77.4	80.4	19.6	76.8	23.2
2	11.1	6.8	1.9	80.2	73.4	26.6	63.9	36.1
3	17.2	14.8	3.1	64.8	73.4	26.6	78.0	22.0
4	12.5	10.0	0.0	77.5	67.5	32.5	62.5	37.5
5	20.0	5.4	4.3	70.3	84.9	15.1	71.6	28.4
6	14.6	6.9	2.1	76.4	72.5	27.5	64.9	35.1
7	7.6	18.5	5.0	68.9	75.6	24.4	71.9	28.1
8	26.1	17.4	8.7	47.8	78.3	21.7	74.1	25.9
9	13.4	8.9	0.7	77.0	65.4	34.6	71.1	29.9
10	28.9	7.4	1.2	62.5	80.9	19.1	79.3	20.7
11	21.7	9.8	1.4	67.1	81.1	18.9	77.6	22.4
12	15.2	10.1	0.0	74.7	70.7	29.3	79.7	20.3
Mean	16.6	10.4	2.6	70.4	75.4	24.6	72.5	27.5

Appendix 7. Percent of eggs laid by H. armigera on 4 different plants.
(Abbreviation: Lu=lucerne, To=tomato, As=aster, Sw=sweetcorn)

Days	Immature plant				Mature plant				Covered mature plant			
	Lu	To	As	Sw	Lu	To	As	Sw	Lu	To	As	Sw
1	42.9	27.3	24.0	5.8	11.4	18.6	38.3	31.7	10.1	16.0	47.9	26.0
2	43.7	33.6	17.7	5.0	8.3	19.7	41.7	30.3	10.3	19.2	39.7	30.8
3	39.7	28.1	19.8	12.4	9.2	15.4	43.0	32.4	16.3	13.6	41.6	28.5
4	45.7	25.7	17.2	11.4	7.9	17.6	42.4	32.1	12.8	17.7	40.2	29.3
5	52.3	22.1	18.1	7.5	9.8	16.4	43.9	29.8				
6	51.7	18.3	24.0	6.0	9.9	16.6	44.4	29.0				
Mean	46.0	25.9	20.1	8.0	9.4	17.4	42.3	30.9	12.4	16.6	42.4	28.6