The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) and its biological control in the Eastern Cape Province, South Africa

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Abstract

The diamondback moth, *Plutella xylostella* (L.), is a pest on crucifer crops worldwide, damaging the leaves, florets and seed pods of many crucifers including cabbage, cauliflower, broccoli and canola. It has been controlled using broad-spectrum insecticides, but this has led to a rapid build-up of insecticide resistance. In the Grahamstown area of the Eastern Cape Province, South Africa, diamondback moth showed resistance to cypermethrin (a pyrethroid) on commercially grown cabbages. Therefore it is imperative that other methods of control be adopted, including both cultural control and biological control using parasitoids, and that these are incorporated into an Integrated Pest Management (IPM) programme.

The diamondback moth and its parasitoids were monitored weekly from April 1997 to November 1999 at three sites near Grahamstown. One site was a commercial farm with an active insecticide spraying program; the others were unsprayed. Infestation levels were highest during spring (September to November) and autumn (March to May). Nine species of parasitoids were associated with the diamondback moth, with abundances being highest over spring and early summer (September to December). *Cotesia plutellae* (Kurdjumov) dominated the sprayed site, while the unsprayed sites yielded a complex of parasitoids, including *C. plutellae*, *Diadegma mollipla* (Holmgren), *Diadromus collaris* Gravenhorst and *Oomyzus sokolowskii* (Kurdjumov). Parasitism levels ranged between 10 and 90%. There was a large amount of site-to-site and year-to-year variation. Parasitoids were an effective mortality factor against the diamondback moth.

The effects of temperature on development and mortality, and of field size and non-crop plants on the distribution of diamondback moth and its parasitoids, were investigated. The results show that high temperatures can depress pest populations, and that the size and surroundings of fields can be manipulated to improve cultural control of the diamondback moth.

Suggestions for effective IPM in the Eastern Cape Province include a reduction in insecticide applications, the use of bioinsecticides, for example *Bacillus thuringiensis* Berliner (*Bt*) and the encouragement of indigenous parasitoids by planting suitable nectar sources. Cultural control methods are also important and involve removal of cabbage refuse after harvest, management of wild crucifers around cabbage fields, scouting and monitoring the moth population and determining the optimal field size to assist with control by parasitoids.

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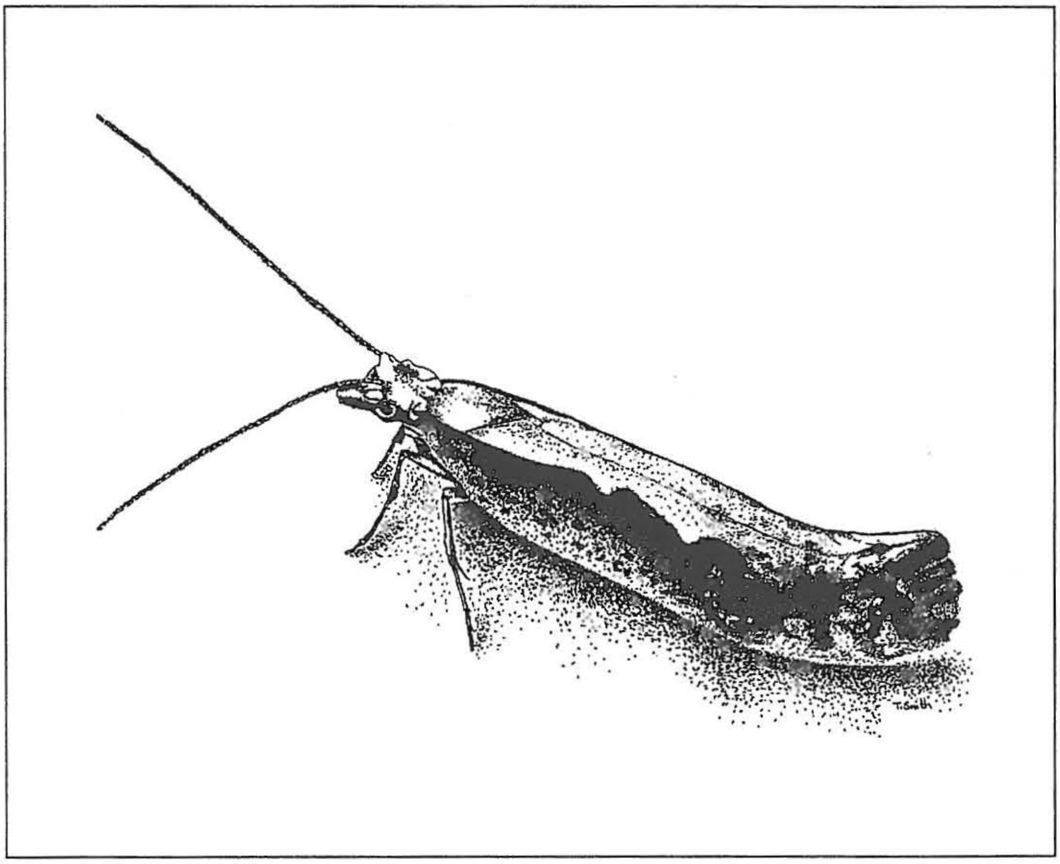
Dedicated to my parents,
Clare and Allan Smith



The diamondback moth, *Plutella xylostella* (L.)

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Chapter 1:

The diamondback moth and its control

1.1. The diamondback moth

The diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) is a cosmopolitan species occurring in all the major zoogeographical regions (Annecke & Moran, 1982). It has adapted to different climatic conditions and is found in temperate and tropical regions and in the colder polar regions, including Iceland and Russia (Bonnemaison, 1965; Ooi, 1986; Salinas, 1986). The larvae feed on and severely damage cruciferous crops like cabbage, cauliflower, broccoli, mustard, rapeseed, collards and Chinese cabbage, some of which form the staple diet for large portions of many countries' populations (Talekar & Shelton, 1993).

The diamondback moth larvae feed on leaves, growth tips, flowers and seed pods (Ramachandran *et al.*, 1998a). Different crops show varying degrees of susceptibility to damage at different stages in their growth. Many of them are more susceptible at the seedling stage, at flowering or at seed setting (Mustata, 1992; Mumford & Knight, 1997). In the leafy crucifer varieties the larvae feed on the leaf surface, leaving the upper epidermis intact, forming characteristic windows. In cauliflower and broccoli they also damage the florets. Oilseed rape is cultivated in many parts of the world for the production of oil, and canola is the term used for Brassica oils of a certain quality. *Brassica napus* L. is currently the most important canola producer (Ramachandran *et al.*, 1998a) and the diamondback moth feeds on the stems, flowers and seed pods (Dosdall, 1994; Justus & Mitchell, 1996, Mosiane, 2001).

The origins of the diamondback moth have been debated extensively. It was thought to have originated in the Mediterranean region (Hardy, 1938; Ooi, 1986; Norris, 1987) mainly because cultivated crucifers are considered to have originated in Europe. The diamondback moth has now spread to all parts of the world where crucifers are grown (Annecke & Moran, 1982; Talekar & Shelton, 1993). Kfir (1997b,1998) suggested that the diamondback moth originated in South Africa because of the number of indigenous parasitoids associated with the diamondback moth; the extensive range of wild brassicas, most of which are indigenous; and the occurrence of the bisexual form of one of the parasitoids, *Diadromus collaris* Gravenhorst (Hymenoptera: Ichneumonidae), suggesting that this parasitoid evolved in South Africa and spread to Europe. Liu *et al.* (2000) showed, using some of the same arguments, that it was also possible for the diamondback moth to have originated in China.

In temperate regions the diamondback moth is present throughout the year, but in the cooler parts of the world it is only present in the warmer summer months. The diamondback moth does not overwinter in these cooler areas (Harcourt, 1957; Butts & McEwan, 1981; Smith & Sears, 1982), Dosdall (1994) found evidence of overwintering in Alberta, Canada, but this only occurred in one year when the environmental conditions in the area were more favourable than usual. The diamondback moth is very mobile, is capable of transoceanic movement and can migrate up to 3000 kilometers (Chu, 1986). In Japan and Canada the moth moves from the warmer southern areas to the cooler northern area in the spring (Harcourt, 1957, 1961,1986; Koshihara, 1986; Honda, 1992a, 1992b). It is this ability to move great distances, together with the spread of crucifers that has resulted in the worldwide distribution of this pest. In 1986 a population of diamondback moth was discovered on Marion Island in the sub-Antarctic (Crafford & Chown, 1987) feeding on the native Kerguelen cabbage (*Pringlea antiscorbutica* R. Br.). It was originally thought that the moth was brought onto the island with fresh crucifers from South Africa but now the possibility of long-distance migration has been considered (Crafford & Chown, 1990; Chown & Avenant, 1992).

1.2. Control of the diamondback moth

In the past, control of the diamondback moth was mostly by non-selective insecticides, such as organophospates, carbamates and pyrethroids (Talekar & Shelton, 1993; Verkerk & Wright, 1996b). By 1993 the annual chemical cost for managing this species was estimated to be over $ 1 billion a year worldwide (Talekar, 1992). However, due to the continued use of these broad-spectrum insecticides, resistance in the moth has become a problem. In 1953 it became the first crop pest in the world to develop resistance to DDT (Ankersmit, 1953). Since then resistance to a number of insecticides has been reported around the world (Miyata *et al.*, 1986; Shelton, *et al.*, 1993b; Kuwahara *et al.*, 1995). Growers use only those chemicals that are still effective and in many countries, for example Japan, very few of the registered chemicals are still being used (Sakai, 1986).

This rapid build-up of resistance to insecticides has resulted in the uncontrolled use of chemicals. Growers increase the dosage, use mixtures of several chemicals in so-called 'cocktails' or spray very frequently, sometimes as often as every 2 days (Chua & Ooi, 1986; Iman *et al.*, 1986; Magallona, 1986; Ooi, 1986; Sastrosiswojo & Sastrodihardjo, 1986; Morallo-Rejesus *et al.*, 1997). Resistance has also resulted in the ever-increasing demand for new insecticides to be developed. Apart from the build-up of resistance to these insecticides, there are also other problems including destruction of natural enemies; resurgence of pest populations; possibility of secondary pests developing; and health and environmental concerns, including contamination of water supplies and the safety of those using the insecticides (Stern *et al.*, 1959; Lim *et al.*, 1986; Kadir, 1992; Alam, 1992; Soares & Quick, 1992; Wyman, 1992). There is also an increasing demand by consumers for good quality vegetables that are both insect-free and insecticide-free. It has become necessary that other forms of control are considered for the control of the diamondback moth. These control methods include cultural control, host plant resistance, alternative chemicals (for example synthetic pheromones) and biological control using parasitoids, predators and pathogens.

1.2.1. Cultural control

Cultural control methods include intercropping, sprinkler irrigation, trap cropping and crop rotation. Intercropping involves growing two or more crop species together with the one species providing a chemical or physical barrier to prevent pest damage. One of the crops that has shown the greatest success for diamondback moth control is the tomato (Chelliah & Srinivasan, 1986; Magallona, 1986; Talekar *et al.*, 1986; Bach & Tabashnik, 1990; Finch & Collier, 2000). Intercropping with non-crop plants, for example herbs, has also been used as some of these plants have repellent properties (Dover, 1986). However, intercropping is more likely to succeed in small-scale cultivation and not in large-scale farming practises (Talekar *et al.*, 1986) as it is labour intensive, requires precise timing in planting (Chelliah & Srinivasan, 1986) and the marketable yields are not always different from when insecticides have been used (Magallona, 1986).

Trap cropping involves the planting of an economically less important, but more attractive, brassica amongst the crucifer crop (Talekar & Shelton, 1993; Mitchell *et al.*, 2000). This helps to attract the diamondback moth away from the important crop. Trap cropping with Indian mustard (*Brassica juncea* (L.) Czern.) has been tried in a number of countries, including India, USA and South Africa with varying success (Srinivasan & Krishna Moorthy, 1992; Luther *et al.*, 1996; Bender *et al.*, 1999; Charleston & Kfir, 2000). Another effective means of control is crop rotation as this prevents the continuous presence of the moths (Lim, 1992).

Sprinkler irrigation has been found to be effective at reducing moth populations (Tabashnik & Mau, 1986; Talekar *et al.*, 1986; Andrews *et al.*, 1992; Lim, 1992). This practise is expensive and not very practical on a large scale. Successful control has generally been on watercress farms where it is easier to manage (Nakahara *et al.*, 1986; Tabashnik & Mau, 1986). It is known that rainfall is a major mortality factor for the eggs and the young larvae, therefore by using sprinklers a similar effect is created with the eggs and larvae being washed off the leaves and drowning. It also has been found to impead the flight and mating of the adult moths, which leads to suppression of oviposition (Talekar *et al.*, 1986).

1.2.2. Host plant resistance

Different crucifer species have varying degrees of resistance to insect attack mainly due to differences in the plant surface, for example waxiness, trichomes, toxins and hardness of the plant tissues (Radcliffe & Chapman, 1966; Wright & Verkerk, 1995; Andrahennadi & Gillot, 1998). Cultivar choice can be an important form of control as some cultivars show more resistance to the diamondback moth than others (Lin *et al.*, 1983). This can result in differences in larval duration, survival and fecundity of the diamondback moth (Vail *et al.*, 1991; Verkerk & Wright, 1994a).

One of the plant surface characteristics that has influenced feeding by the diamondback moth is the wax bloom on the leaves. Normal-bloom cabbages can show resistance to the diamondback moth as a result of chemical properties (Eigenbrode & Shelton, 1992; Talekar & Shelton, 1993;

Verkerk & Wright, 1996a). However, it has been found that the physical properties of glossy surface waxes show higher resistance to the diamondback moth larvae even though they can be the preferred sites for oviposition (Eckenrode *et al.*, 1986; Dickson *et al.*, 1990; Stoner, 1992; Eigenbrode & Pillai, 1998). This leaf trait is found in the dark green, glossy cauliflower PI 234599 line and up to 95% resistance to pests has been found (Dickson *et al.*, 1990; Eigenbrode & Shelton, 1992; Talekar & Shelton, 1993). Unfortunately, crucifers with this trait are not yet commercially available. Generalist predators are more effective at reducing the population of diamondback moth on glossy cabbages than on those with a wax bloom, possibly because they are more mobile on glossy plant surfaces (Stoner, 1992; Eigenbrode *et al.*, 1996).

Transgenic crops which incorporate genes from *Bacillus thuringiensis* Berliner (*Bt*) have been used in other crop systems and have potential for crucifer crops (Ramachandran *et al.*, 1998b; Tabashnik *et al.*, 1998). They are effective in controlling *Bt*-susceptible diamondback moth but not *Bt*-resistant moths. Transgenic crops are more effective if they contain multiple toxins and are used together with non-transgenic plant refuges to help delay resistance (Riggin-Bucci & Gould, 1997; Roush, 1997a , 1997b; Roush, 1998; Verkerk *et al.*, 1998).

1.2.3. Alternative chemicals

Apart from the traditional chemical insecticides which are continually being developed and improved, alternative chemicals are also being used. These include sex pheromones, botanical insecticides and insect growth regulators.

1.2.3.1. Sex pheromones

Synthetic sex pheromones are used in diamondback moth control, either through the disruption of communication between the sexes or through mass trapping of the male moths (Nemoto *et al.*, 1992). Ohbayashi *et al.* (1992) found that mass trapping of the males was not very effective and therefore sex pheromones should be used to disrupt communication. The female diamondback moth releases a sex pheromone that attracts the male and results in mating. However, if the entire field is covered in sex pheromone, communication is confused and mating does not occur (Ohbayashi *et al.*, 1992). To be of any use the synthetic sex pheromone needs to be found in very high concentrations throughout the growing season and if it works it can reduce the need for insecticides by as much as half (Ohbayashi *et al.*, 1992). The use of sex pheromones has been limited due to the cost, the short distances over which it works and its low level of persistence in the field (Lee *et al.*, 1995). Successful mating disruption has been reported in Japan (Chow, 1992), Taiwan (Ohno *et al.*, 1992) and Florida, USA (McLaughlin *et al.*, 1994). More recently studies have suggested that mating disruption of the diamondback moth using the present technology does not provide suitable control (Shelton *et al.*, 1997; Schroeder *et al.*, 2000). Sex pheromone traps are useful for monitoring populations of diamondback moth in the field to determine times of peak adult activity and therefore suitable timing for control (Baker *et al.*, 1982; Leibee & Capinera, 1995; Shirai & Nakamura, 1995).

1.2.3.2. Botanical insecticides

Botanical insecticides are particularly important in developing countries were many of the growers cannot afford commercial insecticides (Schmutterer, 1992). In many cases the plants are easily accessible to the growers, who are able to make their own formulation. They pose no threat to humans, are biodegradable and environmentally friendly (Banaag *et al.*, 1998). Many plant species contain secondary substances that are detrimental to insects. They can either be toxic, inhibit growth and development, affect feeding and ingestion, or affect fecundity and fertility (Morallo-Rejesus, 1986; Chen *et al.*, 1996; Perera *et al.*, 2000). Eighty-two plant species have been reported to be toxic to the diamondback moth (Morallo-Rejesus, 1986). Some of the most effective include neem (*Azadirachta indica* A.) and a related species, chinaberry or syringa (*Melia azedarach* L.) (Andrews *et al.*, 1992; Lim, 1992; Schmutterer, 1992; Srinivasan & Krishna Moorthy, 1992; Chen *et al.*, 1996; Saucke *et al.*, 2000; Charleston *et al.*, 2001). Extracts from the rhizome of the tropical yam, *Dioscorea hispida* Schlussel have been used in the Philippines (Banaag *et al.*, 1997, 1998).

1.2.3.3 Insect growth regulators

Insect growth regulators that interfere with chitin formation, like diflubenzuron, teflubenzuron and chlorfluazuron have been used to control the diamondback moth (Becker, 1986; Rushtapakornchai & Vattanatangum, 1986; Sagenmueller & Rose; 1986, Chalfant, 1992; Furlong & Wright, 1994). They can be as effective as synthetic chemicals and are harmless to most beneficial insects. However, resistance has developed to these compounds (Cheng *et al.*, 1992; Jansson, 1992; Kobayashi *et al.*, 1992; Sun, 1992; Syed, 1992; Furlong & Wright, 1994; Iqbal & Wright, 1997).

1.2.4. Sterile insect technique

The use of a sterile insect technique through irradiation of males has been attempted in the diamondback moth (Sastrodihardjo, 1986). Lepidopteran pests need higher doses of radiation than those used for other insect groups, which can cause changes in their competitiveness and performance in the field (Bahari, 1994; Bloem & Carpenter, 2001). It is possibly because of this that this method has not been widely used for the control of the diamondback moth.

1.2.5. Biological control

There are a wide range of pathogens that can control the diamondback moth including viruses, fungi and bacteria. Other biological control methods that have been used against the diamondback moth include nematodes, predators and parasitoids.

1.2.5.1. Viruses

A number of viruses have been found that infest the larvae of the diamondback moth including granulosis virus (GV) and nucleopolyhedrosis vius (NPV) (Asayama, 1986; Koshihara, 1986; Wilding, 1986; Kadir, 1992; Talekar, 1996). These viruses cause the segments of the larva to swell and to change colour, and result in the death of the larvae. Viruses have not been used extensively as their efficacy is reduced by UV radiation, unsynchronised host populations (Kadir, 1992), high temperatures (Talekar, 1996) and no stable formulations have been developed.

1.2.5.2. Fungi

Fungi have been used in the control of a number of insect species. *Zoophthora radicans* (Brefeld), *Beauveria brassiana* (Balsamo) Vuillemin, *Metarhizium anisopliae* Metschnikoff (Sorokin), *Pandora blunckii* (Lakon ex Zimm.) and *Paecilomyces fumosoroseus* (Wize) Brown & Smith are just some of the fungi that have been used in the control of the diamondback moth (Ooi, 1986; Wilding, 1986; Thomas & Ferguson, 1989; Lim, 1992; Riethmacher *et al.*, 1992; Furlong *et al.*, 1997; Shelton *et al.*, 1998; Vandenberg *et al.*, 1998a, 1998b). They usually infect larvae but can also infect pupae. In 1940 Ullyett & Schonken reported that *Zoophthora radicans* (Brefeld) was sometimes so effective in South Africa that the parasitoids were eliminated due to a lack of hosts (cited by Wilding, 1986).

1.2.5.3. Bacteria

By far the most effective and widely used pathogen is the bacterium *B. thuringiensis* (*Bt*) formulated into a bioinsecticide (Andrews *et al.*, 1992; Morallo-Rejesus & Sayaboc, 1992). This bacterium produces an endotoxin that paralyses the gut, causing feeding to cease and eventually leads to death of the larva (Wilding, 1986). However its effectiveness is limited by having a short residual activity under field conditions due to rapid degradation by UV radiation. Lethal doses are therefore only present for very short periods and frequent applications are necessary (Soares & Quick, 1992). Formulations of *Bt* have been produced which are specific to species of Lepidoptera and have no effect on humans, vertebrates or most of the beneficial insects, like parasitoids (Brunner & Stevens, 1986; Lim, 1992; Mori, 1992; Soares & Quick, 1992).

Even though resistance to *Bt* had been documented in a number of insect pests in laboratory conditions, it was initially thought that resistance in field situations was unlikely. However, Tabashnik *et al.* (1990) reported resistance of field populations to *Bt* in Hawaii. It was therefore suggested that, if *Bt* was used at the same frequency as the more conventional insecticides, a similar resistance problem would develop. High levels of resistance to *Bt* by diamondback moth have since been reported (Jansson, 1992; Syed, 1992; Shelton & Wyman, 1992; Tabashnik *et al.*, 1992; Tanaka, 1992; Shelton *et al.*, 1993a; Liu & Tabashnik, 1997a; Tabashnik *et al.*, 1997). It is therefore only effective when used with another method of control in an IPM programme, for example other biological control options, plant resistance or cultural control (Shelton *et al.*, 1993a; Talekar & Shelton, 1993; Ivey & Johnson, 1997; Díaz-Gomez *et al.*, 2000). A better understanding of resistance to *Bt* is required to help in the development of resistance management strategies (Tabashnik *et al.*, 1991; Tabashnik, 1994; Tabashnik *et al.*, 1998) which should be used to slow down *Bt*-resistance in areas where it is still effective (McGaughey, 1994; Liu & Tabashnik, 1997b).

1.2.5.4. Nematodes

Infective juvenile stages of entomopathogenic nematodes from the families Steinernematidae and Heterorhabditidae have been used in commercial formulations against the diamondback moth (Baur *et al.*, 1997). Their effectiveness is limited by temperature, and the ability to survive desiccation and UV radiation. However, studies have shown that with an optimal spraying programme, careful application techniques and timing, control of the diamondback moth can be achieved (Baur *et al.*, 1995; Mason & Wright, 1997; Baur *et al.*, 1998).

1.2.5.5. Predators

Predators found in association with the diamondback moth include spiders (Aranaea) (Koshihara, 1986; Wakisaka *et al.*, 1992; Muckenfuss & Shepard, 1994), hoverflies (Syrphidae: Diptera), lacewings (Chrysopidae: Neuroptera) and a variety of Coleoptera including Coccinellidae, Staphylinidae and Carabidae (Koshihara, 1986; Alam, 1992; Wakisaka *et al.*, 1992; Schellhorn &

Sork, 1997; Suenaga & Hamamura, 1998, 2001). Birds have also been known to feed on the diamondback moth (Ullyett, 1947b; Harcourt, 1960; Talekar & Shelton, 1993).

1.2.5.6. Parasitoids

The eggs and the immature stages of the diamondback moth are attacked by parasitoids. Biocontrol using parasitoid wasps has shown various degrees of success in different countries around the world with different species dominating, depending on the conditions (Goodwin, 1979). Lim (1986) found that records of natural control of the diamondback moth suggest that it has only become a pest in countries where natural enemies, particularly parasitoids, are ineffective or absent. Many countries where the diamondback moth is a pest, for example parts of southeast Asia, do not have their own parasitoid complexes for control against the moth and as a result species have been introduced from other regions. Successful control by parasitoids depends on the conditions under which they are used. Insecticides and hyperparasites have resulted in reducing the effect of parasitoids (Chen & Su, 1986; Lim, 1986; Sastrosiswojo & Sastrodihardjo, 1986; Alam, 1992, Morallo-Rejesus & Sayaboc, 1992; Idris & Grafius, 1993c).

1.3. Integrated Pest Management (IPM)

It is becoming more widely recognised that Integrated Pest Management (IPM) is one of the few solutions to the diamondback moth problem. This involves using a number of control methods in conjunction with one another, the most important being the effective use of biological parasitoids (Ooi, 1986; Lim, 1992; Ooi, 1992; Lim *et al.*, 1997). IPM programmes are needed to reduce the use of insecticides but at the same time, increase the economic yield of crucifer crops in countries around the world (Lim, 1992).

1.4. Outline of the study

This study examines the diamondback moth populations in the Grahamstown area of the Eastern Cape Province in both an insecticide and an insecticide-free environment. The history of diamondback moth research in the country and the study sites are introduced (Chapter 2). The possibility of resistance to chemicals that have been used in the past are investigated (Chapter 3) and the development and mortality of the diamondback moth immature stages with respect to temperature are determined (Chapter 4). The seasonal population fluctuations of the moth were recorded and the impact of the abiotic factors, including temperature, humidity, rainfall and wind speed on these fluctuations are considered (Chapter 5). The parasitoids associated with the diamondback moth were determined (Chapter 6), their seasonal fluctuations recorded (Chapter 7) and the trends in parasitism rates investigated (Chapter 8). The edge distributions and the distances moved into fields by the moths and their parasitoids were determined with regards to improving cultural practices (Chapter 9). Oviposition and survival by the diamondback moth on alternative host plants was investigated (Chapter 10). The information obtained in each of these chapters was considered with the aim of suggesting ideas for an Integrated Pest Management programme in the Eastern Cape Province (Chapter 11).

The aims of this thesis were therefore:
- to test for an indication of insecticide resistance in the diamondback moth
- to investigate development and mortality rates of the diamondback moth at different temperatures
- to monitor seasonal population fluctuation in the diamondback moth
- to determine the parasitoid species present
- to monitor the population fluctuations of the parasitoid species
- to determine trends in parasitism rates
- to investigate edge distributions in the diamondback moth and its parasitoids
- to investigate oviposition and survival rates of the diamondback moth on alternate host plants
- to suggest possible ideas for incorporation into an IPM programme in the area.

Chapter 2:

The diamondback moth in South Africa and study sites

2.1. Introduction

Brassicas are an important crop in South Africa, with large portions of the population relying on crucifer crops, especially cabbage (*Brassica oleracea* var. *capitata* L.), as part of their staple diet. Cabbages can be grown in most parts of South Africa throughout the year but they grow best in cool, humid climates. In summer certain areas of the country are too hot for successful cultivation (Steÿl, 1998). Cabbages are grown both on a large commercial scale, as a cash crop, and on a smaller subsistence scale. About 80% of small-scale rural farmers grow cabbage as a subsistence crop and 7 500 ha of cabbage is under commercial cultivation (Charleston, 1998). Other brassicas grown commercially in South Africa include broccoli and cauliflower, which are grown for both the fresh and frozen food market, and canola, which is produced for oil.

The cost of cabbage cultivation is relatively low and, provided the grower has a market close by, a profit can easily be made. Small-scale growers do not have many of the expenses of large-scale growers and, depending on their circumstances, could make a good living from growing cabbage (Steÿl, 1998).The practises of cabbage crop production differ greatly between small- and large-scale growers, including methods of soil preparation, planting, maintenance, pest management and harvesting. The requirements for and access to information, equipment and products are very different in the two groups.

One of the main problems with brassica cultivation in South Africa is the control of pests, especially the diamondback moth. Control of commercial cabbages has mainly been through the use of broad-spectrum insecticides such as pyrethroids and organophosphates. In small-scale subsistence farming, commercial pesticides are not always available and other methods, including cultural methods are used to control the pest. Many of the successful control methods used in other countries are not always feasible in South Africa and more economical and accessible methods of control need to be formulated. In the immediate vicinity of Grahamstown, Eastern Cape Province (Fig. 2.1), both large-scale commercial cabbage farming and small-scale subsistence farming are practised.

2.2. Commercial farming in the Eastern Cape Province

Cabbage is one of the most commonly grown, commercial vegetable crops in the Grahamstown area and is sold locally to shops, markets and hawkers as a cash crop. Other crucifer crops, for example cauliflower and broccoli, are used in the frozen vegetable market. Large-scale commercial growers rely on weekly calender spraying, with broad-spectrum pesticides and *Bacillus thuringiensis* Berliner (*Bt*) products are used occasionally. Diamondback moth is not the only problem pest on cabbage but it is one of the most destructive. Damage can also be done by other lepidopteran larvae for example, the cabbage looper, *Tricoplusia orichalcea* (F.) and the American bollworm, *Helicoverpa armigera* (H.); aphids (*Brevicoryne brassica* L.) and thrips (*Thrips tabaci* (Lindman)). Hail, theft and feeding by porcupines (*Hystrix africaeaustralis* Peters) and antelope, for example the common duiker (*Sylicapra grimmia* L.) also result in loss in cabbage production.

2.3. Subsistence farming in the Eastern Cape Province

The Eastern Cape is one of the poorest provinces in South Africa and many people rely on growing their own food in small, family gardens. The vegetables grown vary depending on what is available in terms of seedlings, water and the financial situation of the family. Cabbage is one of the most commonly grown vegetables, but carrots, sweet potatoes, onions, beans, spinach, lettuce, tomatoes and beetroot are also grown. Fertilizer is usually added in the form of cattle manure or wood ash but only if it is available. Commercial chemical pesticides are not often used because of the cost. Instead, growers use a variety of household substances including household detergent, ammonia, tobacco extracts and wood ash. Most of the vegetables are used by the family, and any excess is sold. There is very little understanding regarding insect pests and most of the growers cannot distinguish between pest insects and beneficial insects. In these communities education and training on insect pests and their control is vitally important.

2.4. Study sites

The three sites sampled in this study were all situated within 50 kilometers of Grahamstown (33°19'S 26°32'E) in the Eastern Cape Province, South Africa (Fig. 2.1). Grahamstown is situated in a transitional zone between a sub-tropical and a temperate climatic region. The average summer temperature range (December to February) is between 20 and 25°C and the average winter temperature range (May to July) is between 12.5 and 15°C. Rainfall can be year round as Grahamstown lies on the border of the summer and winter rainfall areas. Average rainfall varies between 250 mm and 750 mm. The occurrence of frost in the winter months is low, usually below 20%.

The first site, Site 1, included two commercial cabbage farms, while Site 2 and 3 were planted purely for the purpose of this study. The number of cabbages grown at the sites varied, with the commercial growers planting about 30 000 seedlings every 6 weeks. At Sites 2 and 3, only 1000 - 1500 cabbages where planted every 6 weeks due to limitations of space, time and labour. At Site 1 calendar pesticide spraying programs were used, but at Site 2 and 3 the cabbages were pesticide-free.

2.4.1. Site 1

Site 1 included two neighbouring farms in Belmont Valley, Grahamstown. The two farms were included together because of their close proximity and the very similar farming practises. Sampling was carried out at the first farm, Willow Glen (33°19'10"S 26°36'45"E) from April 1997 to January 1998. Cabbage cultivation was discontinued at this site after January 1998, so sampling continued at the neighbouring farm, Lower Melrose (33°19'45"S 26°38'45"E). Cabbage sampling was carried out here from January 1998 to October 1999, after which cabbage cultivation stopped. Cabbages were grown throughout the sampling period.

Other crops grown included cauliflower, broccoli, paprika, pumpkin, carrots and tomatoes. The surrounding vegetation consisted of valley bushveld (Low & Rebelo, 1996) with a grass and/or weed area separating this from the ploughed fields. This site underwent a pesticide spraying programme with products containing cypermethrin (pyrethroid) and mevinfos (organophosphate) as the active ingredients. A bioinsecticide, Dipel, containing *Bt* was used periodically.

2.4.2. Site 2

Site 2 was situated on Brentwood Farm (33°29'32"S 26°09'10"E), a dairy farm, situated 50 km west of Grahamstown. This area is a dairy, beef, goat and sheep farming area and cabbages had not previously been grown as a commercial crop. Sampling took place from April 1997 until October 1999. The surrounding vegetation consisted of pastures, lurcern and natural valley bushveld (Low & Rebelo, 1996). There was no pesticide spraying programme at this site.

2.4.3. Site 3

Site 3 was situated on Rhodes University property in Grahamstown (33°18'S 26°31' E). Cabbages had been previously grown in the area as a subsistence crop to provide food for a family. Sampling took place from August 1997 to October 1999. The surrounding vegetation consisted mainly of grassland, with elements of false fynbos (Low & Rebelo, 1996). There was no pesticide spraying programme at this site.

2.5. Previous work on the diamondback moth in South Africa

The diamondback moth has a much lower pest status in South Africa than in other parts of the world that have similar climates (Kfir, 1997b; Kfir, 1998), but it does still cause serious damage to crucifer crops grown by both subsistence and commercial growers.Very little work has been done in South Africa on the diamondback moth in comparison to other parts of the world. The first study was done in 1917 by Gunn and control of the moth was through arsenical sprays, tobacco extract and tar emulsion. Ullyett (1947b) did an intensive study on the mortality factors of the diamondback moth, and found parasitoids to be important. Recently studies have been done by Dennill & Pretorius (1995), Kfir (1996, 1997a, 1997b & 1998), Charleston (1998), Charleston & Kfir (2000) and Mosiane (2001). These studies, as with the one by Ullyett, have all been done in the Pretoria area of the Gauteng Province (Fig. 2.1). In the Eastern Cape Province studies on the diamondback moth have only been recently initiated. Waladde *et al.* (2001) investigated the parasitoids associated with the diamondback moth in the Alice area, 70 kilometers northeast of Grahamstown. The study reported in the following chapters is the only other known study on the diamondback moth in the Eastern Cape Province.

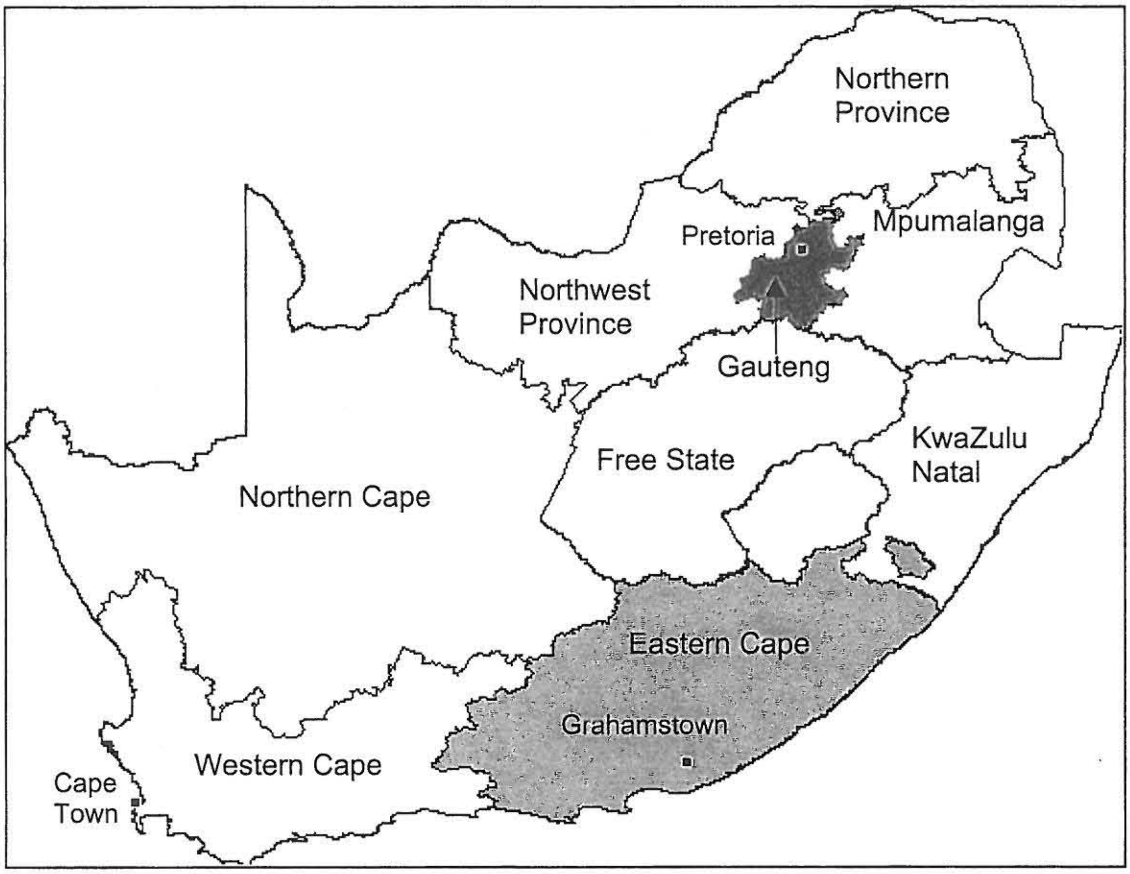

Figure 2.1. Map of South Africa showing the position of Grahamstown in the Eastern Cape Province and Pretoria in the Gauteng Province.

Chapter 3:

Occurrence of insecticide resistance

3.1. Introduction

Resistance by the diamondback moth to the commercially used chemicals has been reported worldwide (Miyata *et al.*, 1986; Yeh *et al.*, 1986; Shelton *et al.*, 1993b; Kuwahara *et al.*, 1995) and new insecticides are continually being developed as existing ones become useless. However, the diamondback moth has been found to develop resistance very quickly to many of these new formulations (Ninsin *et al.*, 2000; Shelton *et al.*, 2000). These new formulations include development of insecticides commonly known as 'softer insecticides' which are very active against pests but do not affect many of the beneficial insects. An example is spinosad, but resistance to this insecticide has already been discovered (Zhao *et al.*, 2002). Cross resistance and multiple resistance have also developed between a number of insecticides (Cheng, 1986; Miyata *et al.*, 1986; Shelton *et al.*, 2000).

An additional problem of using insecticides is the effect that these have on parasitoids and other beneficial insects, both directly and indirectly (Haseeb *et al.*, 2000). Laboratory experiments have often shown that insecticides are very toxic to parasitoids (Idris & Grafius, 1993a), but field trials have shown that some parasitoids are not as severely affected by insecticides (Idris & Grafius, 1993b).

At Site 1 in 1999 the grower experienced problems with very high numbers of diamondback moth larvae even though cypemethrin, a pyrethroid, had been sprayed regularly. Resistance to pyrethroids is common and in the USA it has been reported in Georgia (Chalfant, 1992), Florida (Jansson, 1992; Leibee & Savage, 1992) and Texas (Plapp *et al.*, 1992). Shelton & Wyman (1992) confirmed widespread resistance by 1988, particularly in the southern states but also in some of the northern states. In Japan resistance to pyrethroids was reported all over the country by 1990 (Yasudomi *et al.*, 1992). In Malaysia resistance was reported in both the highlands and the lowlands (Syed, 1992). Some cabbage growing areas in South Africa have reported resistance to a number of insecticides, including pyrethroids (Sereda *et al.*, 1997).

This chapter represents a range-finding pilot study done to determine if diamondback moth from Site 1 were resistant to cypermethrin. In addition the effect of cypermethrin on the adults of the dominant parasitoid species, *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) was also tested.

3.2. Materials and methods

3.2.1. Diamondback moth resistance

Larvae of a suspected resistant strain of diamondback moth were collected from the field at Site 1. The larvae were reared in the laboratory at 25°C and 16:8 hours light:dark. The emerging adults were allowed to lay eggs and the resulting larvae were used to determine for resistance. Larvae from a laboratory culture originally collected at Site 2, an unsprayed site, were also tested for resistance. For the purpose of this study, this population was called the susceptible strain, even though it was only in the laboratory for 18 months. A pyrethroid, Ripcord, with cypermethrin as the active ingredient was used. The recommended dose was 0.02g a.i./l. A concentration series was made up ranging from 2×10^{-4}g a.i./l to 1.2g a.i./l.

A leaf-dip bioassay was used to determine resistance and susceptibility of the diamondback moth larvae. The methods followed those of Sereda *et al.* (1997). Leaf-dip bioassays are representative of application methods in the field (Tabashnik & Cushing, 1987). Leaf disks (8cm in diameter) were cut from insecticide-free cabbage leaves. Each leaf disk was immersed for 5 seconds in a particular concentration of cypermethrin, the disks were then air-dried for 2 hours. The concentrations used for the susceptible strain were 2×10^{-4}, 0.001, 0.002, 0.005, 0.01, 0.015, 0.02, 0.04 and 0.08g a.i./l. Those used for the suspected resistant strain (Site 1) were 0.002, 0.01, 0.02, 0.04, 0.06, 0.08, 0.12, 0.16, 0.2, 0.4, 0.8 and 1.2g a.i./l. A control of insecticide-free de-ionized water was used in each experiment. When the leaf disks were dry, each disk was placed in a plastic petri dish with filter paper of the same diameter. Ten second and third instar larvae were placed on each leaf disk and the petri dishes were kept in a constant environment room at 25°C and 16:8 hours light:dark. The number of dead larvae in each petri dish was recorded at 48 hrs, 72 hrs, 96 hrs and 120 hrs. The percentage mortality of larvae at each concentration was determined. Larvae that survived were allowed to pupate and pupation and eclosion rates were determined. Using PROBIT v. 1.5 (US EPA Toxicity Data Analysis Software, 1994), the LC_{50} was determined for the suspected resistant strain and the nominal susceptible strain. The outliers were removed from the probit analysis (0.005g a.i./l from the resistant strain and $2 \times 10^{-4}$and 0.001g a.i./l from the susceptible strain). The only effect of this would have had was to decrease the likelihood of getting a significant difference.

3.2.2. Parasitoid resistance

Cotesia plutellae cocoons were collected from Site 1 and allowed to emerge in the laboratory. The leaf-dip bioassay described in the previous experiment was used. The concentrations of cypermethrin used were 0.002, 0.01, 0.02, 0.04, 0.06, 0.08, 0.12, 0.16, 0.2, 0.4, 0.8 and 1.2g a.i./l. A control was set up using insecticide-free de-ionized water. When the *C. plutellae* adults emerged, 10 individuals were placed in each petri dish and mortality after 48, 72, 96 and 120 hours was recorded.

3.3. Results

3.3.1. Diamondback moth resistance

Larvae from the suspected resistant strain were observed feeding on the leaf disks and windows were found at all concentrations less than 0.04g a.i./l. Feeding activity of the larvae from the susceptible strain varied at the different concentrations and windows were seen on the control, 2×10^{-4}, 0.002 and 0.005g a.i./l leaf disks.

Mortality was significantly higher (Fig. 3.1) in the susceptible strain than in the resistant strain ($t = -3.23$, $p = 0.02$, $t = -3.51$, $p = 0.02$, $t = -3.67$, $p = 0.01$ and $t = -3.73$, $p = 0.01$ at 48, 72,96 and 120 hours respectively) while pupation (Fig. 3.2) and moth eclosion (Fig. 3.3) were significantly lower ($t = 7.0$, $p = 0.01$ and $t = 13.42$, $p = 0.00002$, respectively). There was no mortality in any of the controls at any of the concentrations tested. Paired t-tests were done between the suspected resistance and susceptible strains of the diamondback moth at the 5 concentrations common to both strains. These were all significant (Table 3.1) and this information suggests that the diamondback moth population at Site 1 is resistant to cypermethrin.

There was at least a degree of magnitude difference between the estimated LC_{50}'s of the resistant and susceptible strain at every census (Table 3.2). The fiducial limits never overlapped between strains at any exposure time (Table 3.2) which implies that there was a statistically significant difference in LC_{50} between the two strains. The LC_{50} was higher for the resistant strain than the susceptible strain in each case. The response curve was not monotonic and as a result no further analysis was carried out. The resistance ratios were all greater than 50 (Table 3.2).

3.3.2 Parasitoid resistance

Survival of *C. plutellae* adults, when exposed to cypermethrin on contact, was high until exposed to 1.2g a.i/l. At this concentration all the wasps died after 24 hours. One death was found after 24 hours at a concentration of 0.2g a.i./l and 1 death was found after 48 hours at concentrations of 0.12g a.i./l and 0.4g a.i./l respectively. All the other wasps were still alive at 120 hours (Fig. 3.4).

3.4. Discussion

The larvae from Site 1 showed a higher degree of resistance to cypermethrin than the larvae originally collected from Site 2. The resistant strain reached 100% mortality at 1.2g a.i./l while the susceptible strain reached 100% mortality at 0.08g a.i./l (Fig. 3.1). The rate of pupation was very low in the susceptible strain but in the resistant strain it was high until a concentration of 0.12g a.i./l of cypermethrin was used (Fig. 3.2). No moth eclosion was found in the susceptible strain, but in the resistant strain eclosion was above 50% until a concentration of 0.12g a.i./l of cypermethrin was used (Fig. 3.3). The resistance ratio (RR) showed that the larvae from Site 1 had 108, 59.7, 62.8 and 76.7-fold resistance to cypermethrin after 48, 72, 96 and 120 hours respectively. These resistant ratios for pyrethroids are much lower than in other parts of the world. Ho *et al.* (1983) found that cypermethrin was very effective against a susceptible strain of diamondback moth but that the resistant strain was more than 30 000-fold resistant to cypermethrin. Although the LC_{50} was determined for each strain, no further analysis could be done due to the lack of a monotonic response. This was a pilot study, using an unreplicated regression method and it did show that resistance to cypermethrin was found at Site 1, but further studies need to be done to confirm these results. As this study was a range-finding study and not a definitive study, the concentrations used for the susceptible strain were not extended below 2×10^{-4}g a.i./l. However in future work this needs to be done to confirm a lower mortality in the susceptible strain.

Sereda *et al.* (1997) determined resistance to deltamethrin, a pyrethroid, using a three dose assay with the recommended dose, half the recommended dose and twice the recommended dose. No LC_{50} levels were determined for any of the populations. Results showed that after 48 hours five of the six tested populations showed resistance to deltamethrin. Resistance to pyrethroids builds up more quickly in the diamondback moth than resistance to organophosphates and carbamates (Hama, 1992; Yu & Nguyen, 1996). In Florida the diamondback moth showed a 2100- to 82400-fold resistance to pyrethroids, a 20- to 73-fold resistance to organophosphates and a 400- to 500-fold resistance to carbamates (Yu & Nguyen, 1996). In Adelaide, Australia, an 8- to 400-fold resistance to pyrethroids was found, while a 5- to 200-fold resistance in organophosphates and a 6-fold resistance to a carbamate insecticide was found (Baker & Kovaliski, 1999). Resistance to pyrethroids is more stable than resistance to organophosphates and remains within a population for longer after application is stopped. Cross-resistance is also much higher amongst pyrethroids than in the organophosphates. For these reasons pyrethroids should not be used in rotational applications (Hama, 1992).

Cypermethrin, except at very high doses, did not have an effect on adult *C. plutellae* (Fig. 3.4) which might suggest resistance in the parasitoid population at these concentrations, but no *C. plutellae* from a susceptible population were tested so this cannot be confirmed. However, Mani & Krishna Moorthy (1984) and Kao & Tzeng (1992) found that pyrethroids had no effect on adult *C. plutellae*. Some parasitoid populations have developed high levels of resistance to insecticides (Sastrodihardjo, 1986; Xu *et al.*, 2001b). It has been suggested that resistance to insecticides takes longer to develop in parasitoids than in the diamondback moth (Xu *et al.*, 2001b). Even though adult parasitoids are not always directly affected by insecticides, parasitism rates are altered because the developing parasitoids within the host larvae are killed (Chilcutt & Tabashnik, 1997b,1999; Haseeb *et al.*, 2000). For effective control of the diamondback moth using parasitoids, selective insecticides with a low toxicity to beneficial insects are needed, for example *Bt* and growth regulators, and timing of applications is important (Iman *et al.*, 1986; Lim *et al.*, 1986; Waterhouse, 1992; Idris & Grafius, 1993b; Muckenfuss & Shepard, 1994; Iqbal *et al.*, 1996; Chilcutt & Tabashnik, 1997a, 1999; Roush, 1997b; Hill & Foster, 2000).

Apart from the continuous use of insecticides, other factors are also important in the development of resistance. These include high temperatures, extended growing seasons and a rapid generation rate of the pest (Jannson, 1992; Talekar *et al.*, 1992). A number of management strategies have been developed to slow down and help prevent resistance. These include rotation of chemicals, revolving doses, having unsprayed refugia, using transgenic crops and avoiding the mixing of chemicals (Sakai, 1986; Hama, 1992; Miyata, 1992; Sun, 1992; Liu & Tabashnik, 1997a; Riggin-Bucci & Gould, 1997; Roush, 1997a, 1997b; Gardner *et al.*, 1998). Resistance monitoring is necessary and it is very important that management strategies are put into place before resistance becomes a problem (Cheng *et al.*, 1992; Plapp *et al.*, 1992; Sun, 1992; Perez & Shelton, 1997). Resistance management strategies should be used together with biological and cultural control methods in order to provide the best results (Cheng *et al.*, 1992; Tabashnik *et al.*, 1992; Gardner *et al.*, 1998; Díaz-Gomez *et al.*, 2000; Shelton *et al.*, 2000, Zhao *et al.*, 2002).

3.5. Conclusion

Resistance to insecticides used against the diamondback moth has been found in areas of South Africa, including Gauteng, Free State and North West Province (Sereda *et al.*, 1997), and the problem is spreading. In the Eastern Cape Province resistance is suspected in many areas and this chapter confirms its existence on a commercial farm in the Grahamstown area. T-tests showed a statistically significant difference between the suspected resistant and susceptible strains. The fiducial limits for the estimated LC_{50}'s did not overlap which also implied a statistically significant difference between the strains. This pilot study was carried out to show that there was a need for other control mechanisms in the Grahamstown area and the importance of addressing problems regarding insecticide resistance.

Table 3.1. Results of the paired t-tests on the mortality of the suspected resistant and susceptible strain of the diamondback moth at the 5 concentrations of cypermethrin common to both. All values are significant ($p < 0.05$).

48 hours	72 hours	96 hours	120 hours
$t = -4.14$	$t = -4.83$	$t = -5.30$	$t = -5.48$
$p = 0.01$	$p = 0.01$	$p = 0.01$	$p = 0.01$

Table 3.2. Estimated LC_{50}'s with 95% fiducial limits, the slope and standard error (SE) and the chi-square for homogeneity for two strains of diamondback moth larvae, a suspected resistant strain (R) and a susceptible strain (S) at four time intervals. The resistance ratio (RR) is provided.

	Resistant strain					Susceptible strain					
	LC_{50}	Fiducial limits		Slope (SE)	Chi square	LC_{50}	Fiducial limits		Slope (SE)	Chi square	Resistant Ratio (RR)
		lower	upper				lower	upper			
48 hrs	16.2	7.51	81.1	1.70 (0.51)	24.2	0.15	0.002	0.37	0.87 (0.34)	7.06	108
72 hrs	8.95	3.95	27.3	1.81 (0.53)	26.1	0.15	0.003	0.35	0.93 (0.35)	4.93	59.7
96hrs	7.53	3.84	16.5	1.79 (0.44)	18.7	0.12	0.01	0.27	1.17 (0.38)	5.07	62.8
120hrs	6.90	3.65	13.9	1.82 (0.42)	17.0	0.09	0.01	0.19	1.57 (0.50)	0.98	76.7

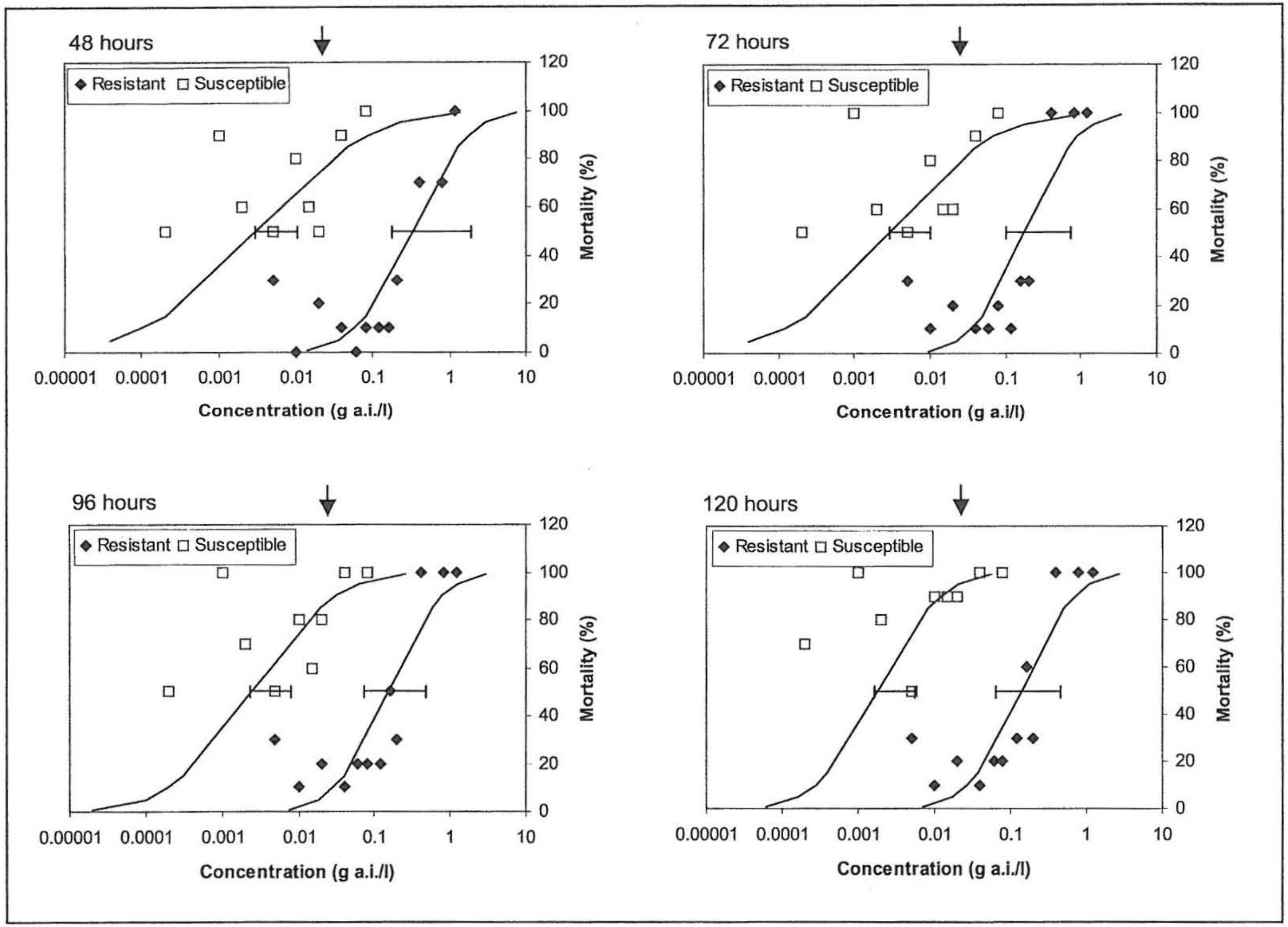

Figure 3.1. Mortality of a suspected resistant and a susceptible strain of diamondback moth larvae at a number of concentrations of cypermethrin at four time intervals, showing the probit curves. 95% fiducial limits are given for the resistant and susceptible LD_{50}'s at each time interval. Arrows show the manufacturers recommended dose for cypermethrin.

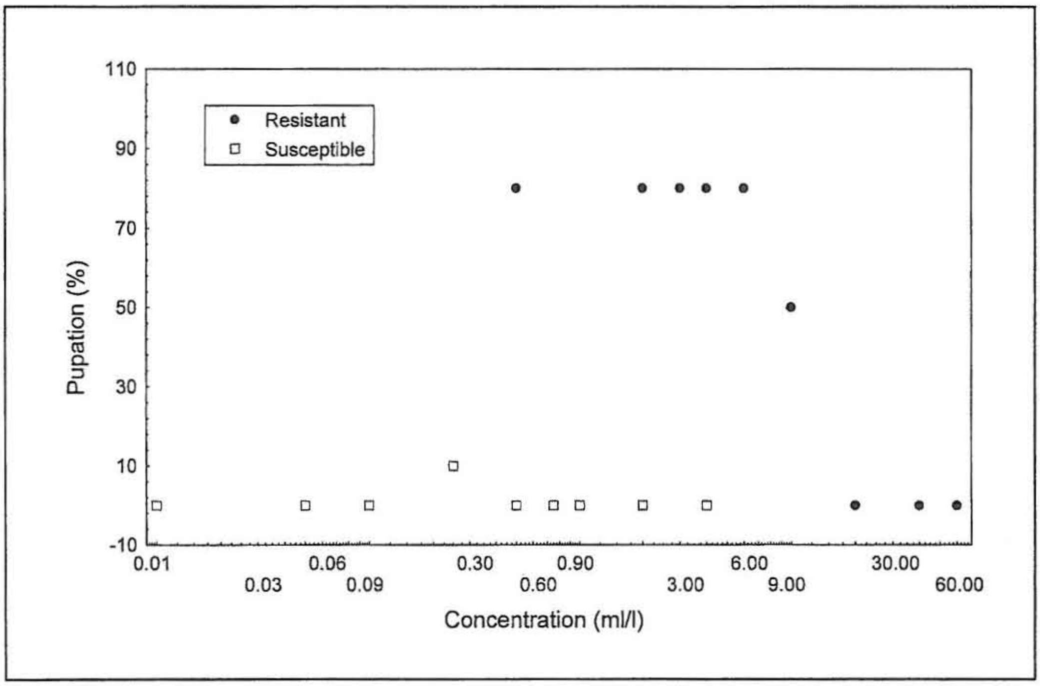

Figure 3.2. Pupation of a suspected resistant and a susceptible strain of diamondback moth at a number of concentrations of cypermethrin.

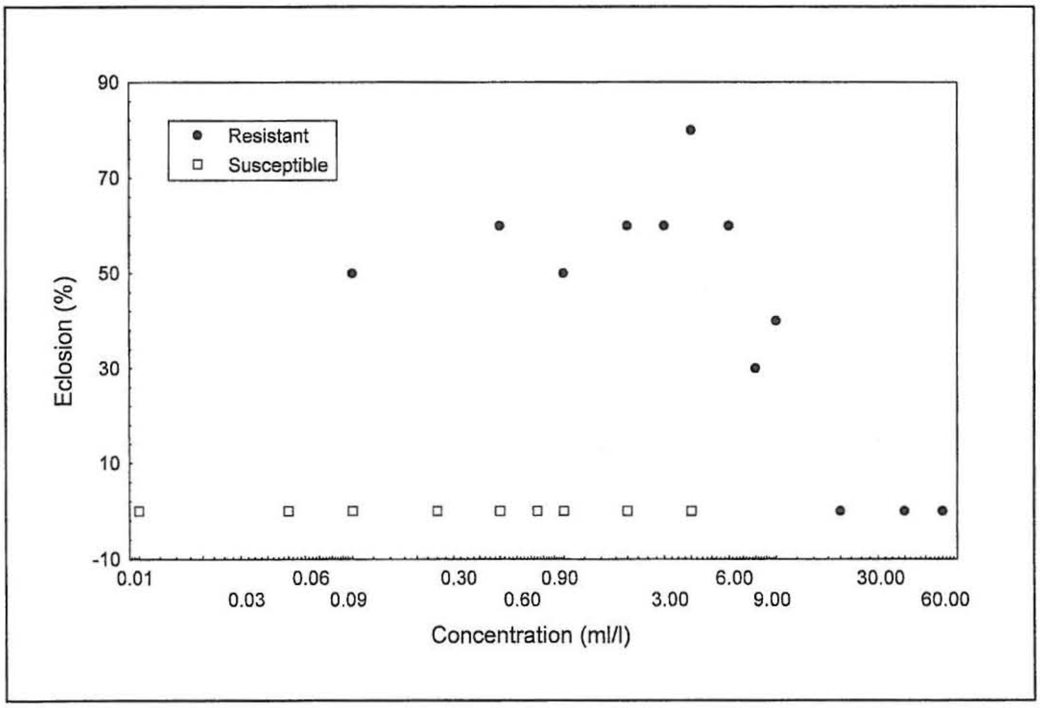

Figure 3.3. Eclosion of a suspected resistant and a susceptible strain of diamondback moth at a number of concentrations of cypermethrin.

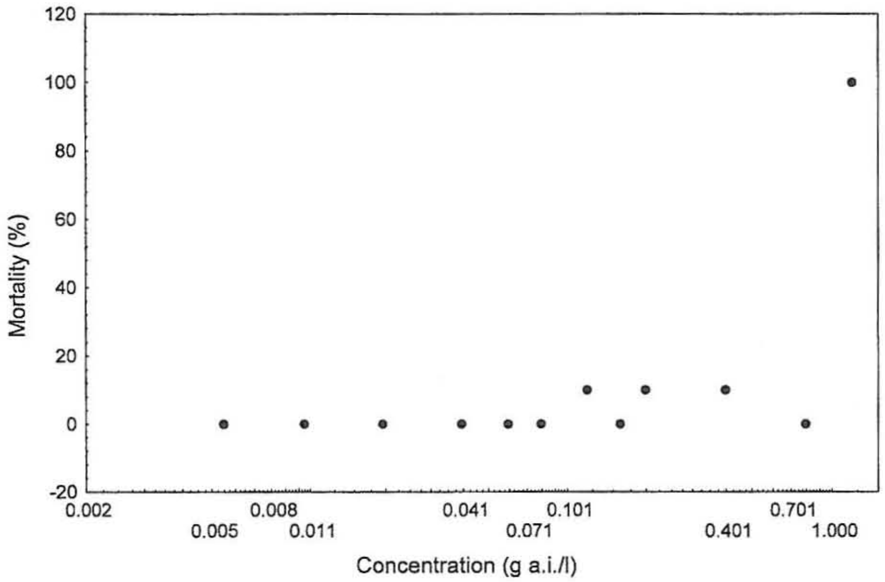

Figure 3.4. Mortality of adult *Cotesia plutellae* parasitoids exposed to a number of concentrations of cypermethrin after 120 hours.

Chapter 4:

Effects of temperature on development and mortality

4.1. Introduction

The rate of development in insects depends to a large extent on temperature (Higley & Haskell, 2001). The biochemical reactions that result in growth and development are controlled by enzyme reactions which are commonly temperature-dependent (Sharpe & DeMichele, 1977; Higley *et al.*, 1986; Higley & Haskell, 2001). As a result, models for predicting the development rates for a number of insect species have been successfully developed. Generally, the relationship between temperature and development is a sigmoid development curve, with the relationship being curvilinear (nonlinear) at low and high temperatures and practically linear in between (Higley *et al.*, 1986; Higley & Haskell, 2001; Pedigo, 2002). In agriculture, modelling thermal accumulation in pest species is important in predicting outbreaks (Higley & Haskell, 2001; Pedigo, 2002). It also helps to determine the best time to apply control measures, particularly insecticide applications.

The adult diamondback moths are inactive during daylight hours. They mate at dusk on the same day as emergence and oviposition occurs soon after mating (Harcourt, 1957). The gravid female diamondback moth lays small, oval, yellow eggs on the undersurface of the leaves of the host plant, usually along the midrib or the veins. The number of eggs laid varies but they can lay as many as 300 per moth (Ullyett, 1947b; Chen & Su, 1986). First instar larvae hatch and begin feeding by mining into the leaf tissue. From the second instar the larvae feed on the exterior of the leaf, usually on the underside. They leave the wax layer on the upper epidermis of the leaf intact, forming characteristic windows (Harcourt, 1957). The fourth instar pupates, spinning a loosely woven cocoon.

The length of all stages in the lifecycle of the diamondback moth depends on temperature (Ullyett, 1947b) and a number of authors have studied development of the diamondback moth at different temperatures (Chelliah & Srinivason, 1986; Wakisaka *et al.*, 1992; Salinas, 1986). Generally, development is slow at lower temperatures but increases as temperatures increase. Once an optimum is exceeded, development time decreases again. The degree days (thermal summation) and the developmental zero (thermal threshold) for the diamondback moth has been determined in a number of countries (Butts & McEwen, 1981; Honda, 1992b; Kmec & Weiss, 1997; Godin & Boivin, 1998b) all of which are outside Africa.

Very little work has been reported regarding geographical variation within the diamondback moth. In most published studies, no statistically significant geographical differences have been found between the thermal tolerances or larval development of the diamondback moth (Shirai, 2000). The diamondback moth is a very mobile species and migration is known to occur especially in the northern hemisphere, for example in Canada (Harcourt, 1986) and Japan (Koshihara, 1986). This may be the reason for the small geographical variation in thermal tolerances (Shirai, 2000). South Africa is fairly isolated in relation to other parts of the world and as such any differences in thermal tolerances would be worth investigating.

4.2. Material and methods

The diamondback moths used in these experiments were originally collected from Site 1 (see Chapter 2). The colony was maintained in a constant environment room at 25°C, 16:8 hours light:dark. Three cabbage leaves, removed from insecticide-free plants, were placed in a cage with the established colony. After 24 hours the leaves were removed, the number of eggs counted and the leaves placed together in a KBW 240 Precision growth chamber set at one of the six experimental temperatures (10°C, 15°C, 20°C, 25°C, 30°C and 35°C). The number of eggs used at each temperature were 378, 500, 303, 200, 190 and 330 at 10°C, 15°C, 20°C, 25°C, 30°C and 35°C respectively. The leaves were checked daily and the dates of hatching, moulting of the instars, and dates of pupation and eclosion of the moths were recorded. A minimum and maximum development time for each stage was determined and analysis was based on the mean at each temperature. The same process was carried out for each of the temperatures.

The development rate of the diamondback moth at each of the six temperatures was determined. Two methods were used to determine the thermal summation and the development zero of the diamondback moth. The first method was the traditional linear method where it is accepted that the linear portion of the development curve is suitable to provide the information (Sharpe & DeMichele, 1977; Pruess, 1983; Higley *et al.*, 1986; Lamb, 1992; Higley & Haskell, 2001). The developmental zero is determined by finding the x-intercept of the linear portion of the graph but it only gives an estimate of the minimum developmental temperature. Determining the maximum developmental temperature is very rarely done and often overestimates the rate of development (Higley *et al.*, 1986). This method for modelling insect development is widely used because it requires minimal data for formulation, it is easy to calculate and apply, and often gives approximately and practically correct values (Wagner *et al.*, 1984). However, it is only valid over intermediate temperatures, and under- and overestimations of the thermal summations are found at low and high temperatures respectively (Sharpe & DeMichele, 1977; Wagner *et al.*, 1984; Worner, 1992). The second method used was the reduced major axis regression method described by Ikemoto & Takai (2000) where the product of the development time and the temperature (DT) is plotted against development time (D). Ikemoto & Takai (2000) found that this method showed greater precision when determining the thermal summation and the thermal threshold of organisms.

4.3. Results

4.3.1. Development of the diamondback moth at different temperatures

At 10°C development was slow, but as temperatures increase the development time decreased. At 35°C the development time increased again (Fig. 4.1). The data collected at 35°C was not used to determine the thermal summation or the developmental zero as the point did not lie on the linear section of the development curve.

4.3.2. Determining thermal summation and thermal thresholds

4.3.2.1. Method 1 (linear method)

Using least square regression with 95% confidence intervals, one generation required 391.5 degree days (DD) above a threshold of 3.8°C to complete development from egg to adult (s.e. for intercept = 0.0002; s.e. for slope = 0.00001; $r = 0.98$, $r^2 = 0.96$, $p = 0.003$). The confidence interval (Fig. 4.2) suggested that the developmental zero could lie from below 0°C up to 8.5°C. Figure 4.2 suggested a possible inflection at 20°C which is therefore considered to be the developmental optimum because it is where the gradient of the graph is steepest.

4.3.2.2. Method 2 (reduced major axis regression)

Using reduced major axis regression with 95% confidence intervals, development took 487.4 DD (s.e. = 45.8) above a threshold of 4.8°C (s.e. = 1.27) to complete one generation ($r = 0.89$, $r^2 = 0.79$, $p = 0.04$). Because of the greater precision using this method, values for DT were calculated for the diamondback moth in a number of countries using the available literature (Table 4.1). For those countries where sufficient information was available (England, Japan and Taiwan) the K-values and the D_0's were calculated (Table 4.1). All of the K-values lay within the confidence limits of the Eastern Cape data (Fig. 4.3).

4.3.3. Proportion of time spent at different stages

A chi-squared test for homogeneity showed a significant difference between the time spent at the different stages of the lifecycle ($\chi^2 = 246.1912$, $p = 0.000$). The proportion of time spent at the egg stage was fairly consistent at all six temperatures (Fig. 4.1, Fig. 4.4). The proportion of time spent in the 1st instar stage was less at the higher temperatures while the 2nd, 3rd and 4th instars took relatively longer. The pupae spent a similar proportion of time (between 15 and 25%) at all the temperatures (Fig. 4.4).

4.3.4. Thermal summation and developmental zero for different stages

At different temperatures the developmental rate for the eggs, larvae and pupae varied. The development rate for the larvae and pupae decreases at temperatures above 30°C. The development rate for the eggs reached a maximum at 25°C, but it did not decrease after this temperature. Both the traditional linear method, using least square regression with 95% confidence intervals (Fig. 4.5), and the method by Ikemoto & Takai (2000), using major axis regression with 95% confidence intervals (Fig. 4.6), were used to determine the thermal summation and the developmental zero for each stage. Table 4.2 provides the thermal summation and the developmental zero for the egg, larval and pupal stages which were determined using the more reliable Ikemoto & Takai (2000) method.

4.3.5. Survival rates

Survival of the moth is very poor at low and high temperatures. Even at its peak, survivorship was only 70% and it only occurred over a narrow temperature range (Fig. 4.7).

4.4. Discussion

4.4.1. Development of the diamondback moth at different temperatures

Development takes longer at the lower temperatures (10°C and 15°C). As temperature increases, development time decreases until 30°C, after which development time increases again. Hardy (1938) stated that the diamondback moth could breed and develop at temperatures from 10°C to 40°C and that the adults were active up until 50°C. A number of studies have determined the temperature tolerances of the diamondback moth and most of them show that the development rate is reduced above 30°C. Wakisaka *et al.* (1992) found that temperatures above 30°C delayed development, reduced the survival of the larvae and reduced the fecundity of the females. Recently, Liu *et al.* (2002) showed that at constant temperatures the diamondback moth developed successfully from 8 to 32°C. At temperatures from 4 to 6°C and from 34 to 40°C partial and complete development of the individual stages occurred. Shirai (2000) examined nine populations of diamondback moth from both tropical and temperate regions to determine if those from tropical regions showed a high-temperature tolerance. He found that egg production and larval development were similar in both the temperate and tropical regions indicating that there is no difference in their temperature tolerances. This may be because temperate regions can also reach high temperatures during midsummer and they experience a broader range of temperatures than tropical regions. Larvae developed between 15 and 30°C but at 32.5°C development was inhibited (Shirai, 2000).

The optimum development temperature for the diamondback moth is probably between 20°C and 25°C. Chen & Su (1986) found a similar optimum for the diamondback moth in Taiwan. The inflection in the development curve (Fig. 4.2) occurs at about 20°C while the mortality curve (Fig. 4.7) shows an optimum survival at 25°C. The temperature for the most rapid development is higher than that found by Yamada & Kawasaki (cited by Koshihara, 1986), Wakisaka *et al.* (1992) and Shirai (2000), who all found the maximum to be below 30°C. Yamada & Kawasaki (cited by Koshihara, 1986) found the percentage of adult emergence was higher between 22.5°C and 27.5°C, and that after 30°C adult emergence reduced rapidly. Wakisaka *et al.* (1992) found that adult emergence was high between 25°C and 30.5°C but decreased at 33°C and Shirai (2000) found that at 35°C survival was 0%.

The length of the lifecycle and the length of the different stages found at the various constant temperatures used in this study (Fig. 4.1) compared well to previous studies (Table 4.1), particularly those in more temperate regions, for example in Japan (Yamada & Kawasaki (cited by Koshihara, 1986); Wakasaki *et al.*, 1992), Taiwan (Chen & Su, 1986), Missouri (Biever & Boldt, 1971) and Canada (Harcourt, 1957). In the more tropical countries like Malaysia (Ooi, 1986) and Lesser Antilles (Bennett & Yaseen, 1972) the length of development was more rapid. On Marion Island, a sub-Antactic island, the larval duration and the length of the lifecycle of the diamondback moth that were determined using a temperature range between15 and 18°C (Crafford & Chown, 1990), and the results were very similar to those found in the Eastern Cape Province. The range in the length of development in the Eastern Cape was also very similar to that found by Gunn (1917) in the Pretoria region. Very few studies have investigated development at the lower temperatures (below 15°C).

4.4.2. Determining thermal summation and thermal thresholds

The two methods used to determine the thermal summation and thermal threshold gave different results. Ikemoto & Takai (2000) found that problems in determining the linear temperature ranges, discrepancies at low and high temperatures and imprecision in the estimation of the x-intercept could all be solved using their revised method, which provides a more reliable estimate. The developmental zero for Method 1 (linear method) was found to be lower than that for Method 2 (reduced major axis regression method), indicating that Method 1 underestimated the developmental zero. This is often the case when using the x-intercept approach. However, the developmental zero for Method 2 did fall into the confidence interval for Method 1 (Fig. 4.1). In the Eastern Cape population the thermal summation is much higher and the developmental zero much lower than those found in other populations around the world (Table 4.3).

Butts & McEwen (1981) found that 293 degree days above a threshold temperature of 7.3°C was required to complete one generation, even with the overlap of generations in the diamondback moth it was possible to accurately predict when the various stages were present in Canada. Godin & Boivin (1998b) determined that an average of 352.7 degree days above 7.3°C was required to complete one generation. However, they decided that the overlap of generations in the diamondback moth made it difficult to predict their occurrence using degree day accumulations. Degree day models do have their limitations in the field but in the Eastern Cape study they were not used for the timing of developmental events but as an index of population growth rate in the field. Liu *et al.* (2002) showed that when predicting diamondback moth in the field, the degree day model can be used in areas were temperatures range between 10 and 30°C for most of the time.

The developmental zero (Table 4.3) found for the diamondback moth in the Eastern Cape population is much lower than that found in other studies, which indicates that the South African population of the diamondback moth may be a distinct strain. The diamondback moth population on Marion Island in the sub-Antarctic is also able to survive at very low temperatures (between 4 and 7.5°C) during the summer months. To determine whether the South African population is different from other populations, genetic work needs to be done. Genetically, very few geographical variations have been found between populations of the diamondback moth. Caprio & Tabashnik (1992), Noran & Tang (1997) and Kim *et al.* (1999) used allozymes and found very little variation between populations in Hawaii, Malaysia and China, respectively. Chang *et al.* (1997) examined the variation amongst 6 geographic strains of the diamondback moth using mitochondrial DNA sequencing. They stated that variation was not correlated to geographical location. Thermal tolerances of widely distributed species also show very few geographic variations (Shirai, 2000). The diamondback moth is a migratory species and highly mobile and it is considered unlikely that it will show geographical thermal differences (Shirai, 2000). Pichon *et al.* (2001) have shown that although there are some biological and genetic differences in populations from around the world, they are not correlated with geographic distances.

4.4.3. Thermal summation and developmental zero for different stages

The thermal summation and developmental zero for different stages of an insects lifecycle are rarely considered in developmental studies. However, where they have been done, many insects are found to have different threshold temperatures at different stages of the lifecycle (Higley *et al.*, 1986). Davison (1969) examined the different stages of *Calliphora vicina* (Diptera: Calliphoridae) and found that the eggs were less temperature resistant than the pupal stage. These changes in tolerance between the stages are a result of changes taking place during development. The thermal summation and the developmental zero for the different stages of the diamondback moth vary in the Eastern Cape population (Table 4.2). The pupal stage has the highest developmental zero, followed by the egg and then the larval stages, which may indicate a tolerance to lower temperatures in the more mobile stages of the lifecycle. Koshihara (1986) reported the developmental threshold and the thermal summation for the egg, larvae and pupae for a number of localities in Japan. The developmental thresholds are much higher than those found in the Eastern Cape study. The thermal summation for the egg and larval stages in the Easter Cape population are slightly higher than those found in Japan but for the pupal stage they are similar.

When generations overlap significantly, Butts & McEwen (1981) suggest that efficient insecticide applications would include spraying at 80 -120 degree days after adult emergence, when larvae would be at the 1st and 2nd instar stages of the lifecycle. Larvae should then be counted between 180 and 220 degree days (3rd and 4th instars) to determine whether a second application is required. These thermal accumulations agree with those found for the different stages of the diamondback moth in the Eastern Cape (Table 4.2). In warmer areas where the diamondback moth is present all year and generations overlap it may still be possible to use thermal accumulations by having a regional break in cabbage cultivation. This would cause a crash in the population and result in synchronising the generations. Thermal accumulations can also be used to determine the time for release of parasitoids that attack a particular stage in the lifecycle of the diamondback moth (Godin & Boivin, 1998b).

4.5. Conclusion

The development of the diamondback moth at different temperatures can provide useful information for pest management. In the Eastern Cape control of the diamondback moth using insecticides has been by calender spraying. By establishing the mortality and the generation time of the moth, the interval between population increases can be determined and insecticide application methods adapted. The variation found between the thermal summation and developmental zero in the Eastern Cape population in comparison with other studies could mean that the South African population of the diamondback moth is a geographically adapted strain and is able to withstand different thermal limits. Further work needs to be done, especially at the higher and lower temperature ranges to determine these thermal limits.

Table 4.1. Length of development of the different stages in the lifecycle of the diamondback moth from various countries under various temperature conditions. The thermal summation (K) (°Ch) and developmental zero (D_0), determined by Method 2 (reduced major axis regression), are given where data were available. DT and K have been calculated for the available data in degree hours (°Ch).

Country	Temperature (°C)	Length of development (days)				DT (°Ch)	K (°Ch)	D_0	Source
		Egg	Larvae	Pupae	Total				
Canada	Variable	4-8	9-30	5-15	18-53	-	-	-	Harcourt (1957)
USA - Missouri	23	3	11	5	19	10488	-	-	Biever & Boldt (1971)
England	10	13	-	-	-	-	6359.3	7.6	Hardy (1938)
	15	6	17	11.5	34.5	12420			
	20	4.5	10.5	8	23	11040			
	25	3	7.25	4	14.25	8550			
	30	2.5	6.5	3	12	8640			
	35	1.5	5.25	-	-	-			
Japan	25				15.2	9120	5892.4	11.6	Wakasaki *et al.* (1992)
	27				14.9	9655.2			
	28.5				13.8	9439.2			
	30.5				12.8	9369.6			
	33				14.8	11721.6			
Japan	20	4.1	13.5	5.4	23	11040	7342.5	6.6	Yamada & Kawasaki (cited by Koshihara, 1986)
	25	3.0	9.2	3.8	16	9600			
	30	2.4	7.8	3.2	13.4	9648			
India	Variable	3-6	14-21	7-11	24-38	-	-	-	Chelliah & Srinivasan (1986)
Northwestern Himalaya	Variable	5-7	9-13	4-6	18-26	-	-	-	Bhalla & Dubey (1986)

Table 4.1 continued

Country	Temperature (°C)	Length of development (days)				DT (°Ch)	K (°Ch)	D_0	Source
		Egg	Larvae	Pupae	Total				
Taiwan	20				23	11040	6762.5	7.6	Chen & Su (1986)
	25				15.5	9300			
	30				13	9360			
Lesser Antilles	variable	2	8-10	3-4	13-16	-	-	-	Bennett & Yaseen (1972)
Venezuela	12 - 25	6.48	21.68	13.38	41.54	-	-	-	Salinas (1986)
	20	5.79	15.14	9.07	30	14400			
Malaysia -	Variable						-	-	Ooi (1986)
Lowlands		3	6	4	13	-			
Highlands		6	14	7	27	-			
Marion Island	15-18		20-30		40-50	-	-	-	Crafford & Chown (1990)
South Africa - Pretoria	Variable	5-8	15-30	5-14	25-52	-	-	-	Gunn (1917)
South Africa - Eastern Cape	10	14.5	32	14.5	61	14640	11697.6	4.8	
	15	7.5	28	7.5	43	15480			
	20	5	12	4.5	21.5	10320			
	25	3.5	10.5	4	18	10800			
	30	3.5	9.5	2.5	15.5	11160			
	35	3.5	11	3	17.5	14700			

Table 4.2. Thermal summation (K) and development zero (D_0), including standard errors (SE), for the different stages of the diamondback moth in the Eastern Cape, using Method 2 (reduced major axis regression). Thermal summation is shown in degree days (DD).

	K (DD) (±SE)	D_0 (°C) (±SE)
Egg	79.5 ± 6.3	4.5 ± 0.8
Larva	222.5 ± 47.2	4.3 ± 2.3
Pupa	69.0 ± 6.2	5.4 ± 0.8

Table 4.3. Published thermal summation (K) and developmental zeros (D_0) for the diamondback moth in different countries. Thermal summation is shown in degree days (DD).

Country	K (DD)	D_0 (°C)	Source
Japan	274	8.5	Yamada & Kawasaki (cited by Koshihara, 1986)
Japan	299	9.5	Umeya & Yamada (1973) (cited by Honda, 1992b)
Canada - Quebec	352.7	7.3	Godin & Boivin, 1998b
Canada - Ontario	293	7.3	Butts & McEwen (1981)
Canada - Ontario	236	7	Smith & Sears (1982)
Canada - Ontario	283	7.3	Harcourt (cited by Butts & McEwen, 1981)
USA - North Dakota	300	7.5	Kmec & Weiss (1997)
France	225	9.8	Bonnemaison (1965)
South Africa - Eastern Cape	487.4	4.8	This study

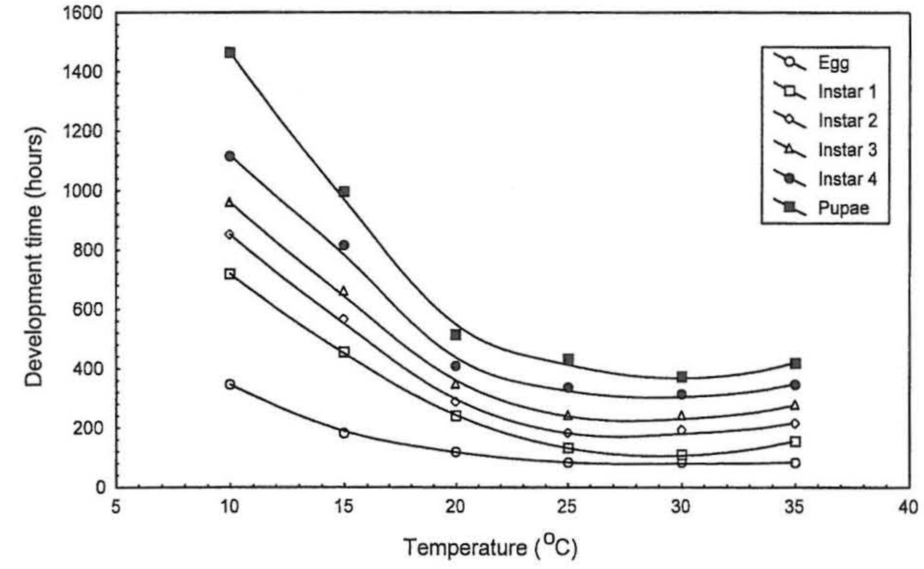

Figure 4.1. Total time to reach developmental landmarks at six different temperatures.

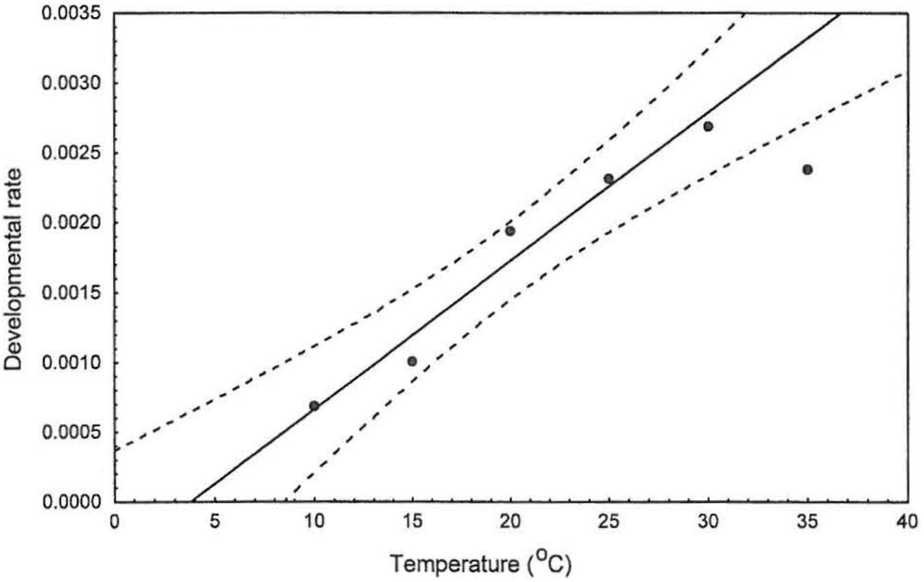

Figure 4.2. Rate of development of the diamondback moth at different temperatures using least square regression with 95% confidence intervals (Method 1).

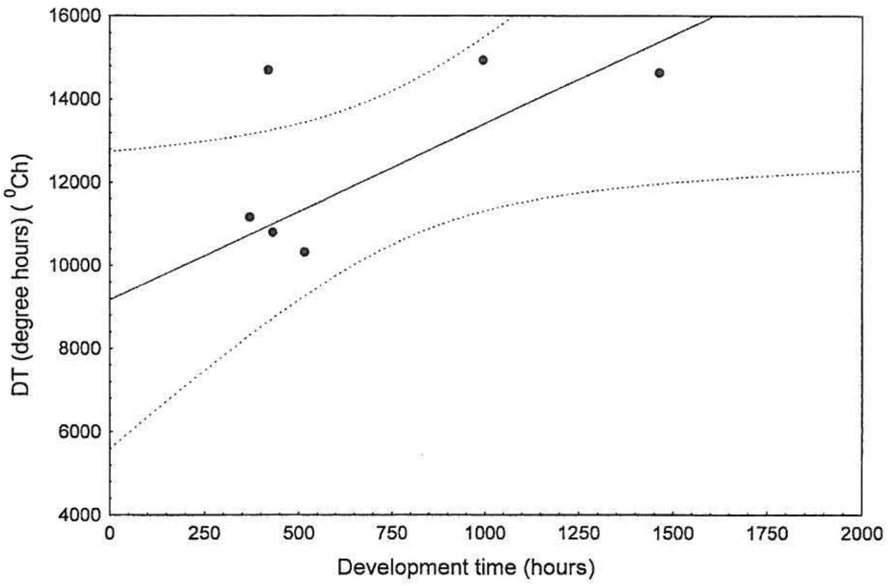

Figure 4.3. Development time of the diamondback moth using the reduced major axis regression with 95% confidence intervals (Method 2) (Ikemoto & Takai, 2000).

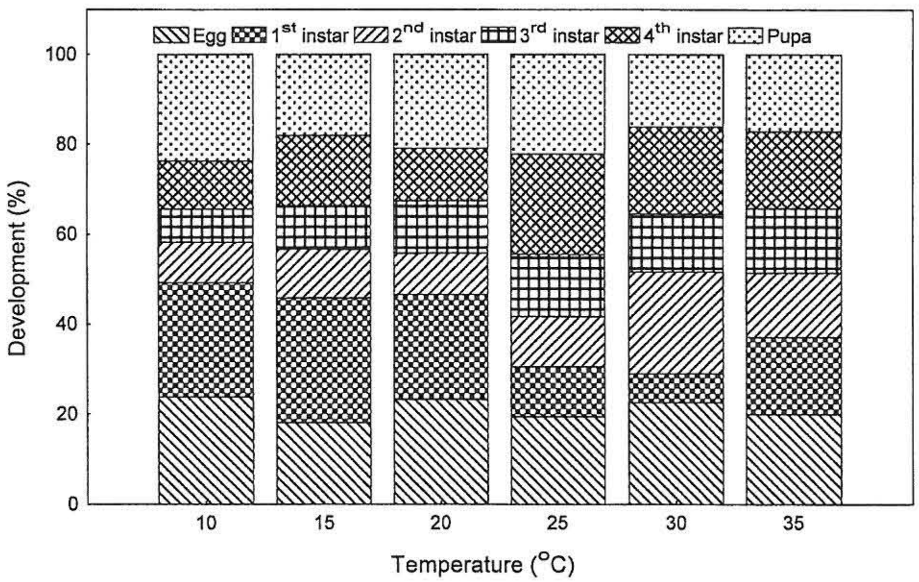

Figure 4.4. Proportion of time spent in each stage of the diamondback moth lifecycle at six different temperatures.

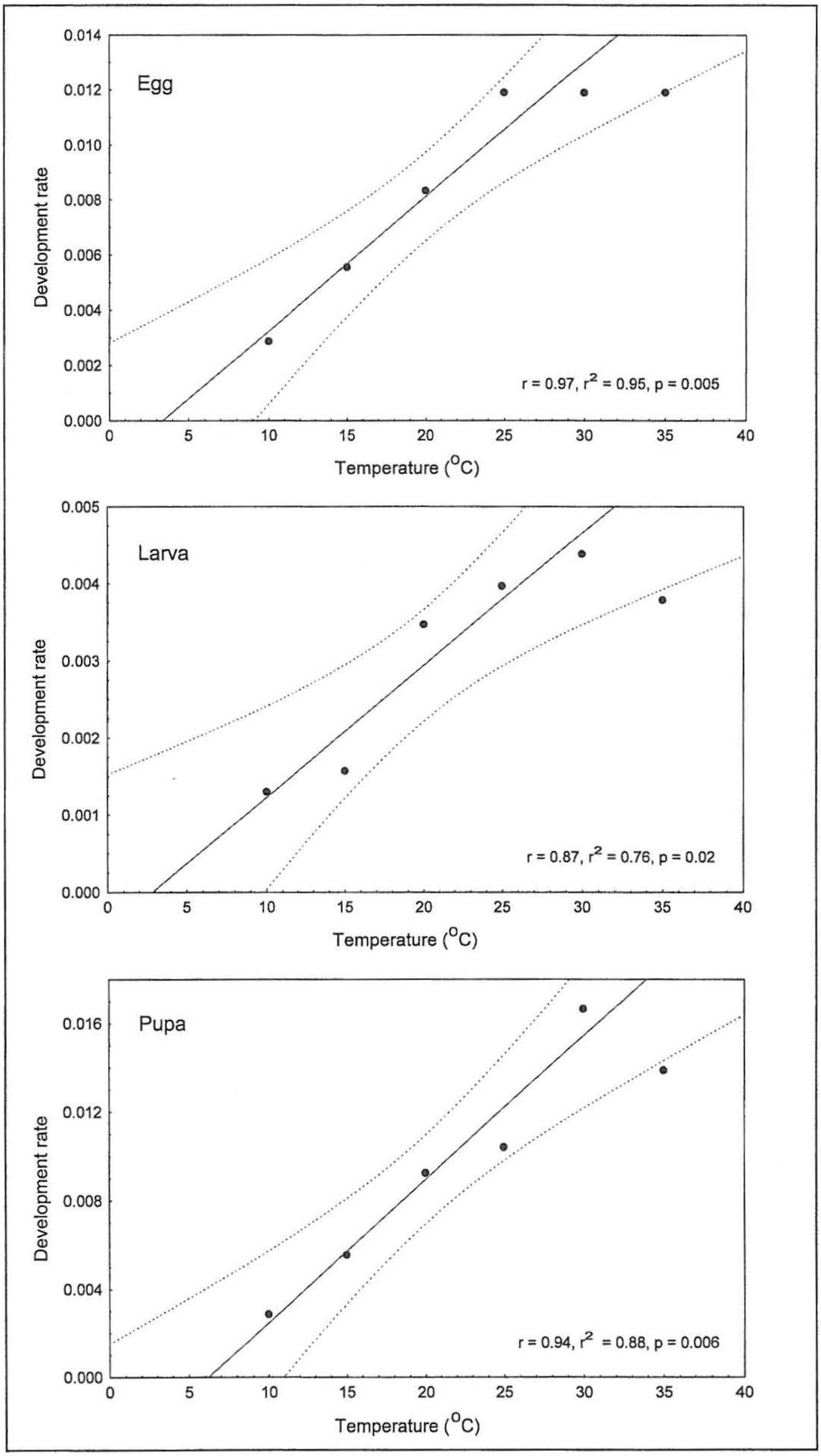

Figure 4.5. The development rate of the different stages of the diamondback moth at different temperatures using least square regression with 95% confidence intervals (Method 1).

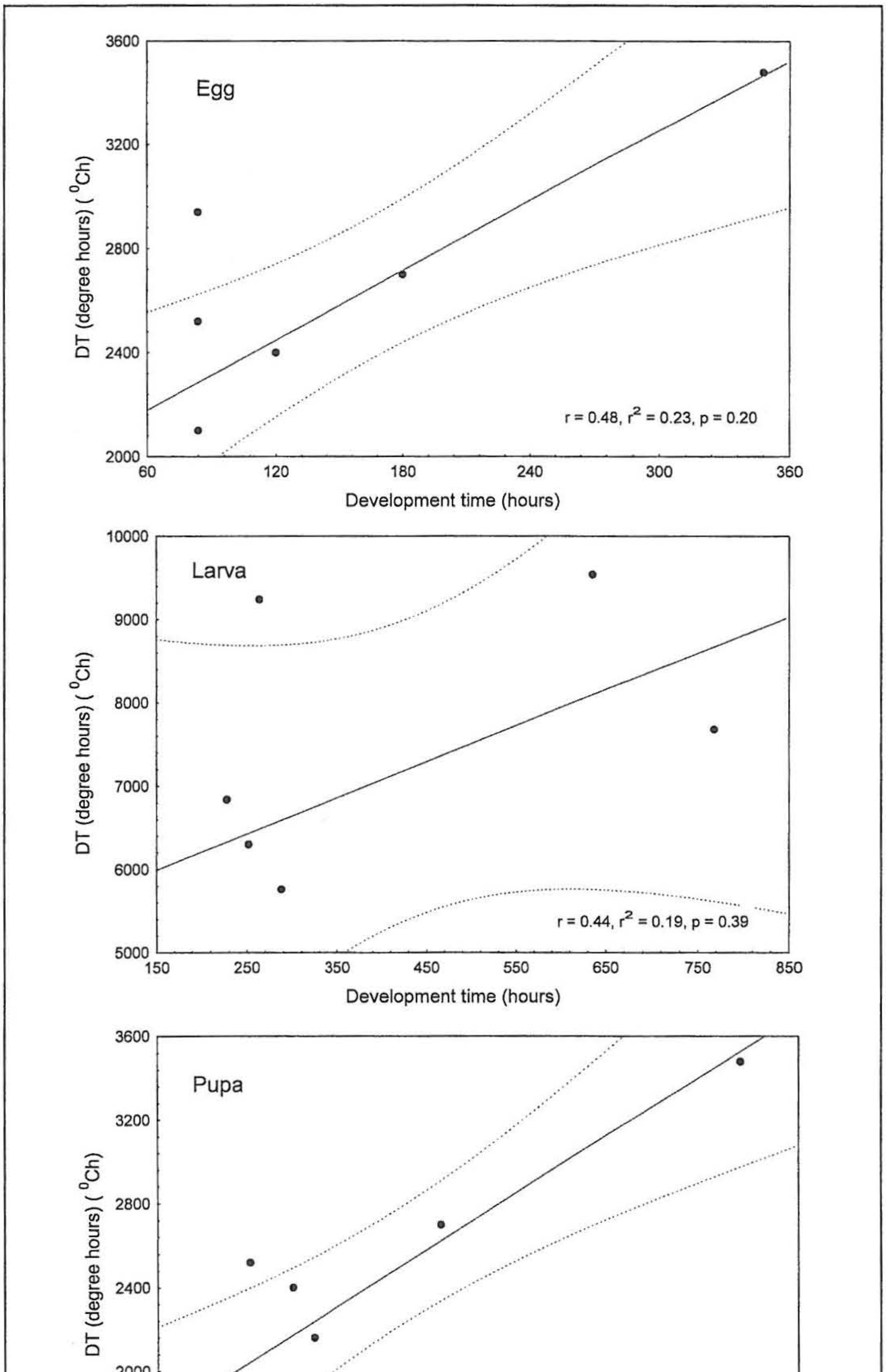

Figure 4.6. Development time of the different stages of the diamondback moth using reduced major axis regression with 95% confidence intervals (Method 2) (Ikemoto & Takai, 2000).

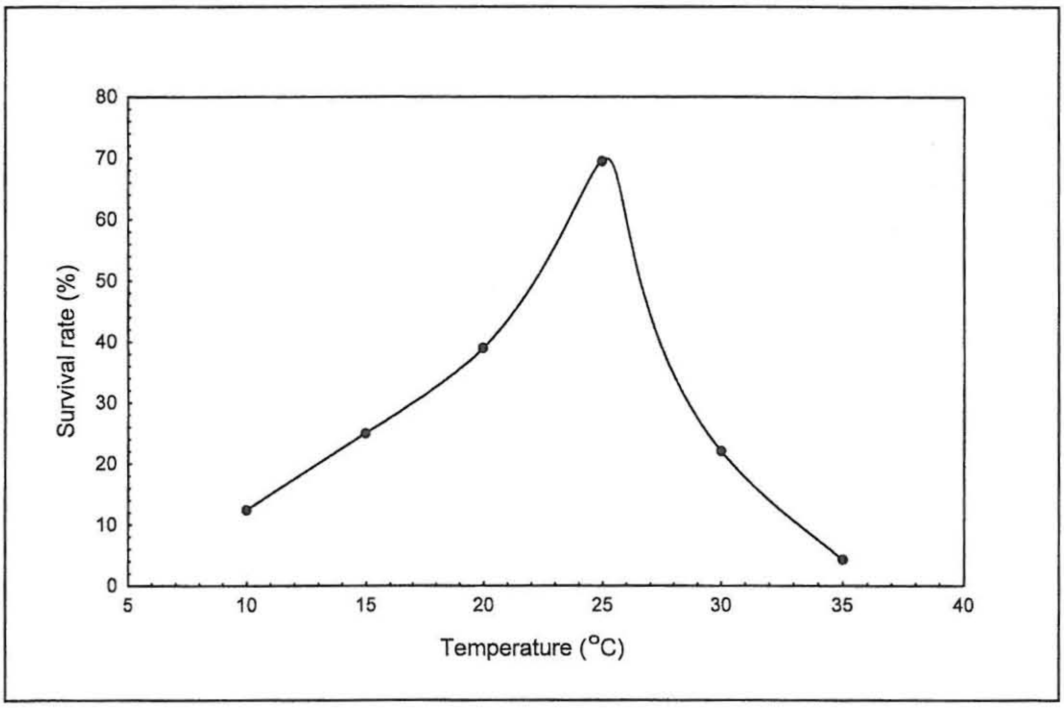

Figure 4.7. Survival rate of the diamondback moth at different temperatures.

Chapter 5:

Population dynamics of the diamondback moth with reference to abiotic factors

5.1. Introduction

In some countries, for example England, the diamondback moth does not cause a large amount of damage but in those countries where economic losses are great, outbreaks occur mainly during the hotter, drier periods of the year. In Thailand and the Cameron Highlands of Malaysia the numbers of diamondback moth are highest and the most damage is done during the drier season from November to May (Ooi, 1986; Rushtapakornchai & Vattanatangum, 1986). The diamondback moth is not always present all year round. In the northern regions of Japan it is only present from spring to autumn but in the central and southern regions it is present all year (Koshihara, 1986). In the northwestern Himalayas diamondback moth are found throughout the year even though temperatures can be very low in winter. The population increases gradually as temperatures get warmer and the highest numbers were found when daily minimum temperatures ranged between 5 and 12°C and a daily maximum of 21 to 36°C (Bhalla & Dubey, 1986).

Insect population densities vary over time and variation can be due to one of two things, either population cycles or population eruptions. Population cycles are periodic and fairly predictable while population eruptions result in outbreaks and can occur suddenly and unexpectedly (Speight *et al.*, 1999). Population cycling is regulated by density-dependant factors that are biotic, such as competition and predation. Population eruptions occur as a result of changes in density-independent factors which are usually environmental (Speight *et al.*, 1999). There is much debate over whether density-dependent or density-independent factors are more important. Density-independent factors cannot regulate populations by themselves, but they can cause large fluctuations in abundances and they can interact with density-dependant factors (Speight *et al.*, 1999).

The diamondback moth does not show diapause at any stage during the lifecycle but population numbers fluctuate throughout the year (Atwal, 1955). These changes are the result of a number of mortality factors and many studies have attempted to determine which of these factors are the most important. Ullyett (1947b) divided these mortality factors into three groups. The first group included environmental conditions, for example temperature, humidity and rainfall, and parasitoids, both of which result in normal seasonal fluctuations of the population. The second group included the residual mortality factors, for example predators, which are difficult to determine in the field as they do not leave much evidence. The third group included catastrophic mortality factors which results in a very high mortality, reducing the population significantly in a very short space of time, for example diseases from fugus, bacteria or viruses, very sudden changes in the physical environment and control through insecticides.

The four abiotic density-independent factors considered in this chapter were humidity, rainfall, wind speed and temperature. Parasitism, a density-dependent biotic factor is considered in the following chapters (Chapters 6 - 8). Some of these environmental factors not only affect the diamondback moth directly but also indirectly through its food source (Atwal, 1955). It is often unclear whether humidity affects insects directly or only indirectly (Dent, 1997). Low humidity is stressful for most insects and results in high mortality rates (Byrne *et al.*, 2002). Wind can influence insects in a number of ways. It is important in assisting migration and dispersal and in distributing chemical signals (Speight *et al.*, 1999). However, if the wind is too strong it can also prevent insects from flying.

Rainfall can affect insect populations both directly and indirectly (Speight *et al.*, 1999). It is an important mortality factor of the diamondback moth larval stages, through wash-off and fungal diseases. Harcourt (1961, 1986) found that rainfall affected the larvae by washing them off the leaves or by drowning them in rain droplets. The younger larvae are dislodged more easily and in Ontario more than half of them die from drowning. Thundershowers can reduce numbers of larvae by 74% while drizzle can reduce them by 20% (Beirne, 1971). In India rainfall was one of the major mortality factors of the first and second instars (Chelliah & Srinivasan, 1986). In Malaysia and the Philippines, when there was a combination of rainfall and high temperatures, fungal disease was an important mortality factor in the larval stages (Ooi, 1986; Poelking, 1992). Adult moth flight is also prevented during wet conditions, which results in a reduction in egg laying (Harcourt, 1986; Talekar *et al.*, 1986).

Temperature seems to be one of the most important environmental factors affecting the fluctuations of diamondback moth populations. In Japan, at temperatures below 30°C, high rates of egg laying, hatching, pupation and emergence were observed, whereas at temperatures above this, these activities were low (Koshihara, 1986). Harcourt (1986) showed that populations were regulated mainly by factors that affected adult moths. Favourable conditions for moth flight and oviposition are high temperatures and low wind velocity while unfavourable conditions include low temperatures, high wind and rainfall which prevent the females from flying and therefore ovipositing. He concluded that the most important factors affecting the diamondback moth population were environmental conditions; fecundity, which is related to photoperiod and the quality of the food plant; and lastly parasitoids. The environmental conditions and fecundity are density-independent, causing fluctuations and outbreaks, while parasitoids are density-dependent and tend to stabilize the population. It has been shown that more eggs are laid at longer photoperiods and that the average fecundity of the diamondback moth population declines during the season. It has therefore been suggested that fecundity is related to photoperiod (Harcourt & Cass, 1966) and is probably due to reduced quality of the food plant as the photoperiod shortens. Harcourt and Cass (1966) and Atwal (1955) compared the relationship of photoperiod and fecundity to the relationship between photoperiod and diapause in other insects. Atwal (1955) suggested that as well as affecting fecundity, photoperiod also influences the rate of diamondback moth development.

Dent (1997) suggested that the effect of biotic factors on mortality should be measured in the field to prevent difficulties associated with translating laboratory experiments to field conditions. In this chapter the population dynamics of the diamondback moth under field conditions were examined with particular reference to density-independent factors including temperature, humidity, rainfall and wind speed.

5.2. Materials and methods

Each site was sampled at weekly intervals from April 1997 to November 1999. The sampling period varied at the different sites (Fig. 5.1): at Site 1 sampling spanned 33 months; at Site 2, 31 months; and at Site 3, 27 months. On each sampling date 30 random cabbage plants were sampled at each site. The numbers of diamondback moth larvae at each instar and pupae were recorded and collected. Instar stage was determined by eye to provided an index of population size and any sampling bias would have been consistent. Climate data for the sampling period, including temperature, rainfall, wind speed and humidity were obtained from the National Weather Bureau in Pretoria, South Africa. Additional rainfall records were obtained from the Rhodes University Weather Station (33°19'S 26°32'E) and Brentwood Farm (Site 2).

The percentage infestation, mean number of larvae per cabbage and relative abundances of each instar and of pupae were determined. Relative abundances were determined annually, from season to season (April of one year to March of the next year) by dividing by the largest sample value in each cycle so the maximum value in any cycle was 1. The peaks of diamondback moth abundance differed from cycle to cycle, so the relative abundances were calculated annually as this made it easier to compare the cycles.

Pearson correlation coefficients were found between the relative abundances of various stages in the diamondback moth lifecycle using STATISTICA v.5 (StatsSoft, 2001). Pearson partial correlations were calculated between relative abundances of each of the immature stages with temperature, rainfall, wind speed and humidity. The correlations were calculated using different time lags to determine which lag period had the strongest relationship with the population. The six weeks prior to the sampling date were considered, with each week being correlated separately. Pearson correlations were done between photoperiod and lunar cycles and relative total abundance of diamondback moth. In the analysis of results, 1st instar larvae were ignored because of the possibility that not all larvae were counted during sampling due to their small size and mining habit at this stage. Mosiane (2001) found a higher number of 1st and 2nd instar larvae using a Berlese funnel compared with visual counting.

5.3. Results

5.3.1. Infestation levels

The percentage of cabbage plants infested by the diamondback moth followed a similar pattern at site 2 and 3 (Fig. 5.1) where highest infestation occurred during the spring months (September to November). Infestation levels were low until the beginning of August 1997. From August until the end of October 1997 infestation was high, reaching 100% at all sites. These levels decreased over November and December 1997. At the sprayed site (Site 1) infestation levels remained high during 1998, generally above 50%. In 1999 infestation levels were slightly lower, but by September they reached 100%. Fluctuations were found at Site 1 throughout the sampling period.

At the two unsprayed sites (Sites 2 and 3) infestation levels remained below 40% until the beginning of September 1998. From September to November 1998 the infestation level increased, dropping again from December 1998 until May 1999. At the end of July 1999 infestation levels at both sites increased, reaching 65% at Site 2 and 80% at Site 3. Infestation was high until the end of November, after which it decreased.

5.3.2. Larval density

The highest mean number of larvae/plant was found during spring (September to November) in each year at all three sites (Fig. 5.2). At the sprayed site (Site 1) the mean number of larvae/plant was less than 1 except from September to November 1997 where it peaked at 7 larvae/plant. In 1998 the mean numbers fluctuated between 1 and 6 larvae/plant, peaking at 10 larvae/plant in October. The mean number then dropped off and remained low at less than 2 larvae/plant until the end of July 1999 where it increased to between 3 and 4 larvae/plant until the end of sampling in October 1999.

At the unsprayed site, Site 2, the mean number of larvae/plant reached 12 during October 1997. In 1998 and 1999 the mean number remained below 1 larva/plant, increasing to between 1 and 2 larvae/plant in September 1998 and to between 2 and 3 larvae/plant in September 1999. At the second unsprayed site, Site 3, the mean number of larvae/plant remained low until October 1997 after which it increased to 4 larvae/plant. Numbers of larvae remained low in 1998 and 1999 until October of each year where they increased to 2 larvae/plant.

5.3.3. Seasonal variation of diamondback moth abundance

At the sprayed site, Site 1, the highest abundance of 2nd, 3rd and 4th larvae and pupae were found from early September to early October 1997 (Fig. 5.3). There was an additional peak in April 1997. The abundance of larvae and pupae peaked during May 1998 and at the end of October 1998. There is no corresponding autumn peak in April and May of 1999 as was found in 1997 and 1998. There were additional minor peaks during March 1998 and during July, August and September of 1999. The abundance of 3rd instars was generally low throughout the study period.

At the first unsprayed site, Site 2, the total abundance of larvae and pupae peaked during September and October 1997 (Fig. 5.4). The abundances remained low during the rest of the study period with two small peaks during September and October of 1998 and 1999. The abundance of the 3rd instar larvae was low throughout the study period except during September and October of 1997.

At Site 3, the second unsprayed site, total abundances peaked in September and October 1997 (Fig. 5.5). Similar peaks were found at the same time in 1998 and 1999, but the total abundances were much lower. There were additional small peaks in March 1998 and August 1998. There was no peak in the autumn months of 1999, but in August 1999 there was an additional peak. The 3rd instar has the lowest abundance of all the stages throughout the study period.

The diamondback larval and pupal abundances peaked at slightly different times at each of the sites (Fig. 5.6). At Site 1 they peaked simultaneously in late September 1997. In 1998 the peak occurred in October and the pupae peaked earlier than the larvae. At Site 2 the larvae and pupae peaked simultaneously in late September 1997. In 1998 and 1999 the peaks, although much smaller, occurred in October. At Site 3 the larvae peaked first in September 1997 followed by the pupae in late November. In 1998 and 1999 the larvae and pupae abundance peaked simultaneously in November and October respectively.

At both the sprayed (Site 1) and unsprayed sites (Sites 2 & 3), the relative abundances of the different larval stages (2nd, 3rd and 4th instar) showed a significant positive correlation between each other and with the total number of larvae. At all of the sites there were significant positive correlations between 2nd, 3rd and 4th instars, total larvae and pupae (Table 5.1). The pattern of absolute and relative magnitudes of the correlations is similar at each site.

5.3.4. Density-independent factors

5.3.4.1. Humidity

Humidity was higher over the summer months (December to February) and lower over the winter months (June to August). At all three sites the highest abundances of both larvae and pupae were found between 65% and 90% relative humidity (Fig. 5.7). Generally, humidity showed a negative correlation with the relative abundances of the immature stages of the lifecycle, but very few of the correlations were significant. Partial correlations (Table 5.2) showed more significant results at Site 3 than at the other sites. At Site 3 the lag periods suggest that it is the adults, the eggs and the early instars that are affected most by humidity.

5.3.4.2. Rainfall

Rainfall varied between the sites and between the years but higher rainfalls were generally found during March to May (autumn) and from August to December (spring and early summer). At Site 1 and 2 the highest abundances of the immature stages were found in periods of lower rainfall, but at Site 3 high abundances were also found during higher rainfall periods (Fig. 5.8). There were only two significant correlations between the relative abundances and rainfall, both at Site 3, one with 3rd instar larvae and the second with pupae (Table 5.3). There was no indication that any particular lag period had any relationship with regard to rainfall.

5.3.4.3. Wind speed

Wind speed was generally higher during the cooler months of the year (June to August) and lower during the warmer months (December to February). The highest abundances of the immature stage at each site were found between 12000 and 24000 m/hour of wind, but there was a slight variation between the sites (Fig. 5.9). Relative abundance of larvae and pupae showed a negative correlation with wind speed (Table 5.4). Significant correlations were found at all three sites. The lag periods suggest that at Site 1 and 2 the early instars were affected by wind and at Site 3 the adult and egg stage were most affected.

5.3.4.4. Temperature

Temperatures started to increase in spring (September to November) and the highest temperatures were found during late summer (February). The highest average temperature did not exceed 24°C, but the maximum temperature reached between 30°C and 35°C at times. Higher numbers of larvae were found at temperatures between 14°C and 20°C at all sites (Fig. 5.10). All the sites show that below 13°C and above 22°C, the number of larvae and pupae decreased (Fig. 5.11).

The relationship between temperature and the relative abundances of the immature diamondback moth is not monotonic (Fig. 5.11) so the r_p value must be interpreted carefully because the correlation analysis assumes that the relationship is monotonic. Significant negative correlations were found between temperature and the relative abundances of the different larval stages and pupae at all of the sites (Table 5.5). This implies that the trend is negative. However, there is a lower threshold (below 14 °C) below which the trend is positive ($r = 0.38$, 0.28 and 0.33 for larvae and $r = 0.24$, 0.28 and 0.54 for pupae at Site 1, 2 and 3 respectively). The lag analyses suggest that all the stages are affected by temperature.

5.3.5. Photoperiod and lunar cycles

A Pearson partial correlation was done with temperature to determine whether photoperiod influenced the relative abundance of diamondback moth larvae and pupae. Only one significant correlation was found, at Site 3, with relative abundance of pupae ($r_p = 0.21$, $p = 0.04$). There was no significant correlation between the lunar cycle and the abundance of diamondback moth stages at any of the sites.

5.4. Discussion

There is considerable variation in infestation levels, larval density and abundance of the diamondback moth over the study period. At the unsprayed sites it is important to separate the first year of the study from subsequent years. The first year is characteristic of what might happen if a switch to biological control occurs, while the subsequent years are characteristic of biological control.

5.4.1. Infestation levels

Infestation levels in the present study varied widely from no infestation at times to 100%

infestation over the spring months (September to November) (Fig. 5.1). Infestation levels in the Gauteng Province of South Africa showed similar results (Kfir, 1997b). In the temperate climate of the northwestern Himalayas, infestation levels ranged from 3% to 73% with the peak infestation being found in spring (mid-April). In India, infestation levels were similar to the Eastern Cape, ranging between 5 and 100% but peak infestation occurred from September to March (Bhalla & Dubey, 1986). The peak infestations in India were found over autumn and winter, probably because, being a tropical region, temperatures are favourable but rainfall is not as high over this period. This indicates that infestation levels in South Africa are fairly consistent with other countries.

At the sprayed site (Site 1), during the second and third year of the study, infestation levels were much higher and fluctuated over greater ranges than at the two unsprayed sites (Sites 2 & 3). This suggests that at the sprayed site where cypermethrin was being used for control of the diamondback moth, it was either resulting in resistance to the insecticide or the destruction of the parasitoids. In South Carolina, numbers of diamondback moth larvae were higher when pyrethroids were used because the chemicals reduced the number of natural enemies (Muckenfuss *et al.*, 1992).

At the two unsprayed sites (Sites 2 and 3) infestation levels reached 100% during the spring of the first year but in subsequent years infestation over the same period did not rise above 85%. This difference is due to the effects of parasitoids and will be discussed in Chapter 8.

5.4.2. Larval density

In the northwestern Himalayas the larval population varied from 3 to 415 larvae/100 plants (Bhalla & Dubey, 1986) and in the Cameron Highlands of Malaysia the larval density varied from 2 to 78 larvae/plant (Ooi, 1979 cited by Ooi, 1986). Ullyett (1947b) found that in the Pretoria region (Gauteng Province) of South Africa the diamondback moth numbers were highest in the early summer (November to January), reaching 11.6 larvae/plant, but, according to Ullyett, this did not result in serious economic damage. Dennill & Pretorius (1995) found only 0.4 larvae/plant in the same area, which they attributed to effective control by insecticides and parasitoids. However, Kfir

(1997b) found that diamondback moth larvae reached as many as 74 per plant during the spring period of 1994. Ullyett (1947b) found that the summer rains led to an epidemic of the fungus, *Zoophthora radicans* (Brefeld), which resulted in high mortality in the diamondback moth, leaving only 2-3 larvae per plant. The numbers remained low for a few months, increasing gradually and by the end of April started to fluctuate dramatically, reaching 26 larvae per plant by May and June. The rainfall and temperature ranges in the Eastern Cape are different to those found in the Pretoria region. Rainfall in the Eastern Cape occurs mainly in the autumn and spring to early summer when temperatures are not very high. It is therefore possible that conditions are not suitable for fungal epidemics and no rapid losses of number of diamondback moth occurred as a result. There has been no indication that fungal epidemics are a regular feature of diamondback moth losses in the Pretoria region.

In a recent study on canola, *Brassica napus* L., in the Gauteng Province diamondback moth numbers peaked at different times of the year at the two sites, the first site from May to August (autumn and winter) and the second site from September to December (spring). However, numbers at the first site remained below 0.3 larva/plant. At the second site they increased to 10 larvae/plant in 1997 (Mosiane, 2001). In the Eastern Cape region of South Africa the number of diamondback moth larvae were highest in spring (September to November) and the density of larvae remained below 12 larvae/plant for the entire study period at all three sites (Fig. 5.2). The same number of larvae/plant was found on the native Kerguelen cabbage on Marion Island over the late summer months (Crafford & Chown, 1990). In the Eastern Cape larval density is fairly consistent with other parts of South Africa but it is generally lower than in other countries, for example Malaysia and northwestern Himalayas.

Action thresholds are used to determine when applications of chemicals are required for diamondback moth control (Pedigo, 2002). Action thresholds were not calculated for this crop but Figure 5.2 shows the variation in action threshold taken from the literature. These action thresholds would not necessarily apply to the Eastern Cape as the threshold is influenced by a number of factors and needs to be determined for each crop. According to Ullyett's (1947b) threshold of 11.6

larvae/plant, the diamondback moth would not cause serious damage in the Eastern Cape and control measures are not needed very often. The thresholds used by Loke *et al.* (1992) of 4 larvae/plant, and Palis (1983) and Muckenfuss & Shepard (1994) of 1 larvae/plant, indicate that in the Eastern Cape, at the unsprayed sites, control measures only need to be applied in the late autumn and early spring. The action threshold suggested by Sastrosiswojo & Sastrohardjo (1986) and Mitchell *et al.* (2000) of 0.3 larvae/plant show control is needed in late autumn, spring and early summer at the unsprayed sites. However, the action threshold used by Beck and Cameron (1992) of 15% infestation (Fig. 5.1) indicated that the only time control measures were not required was during the late autumn and winter. Action thresholds seem to have become increasingly more conservative over time, probably due to their dependence on the market value and a worldwide increase in insecticide resistance.

5.4.3. Seasonal variation of diamondback moth abundance

Seasonal variation in the Eastern Cape was found in the abundances of both the diamondback moth larvae and pupae during this three-year study (Figs. 5.3 - 5.5). The diamondback moth was found all year round, although population numbers reached very low levels at certain times of the year. The main peaks in abundance of immature diamondback moth in the Eastern Cape study were during spring, with additional smaller peaks over the autumn months. A similar pattern was found in a number of other countries, for example Japan (Wakisaka *et al.*, 1992) and Malaysia (Ooi, 1986). At the sprayed site, Site 1, abundances fluctuated throughout the study period which suggests sudden reductions in abundances probably due to insecticide applications (Fig. 5.3). The abundances in 1999 were lower than in 1998, possibly because the insecticide was changed from cypermethrin (a pyrethroid) to mevinfos (an organophosphate). Abundances had remained high during 1998 even with the use of cypermethrin, and resistance to this chemical was determined (Chapter 3).

At the first unsprayed site, Site 2, very high abundances were found during spring of the first year of planting, after which the abundances were reduced drastically (Fig. 5.4). Crucifers had not been previously grown at this site and the lag in control is possibly due to the effective impact by parasitoids once they became established (Chapter 7 and 8). At the second unsprayed site, Site 3, there was a similar pattern, with higher abundances in the first year of planting compared to the following two years (Fig. 5.5). However, at this site, additional peaks were more obvious in the autumn months. A study conducted over two years in southeastern New Brunswick, Canada, showed that diamondback moth populations peaked in July and August (summer) and that in the first year of the study, the numbers of larvae and pupae were higher than in the second year (Maltais *et al.*, 1998). No explanation was given for this difference in numbers between the two years. In the Eastern Cape the sprayed and the unsprayed sites had very different numbers of cabbages present which might have affected the population of diamondback moth. However, the results show a continuous pattern of diamondback moth at all three sites suggesting that the populations are stable. Therefore the differences in the number of cabbages grown at each site is not important.

In some parts of the world, for example Canada and Japan, where the winters are too cold for their survival, the population relies on migrants moving back into the areas during the spring (Harcourt, 1986; Honda, 1992a, 1992b). Seasonal variation has been found in most countries. For example, in Central Mexico the diamondback moth occurs in significant numbers in spring, from April to September (McCully & Salas Araiza, 1992). In Australia the moth is present all year but in the hot dry summer months the population decreases (Goodwin, 1979). Generally, diamondback moth numbers increase in the drier periods of the year, for example in India, Malaysia, Indonesia and Jamaica (Bhalla & Dubey, 1986; Ooi, 1986; Iman *et al.*, 1986; Alam, 1992). In Thailand damage was highest during the dry seasons but Kuwahara *et al.* (1995) found that numbers could remain high throughout the rainy season as long as there was a food source available. Kmec & Weiss (1997) did a study over three years, investigating the population fluctuations of the diamondback moth on the host plant *Crambe abyssinica* (Hochst. ex R.E. Fries). They suggested that the differences in the populations over the three years was due to the weather. During the summer season (June to August) in the first two years it was cold and wet and moth numbers declined. In the third year the weather was warmer and drier and moth numbers increased.

The significant positive correlations between the different stages in the lifecycle of the diamondback moth at all three sites (Table 5.1) implies that each stage recruits from the previous stage for the continuation of the lifecycle, suggesting that there is little migration of moths. It also indicates that when sampling, the abundance of 4th instars may provide a suitable indication of the total larval abundances. This would make scouting for the diamondback moth within a crop more efficient. It also provides a cross-validation that smaller instars were being detected during the sampling process.

5.4.4. Density-independent factors

The major mortality factors influencing the diamondback moth include environmental conditions, for example temperature, humidity and rainfall; natural enemies, including parasitoids, predators and bacterial and fungal diseases; the type and quality of the food plant and the fecundity of the female moth (Ullyett, 1947b; Harcourt, 1986). Authors have found that different factors are important in different areas (Wakisaka *et al.*, 1992). Ullyett (1947b) stated that weather rarely has a direct effect on fluctuations but may affect them indirectly. He showed that mortality is dependant on the density of the diamondback moth population, which indicates that total mortality is probably dominated by biotic factors and may be regulated mainly by parasitoids. Harcourt (1986) decided that weather, which is density-independent, was the principle factor that causes population fluctuations and was the cause of outbreaks. However, Ullyett (1947b) also stated that each mortality factor plays an important part in population fluctuations and that it is impossible to try to evaluate each one separately as they all work together. The relative importance of the different mortality factors also change with time; some are persistent but vary in intensity and others are intermittent (Ullyett, 1947b).

There is no overall pattern to indicate how humidity affects abundance at the different sites, but the relationship is negative, suggesting that high humidity is unfavourable (Fig. 5.7, Table 5.2). There is an indication that it is the adults, eggs and early larval stages that are affected most by humidity. The influence of humidity on fluctuations of the diamondback moth population is not clear. Møller (1988) determined that hatching success was dependent on relative humidity as well as temperature. Wakisaka *et al.* (1992) found that at high humidity (100%) the mortality rate of the larvae was 70% but at humidities less than 90%, only 30% of the larvae died. The population numbers were, however, not affected by humidity (Koshihara, 1986). It has been shown that the microclimate around the leaf is at saturation point at all times, so any change in atmospheric humidity would not have any great effect on eggs, larvae or pupae in the field (Hardy, 1938; Ullyett, 1947b).

Rainfall was high enough to have an impact on diamondback moth larvae and its effect was noticed in the field. Figure 5.8 shows a clear relationship between larval and pupal abundances and rainfall. However, it did not have a statistically detectable effect on the diamondback moth stages in this study, even after taking other climatic factors into account (Table 5.4). The egg and first instar stages where not included in the correlations and it is these stages that are most susceptible to wash-off by rain (Hardy 1938; Harcourt, 1986). Even if only the eggs and first instars are affected, it should show up in later instars as an indirect effect. Rainfall is often suggested to be an important mortality factor, but Ullyett (1947b) decided that it was very unlikely to be a direct factor and that it probably resulted in mortality indirectly through fungal diseases. Other authors have reported a direct relationship (Harcourt, 1986; Sastrodihardjo, 1986; Poelking, 1992). Wakisaka *et al.* (1992) found that wash-off of eggs and larvae due to rain and the drowning of young larvae after rain were the major causes of mortality in their study in Japan. In a study carried out in South Carolina, neither simulated nor natural rainfall caused major larval mortality. This could have been because collards were used, which might provide more protection for larvae than other crucifers (Muckenfuss *et al.*, 1992).

Wind speed showed an effect at all of the sites (Table 5.4), and there is a suggestion from the lag periods that the adult stages were affected the most. Wind is thought to affect the flight of the adult moths and therefore oviposition. If the wind is too strong then the moths are unable to fly. Harcourt (1986) stated that high temperature and low wind velocity were the conditions most suitable for adult flight and oviposition, while low temperature, high wind velocity and rainfall grounded the female moths and therefore oviposition was drastically reduced.

Temperature shows the greatest climatic impact on the diamondback moth in the Eastern Cape. As temperatures started to increase, the abundance of the diamondback moth larvae and pupae increased (Fig. 5.10). Temperature was negatively correlated with the different diamondback moth stages in this study (Table 5.5), which suggests that as temperature increases the abundance of the diamondback moth larvae and pupae decreases. However, the relationship is not monotonic and below 14°C the relationship appears to be positive (Fig. 5.11). The mortality curve due to temperature (Fig. 4.7, Chapter 4) shows that survivorship in the moth is non-linear. The population of diamondback moth increases as the temperature starts to increase in spring at all three of the sites. Populations of diamondback moth are found to decline in the summer months (Koshihara, 1986, Wakisaka *et al.*, 1992). This is thought to be due to the increase in temperature, but temperatures in the field do not often reach levels high enough to cause these declines. This suggests that it could be the temperature at a microclimate level and not ambient temperature that is important (Mohandass & Zaluki, 2001). On Marion Island, in the summer, temperatures amongst the leaves of the Kerguelen cabbages were up to 10°C higher than ambient temperature (Crafford & Chown, 1990). Wakisaka *et al.* (1992) suggests that in mid-summer the ground surface temperature is higher than the average temperature and that this affects the diamondback moth population. Food availability is also an important factor, in some countries, for example Taiwan and Japan, crucifers are not grown in the hotter summer months (Chen & Su, 1986; Koshihara, 1986; Wakisaka *et al.*, 1992).

5.4.5. Photoperiod and lunar cycles

The abundance of the diamondback moth larvae and pupae increases in relation to the increase of photoperiod over spring and summer, but no significant correlation was found with photoperiod and this relationship is probably due to an increase in temperature and not photoperiod. In other studies photoperiod has been found to have an influence on the diamondback moth. Atwal (1955) found that development was reduced when photoperiod was short and this, together with low temperatures, resulted in very slow development of the diamondback moth. He also suggested that photoperiod has an indirect effect on larval development through food quality. Harcourt & Cass

(1966) showed that fecundity was related to photoperiod, through changes in the quality of the food plant. Møller (1988) showed that pupation, emergence and copulation all depended on photoperiod and Talekar *et al.* (1994) showed that photoperiod may play a part in oviposition but it is not the only factor. These events in the lifecycle are probably influenced by photoperiod because they are all related to the behaviour of the adult moth.

It was thought that lunar cycle might have an influence on the abundance of diamondback moth as the adults are active at night, copulating and ovipositing at dusk. However, field counts of larvae and pupae did not show a relationship with the lunar cycle in the Eastern Cape study. There is a possibility that a correlation may be found if sampling is done using pheromone traps. However, Mosiane (2001) found no such correlation in the Pretoria region when pheromone traps were used. No pheromone trapping was done in the Grahamstown area.

5.5. Conclusion

Information on the seasonal fluctuations within populations are important for the successful control of the diamondback moth, especially for the timing of insecticide applications (Butts & McEwen, 1981; Kuwahara *et al.*, 1995). In the Eastern Cape the abundance of the diamondback moth was highest over the spring months and although the moth was present all year the abundances were low over the winter months. Seasonal population studies are also important in determining the economic threshold for effective pest management strategies (Kmec & Weiss, 1997), unfortunately a threshold was not determined for this study. There was variation in infestation levels and abundance of the diamondback moth between the sites and between the years. Although density-independent factors, like temperature, humidity and wind speed play a role in density fluctuations within the population, these factors were difficult to evaluate for their importance in the population fluctuations. Temperature was important and showed a negative correlation, but rainfall appeared to be unimportant. The effect of humidity was ambiguous and the effect of wind speed, although present, was also difficult to interpret.

Table 5.1. Pearson correlation coefficients between larval and pupal diamondback moth relative abundance. Significant correlations ($p < 0.05$) are shown in bold.

Site		2nd instar	3rd instar	4th instar	Total larvae
1	2nd instar	-			
	3rd instar	**0.84**	-		
	4th instar	**0.71**	**0.77**	-	
	Total larvae	**0.87**	**0.84**	**0.93**	-
	Pupae	**0.54**	**0.56**	**0.74**	**0.67**
2	2nd instar	-			
	3rd instar	**0.81**	-		
	4th instar	**0.79**	**0.89**	-	
	Total larvae	**0.92**	**0.92**	**0.95**	-
	Pupae	**0.58**	**0.63**	**0.73**	**0.68**
3	2nd instar	-			
	3rd instar	**0.75**	-		
	4th instar	**0.78**	**0.89**	-	
	Total larvae	**0.89**	**0.92**	**0.93**	-
	Pupae	**0.57**	**0.58**	**0.65**	**0.6**

Table 5.2. Pearson partial correlation coefficients between humidity and relative abundances of diamondback moth immature stages at the three sites over six lag periods (w_1 to w_6) of 7 days each. Significant partial correlations are shown in bold ($p < 0.05$).

Stage	Week	Site 1	Site 2	Site 3
2nd instar	w_1	**- 0.24 (p = 0.01)**	- 0.14 (p = 0.13)	**- 0.28 (p = 0.01)**
	w_2	- 0.17 (p = 0.07)	- 0.08 (p = 0.37)	**- 0.30 (p =0.003)**
	w_3	- 0.54 (p = 0.58)	- 0.04 (p = 0.65)	**- 0.22 (p = 0.03)**
	w_4	0.01 (p = 0.94)	- 0.08 (p = 0.36)	**- 0.25 (p = 0.01)**
	w_5	- 0.05 (p = 0.63)	- 0.11 (p = 0.22)	- 0.16 (p = 0.13)
	w_6	0.05 (p = 0.64)	- 0.04 (p = 0.70)	- 0.11 (p = 0.28)
3rd instar	w_1	- 0.15 (p = 0.13)	- 0.13 (p = 0.15)	- 0.16 (p = 0.13)
	w_2	**- 0.20 (p = 0.04)**	- 0.09 (p = 0.33)	**- 0.25 (p = 0.02)**
	w_3	- 0.12 (p = 0.27)	0.01 (p = 0.95)	- 0.01 (p = 0.92)
	w_4	- 0.06 (p = 0.57)	0.01 (p = 0.92)	- 0.05 (p = 0.66)
	w_5	- 0.10 (p = 0.34)	- 0.07 (p = 0.45)	0.01 (p = 0.92)
	w_6	0.03 (p = 0.80)	- 0.03 (p = 0.77)	0.01 (p = 0.93)
4th instar	w_1	- 0.05 (p = 0.62)	- 0.16 (p = 0.09)	- 0.16 (p = 0.12)
	w_2	- 0.15 (p = 0.13)	- 0.15 (p = 0.12)	- 0.20 (p = 0.05)
	w_3	- 0.05 (p = 0.62)	- 0.08 (p = 0.40)	- 0.13 (p = 0.20)
	w_4	0.03 (p = 0.78)	0.07 (p = 0.47)	- 0.13 (p = 0.21)
	w_5	- 0.07 (p = 0.46)	- 0.16 (p = 0.09)	- 0.09 (p = 0.41)
	w_6	- 0.01 (p = 0.94)	- 0.11 (p = 0.22)	- 0.13 (p = 0.22)
Total larval	w_1	- 0.12 (p = 0.20)	- 0.15 (p = 0.09)	**- 0.21 (p = 0.05)**
	w_2	- 0.15 (p = 0.11)	- 0.14 (p = 0.12)	**- 0.26 (p = 0.01)**
	w_3	- 0.05 (p = 0.59)	- 0.07 (p = 0.44)	- 0.13 (p = 0.22)
	w_4	0.02 (p = 0.85)	- 0.08 (p = 0.37)	- 0.15 (p = 0.14)
	w_5	- 0.06 (p = 0.54)	- 0.15 (p = 0.10)	- 0.04 (p = 0.70)
	w_6	0.04 (p = 0.72)	- 0.08 (p = 0.36)	- 0.05 (p = 0.65)

Table 5.2 continued

Stage	**Week**	**Site 1**	**Site 2**	**Site 3**
Pupae	w_1	- 0.08 (p = 0.37)	**- 0.22 (p = 0.02)**	- 0.17 (p = 0.11)
	w_2	- 0.07 (p = 0.47)	- 0.14 (p = 0.14)	- 0.14 (p = 0.19)
	w_3	- 0.12 (p = 0.21)	- 0.11 (p = 0.22)	- 0.17 (p = 0.10)
	w_4	0.03 (p = 0.68)	- 0.08 (p = 0.40)	- 0.13 (p = 0.20)
	w_5	- 0.09 (p = 0.33)	0.001 (p = 1.0)	- 0.10 (p = 0.36)
	w_6	0.01 (p = 0.92)	- 0.02 (p = 0.83)	- 0.18 (p = 0.08)

Table 5.3. Pearson partial correlation coefficients between rainfall and relative abundances of diamondback moth immature stages at the three sites over six lag periods (w_1 to w_6) of 7 days each. Significant partial correlations are shown in bold ($p < 0.05$).

Stage	**Week**	**Site 1**	**Site 2**	**Site 3**
2nd instar	w_1	- 0.01 (p = 0.90)	- 0.01 (p = 0.96)	0.10 (p = 0.33)
	w_2	- 0.04 (p = 0.67)	- 0.09 (p = 0.31)	- 0.06 (p = 0.58)
	w_3	0.06 (p = 0.56)	- 0.03 (p = 0.72)	- 0.02 (p = 0.82)
	w_4	- 0.05 (p = 0.58)	- 0.03 (p = 0.78)	- 0.03 (p = 0.74)
	w_5	0.001 (p = 1.0)	- 0.01 (p = 0.88)	- 0.04 (p = 0.67)
	w_6	- 0.08 (p = 0.40)	- 0.08 (p = 0.38)	0.15 (p = 0.16)
3rd instar	w_1	0.06 (p = 0.57)	- 0.04 (p = 0.67)	0.17 (p = 0.09)
	w_2	0.05 (p = 0.63)	- 0.15 (p = 0.10)	- 0.04 (p = 0.69)
	w_3	- 0.001 (p = 0.10)	- 0.06 (p = 0.49)	**- 0.21 (p = 0.04)**
	w_4	- 0.04 (p = 0.09)	- 0.05 (p = 0.62)	- 0.08 (p = 0.42)
	w_5	0.15 (p = 0.13)	0.03 (p = 0.78)	- 0.13 (p = 0.22)
	w_6	- 0.04 (p = 0.66)	- 0.09 (p = 0.33)	0.09 (p = 0.37)
4th instar	w_1	- 0.07 (p = 0.45)	- 0.02 (p = 0.82)	0.12 (p = 0.25)
	w_2	0.03 (p = 0.78)	- 0.09 (p = 0.33)	- 0.01 (p = 0.90)
	w_3	0.08 (p = 0.40)	- 0.05 (p = 0.59)	- 0.09 (p = 0.39)
	w_4	- 0.01 (p = 0.90)	- 0.03 (p = 0.77)	- 0.08 (p = 0.46)
	w_5	0.12 (p = 0.22)	0.01 (p = 0.89)	- 0.02 (p = 0.86)
	w_6	- 0.03 (p = 0.78)	- 0.03 (p = 0.73)	0.06 (p = 0.54)
Total larval	w_1	- 0.06 (p = 0.56)	- 0.007 (p =0.93)	0.12 (p = 0.30)
	w_2	- 0.002 (p = 1.0)	- 0.10 (p = 0.30)	- 0.05 (p = 0.66)
	w_3	0.04 (p = 0.67)	- 0.03 (p = 0.71)	- 0.12 (p = 0.27)
	w_4	- 0.05 (p = 0.57)	- 0.03 (p = 0.76)	- 0.06 (p = 0.55)
	w_5	0.11 (p = 0.26)	0.001 (p = 1.0)	- 0.08 (p = 0.41)
	w_6	- 0.07 (p = 0.50)	- 0.06 (p = 0.52)	0.07 (p = 0.49)

Table 5.3 continued

Stage	**Week**	**Site 1**	**Site 2**	**Site 3**
Pupal	w_1	- 0.03 (p = 0.73)	0.03 (p = 0.71)	**0.23 (p = 0.03)**
	w_2	- 0.10 (p = 0.30)	- 0.13 (p = 0.14)	- 0.05 (p = 0.63)
	w_3	0.06 (p = 0.50)	- 0.05 (p = 0.58)	0.02 (p = 0.85)
	w_4	- 0.10 (p = 0.31)	- 0.06 (p = 0.50)	- 0.12 (p = 0.27)
	w_5	- 0.04 (p = 0.63)	- 0.06 (p = 0.51)	- 0.05 (p = 0.66)
	w_6	- 0.07 (p = 0.48)	- 0.03 (p = 0.72)	- 0.03 (p = 0.77)

Table 5.4. Pearson partial correlation coefficients between wind speed and relative abundances of diamondback moth immature stages at the three sites over six lagged periods (w_1 to w_6) of 7 days each. Significant partial correlations are shown in bold ($p < 0.05$).

Stage	**Week**	**Site 1**	**Site 2**	**Site 3**
2nd instar	w_1	**- 0.28 (p = 0.003)**	**- 0.28 (p = 0.002)**	**- 0.20 (p = 0.05)**
	w_2	- 0.12 (p = 0.23)	**- 0.20 (p = 0.03)**	**- 0.32 (p = 0.002)**
	w_3	- 0.09 (p = 0.35)	- 0.13 (p = 0.17)	**- 0.32 (p = 0.002)**
	w_4	- 0.01 (p = 0.92)	- 0.16 (p = 0.07)	**- 0.25 (p = 0.02)**
	w_5	- 0.05 (p = 0.61)	- 0.17 (p = 0.07)	- 0.13 (p = 0.20)
	w_6	0.003 (p = 0.97)	- 0.12 (p = 0.17)	- 0.08 (p = 0.47)
3rd instar	w_1	**- 0.25 (p = 0.01)**	**- 0.27 (p = 0.003)**	- 0.15 (p = 0.16)
	w_2	- 0.13 (p = 0.19)	- 0.15 (p = 0.09)	**- 0.29 (p = 0.01)**
	w_3	- 0.13 (p = 0.18)	- 0.05 (p = 0.58)	**- 0.24 (p = 0.02)**
	w_4	- 0.03 (p = 0.77)	- 0.10 (p = 0.25)	**- 0.21 (p = 0.04)**
	w_5	- 0.01 (p = 0.90)	- 0.12 (p = 0.18)	- 0.10 (p = 0.35)
	w_6	0.09 (p = 0.38)	- 0.10 (p = 0.26)	- 0.08 (p = 0.45)
4th instar	w_1	- 0.13 (p = 0.17)	**- 0.27 (p = 0.002)**	- 0.18 (p = 0.09)
	w_2	- 0.17 (p = 0.08)	**- 0.23 (p = 0.01)**	**- 0.22 (p = 0.03)**
	w_3	- 0.09 (p = 0.38)	- 0.12 (p = 0.23)	**- 0.27 (p = 0.01)**
	w_4	- 0.03 (p = 0.77)	- 0.13 (p = 0.15)	**- 0.28 (p = 0.01)**
	w_5	- 0.07 (p = 0.49)	- 0.16 (p = 0.08)	- 0.02 (p = 0.86)
	w_6	0.06 (p = 0.54)	- 0.15 (p = 0.09)	0.06 (p = 0.54)
Total larval	w_1	**- 0.23 (p = 0.02)**	**- 0.28 (p = 0.002)**	- 0.18 (p = 0.09)
	w_2	- 0.16 (p = 0.09)	**- 0.22 (p = 0.01)**	**- 0.32 (p = 0.002)**
	w_3	- 0.11 (p = 0.26)	- 0.12 (p = 0.19)	**- 0.29 (p = 0.01)**
	w_4	- 0.02 (p = 0.82)	- 0.15 (p = 0.09)	**- 0.27 (p = 0.01)**
	w_5	- 0.04 (p = 0.67)	- 0.16 (p = 0.07)	- 0.11 (p = 0.26)
	w_6	0.07 (p = 0.45)	- 0.13 (p = 0.15)	- 0.09 (p = 0.35)

Table 5.4 continued

Stage	**Week**	**Site 1**	**Site 2**	**Site 3**
Pupal	w_1	- 0.05 (p = 0.58)	**- 0.29 (p = 0.001)**	- 0.20 (p = 0.06)
	w_2	- 0.08 (p = 0.40)	**- 0.34 (p = 0.0002)**	- 0.18 (p = 0.09)
	w_3	- 0.11 (p = 0.25)	**- 0.22 (p = 0.02)**	**- 0.30 (p = 0.004)**
	w_4	- 0.07 (p = 0.47)	**- 0.19 (p = 0.04)**	**- 0.29 (p = 0.004)**
	w_5	- 0.04 (p = 0.71)	- 0.15 (p = 0.10)	- 0.14 (p = 0.18)
	w_6	0.02 (p = 0.78)	**- 0.18 (p = 0.05)**	**- 0.26 (p = 0.01)**

Table 5.5. Pearson partial correlation coefficients between temperature and relative abundances of diamondback moth immature stages at the three sites over six lagged periods (w_1 to w_6) of 7 days each. Significant partial correlations are shown in bold ($p < 0.05$).

Stage	**Week**	**Site 1**	**Site 2**	**Site 3**
2nd instar	w_1	**- 0.33 (p = 0.001)**	**- 0.23 (p = 0.01)**	- 0.13 (p = 0.22)
	w_2	**- 0.25 (p = 0.01)**	**- 0.18 (p = 0.04)**	**0.03 (p = 0.01)**
	w_3	**- 0.27 (p = 0.01)**	**- 0.19 (p = 0.04)**	**- 0.38 (p = 0.0001)**
	w_4	**- 0.27 (p = 0.004)**	**- 0.29 (p = 0.01)**	**- 0.35 (p =0.001)**
	w_5	**- 0.30 (p = 0.002)**	**- 0.26 (p = 0.003)**	**- 0.28 (p = 0.01)**
	w_6	**- 0.31 (p = 0.001)**	**- 0.34 (p = 0.0001)**	**- 0.34 (p =0.001)**
3rd instar	w_1	**- 0.35 (p = 0.0002)**	**- 0.27 (p = 0.002)**	- 0.04 (p = 0.7)
	w_2	**- 0.24 (p = 0.01)**	**- 0.20 (p = 0.03)**	- 0.16 (p = 0.13)
	w_3	**- 0.26 (p = 0.01)**	**- 0.18 (p = 0.05)**	**- 0.33 (p = 0.001)**
	w_4	**- 0.24 (p = 0.01)**	**- 0.26 (p =0.003)**	**- 0.34 (p = 0.001)**
	w_5	**- 0.24 (p = 0.01)**	**- 0.29 (p = 0.001)**	**- 0.25 (p = 0.01)**
	w_6	**- 0.23 (p = 0.02)**	**- 0.30 (p = 0.001)**	**- 0.28 (p = 0.01)**
4th instar	w_1	**- 0.21 (p = 0.03)**	**- 0.26 (p = 0.004)**	- 0.14 (p = 0.17)
	w_2	**- 0.25 (p = 0.01)**	**- 0.26 (p = 0.003)**	- 0.16 (p = 0.11)
	w_3	**- 0.23 (p = 0.02)**	**- 0.23 (p = 0.01)**	**- 0.31 (p = 0.002)**
	w_4	**- 0.21 (p = 0.03)**	**- 0.27 (p =0.003)**	**- 0.39 (p = 0.0001)**
	w_5	**- 0.22 (p = 0.02)**	**- 0.28 (p = 0.002)**	**- 0.26 (p = 0.01)**
	w_6	- 0.15 (p = 0.13)	**- 0.34 (p = 0.0001)**	**- 0.31 (p = 0.002)**
Total larval	w_1	**- 0.31 (p = 0.001)**	**- 0.26 (p=0.003)**	- 0.09 (p = 0.38)
	w_2	**- 0.29 (p = 0.003)**	**- 0.24 (p = 0.01)**	**- 0.30 (p = 0.01)**
	w_3	**- 0.28 (p = 0.004)**	**- 0.23 (p = 0.01)**	**- 0.36 (p = 0.0004)**
	w_4	**- 0.26 (p = 0.01)**	**- 0.28 (p = 0.002)**	**- 0.38 (p = 0.0001)**
	w_5	**- 0.27 (p = 0.01)**	**- 0.28 (p = 0.002)**	**- 0.32 (p= 0.002)**
	w_6	**- 0.24 (p = 0.01)**	**- 0.35 (p = 0.0001)**	**- 0.33 (p = 0.001)**

Table 5.5 continued

Stage	**Week**	**Site 1**	**Site 2**	**Site 3**
Pupae	w_1	- 0.12 (p = 0.20)	- 0.14 (p = 0.11)	- 0.05 (p = 0.60)
	w_2	**- 0.19 (p = 0.04)**	**- 0.30 (p = 0.001)**	- 0.02 (p = 0.83)
	w_3	**- 0.23 (p = 0.01)**	**- 0.25 (p = 0.01)**	- 0.17 (p = 0.10)
	w_4	**- 0.26 (p = 0.004)**	**- 0.24 (p = 0.01)**	**- 0.27 (p = 0.01)**
	w_5	**- 0.19 (p = 0.04)**	**- 0.28 (p = 0.001)**	- 0.12 (p = 0.25)
	w_6	- 0.18 (p = 0.06)	**- 0.33 (p = 0.0002)**	**- 0.25 (p = 0.02)**

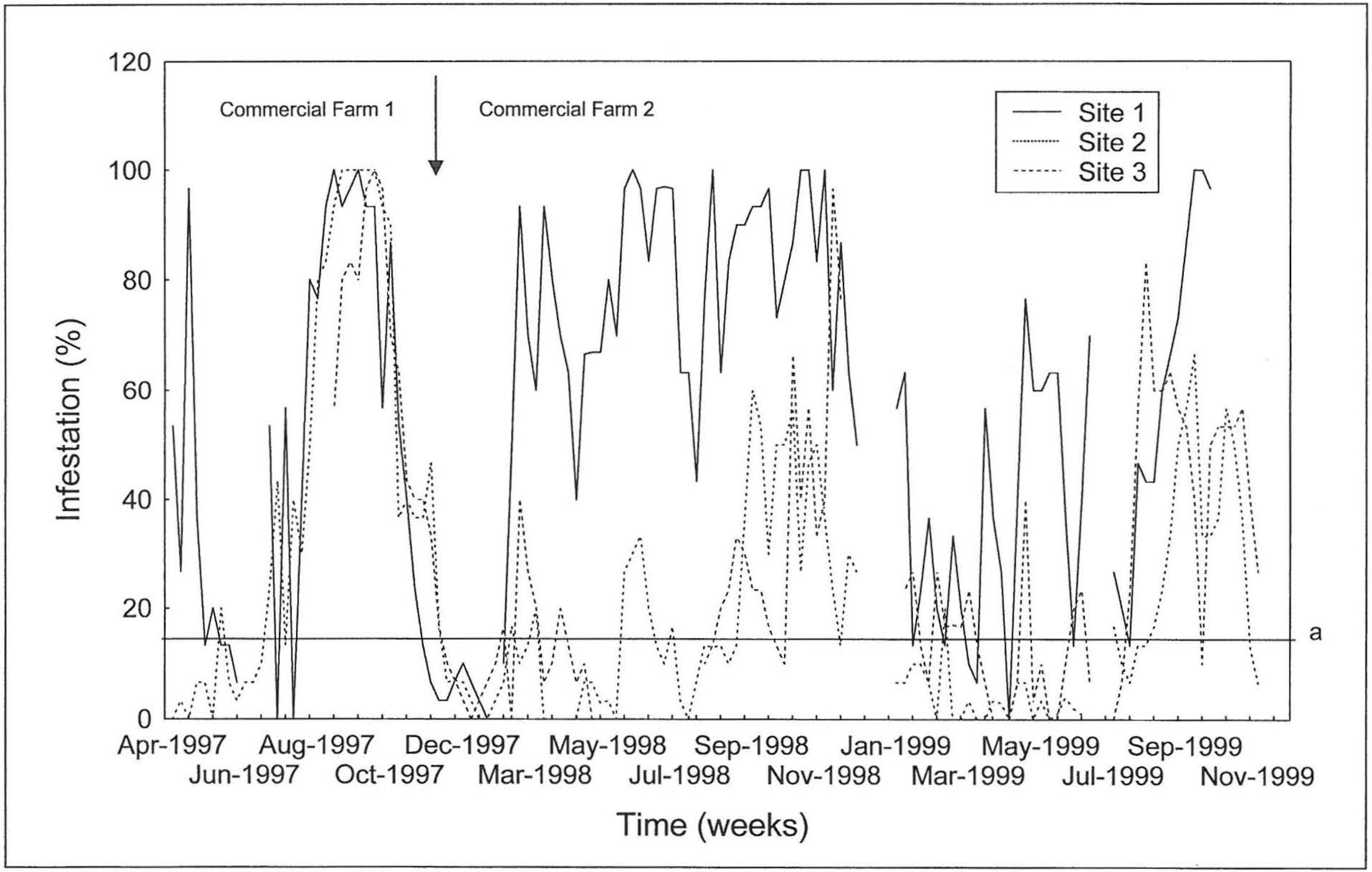

Figure 5.1. Infestation of the diamondback moth at the three sites over the study period. The line labelled 'a' shows the 15% action threshold suggested by Beck & Cameron (1992). The arrow shows when sampling at Site 1 was moved from the first commercial farm to the second farm.

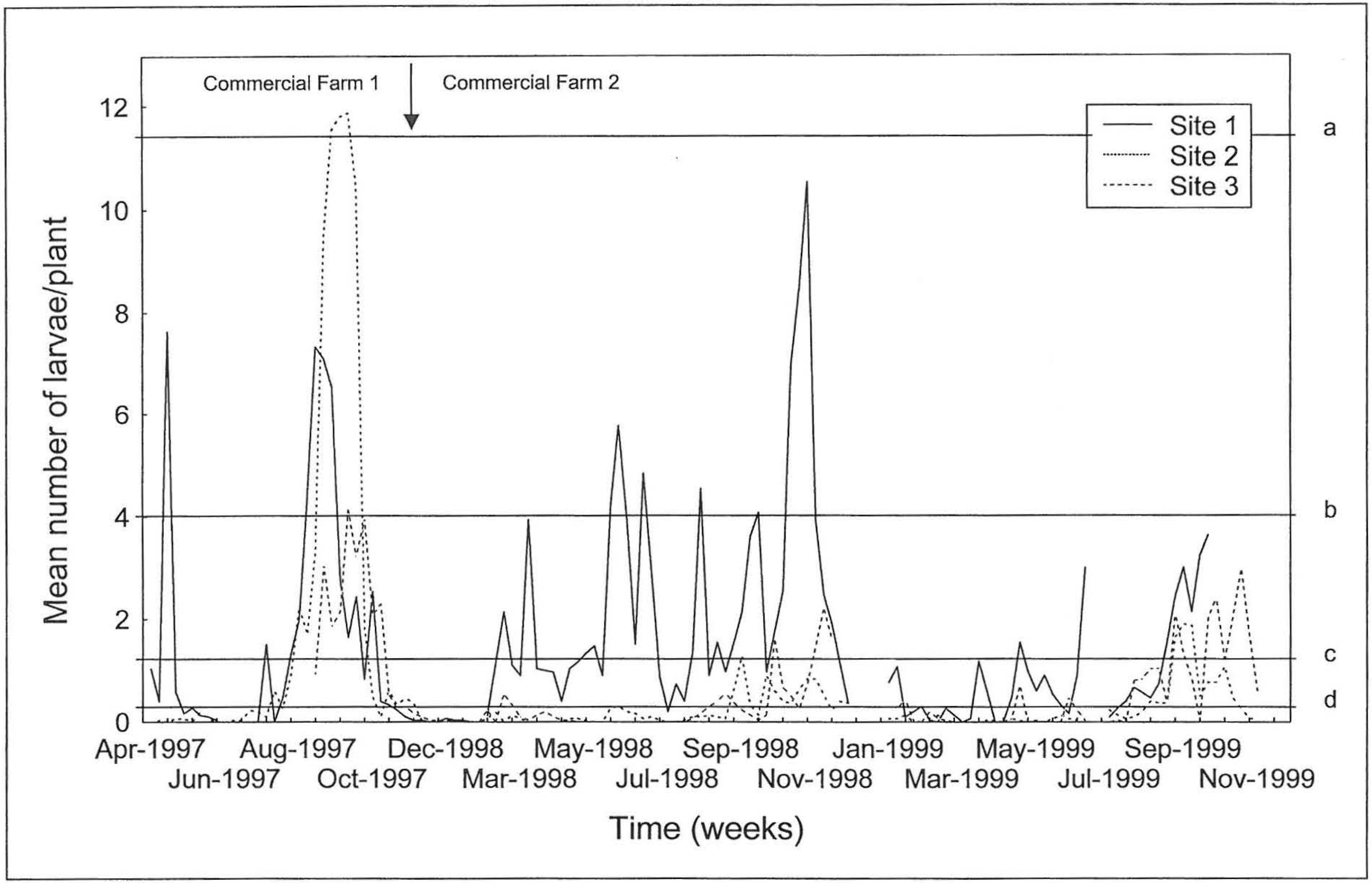

Figure 5.2. Mean number of larvae/plant at each site over the study period. a shows the economic threshold used by Ullyett (1947), b shows the economic threshold used by Loke *et al.* (1992), c shows the threshold used by Palis (1983) and Muckenfuss & Shepard (1994), d shows the action threshold used by Sastrosiswojo & Sastrodihardjo (1986) and Mitchell *et al.* (2000). The arrow shows when sampling at Site 1 moved from the first commercial farm to the second farm.

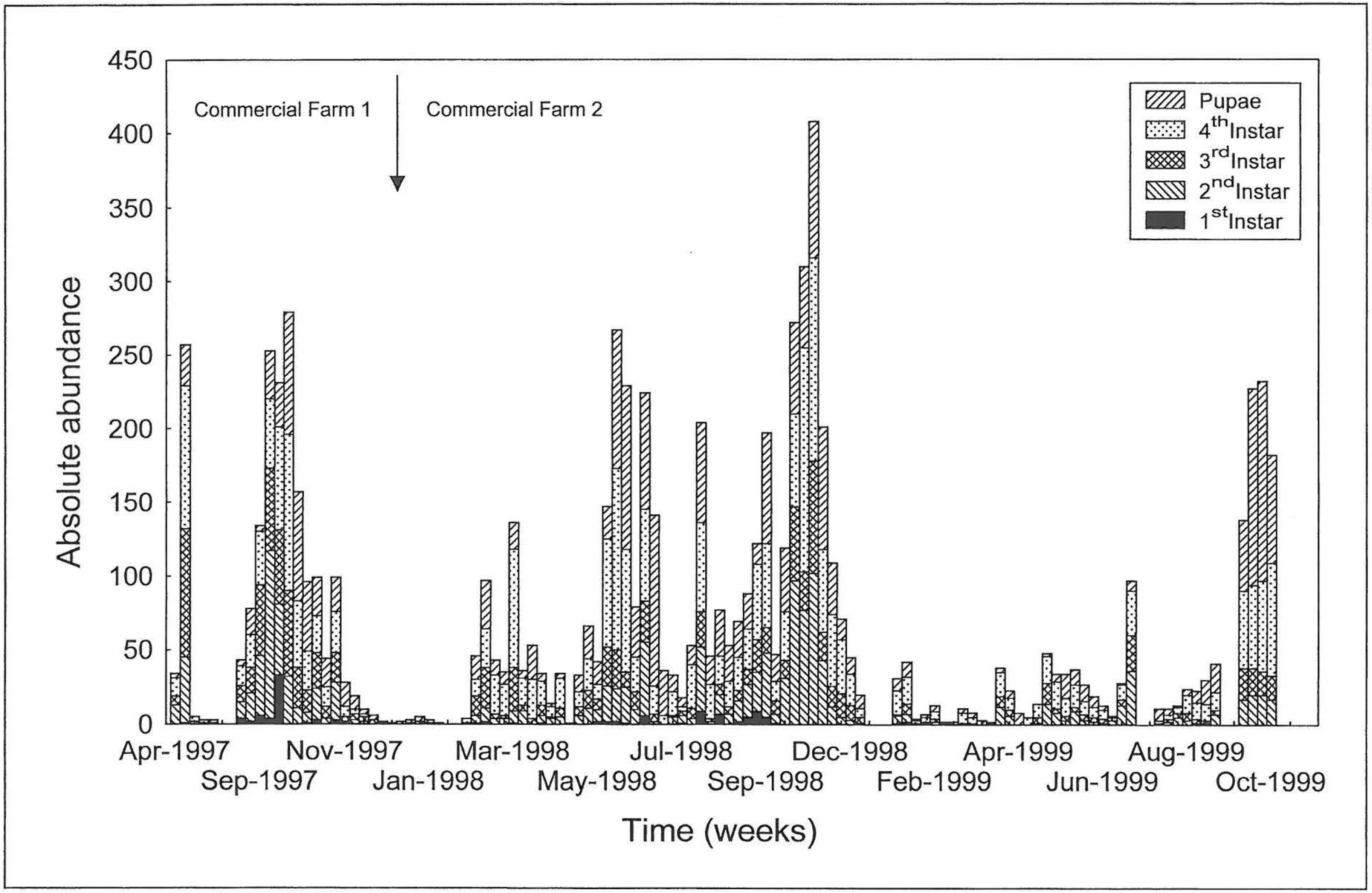

Figure 5.3. Absolute abundance of diamondback moth larvae and pupae at Site 1 from April 1997 to October 1999. The arrow shows when sampling moved from the first commercial farm to the second commercial farm.

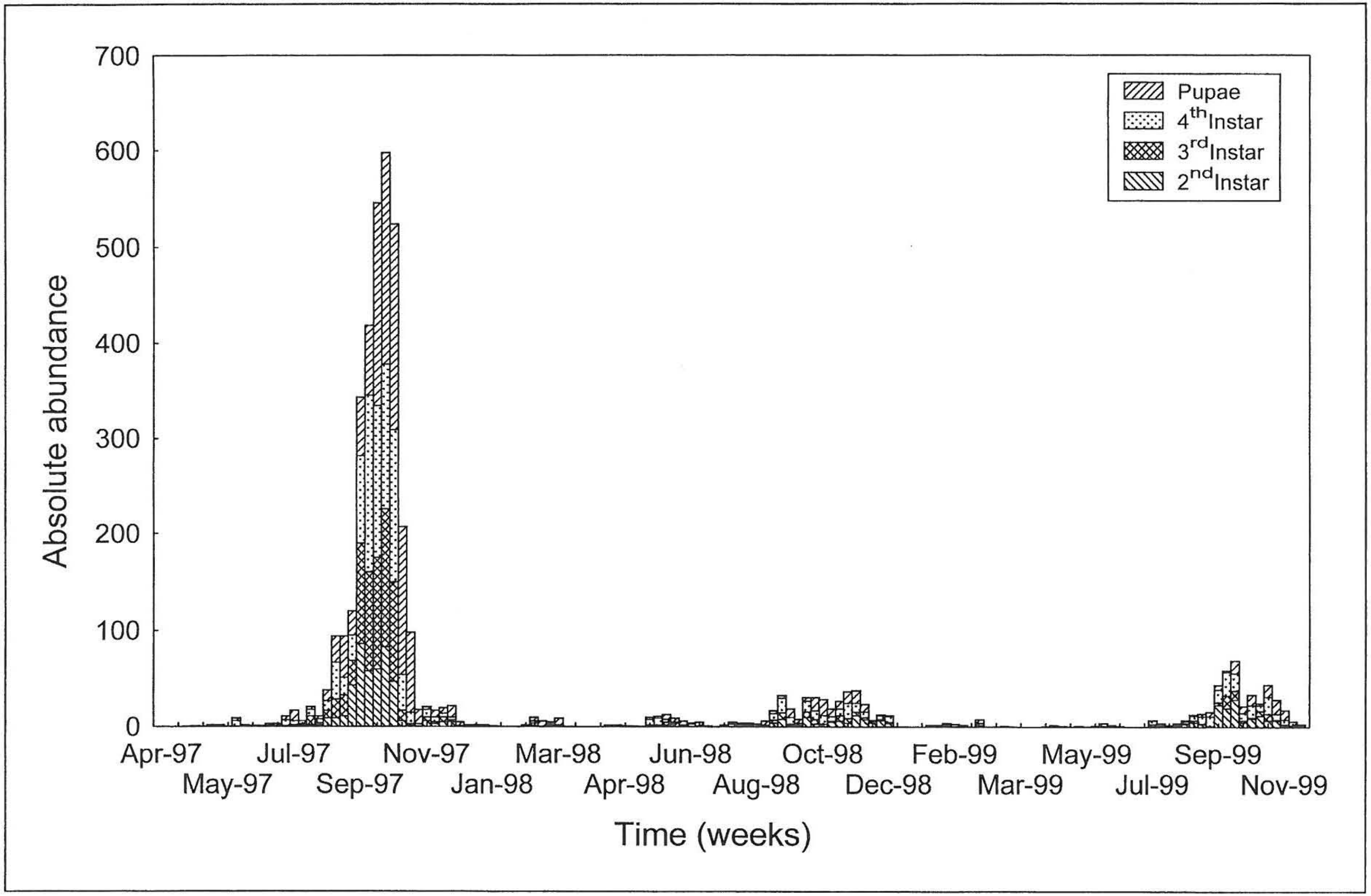

Figure 5.4. Absolute abundance of the diamondback moth larvae and pupae at Site 2 from April 1997 to November 1999.

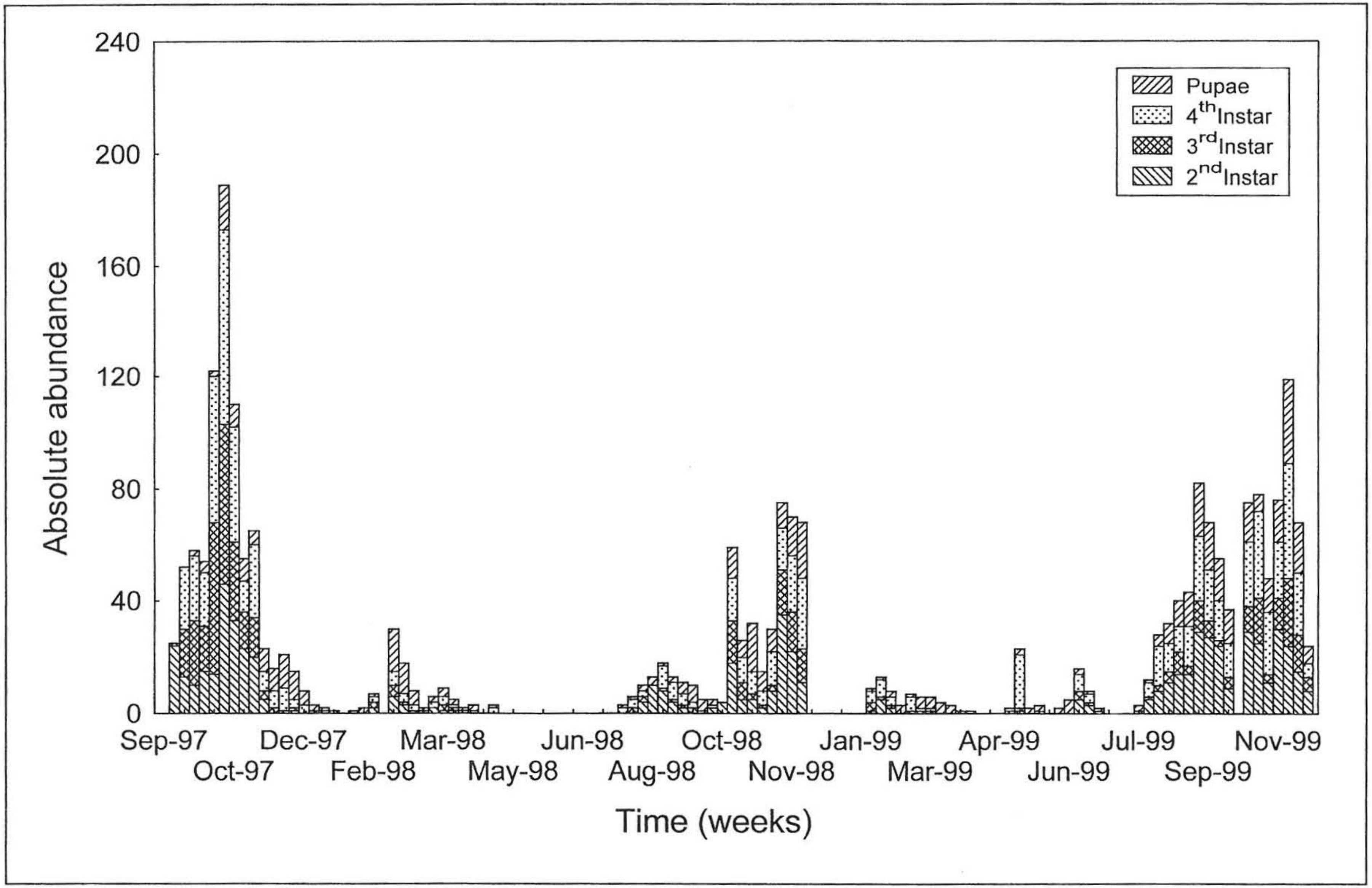

Figure 5.5. Absolute abundance of diamondback moth larvae and pupae at Site 3 from September 1997 to November 1999.

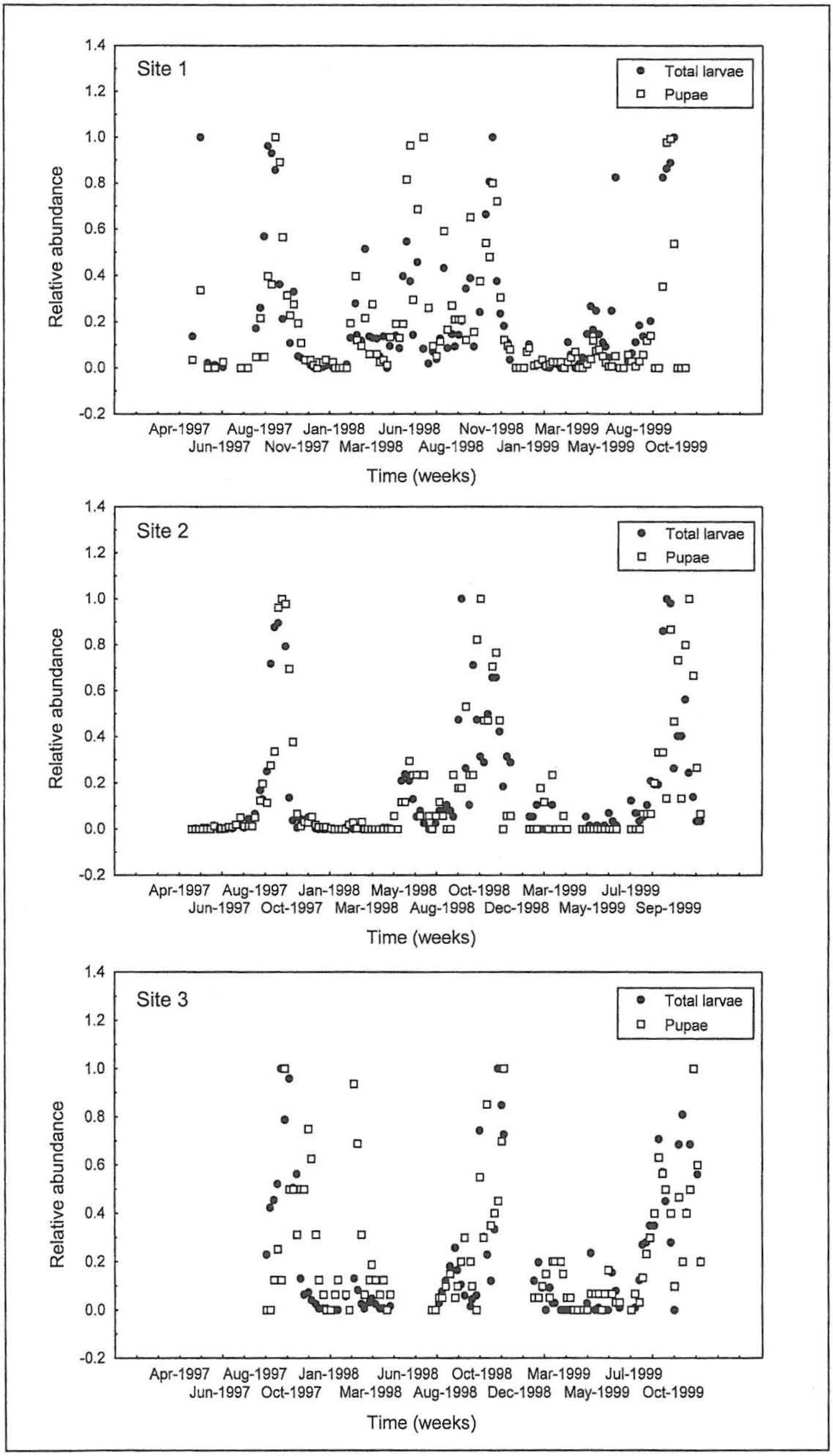

Figure 5.6. Relative abundance of diamondback moth larvae and pupae at each site over the study period.

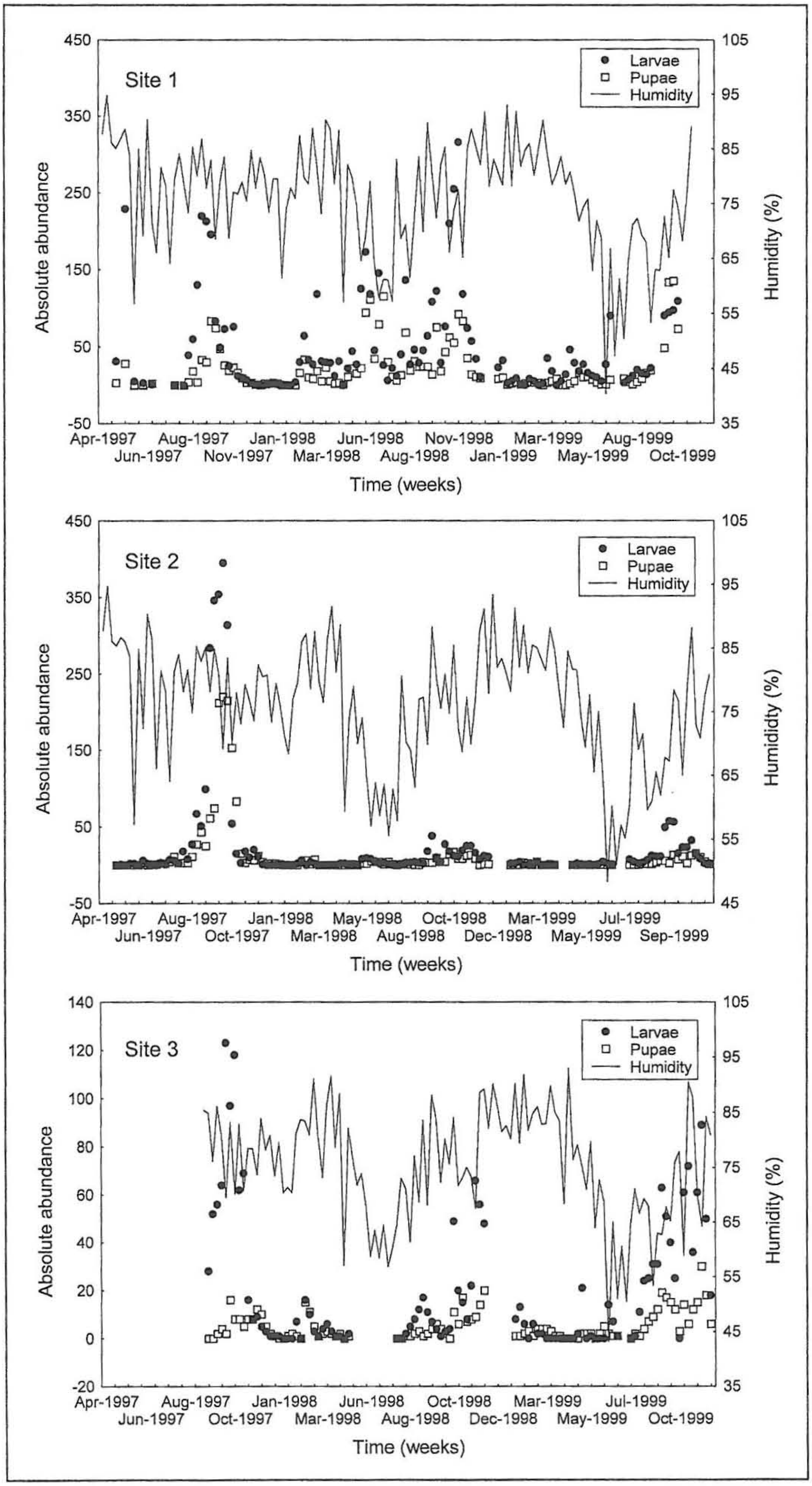

Figure 5.7. Relative humidity and the absolute abundance of diamondback moth larvae and pupae at each site over the study period.

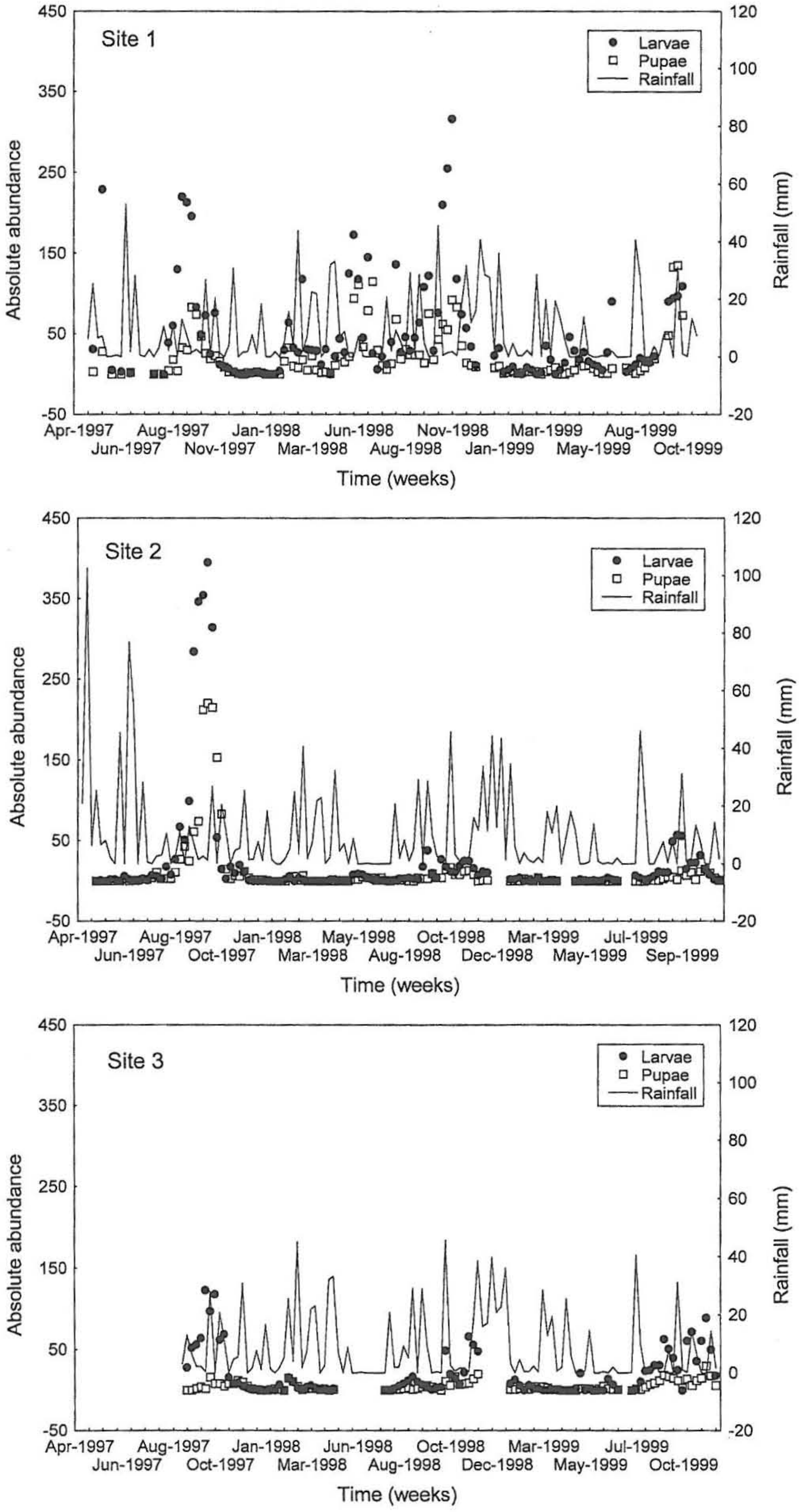

Figure 5.8. Rainfall and the absolute abundance of diamondback moth larvae and pupae at each site over the study period.

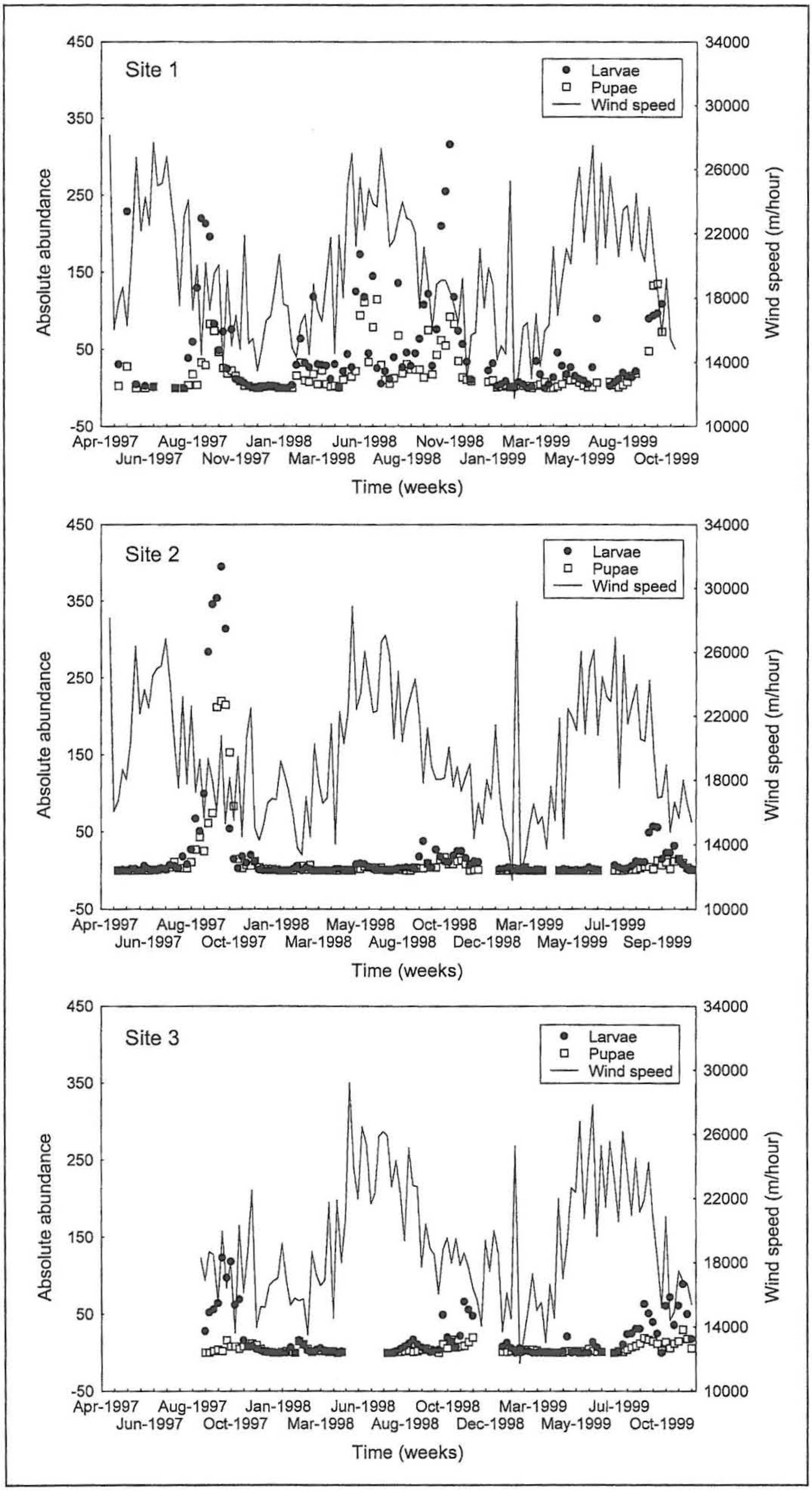

Figure 5.9. Wind speed and the absolute abundance of diamondback moth larvae and pupae at each site over the study period.

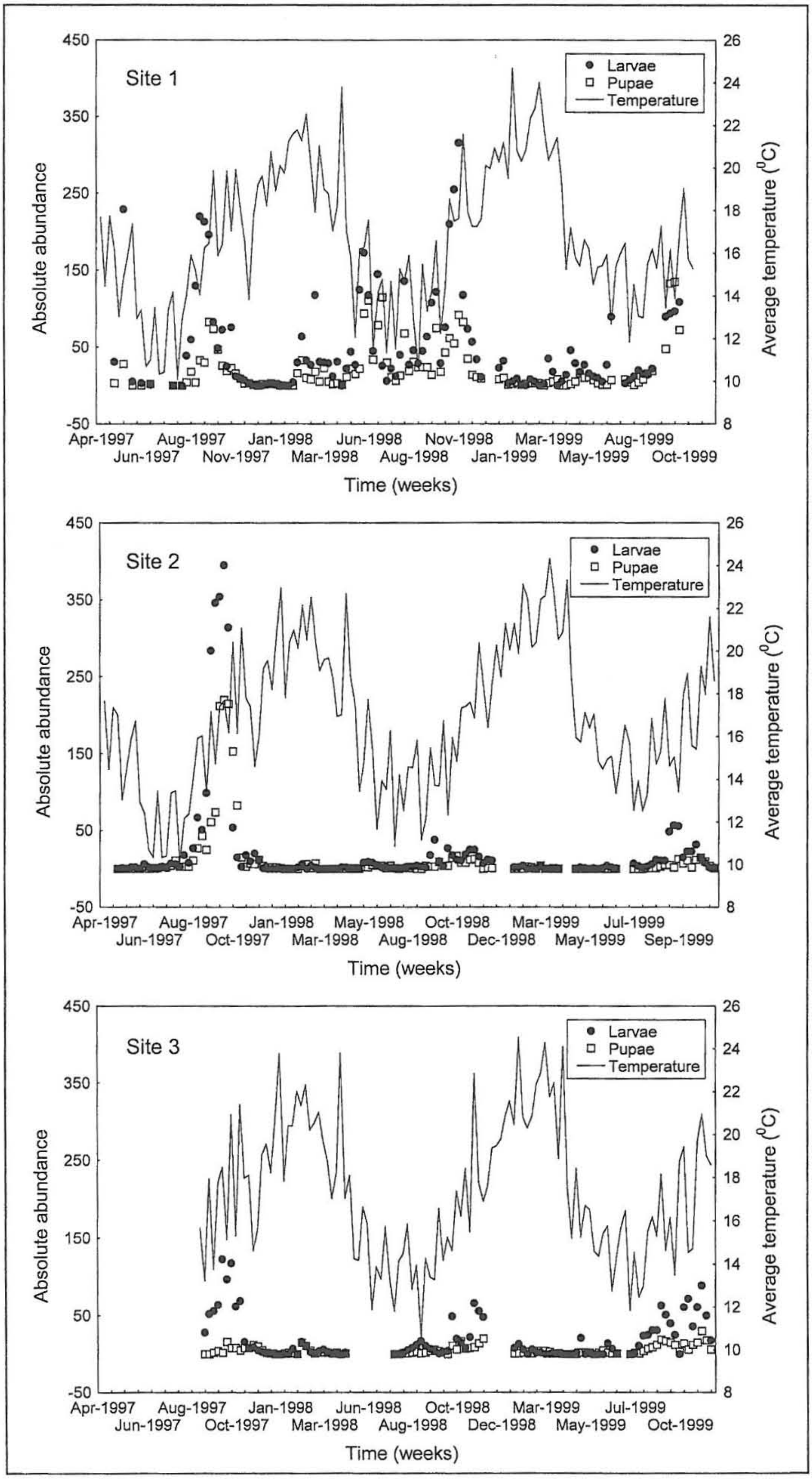

Figure 5.10. Average temperature and the absolute abundance of the diamondback moth larvae and pupae at each site over the study period.

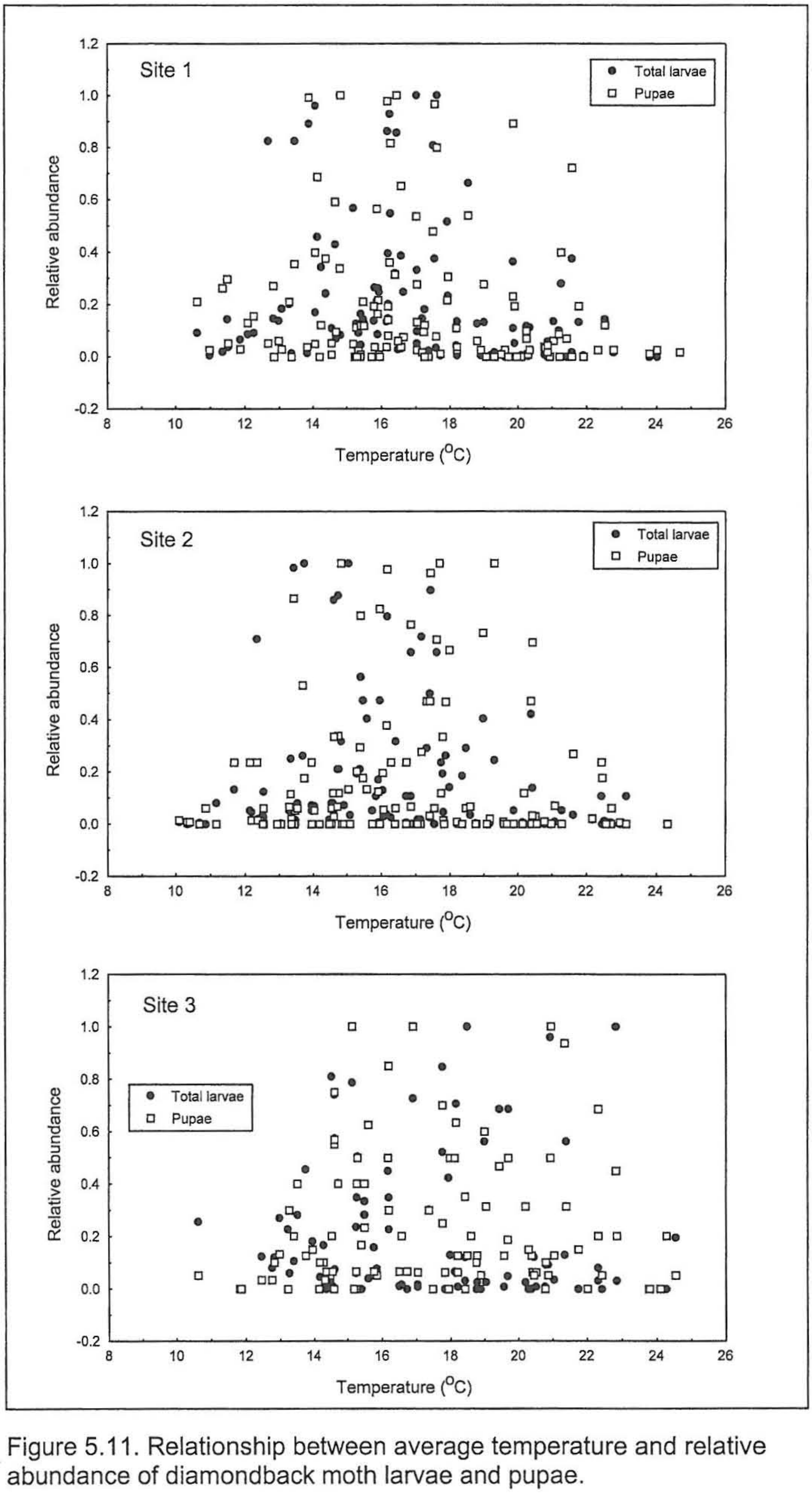

Figure 5.11. Relationship between average temperature and relative abundance of diamondback moth larvae and pupae.

Chapter 6:

Parasitoid species associated with the diamondback moth

6.1. Introduction

Natural enemies used for biological control include parasitoids, predators, bacteria, fungi and viruses, and they can be important mortality factors. There are three types of biological control used against insect pests including classical biological control, conservation of existing biological control agents, and augmentative releases. Classical biological control involves the introduction and release of natural enemies from a pest's country of origin (Murdoch *et al.*, 1985; Strand & Obrycki, 1996). However, it is important that existing natural enemies are encouraged and managed to improve and provide suitable control. This contributes towards successful Integrated Pest Management (IPM) within cropping systems (Luck *et al.*, 1988) and involves methods like intercropping, timing of insecticide applications and habitat manipulation (Strand & Obrycki, 1996, Gurr & Wratten, 1999). Augmentative biological control involves mass-rearing and release of natural enemies in areas where a pest is a problem (Strand & Obrycki, 1996). Successful biological control results in the natural enemy providing a low, stable host population equilibrium and the following features are important: the natural enemy must be host-specific, in synchrony with the host, able to increase in number as the host does, generally need only one host individual to complete its lifecycle, and have a high searching ability (Murdoch *et al.*, 1985).

As many as 90 species of parasitoid have been associated with the diamondback moth worldwide (Goodwin, 1979) but not all of them are effective, and usually only a few predominate (Lim, 1986). Even these do not often provide full control of the diamondback moth and their potential as biocontrol agents varies depending on the host and the environment (Lim, 1986). Parasitoids have been introduced into countries where indigenous parasitoids are unable to provide control, for example Malaysia. In some cases these introduced species have been successful but in others they have failed (Table 6.1 & 6.2, Appendix 1). Many of the failures are due to the continued use of insecticides and the existence of hyperparasitoids (Velasco, 1983a; Chen & Su, 1986; Lim, 1986; Sastrosiswojo & Sastrodihardjo, 1986; Ooi, 1986; Alam, 1992; Morallo-Rejesus & Sayaboc, 1992; Waterhouse, 1992).

The poor understanding of systematics of the Hymenoptera involved has also hampered the use of parasitoids, for example *Cotesia plutellae* (Kurdjumov) and members of the genus *Diadegma*. There are indications from field studies that *C. plutellae* could be made up of a complex of two or more species and *Diadegma* is a large genus of ichneumonids that are very difficult to separate using traditional morphological characters (Fitton & Walker, 1992). Only recently have Azidah *et al.* (2000) identified the *Diadegma* sp. from sub-Saharan Africa as *Diadegma mollipla* (Holmgren). Information on host-parasitoid records are often provided in published lists, but much of this information is inaccurate (Noyes, 1994). Noyes (1994) put together a list of parasitoid species that have been recorded for the diamondback moth but states that it is likely that only a third of the list is correct and the rest require confirmation or are incorrect. There are a number of reasons why much of the information collected on parasitoids is unreliable. Some of these include incorrect collecting in the field, misidentification of the host or parasitoids, disregard for a taxonomist's opinion and misspelling of species names (Noyes, 1994).

Ullyett (1947b) found that in South Africa the diamondback moth had a suite of indigenous parasitoids that were able to provide sufficient control on crucifers. He noted that the species were very similar to those that were found in the moth's presumed country of origin. He suggested that if an introduced species has habitat and environmental requirements that are similar to those of a indigenous species, then there is a possibility that the parasitoids of the indigenous species will use the introduced species as an alternative host (Ullyett, 1947a). Kfir (1997a, 1997b, 1998) has discovered a rich parasitoid fauna in the Pretoria region of South Africa (Table 6.1) including both primary parasitoids and hyperparasitoids. This chapter introduces the parasitoids associated with the diamondback moth in the Grahamstown area of the Eastern Cape.

6.2. Material and methods

The same sampling procedure was carried out as in the previous chapter (Chapter 5). The diamondback moth larvae and pupae collected from the three study sites were reared in a constant environment room at 25°C and 16:8 hours light:dark. Each larva was placed in a standard plastic petri dish (8 cm in diameter) with portions of fresh cabbage leaves. The petri dishes were cleaned daily to avoid moisture build-up and the larvae were provided with fresh leaf material every second day until they pupated. Pupae collected in the field were also placed in petri dishes. Parasitoid wasps that emerged were identified.

6.3. Results

Nine species of parasitoid wasp were found during the study, including both primary parasitoids and hyperparasitoids. Table 6.2 shows the species found, whether they are primary or hyperparasitoids, and their stage of attack in the diamondback moth lifecycle.

6.4. Discussion

Natural enemies, particularly parasitoids, have become very important in control of the diamondback moth. Lim (1986) considered success by parasitoids to be high and he attributes the failures to management problems and improper research techniques. There is also an indication that in countries where there were effective parasitoids, the diamondback moth has not become as much of a problem as in those countries lacking parasitoids.

All of the parasitoid species collected in the Grahamstown area of the Eastern Cape (Table 6.2) have been collected by Kfir (1997a, 1997b, 1998) in the Pretoria region of South Africa. Kfir (1997a, 1997b, 1998) has also collected a number of additional species (Table 6.1), including egg-larval parasitoids, that were not collected in the Grahamstown area. Unfortunately, diamondback moth eggs and first instars were not collected from the field in the Grahamstown area because they were difficult to find due to their small size. Dennill & Pretorius (1995) found only one species of parasitoid wasp, *Apanteles halfordi* Ullyett, in the Pretoria region of South Africa, but their study was only a year long. The species was also incorrectly identification and has since been identified as *C. plutellae* (R. Kfir, pers. comm.). Ullyett (1947b) found a total of 11 parasitoid species, of which *A. halfordi* was one of the most important. In a study carried out by Waladde *et al.* (2001) in the Alice area of the Eastern Cape six parasitoids were found, including, *C. plutellae*, *A. halfordi* (= *Apanteles eriophyes* Nixon (Prinsloo, in press)), *Diadromus collaris* Gravenhorst, *Oomyzus sokolowskii* (Kurdjumov) and the hyperparasitoid, *Hokeria* sp.

Eight species of hyperparasitoids were found in the Pretoria region of South Africa (Kfir, 1998). Two of the major species were *Pteromalus* sp., which parasitizes *C. plutellae*, *A. halfordi* and *D. collaris* cocoons, and *Mesochorus* sp., which develops inside *C. plutellae* and *A. halfordi* (Kfir, 1997a, 1997b). These hyperparasitoids were mainly active in spring and the majority of parasitoids emerging from field samples over this time were hyperparasitoids (Kfir, 1997b). Hyperparasitoids were rare in the Grahamstown region of the Eastern Cape, with only three species being found. These included *Pteromalus* sp., *Mesochorus* sp. and *Proconura* sp.

6.5. Conclusion

This chapter has shown that there are a number of parasitoids associated with the diamondback moth in the Grahamstown area of the Eastern Cape. In the following two chapters the population fluctuations and the impact of four of these parasitoids species on the diamondback moth are determined.

Table 6.1. Parasitoid wasps associated with the diamondback moth in the Pretoria region (Gauteng Province) of South Africa (Kfir, 1998).

Family	**Species**	**Stage**
Braconidae	*Chelonus curvimaculatus* Cameron	Egg-larval parasitoid
	Chelonus sp.	Egg-larval parasitoid
	Apanteles halfordi Ullyett	Larval parasitoid
	Cotesia plutellae (Kurdjumov)	Larval parasitoid
	Habrobracon brevicornis (Wesmael)	Larval parasitoid
Ichneumonidae	*Diadegma mollipla* (Holmgren)	Larval-pupal parasitoid
	Itoplectis sp.	Larval-pupal parasitoid
	Diadromus collaris Gravenhorst	Pupal parasitoid
	Mesochorus sp.	Hyperparasitoid
	Unidentified	Pupal parasitoid
Eulophidae	*Oomyzus sokolowskii* (Kurdjumov)	Larval-pupal parasitoid
	Tetrastichus howardi (Olliff)	Pupal parasitoid
	Tetrastichus sp.	Hyperparasitoid
Chalcididae	*Brachymeria* sp.	Pupal parasitoid
	Brachymeria sp.	Hyperparasitoid
	Hockeria sp.	Pupal parasitoid
	Hockeria sp.	Hyperparasitoid
	Proconura sp.	Hyperparasitoid
Ceraphronidae	*Aphanogmus fijiensis* (Ferriere)	Hyperparasitoid
Eurytomidae	*Eurytoma* sp.	Hyperparasitoid
Pteromalidae	*Pteromalus* sp.	Hyperparasitoid

Table 6.2. Parasitoids found in the Grahamstown area of the Eastern Cape Province, South Africa. The table gives the type of parasitoid and its stage of attack.

Super family	**Family**	**Species**	**Type**	**Stage of attack**
Ichneumonoidea	Braconidae	*Cotesia plutellae* (Kurdjumov)	Primary parasitoid	Larval
		Apanteles halfordi Ullyett	Primary parasitoid	Larval
	Ichneumonidae	*Diadromus collaris* Gravenhorst	Primary parasitoid	Pupal
		Diadegma mollipla (Holmgren)	Primary parasitoid	Larval-pupal
		Itoplectis sp.	Primary parasitoid	
		Mesochorus sp.	Hyperparasitoid	Developing parasitoid larvae
Chalcidoidea	Eulophidae	*Oomyzus sokolowskii* (Kurdjumov)	Primary and hyperparasitoid	Larval-pupal
	Pteromalidae	*Pteromalus* sp.	Hyperparasitoid	Parasitoid cocoons
	Chalcididae	*Proconura* sp.	Hyperparasitoid	Parasitoid cocoons

Chapter 7:

Population dynamics of the parasitoid species associated with the diamondback moth

7.1. Introduction

Various parasitoid species are associated with the diamondback moth in different parts of the world (Table 1 & 2, Appendix 1). In most cases it is the same few parasitoids that are effective against the diamondback moth, which suggests that increases in moth abundance are due to the absence of one or more crucial parasitoids (Lim, 1986). This is probably why so many introductions of parasitoids have been unsuccessful. The community structure and the abundance of these parasitoids vary from season to season and year to year. The reasons for these variations could be due to a number of factors including competition with other parasitoid species, environmental factors and density of the diamondback moth (Pimentel, 1961a; Goodwin, 1979; Ooi, 1992; Liu *et al.*, 2000; Saucke *et al.*, 2000)

In this chapter the abundance of the parasitoids associated with the diamondback moth in the Eastern Cape province were determined. The community structure of the parasitoid species was established for the study period and the effect of environmental factors, including temperature, humidity, wind speed and rainfall were investigated.

7.2. Materials and methods

The diamondback moth larvae and pupae collected from the three study sites (Chapter 5) were used to determine the abundance of the different parasitoid species in the field. The larvae and pupae were reared in a constant environment room (Chapter 6). The dates of pupation and emergence of either moth or parasitoid were recorded. Relative abundances of the parasitoids were determined using the method described in Chapter 5. Pearson correlation coefficients and Pearson partial correlation coefficients were determined between the relative abundances of the parasitoid species at the three sites using STATISTICA v.5 (StatsSoft, 2001). Occurrence of parasitoids were correlated with climatic conditions, including temperature, rainfall, humidity and wind speed using Pearson partial correlations (STATISTICA v.5 (StatsSoft, 2001)). The climate data were obtained from the National Weather Bureau in Pretoria, South Africa.

7.3. Results

7.3.1. Abundance of parasitoid species

The abundance of the parasitoids varied between sites and between months during the study (Figs. 7.1 - 7.3). Site 1 had the highest abundance while Site 3 had the lowest. The most abundant parasitoids at Site 1 was *Cotesia plutellae* (Kurdjumov), at Site 2 *Diadegma mollipla* (Holmgren) and at Site 3 both *C. plutellae* and *D. mollipla*. *Apanteles halfordi* (Ullyett), *Itoplectis* sp., and the hyperparasitoids were very rare and were excluded from further analyses.

At Site 1 (Fig. 7.1) *C. plutellae* was generally present throughout the study. *Diadegma mollipla* was present in spring 1997, but in 1998 and 1999 abundance was very low. *Diadromus collaris* Gravenhorst and *Oomyzus sokolowskii* (Kurdjumov) were present at various times throughout the study but their abundances was low and sporadic until September 1999. At Site 2 (Fig. 7.2) and Site 3 (Fig 7.3) the parasitoid species were generally only present over the spring and the summer. Abundances were highest in the first year of planting at Site 2. Unfortunately at Site 3 sampling was interrupted frequently during the first year of planting.

7.3.2. Parasitoid community structure

Each species of parasitoid contributed to the parasitoid complex in varying degrees and at different times during the study. At Site 1 (Fig. 7.4) *C. plutellae* was the most dominant parasitoid, except during spring in the first year (1997), when *D. mollipla* was dominant, and in spring of the last year (1999) when *D. collaris* was dominant.

At Site 2 (Fig. 7.5) it was difficult to determine the dominant parasitoid species as the abundance of parasitoid species varied throughout the study. In the first year the dominant parasitoids were *D. mollipla*, *O. sokolowskii* and *D. collaris*. In the second year of the study dominance shifted between *C. plutellae* and *O. sokolowskii,* and in the third year dominance shifted among all the parasitoid species. At Site 3 (Fig. 7.6) dominance shifted between *C. plutellae*, *D. mollipla* and *O. sokolowskii* throughout the study.

Significant positive correlations ($p < 0.05$) were found between Site 1 and 2 (*C. plutellae*, *D. mollipla*, *D. collaris* and *O. sokolowskii*) and between Site 1 and 3 (*C. plutellae*, *D. collaris* and *O. sokolowskii*) regarding the relative abundances of the parasitoid species (Table 7.1). A significant positive correlation ($p < 0.05$) was also found between all the species at all the sites (Tables 7.2 a - c) but only *C. plutellae* and *D. collaris* showed a significant partial correlation at all three sites (Tables 7.3 a - c).

7.3.3. Effect of climate

Partial correlations were calculated between the relative abundances of *C. plutella*, *D. mollipla*, *D. collaris* and *O. sokolowskii* and climatic conditions including humidity, temperature, rainfall and wind speed at each of the sites (Tables 7.4 a - d). Lagged partial correlations were done from 1 week prior to sampling to 6 weeks prior to sampling to determine whether there was a delayed effect.

The only significant correlations with humidity were found at Site 3, but no pattern could be determined. Significant negative correlations did occur between temperature and the parasitoid species but the correlations were generally not very strong. There were significant negative correlations between wind speed and some of the parasitoid species but no pattern could be determined. There were very few significant correlation between rainfall and the parasitoid species. Those that were present were positive but again no pattern was found.

7.4. Discussion

7.4.1. Abundance of parasitoid species

At the three sites, the parasitoids are most abundant during the spring and early summer months from September to December, with an additional peak in abundance at some of the sites in the autumn months from March to May (Figs. 7.1 - 7.3). The abundance of the parasitoids varied between the different sites. At Site 2 (Fig. 7.2) the abundance of parasitoids was high during September and October of 1997, but over the same period in 1998 and 1999, where a similar pattern should have occurred, the abundance was much lower. At this site the abundance of diamondback moth larvae decreased after 1997 (Fig. 5.4, Chapter 5). This site was unsprayed and it is possible that the parasitoids were able to reduce the diamondback moth larvae to sufficiently low levels that the abundance of parasitoids in the following two years dropped as a result of effective biological control. A similar pattern was seen at Site 3, although only two years of data were available. In laboratory and field studies in Taiwan *C. plutellae* and *Diadegma semiclausum* Hellén provided adequate control of diamondback moth when crucifers were grown in an insecticide-free monoculture (Talekar & Yang, 1993). The high abundance of *C. plutellae* at Site 1, the sprayed site, suggests that the parasitoids may either be resistant to or unaffected by insecticides. Liu *et al.* (2000) showed that parasitoids were present and capable of reducing the diamondback moth population even in areas where chemical insecticides were being used.

Cotesia plutellae was generally present all year round at the sprayed site (Site 1) but not at the unsprayed sites (Site 2 and 3). At the two unsprayed sites, the abundance of *C. plutellae* was also much lower than at the sprayed site. In the Alice area of the Eastern Cape, Waladde *et al.* (2001) found that *C. plutellae* was present throughout the year. Liu *et al.* (2000) found that in Hangzhou in China *C. plutellae* was active throughout the year, although it was found in very low numbers during the winter months. *Apanteles halfordi* is found only in South Africa and is active all year in the Pretoria region (Gauteng province) (Kfir, 1997a, 1997b), but in the Eastern Cape region it is present only occasionally and in very low numbers. Kfir (1997a, 1997b) found that *D. collaris* was common in April and May, and August and September whereas in the Eastern Cape it was more common in September and October. Mosiane (2001) found a similar complex of parasitoids on canola in the Gauteng Province of South Africa, which included *C. plutellae*, *D. mollipla*, *D. collaris*, *O. sokolowskii* and *A. halfordi*. He found higher abundances of *A. halfordi* and the hyperparasitoids, all of which were very rare in the Eastern Cape. *Oomyzus sokolowskii* is a gregarious parasitoid and has been found to act as a hyperparasitoid occasionally. It was generally found in the summer months when temperatures were higher.

There was considerable variation regarding the seasonal abundance of the parasitoid species at each site (Table 7.1). In cases where the sample sizes were small (Site 2 and 3) this variation may have been an artifact of sampling.

7.4.2. Parasitoid community structure

Certain species of parasitoid have been found to dominate the parasitoid complex in various parts of the world (Goodwin, 1979). In the Eastern Cape Province different species were dominant at different times of the study at each site and between the different sites (Figs. 7.4 - 7.5). There is evidence that, particularly in sprayed environments, *C. plutellae* is the dominant parasitoid. Pimentel (1961a) looked at pests on cole crops, with the diamondback moth being one of the most abundant, and concluded that species of parasitoids showed varying importance from one season to another. He also showed that the weather and the density of the larvae were important in determining the parasitoid complex in the following year. In some countries where parasitoids have been introduced, the introduced species have often out-competed the indigenous species to become dominant, for example *D. semiclausum* in Victoria, Australia (Goodwin, 1979).

Liu *et al.* (2000) found a negative correlation between *C. plutellae* and *O. sokolowskii* and suggested the possibility of competition between the two species. *Oomyzus sokolowskii* has also been considered as a hyperparasitoid parasitizing *C. plutellae,* but in laboratory and green-house experiments Talekar & Hu (1996) found that it was not a hyperparasitoid and there was potential for competition between the two species. Other authors have considered it to be a facultative hyperparasitoid (Fitton & Walker, 1992; Kfir, 1997a, 1997b; Liu *et al.*, 2000). Talekar & Yang (1993) and Talekar *et al.* (1992) found a significant negative correlation between parasitism of diamondback moth by *C. plutellae* and *D. semiclausum* and they suggested that the two parasitoids complemented each other. The authors found that *C. plutellae* was present early in the season and parasitism by *D. semiclausum* only occurred later in the season. Xu *et al.* (2001a) found that *Diadegma insulare* Cresson and *Microplitis plutellae* Muesbeck were able to successfully co-exist in the field because *D. insulare* was present early in the season, but *M. plutellae* was only present later in the season.

There was a positive relationship between the different parasitoid species in the Eastern Cape (Tables 7.2 a - c) which suggests that there is no competition between the different species and that the various parasitoid species are dominant at various times of the year due to seasonal timing and climate preferences (Figs. 7.4 - 7.5).

7.4.3. Effect of climate

The correlations with climate varied between the different sites with different conditions affecting the parastoids, and no consistent patterns were found. Partial correlations were done with climate lagged up to six weeks prior to sampling to determine whether there was a lag effect between climatic conditions and parasitoid abundance but there was no indication that a particular period had more effect on parasitoid abundance. Wind speed showed a negative correlation with all the species at Site 2. The results suggest that wind had an adverse effect on the parasitoids. Windy weather was found to have an adverse effect on flight and searching ability of *Cotesia glomerata* (L.), a parasitoid of pierids (Gu & Dorn, 2001). Idris and Grafius (1998) found that flight activity of male *D. insulare* was determined by light intensity, and that of females by light intensity, temperature and wind speed. Relative humidity, cloud cover and time of day had no influence.

There were strong negative correlations between temperature and the abundance of various parasitoid species, which varied between the sites (Tables 7.4 a - d). This was partly an artifact of using linear correlations to assess a Gaussian trend. The literature indicates that temperature is one of the most important factors in determining the success of particular parasitoid species (Ooi, 1992; Talekar & Yang, 1991; Yang *et al.*, 1993; Wang *et al.*, 1999; Saucke *et al.*, 2000). In Taiwan where *D. semiclausum* was introduced but only became established in the cool temperate highland areas. In the lowlands it was unable to establish, possibly because of the continued use of insecticides and the higher temperatures. *Diadegma semiclausum* is able to overwinter in freezing temperatures but is sensitive to high temperatures (Talekar *et al.*, 1992; Talekar, 1996). Parasitism by *C. plutellae* was greater at higher temperatures but low below 20°C. Parasitism by *C. plutellae* was high early in the growing season but as the plants grew older it decreased. *Diadegma semiclausum* showed the opposite pattern. It was suggested that this is because temperatures may be high early in the season but get lower as the season progresses (Talekar, 1996; Wang *et al.*, 1999). *Oomyzus sokolowskii* showed higher parasitism at higher temperatures (Talekar & Hu, 1996) and in the Eastern Cape it was generally only present in the late summer when temperatures were higher.

7.5. Conclusion

The diamondback moth in the Grahamstown area of the Eastern Cape is active throughout the year, but infestation levels are highest over the spring months from October to December. The four dominant parasitoid species were present at various times during the year but abundances were highest during the spring and summer. It was at this time of the year that there was a resource available to them in the form of diamondback moth larvae and pupae. *Cotesia plutellae* was more abundant at the sprayed site than at the unsprayed sites, suggesting that it was unaffected by the insecticides used, but the abundance of the other parasitoid species was generally higher at the unsprayed sites. No consistent patterns were found between climate and the parasitoid species when considered on an instantaneous basis in the field.

Table 7.1. Pearson correlation coefficients between the sites and the relative abundance of the different parasitoid species. Significant correlations are in bold ($p < 0.05$).

Site	*C. plutellae*	*D. mollipla*	*D. collaris*	*O. sokolowskii*
1 and 2	**r = 0.37**	**r = 0.20**	**r = 0.59**	**r = 0.41**
1 and 3	**r = 0.43**	r = 0.15	**r = 0.32**	**r = 0.25**
2 and 3	r = 0.19	r = 0.06	r = - 0.04	r = 0.22

Table 7.2 a. Pearson correlation coefficients between the relative abundance of parasitoid species at Site 1. Significant correlations are in bold ($p < 0.05$).

	C. plutellae	*D. mollipla*	*D. collaris*
D. mollipla	**r = 0.31**		
D. collaris	**r = 0.55**	**r = 0.46**	
O. sokolowskii	**r = 0.40**	**r = 0.22**	**r = 0.66**

Table 7.2 b. Pearson correlation coefficients between the relative abundance of parasitoid species at Site 2. Significant correlations are in bold ($p < 0.05$).

	C. plutellae	*D. mollipla*	*D. collaris*
D. mollipla	**r = 0.60**		
D. collaris	**r = 0.39**	**r = 0.27**	
O. sokolowskii	**r = 0.43**	**r = 0.24**	**r = 0.31**

Table 7.2 c. Pearson correlation coefficients between the relative abundance of parasitoid species at Site 3. Significant correlations are in bold ($p < 0.05$).

	C. plutellae	*D. mollipla*	*D. collaris*
D. mollipla	**r = 0.40**		
D. collaris	**r = 0.48**	**r = 0.74**	
O. sokolowskii	**r = 0.45**	**r = 0.63**	**r = 0.53**

Table 7.3 a. Pearson partial correlation coefficients between the relative abundance of parasitoid species at Site 1. Significant correlations are in bold ($p < 0.05$) with the p-values in brackets.

	C. plutellae	*D. mollipla*	*D. collaris*
D. mollipla	0.07 (0.47)		
D. collaris	**0.34 (0.0003)**	**0.04 (0.002)**	
O. sokolowskii	0.08 (0.43)	- 0.09 (0.34)	**0.58 (0.00000)**

Table 7.3 b. Pearson partial correlation coefficients between the relative abundance of parasitoid species at Site 2. Significant correlations are in bold ($p < 0.05$) with the p-values in brackets.

	C. plutellae	*D. mollipla*	*D. collaris*
D. mollipla	**0.54 (0.00000)**		
D. collaris	**0.24 (0.02)**	0.05 (0.62)	
O. sokolowskii	**0.34 (0.0004)**	- 0.05 (0.6)	0.10 (0.3)

Table 7.3 c. Pearson partial correlation coefficients between the relative abundance of parasitoid species at Site 3. Significant correlations are in bold ($p < 0.05$) with p-values in brackets.

	C. plutellae	*D. mollipla*	*D. collaris*
D. mollipla	0.03 (0.81)		
D. collaris	**0.29 (0.01)**	**0.52 (0.000003)**	
O. sokolowskii	**0.25 (0.04)**	**0.38 (0.001)**	0.05 (0.66)

Table 7.4 a. Pearson partial correlation coefficients between the relative abundance of *Cotesia plutellae* and environmental factors including humidity, temperature, rainfall and wind speed. Significant correlations are in bold ($p < 0.05$). P-values in brackets.

	Week	**Site 1**	**Site 2**	**Site 3**
Humidity	w_1	- 0.007 (0.94)	- 0.09 (0.36)	- 0.05 (0.66)
	w_2	- 0.04 (0.65)	- 0.11 (0.29)	0.09 (0.44)
	w_3	- 0.03 (0.73)	- 0.11 (0.28)	- 0.16 (0.18)
	w_4	0.06 (0.52)	- 0.04 (0.73)	- 0.06 (0.64)
	w_5	- 0.06 (0.57)	- 0.07 (0.47)	- 0.12 (0.31)
	w_6	- 0.007 (0.94)	- 0.11 (0.28)	**- 0.23 (0.05)**
Temperature	w_1	0.04 (0.66)	- 0.16 (0.12)	- 0.008 (0.95)
	w_2	- 0.03 (0.76)	**- 0.25 (0.01)**	0.09 (0.46)
	w_3	0.03 (0.79)	**- 0.22 (0.03)**	0.12 (0.33)
	w_4	- 0.001 (0.10)	**- 0.24 (0.02)**	- 0.02 (0.89)
	w_5	0.01 (0.92)	**- 0.24 (0.02)**	- 0.03 (0.81)
	w_6	0.17 (0.08)	**- 0.36 (0.0002)**	0.05 (0.68)
Rainfall	w_1	0.01 (0.92)	0.05 (0.59)	**0.28 (0.01)**
	w_2	0.06 (0.56)	- 0.11 (0.29)	- 0.05 (0.64)
	w_3	0.06 (0.52)	0.01 (0.89)	0.14 (0.24)
	w_4	0.13 (0.18)	0.03 (0.76)	- 0.14 (0.25)
	w_5	**0.24 (0.01)**	0.04 (0.71)	- 0.04 (0.74)
	w_6	- 0.03 (0.78)	0.05 (0.59)	- 0.09 (0.47)
Wind speed	w_1	- 0.09 (0.36)	- 0.17 (0.08)	- 0.18 (0.10)
	w_2	- 0.17 (0.07)	**- 0.24 (0.02)**	- 0.07 (0.53)
	w_3	- 0.14 (0.16)	- 0.16 (0.11)	- 0.18 (0.12)
	w_4	**- 0.12 (0.03)**	- 0.13 (0.21)	- 0.20 (0.09)
	w_5	- 0.09 (0.37)	- 0.11 (0.27)	- 0.20 (0.10)
	w_6	0.07 (0.46)	**- 0.20 (0.05)**	- 0.18 (0.12)

Table 7.4 b. Pearson partial correlation coefficents between the relative abundance of *Diadegma mollipla* and environmental factors including humidity, temperature, rainfall and wind speed. Significant correlations are in bold ($p < 0.05$). P-values in brackets.

	Week	**Site 1**	**Site 2**	**Site 3**
Humidity	w_1	- 0.15 (0.13)	0.03 (0.77)	- 0.16 (0.18)
	w_2	- 0.12 (0.20)	0.06 (0.55)	**- 0.24 (0.04)**
	w_3	- 0.06 (0.53)	- 0.02 (0.85)	- 0.14 (0.22)
	w_4	- 0.02 (0.83)	- 0.003 (0.97)	- 0.22 (0.06)
	w_5	- 0.01 (0.91)	- 0.09 (0.38)	- 0.16 (0.17)
	w_6	- 0.02 (0.88)	- 0.09 (0.37)	**- 0.28 (0.02)**
Temperature	w_1	- 0.07 (0.48)	**- 0.25 (0.01)**	**- 0.03 (0.79)**
	w_2	**- 0.23 (0.02)**	**- 0.27 (0.01)**	- 0.13 (0.26)
	w_3	**- 0.22 (0.02)**	**- 0.24 (0.02)**	- 0.21 (0.08)
	w_4	- 0.22 (0.22)	**- 0.22 (0.03)**	**- 0.36 (0.002)**
	w_5	**- 0.20 (0.03)**	- 0.18 (0.08)	- 0.14 (0.24)
	w_6	**- 0.34 (0.0004)**	**- 0.29 (0.003)**	- 0.20 (0.09)
Rainfall	w_1	- 0.01 (0.89)	0.08 (0.43)	0.08 (0.50)
	w_2	- 0.12 (0.21)	0.01 (0.91)	- 0.03 (0.80)
	w_3	- 0.03 (0.80)	- 0.03 (0.79)	- 0.06 (0.61)
	w_4	0.09 (0.36)	- 0.10 (0.32)	- 0.04 (0.72)
	w_5	- 0.05 (0.62)	- 0.17 (0.10)	- 0.02 (0.88)
	w_6	- 0.12 (0.27)	- 0.001 (0.99)	0.19 (0.10)
Wind speed	w_1	- 0.17 (0.08)	- 0.14 (0.15)	- 0.15 (0.20)
	w_2	**- 0.27 (0.01)**	- 0.10 (0.31)	**- 0.26 (0.03)**
	w_3	- 0.18 (0.07)	- 0.10 (0.31)	- 0.23 (0.06)
	w_4	- 0.14 (0.14)	- 0.09 (0.39)	**- 0.33 (0.01)**
	w_5	- 0.05 (0.60)	**- 0.20 (0.04)**	- 0.12 (0.33)
	w_6	**- 0.19 (0.04)**	- 0.13 (0.21)	- 0.23 (0.06)

Table 7.3 c. Pearson partial correlation coefficients between the relative abundance of *Diadromus collaris* and environmental factors including humidity, temperature, rainfall and wind speed. Significant correlations are in bold ($p < 0.05$). P-values in brackets.

	Week	**Site 1**	**Site 2**	**Site 3**
Humidity	w_1	- 0.17 (0.08)	- 0.18 (0.07)	- 0.15 (0.20)
	w_2	- 0.17 (0.07)	- 0.18 (0.08)	- 0.04 (0.74)
	w_3	- 0.15 (0.13)	0.02 (0.87)	- 0.15 (0.22)
	w_4	- 0.05 (0.61)	- 0.10 (0.34)	- 0.21 (0.08)
	w_5	- 0.11 (0.27)	- 0.09 (0.38)	- 0.09 (0.44)
	w_6	- 0.03 (0.75)	0.12 (0.24)	**- 0.24 (0.04)**
Temperature	w_1	- 0.09 (0.37)	- 0.02 (0.83)	- 0.03 (0.78)
	w_2	- 0.15 (0.13)	- 0.18 (0.07)	- 0.10 (0.42)
	w_3	**- 0.19 (0.05)**	- 0.18 (0.07)	- 0.20 (0.12)
	w_4	**- 0.24 (0.01)**	**- 0.24 (0.02)**	**- 0.24 (0.04)**
	w_5	**- 0.21 (0.03)**	- 0.18 (0.08)	- 0.05 (0.66)
	w_6	**- 0.22 (0.02)**	**- 0.26 (0.01)**	- 0.16 (0.18)
Rainfall	w_1	- 0.04 (0.69)	- 0.03 (0.73)	0.14 (0.26)
	w_2	- 0.004 (0.97)	0.10 (0.33)	- 0.10 (0.41)
	w_3	- 0.03 (0.78)	- 0.12 (0.24)	0.04 (0.76)
	w_4	0.11 (0.25)	0.12 (0.24)	- 0.05 (0.69)
	w_5	0.07 (0.50)	- 0.17 (0.10)	- 0.06 (0.63)
	w_6	- 0.08 (0.39)	- 0.09 (0.37)	- 0.003 (0.98)
Wind speed	w_1	**- 0.21 (0.02)**	**- 0.20 (0.05)**	- 0.16 (0.18)
	w_2	**- 0.22 (0.02)**	**- 0.29 (0.003)**	- 0.20 (0.10)
	w_3	**- 0.25 (0.01)**	- 0.13 (0.21)	**- 0.25 (0.03)**
	w_4	- 0.17 (0.08)	**- 0.20 (0.04)**	**- 0.30 (0.01)**
	w_5	- 0.18 (0.07)	**- 0.20 (0.04)**	- 0.06 (0.63)
	w_6	- 0.15 (0.14)	- 0.05 (0.63)	**- 0.24 (0.04)**

Table 7.4 d. Pearson partial correlation coefficients between the relative abundance of *Oomyzus sokolowskii* and environmental factors including humidity, temperature, rainfall and wind speed. Significant correlations are in bold ($p < 0.05$). P-values in brackets.

	Week	**Site 1**	**Site 2**	**Site 3**
Humidity	w_1	- 0.15 (0.13)	0.03 (0.77)	0.04 (0.74)
	w_2	- 0.05 (0.63)	- 0.07 (0.49)	**- 0.28 (0.02)**
	w_3	- 0.09 (0.33)	- 0.05 (0.64)	- 0.20 (0.10)
	w_4	- 0.002 (0.99)	- 0.006 (0.95)	- 0.08 (0.51)
	w_5	- 0.19 (0.06)	- 0.04 (0.68)	- 0.12 (0.30)
	w_6	0.02 (0.83)	0.03 (0.74)	**- 0.28 (0.02)**
Temperature	w_1	- 0.06 (0.50)	- 0.09 (0.36)	0.16 (0.18)
	w_2	- 0.03 (0.76)	- 0.16 (0.11)	- 0.02 (0.90)
	w_3	**- 0.22 (0.02)**	- 0.12 (0.25)	- 0.04 (0.77)
	w_4	**- 0.19 (0.05)**	- 0.19 (0.06)	- 0.21 (0.08)
	w_5	- 0.16 (0.10)	**- 0.20 (0.05)**	- 0.14 (0.25)
	w_6	- 0.07 (0.49)	**- 0.24 (0.02)**	- 0.02 (0.10)
Rainfall	w_1	0.01 (0.93)	- 0.001(0.10)	- 0.5 (0.70)
	w_2	- 0.05 (0.62)	0.02 (0.81)	0.17 (0.15)
	w_3	- 0.01 (0.90)	- 0.06 (0.53)	0.002 (0.99)
	w_4	0.03 (0.80)	0.01 (0.88)	- 0.04 (0.74)
	w_5	**0.31 (0.001)**	0.13 (0.19)	0.15 (0.20)
	w_6	- 0.08 (0.44)	- 0.01 (0.96)	0.17 (0.15)
Wind speed	w_1	**- 0.20 (0.04)**	- 0.09 (0.36)	0.02 (0.87)
	w_2	- 0.09 (0.36)	**- 0.24 (0.01)**	- 0.13 (0.27)
	w_3	**- 0.28 (0.003)**	- 0.11 (0.25)	**- 0.23 (0.05)**
	w_4	- 0.12 (0.20)	- 0.14 (0.15)	**- 0.23 (0.05)**
	w_5	**- 0.20 (0.04)**	- 0.08 (0.42)	- 0.17 (0.17)
	w_6	- 0.001 (0.99)	- 0.07 (0.51)	- 0.13 (0.27)

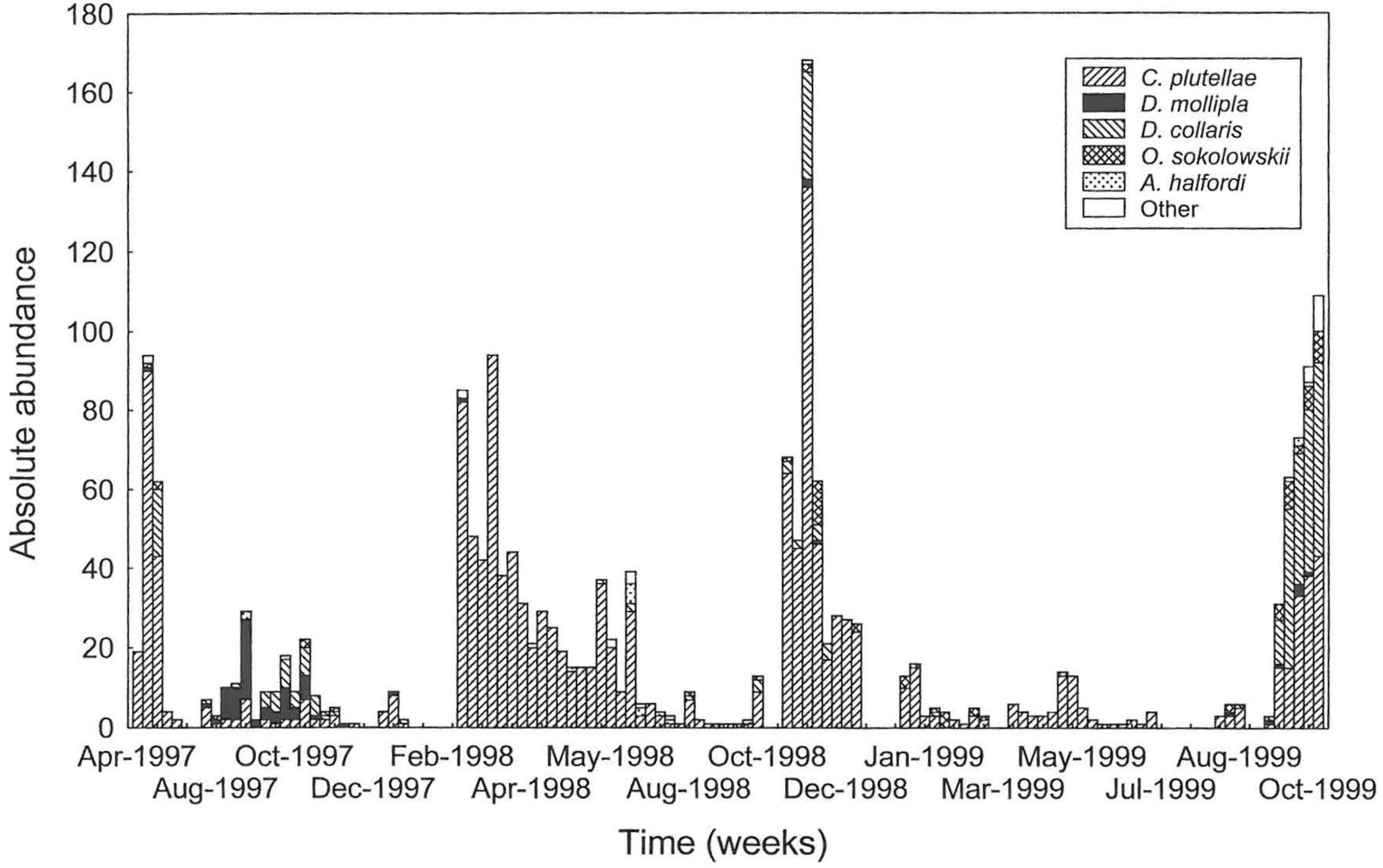

Figure 7.1. Absolute abundance of the parasitoid species associated with the diamondback moth at Site 1 from April 1997 to October 1999. In the legend, "other" includes the very rare *Itoplectis* sp. and the hyperparasitoids.

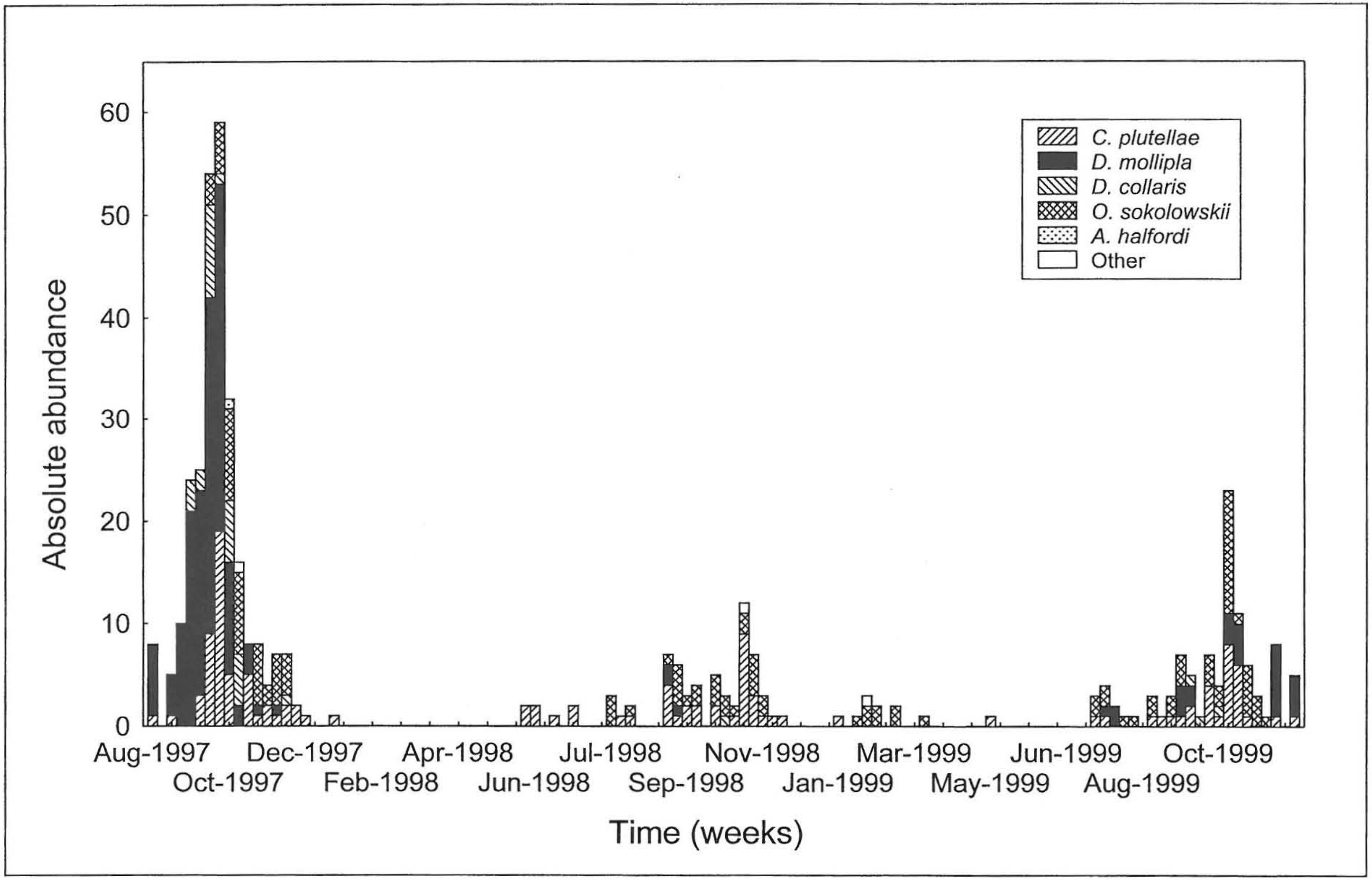

Figure 7.2. Absolute abundance of parasitoid species associated with the diamondback moth at Site 2 from August 1997 to November 1999. In the legend, "other" includes the very rare *Itoplectis* sp. and hyperparasitoids.

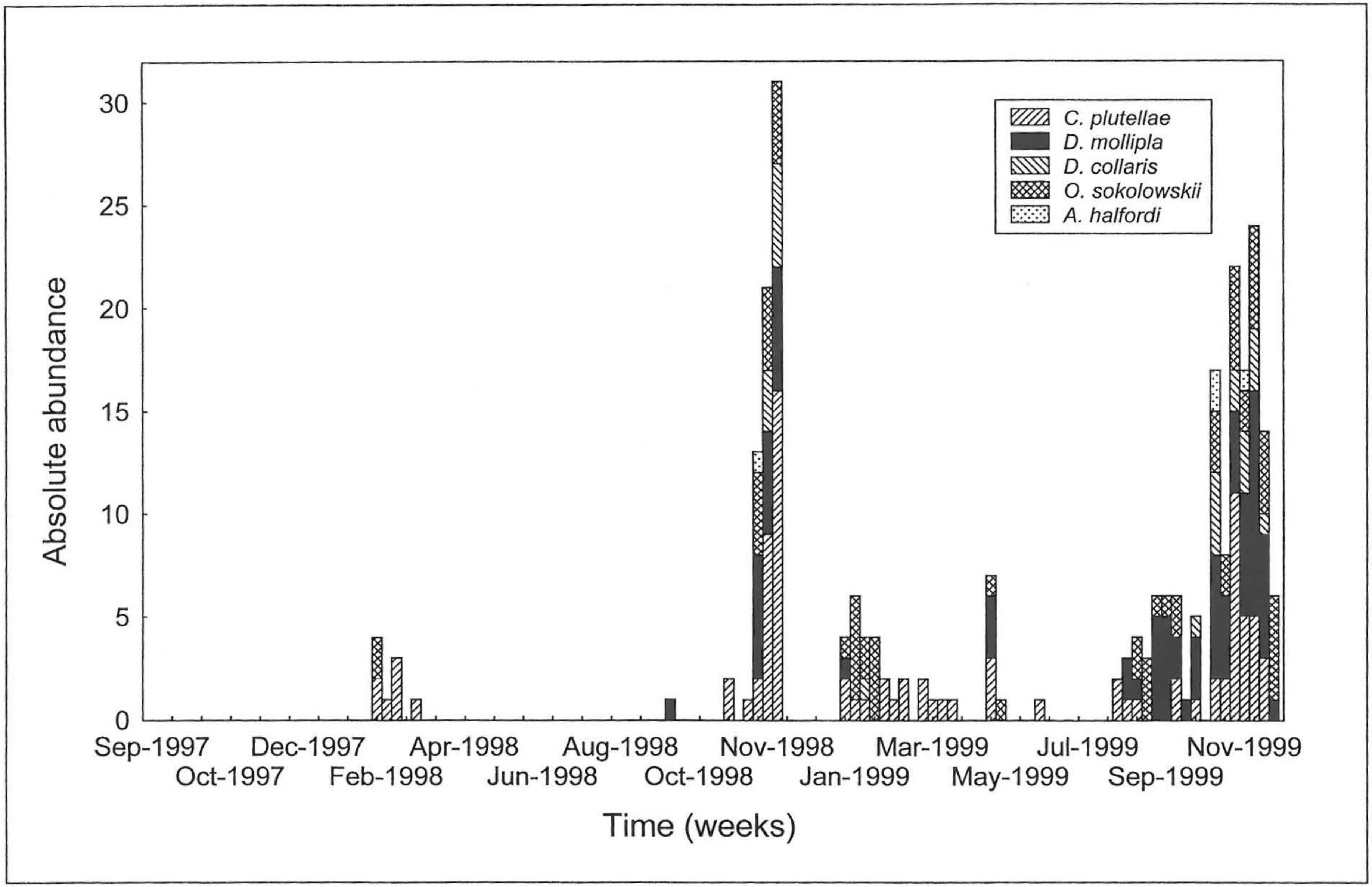

Figure 7.3. Absolute abundance of parasitoid species associated with the diamondback moth at Site 3 from September 1997 to November 1999.

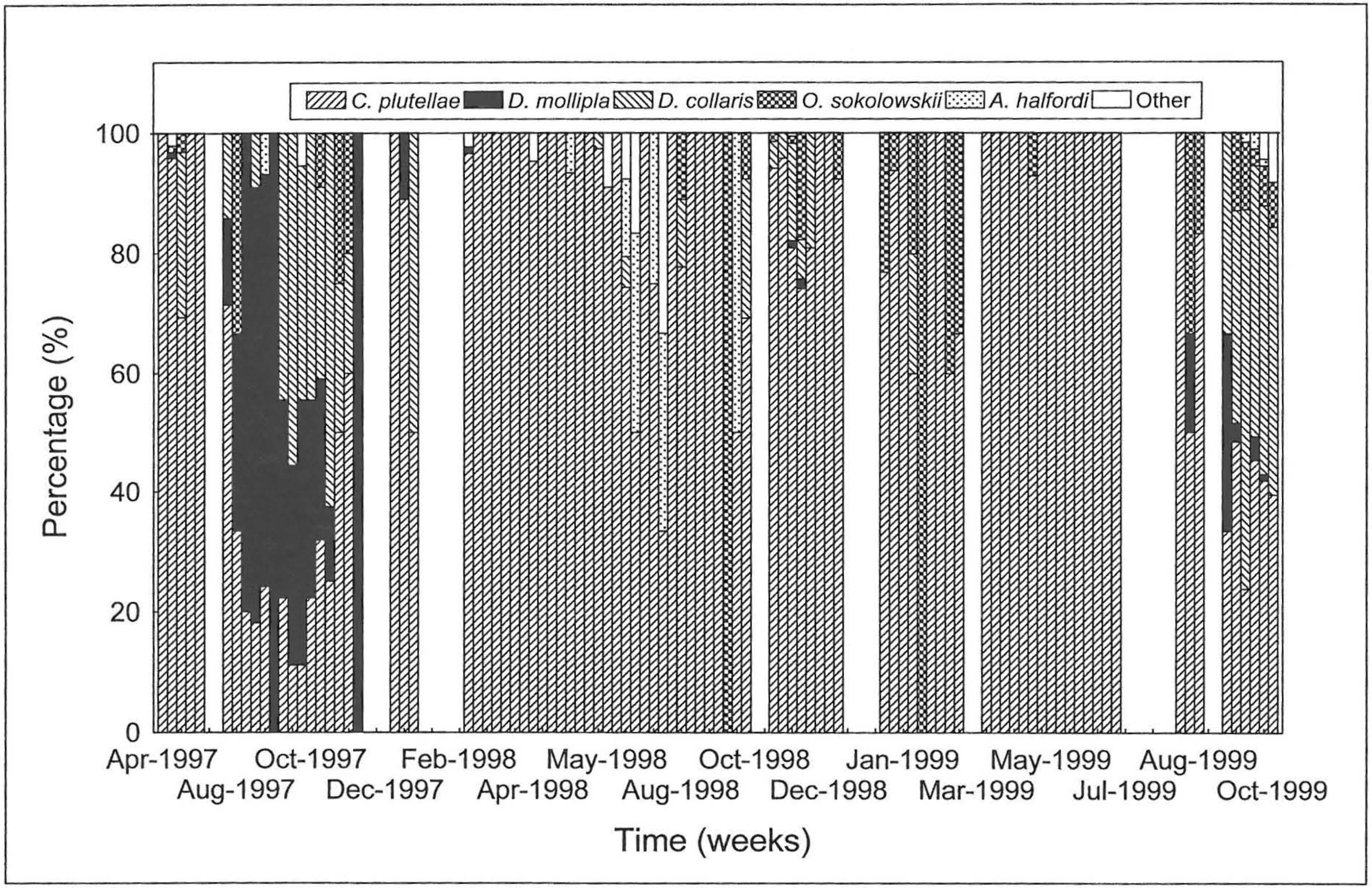

Figure 7.4. Contribution of each parasitoid species to the parasitoid complex at Site 1 from April 1997 to October 1999. In the legend "other" includes the very rare *Itoplectis* sp. and the hyperparasitoids.

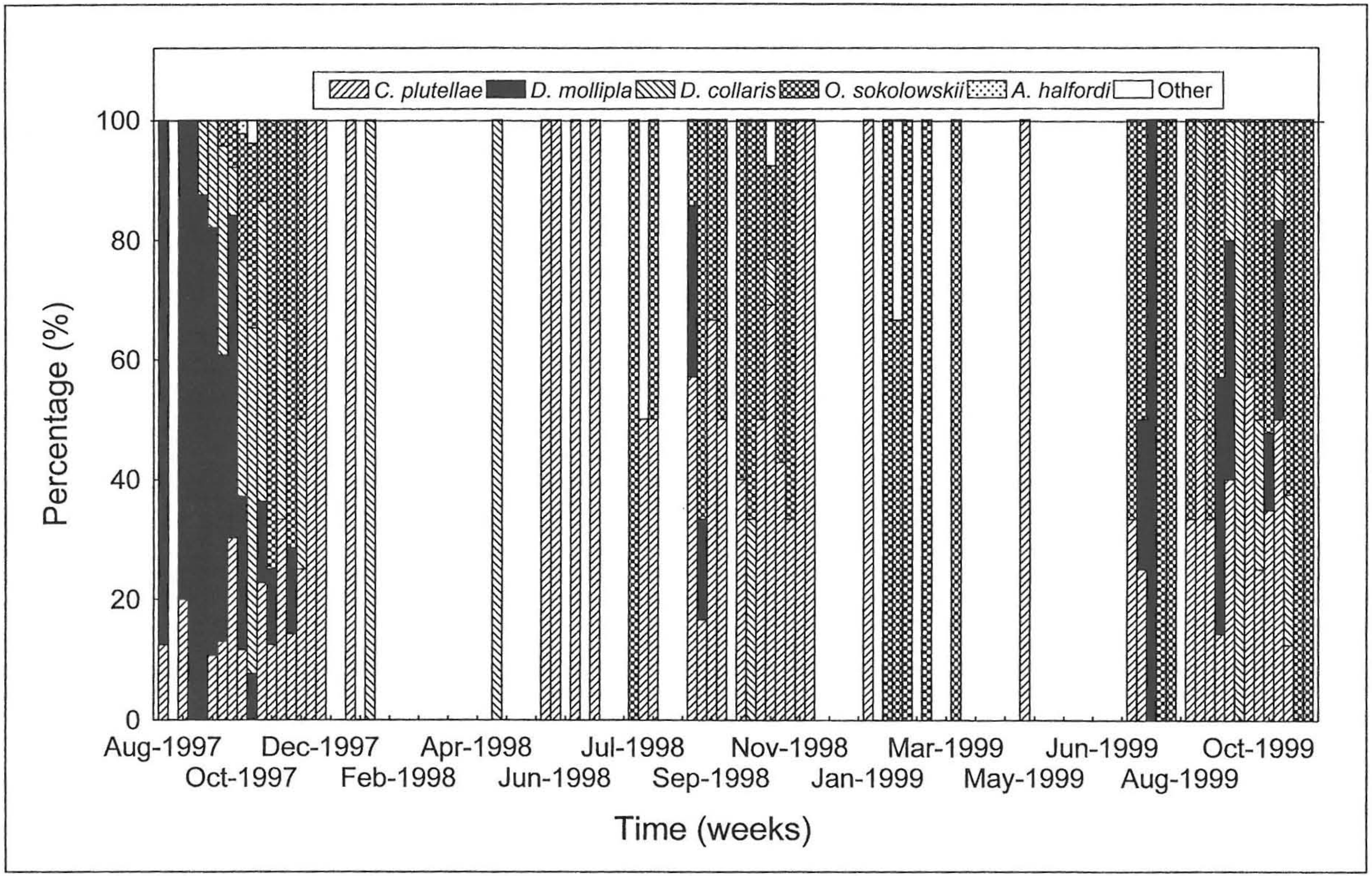

Figure 7.5. Contribution of each parasitoid species to the parasitoid complex at Site 2 from April 1997 to November 1999. In the legend "other" includes the very rare *Itoplectis* sp. and the hyperparasitoids.

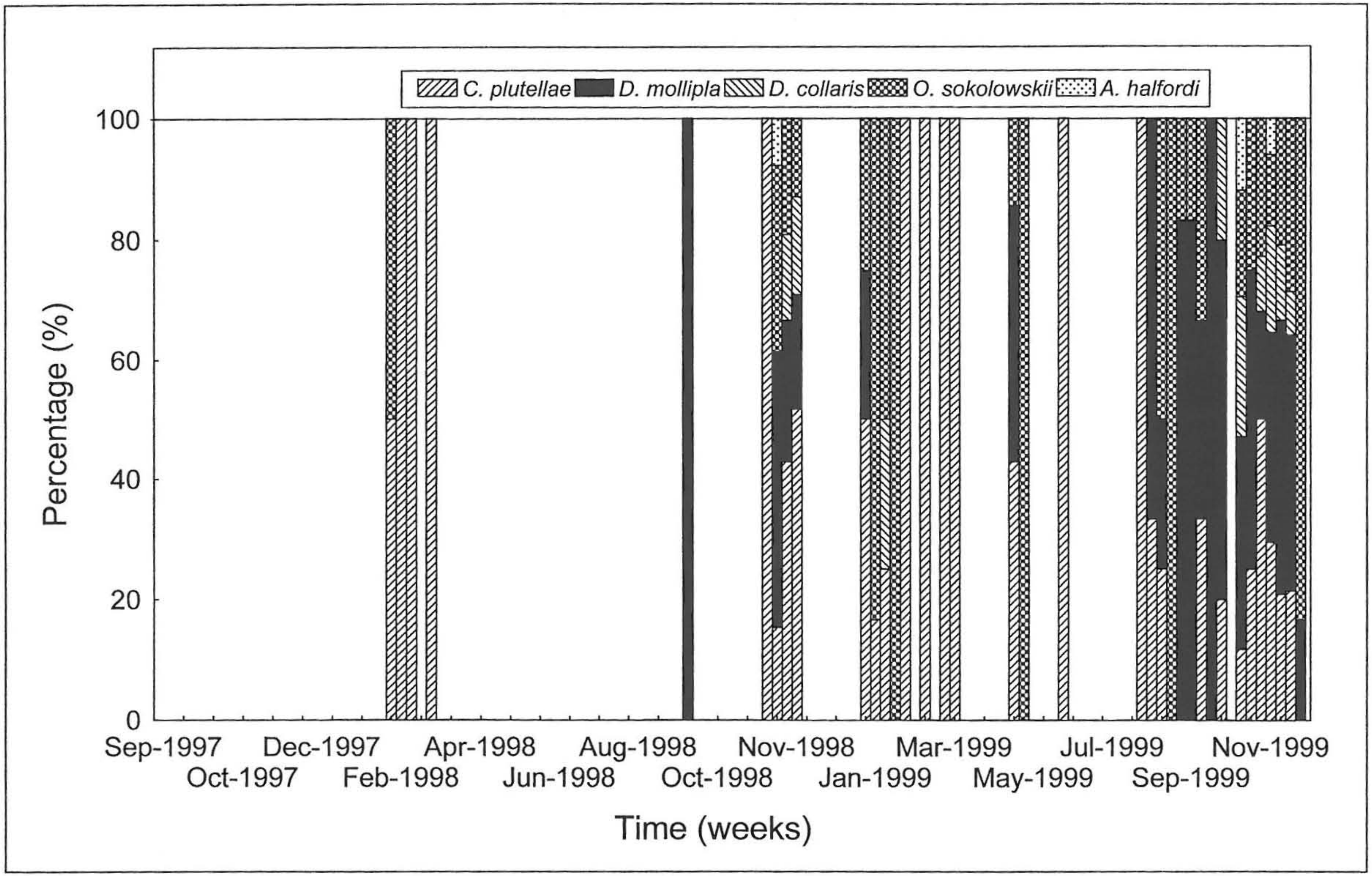

Figure 7.6. Contribution of each parasitoid species to the parasitoid complex at Site 3 from September 1997 to November 1999.

Chapter 8:

Parasitism trends in diamondback moth populations

8.1. Introduction

It is difficult to assess the effectiveness of the parasitoids, but it is important to determine their relative effectiveness and to what extent they can be exploited (Lim, 1986). Not all parasitoids are capable of reducing diamondback moth abundance. Criteria that are important in determining the parasitoid that will be most successful include the following. The parasitoid must have a density-dependent relationship with the host; a high searching behaviour; a low handling time; a high aggregational behaviour; adaptability to the environment; a high fecundity; compatibility with other parasitoids; and finally have other 'good' intrinsic properties, for example, synchronization with the host, host specificity, discriminatory power, the ability to survive host-free periods and a low susceptibility to insecticides (Chua & Ooi, 1986).

Egg parasitoids contribute very little to diamondback moth control (Waterhouse, 1992). They have been recorded in some countries, for example Thailand (Keinmeesuke *et al.*, 1992), but in the Eastern Cape none were found during the study. Larval parasitoids generally predominate and are more effective in their control of the diamondback moth (Waterhouse, 1992; Takekar & Shelton, 1993). Lim (1986) found that the most important species belong mainly to the genera *Diadegma*, *Apanteles* and *Microplitis,* and that only *Diadegma semiclausum* Hellèn and maybe *Diadegma fenestralis* Holmgren were able to provide full control. In Romania 28 primary and secondary Ichneumonid and Braconid parasitoid species were found associated with the diamondback moth, but only a few species, mainly *Diadegma* spp., contributed to reducing the population (Mustata, 1992).

In most studies, the effect of parasitoids on the diamondback moth has been established by determining the rates of parasitism, usually through rearing (Harcourt, 1960; Mitchell *et al.*, 1997a, 1997b) or dissecting (Mitchell *et al.*, 1997a, 1997b) the diamondback moth larvae. Day (1994) showed that in alfalfa weevils and mirids higher parasitism levels were found using the dissection method. However Woods *et al.* (1999) concluded that for the alfalfa caterpillar, *Colias eurytheme* (Boisduval), both methods were similar in accuracy but they preferred the dissection method because it was easier. Waage & Cherry (1992) queried the effectiveness of determining parasitism by these methods and suggested a number of factors that need to be considered. These include the importance of knowing the density of the host population, using the correct host stage to calculate percentage parasitism, and not removing host stages too soon from the population as this might prevent parasitism at a later stage and result in an underestimation of parasitism. Another consideration is that parasitism could affect the length of development of the host which may result in an malestimation of parasitism. The total parasitoid impact should also include host deaths that are caused indirectly by the parasitoid, for example through parasitoid feeding (Van Driesche, 1983).

In temperate regions where distinct generations of the moth can be determined, a quantitative measure of mortality by the parasitoids can be calculated using these methods, but in more tropical climates where there is overlap of the host generations, only a qualitative measure of parasitism between sites and general trends in parasitism can be shown (Waage & Cherry, 1992). In the Eastern Cape region of South Africa the climate tends towards being subtropical and diamondback moth generations overlap in the field. According to Waage and Cherry (1992) the results are qualitative and therefore show trends in parasitism between the different sites. Liu *et al.* (2000) determined rates of parasitism from estimates of host and parasitoid density over a number of sampling dates. They acknowledge that this could cause biases in rates of parasitism but conclude that changes in the rates of parasitism by frequent sampling over several years gives a good indication of seasonal abundance of the parasitoid species. In the Eastern Cape study the sites were sampled weekly and over a three year period which would provide a suitable indication of seasonal abundance of the parasitoids and their relative impact on the diamondback moth.

8.2. Materials and methods

Diamondback moth larvae and pupae were collected in the field and reared in a constant environment room as described in Chapters 5, 6 and 7. Mortalities of diamondback moth larvae and pupae that occurred during the rearing process as a result of factors other than parasitism, were recorded. These mortalities may have been a result of handling, diseases or the delayed effects of insecticides. The rates of moth eclosion and parasitism in the field were determined. The rate of parasitism was determined by the number of parasitised larvae and pupae divided by the total number of hosts collected in each sample (Mills, 1997). Parasitism was related to the sampling date and not the emergence date, and therefore provided an indication of parasitism at a particular time. The percentage parasitism provided an index for tracking total instantaneous parasitism in the field and not a generational parasitism level. Sampling was destructive but this would not have had an impact in the commercial fields (Site 1) because of the size of each field. It may have had an impact at the other two sites (Site 2 and 3) but random sampling was used. At Sites 2 and 3 rates of parasitism reached 100% at times which was probably an artifact of low precision in the small sample sizes.

8.3. Results

8.3.1. Moth eclosion, parasitoid emergence and rearing mortality

Moth eclosion at Site 1 (Fig. 8.1) was generally highest over the spring and early summer, but in 1998 and 1999 eclosion started to increase over the winter period. Parasitoid emergence was low over the spring, but increased over the summer and autumn in all three years of the study. Mortalities, due to rearing, were low for most of 1997, but in 1998 and 1999 this mortality increased.

Many of the samples collected at Site 2 (Fig. 8.2) yielded no diamondback moths or parasitoids and as a result there were large fluctuations in emergence over the sampling period. The highest levels of moth eclosion and parasitoid emergence varied over the three years but generally occurred during spring and summer. Rearing mortality was low in 1997, but varied substantially in 1998 and 1999.

At Site 3 (Fig. 8.3) sampling did not occur during certain months and at other times during the study period no diamondback moth or parasitoids were found. In 1998 moth eclosion was generally high over the spring, summer and early autumn, but in 1999 eclosion increased in the winter and remained high over the spring. Parasitoid emergence was low until late spring in 1998 and increased again during late summer and late spring in 1999. The rearing mortality remained fairly low for the majority of the sample period. On the few occasions that it did increase, sample sizes were very small. Generally, at all three sites when moth eclosion was low, parasitoid emergence was high and vice versa (Figs. 8.1 - 8.3).

At all three sites moth eclosion increased with a decrease in percentage parasitism (Fig. 8.4). At each of the sites there was a significant positive correlation between moth eclosion and parasitoid emergence, moth eclosion and rearing mortality, and parasitoid emergence and mortalities (Table 8.1 a). Moth eclosion, parasitoid emergence and the rearing mortality showed a significant positive correlation between the sites, except for parasitism between Site 2 and 3 (Table 8.1 b).

At Site 1 (Fig. 8.5) the abundances of the moths and parasitoids fluctuated substantially with a number of spikes being found. The two main increases in abundance of the diamondback moth were in autumn and spring. Parasitoid abundance was highest from late summer to early winter, and in late spring. In 1999 abundances of both moths and parasitoids was lower than in 1998. At Site 2 (Fig. 8.6) there were three main peaks in abundance over the study, with the first being much greater than the following two. The highest abundances of both moths and parasitoids was found in spring. Over the rest of the study period the abundances were very low. At Site 3 (Fig. 8.7) the abundance of both the moths and parasitoids were lower than at the other sites. Abundance peaked in spring of each year with additional autumn spikes.

At Site 1 there was no detectable lag period between the peak in moth abundance and the peak in parasitoid abundance (Fig. 8.8). However, at Site 2 and 3, the two unsprayed sites, a lag period was found. At Site 2 moth abundance peaked in September 1997 followed by a peak in parasitoid abundance in October 1997. At Site 3 moth abundance peaked in September and October of 1998 and 1999 respectively, followed by a peak in parasitoid abundance in November of both years.

8.3.2. Percentage parasitism by different species

The rates of parasitism in the field varied at the three sites and between the years. Generally parasitism was highest in the late spring, summer and early autumn. At Site 1 (Fig. 8.9) parasitism by *Cotesia plutellae* (Kurdjumov) fluctuated between 0 and 90% while parasitism by both *Diadegma mollipla* (Holmgren) and *Diadromus collaris* Gravenhorst generally remained below 24%. Parasitism by *Oomyzus sokolowskii* (Kurdjumov) was low and sporadic, never increasing above 40% and parasitism by *Apanteles halfordi* Ullyett remained below 2% when it was present.

At Site 2 (Fig. 8.10) parasitism by *C. plutellae*, *D. mollipla*, *D. collaris* and *O. sokolowskii* generally remained below 50%, 30%, 38% and 40% respectively. At Site 3 (Fig. 8.11) parasitism by *C. plutellae* remained below 30% and parasitism by *D. mollipla*, *D. collaris* and *O. sokolowskii* were each below 20%. At both sites parasitism by certain species increased to 100% at times, but this was due to small sample sizes.

8.3.3. Density-dependence

At all the sites the absolute abundance of parasitoids increased as the absolute abundance of moths increased (Fig. 8.12). All the sites showed significant positive correlations ($p < 0.05$) between the abundance of parasitoids and the abundance of moths ($r = 0.31$, $r = 0.53$ and $r = 0.35$, respectively). This suggests possible density-dependence at all of the sites. The relationship between the different parasitoid species and moth eclosion showed a similar trend at each site (Figs. 8.13 - 8.15). The abundance of parasitoids increased as moth abundance increased, but not all of the relationships were significant (Table 8.2). *Diadegma mollipla* was the only parasitoid that showed a significant correlation at all three sites. The *C. plutellae* population size was only significantly correlated with moth abundance at Site 2 and 3; *D. collaris* at Site 1 and 2 and *O. sokolowskii* at Site 2 and 3.

8.4. Discussion

8.4.1. Moth eclosion, parasitoid emergence and rearing mortality

In the Eastern Cape the diamondback moth population is attacked by parasitoid wasps (Figs. 8.1 - 8.3). The percentage of moth and parasitoid emergence varied during the study period at all three sites. When parasitism was high, moth emergence was low but as parasitism levels drop, so moth emergence increased (Fig. 8.4). This suggests that the parasitoids are having a regulatory effect on the moth population and that sources of mortality due to rearing were fairly constant.

The significant positive correlations with moth eclosion, parasitoid emergence and rearing mortality between the sites indicate that there was considerable site-to-site variation (Table 8.1 b). There was no positive correlation between Site 2 and 3. This may have been due to the lower abundance of parasitoids at Site 3, or as a result of the inconsistent sampling because of the lack of host plants at particular times during the study. Generally when moth abundance was high, parasitoid abundance was low (Figs. 8.5 - 8.7). Studies have shown that as the density of the diamondback moth increases, parasitism decreases (Talekar & Yang, 1991; Yang *et al.*, 1994) which suggests that parasitoids are unable to control the moth at very high densities.

At Site 2 and 3, the unsprayed sites, there was a lag period between the peak in moth abundance and the peak in parasitoid abundance (Fig. 8.8). At Site 2 this lag period was three weeks in all three years. At Site 3 the lag period was longer, five weeks in the second year and six weeks in the third year. Sampling started late in the season in the first year so no lag could be determined. Goodwin (1979) in Victoria, Australia found that the larval parasitoids, *Diadegma semiclausum* Hellèn, *Diadromus collaris* and *Diadegma rapi* Cameron, were syncronised with host numbers but there was a lag during the winter period of about three weeks. It was suggested that because Victoria has a mild climate, the host population was present all year and therefore the parasitoid populations are able to continue to build-up even over the winter. The presence of a lag period over the winter months was possibly due to the slowing down of parasitoid activity or slow moth development

(Goodwin, 1979). Mitchell *et al.* (1997a) found a two week lag between the diamondback moth larvae and percentage parasitism in collards and suggested that the parasitoid, *Diadegma insulare* Cresson, was regulating the diamondback moth populations in the collards. The reason for the lack of a lag phase at Site 1 in the Eastern Cape study was probably due to insecticide spraying at this site and therefore no cycle could develop between the parasitoids and the moth.

8.4.2. Percentage parasitism by different species

Mustata (1992) found that the diamondback moth population in Romania was reduced by between 80 and 90% by a complex of parasitoids which resulted in parasitism levels of 63%. He showed that the relationship between the different species varied from sample to sample in the same locality, from time to time, from year to year and from area to area. Similarly, the percentage parasitism of each of the species found in the Eastern Cape varied throughout the study period and between the sites (Figs. 8.9 - 8.11). It was high at all the sites during the spring months (September to November), dropping to lower levels during the rest of the year.

Liu *et al.* (2000) looked at the seasonal abundance of the parasitoid complex in China, where eight species of primary parasitoids were recorded. Larval and pupal parasitism showed two peaks per year, one in June and July (summer) and the second from September to November (autumn) where parasitism ranged from 10 to 60%, occasionally reaching 80%. The major parasitoids included *C. plutellae*, *D. collaris* and *O. sokolowskii*. Parasitism was mainly due to *C. plutellae*, which was present throughout the year although numbers were low in the winter, and *O. sokolowskii*. A similar situation was found in the Eastern Cape with two main peaks in parasitism by a similar complex of parasitoids. Goodwin (1979) found that in Victoria, Australia, parasitism rates were highest in spring and summer but that very high temperatures in summer reduced both the moth and the parasitoid abundance and in drought conditions these reductions intensified. The parasitism levels in autumn depended on how severely the parasitoids were depleted and on their rate of recovery. Parasitism rates varied between 41-57% during the 3-year study. Victoria has a mild climate and as a result parasitism continued to rise during winter, even though the host population decreased. The Eastern Cape has a similar climate to Victoria and similar patterns in the rates and timing of the highest levels of parasitism were found.

In unsprayed fields in Jamaica, large numbers of adult *C. plutellae* were found flying around the cabbages. In sprayed fields very few adults were seen, but cocoons were still found (Alam, 1992). In the Eastern Cape parasitism by *C. plutellae* reached between 70 and 90% at the sprayed site (Site 1), and at the unsprayed sites (Site 2 and 3) it reached 55% and 50%, respectively. *Cotesia plutellae* appears to have developed some resistance to insecticides at Site 1 (Chapter 3). Waladde *et al.* (2001) found that in the Alice area *C. plutellae* reached parasitism levels between 30 and 50%. When measured in an insecticide-free environment, parasitism was between 90 and 95% for 8 months of the year but during winter and early spring it was below 30%.

Parasitism by *D. mollipla* and *D. collaris* was similar at the sprayed site (Site 1) and the unsprayed sites (Site 2 and 3) but parasitism by *O. sokolowskii* was slightly higher at the unsprayed sites than at the sprayed sites. Occasionally 100% parasitism by *C. plutellae*, *D. mollipla*, *D. collaris* and *O. sokolowskii* was found at the unsprayed sites, but this was generally when diamondback moth numbers were very low. Lasota & Kok (1986) looked at percent parasitism by *D. insulare* in insecticide-free cabbage fields in southwestern Virginia (USA) and found that parasitism was 46% and 69% respectively in the two years of study. This study indicates that parasitism levels in the Eastern Cape reach levels that are similar and in many cases better than those in other parts of the world (Appendix 1). There are concerns about the interpretation of data using percentage parasitism, but in this study these limitations are compensated for by frequent sampling over an extended period and the general trend in parasitism can be shown. This study did not determine generational levels of parasitism, in order to do this the phenologies of both the host and the parasitoids are critical (Van Driesche, 1983).

The positive correlations between primary parasitoid species at the three sites (Table 7.2 a - c, Chapter 7) indicated that the hyperparasitoids had very little impact on the primary parasitoids. In many parts of the world (Velasco, 1983a; Ooi, 1986; Waterhouse, 1992) the efficacy of parasitoids is reduced by hyperparasitoids, but this does not seem to be the case in the Eastern Cape.

Studies have found that the combined parasitism by two or more species often increased the overall levels of parasitism in the diamondback moth (Harcourt, 1960; Lim, 1986). In northeast Florida the combined seasonal parasitism by the introduced *C. plutellae* and the indigenous parasitoid *D. insulare* reached 34% in some fields (Mitchell *et al.*, 1997b). In Jamaica there is a complex of 5 parasitoid species which help to provide suitable control (Alam, 1992). There is an indication from the results in the Eastern Cape that a complex of parasitoids is more effective than a single species. At the sprayed site, Site 1, *C. plutellae* was the dominant species while a complex of species was found at the two unsprayed sites (Site 2 and 3). It was at these unsprayed sites that diamondback moth abundance was reduced. The highest rates of parasitism correspond to periods when the larval parasitoid, *C. plutellae*, and the larval-pupal parasitoids *D. mollipla* and *O. sokolowskii* showed the highest abundances. In Quebec, where the diamondback moth is only present over the summer months, the complex of parasitoids was unable to provide effective control because they were present too late in the season. It was suggested that in this case, parasitoids are needed for the eggs and early instars (Godin & Boivin, 1998a).

8.4.3. Density-dependence

There was a general trend for parasitoid abundance to increase disproportionately as the moth abundance increased (Fig. 8.12). This suggests that the parasitoids are density-dependent and are having a stabilising effect on the diamondback moth population. However, not all of the species showed significant relationships, for example *D. collaris* at Site 3 (Fig. 8.14), and *O. sokolowskii* at Site 1 and 2 (Fig. 8.15). Other factors, including temperature, are also having an impact on the relationship and the combined effect of abiotic and biotic factors make analysis difficult. Density-dependance has been shown in some of the parasitoids associated with the diamondback moth, including *C. plutellae* (Ooi, 1986; Alam, 1992; Ooi, 1992; Rowell *et al.*, 1992; Mitchell *et al.*, 1999; Waladde *et al.*, 2001), and *D. insulare* (Harcourt, 1986; Mitchell *et al.*, 1999). Harcourt (1986) showed that even though *D. insulare* showed density-dependence and had the ability to stabilize the diamondback moth population, the process was gradual and unlikely to happen in the short season in Canada. However, Fox *et al.* (1990) found that parasitoid abundance was directly related to the number of diamondback moth and that the rate of parasitism was independent of diamondback moth density and therefore concluded that *D. insulare* was density-independent.

8.5. Conclusion

The last three chapters (Chapter 6, 7 and 8) have shown that there are a number of parasitoids associated with the diamondback moth in the Grahamstown area of the Eastern Cape Province. Instantaneous measures of parasitism provided a means to determine trends in parasitism rates. These trends showed that the parasitoids were able to provide suitable control in particular circumstances. These circumstances were found when there was a complex of parasitoids acting in an insecticide-free environment as was seen at Site 2 and 3. At Site 1 *C. plutellae* was the dominant parasitoid but moth abundances remained high, possibly due to resistance. At Site 2 and 3 a complex of parasitoids were found and after the first year of the study moth abundance was drastically reduced.

Table 8.1 a. Pearson correlation coefficients between percentage moth eclosion (M), parasitoid emergence (P) and rearing mortality (Mo) at each site. Correlations in bold are significant ($p < 0.05$).

	Site 1	Site2	Site 3
M and P	**r = 0.22**	**r = 0.52**	**r = 0.40**
M and Mo	**r = 0.71**	**r = 0.65**	**r = 0.56**
P and Mo	**r = 0.63**	**r = 0.63**	**r = 0.67**

Table 8.1 b. Pearson correlation coefficients between each of the sites and moth eclosion, parasitoid emergence and rearing mortality. Correlations in bold are significant ($p < 0.05$).

Sites	Moth eclosion	Parasitoid emergence	Rearing mortality
1 and 2	**r = 0.80**	**r = 0.38**	**r = 0.51**
1 and 3	**r = 0.30**	**r = 0.36**	**r = 0.37**
2 and 3	**r = 0.44**	r = 0.14	**r = 0.29**

Table 8.2. Pearson correlation coefficients between absolute abundance of parasitoid species and absolute abundance of the diamondback moth at each site. Correlations in bold are significant ($p < 0.05$).

	C. plutellae	*D. mollipla*	*D. collaris*	*O. sokolowskii*
Site 1	r = 0.18	**r = 0.41**	**r = 0.30**	r = 0.17
Site 2	**r = 0.38**	**r = 0.44**	**r = 0.29**	**r = 0.26**
Site 3	**r = 0.36**	**r = 0.34**	r = 0.17	**r = 0.30**

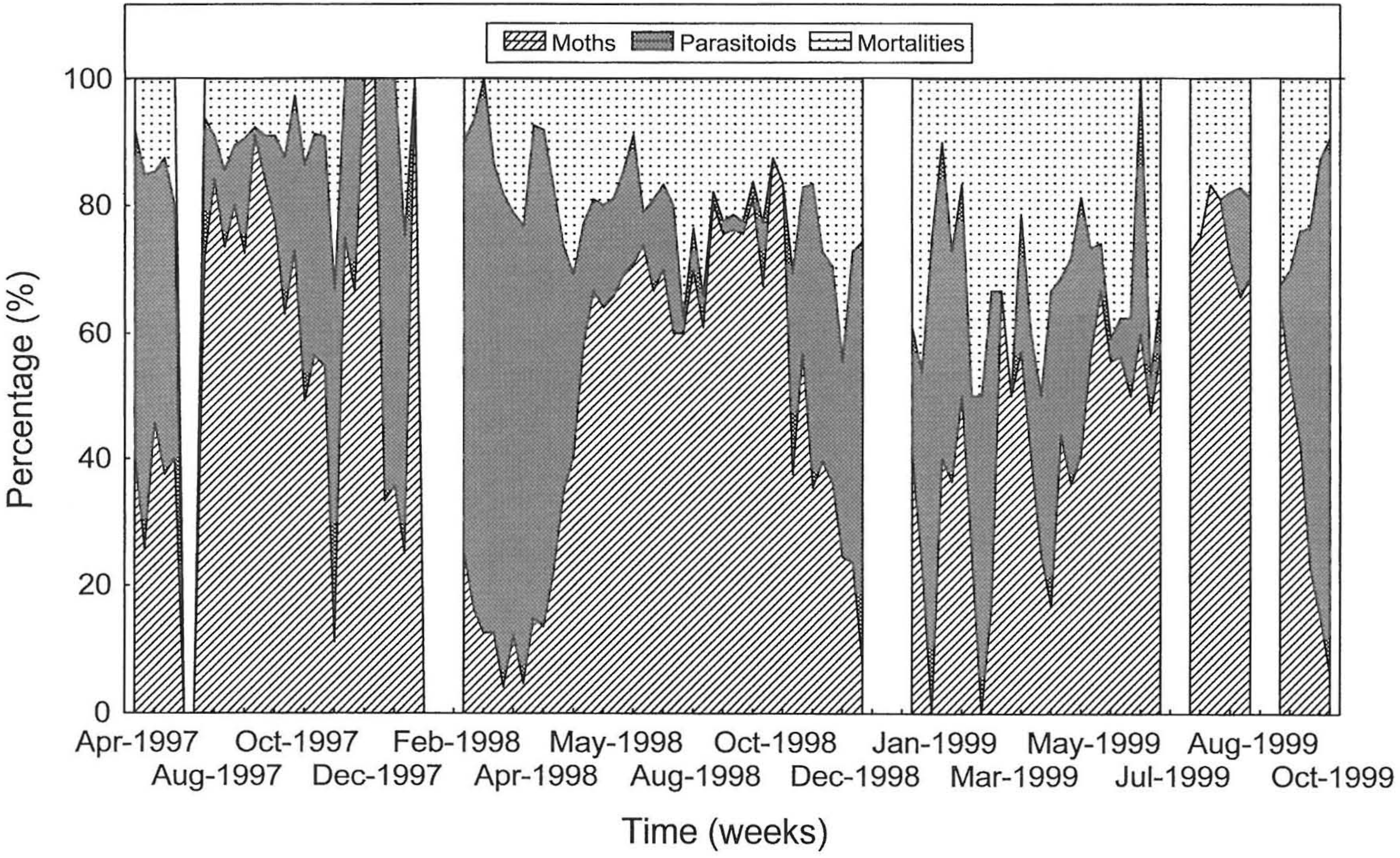

Figure 8.1. Moth eclosion, parasitoid emergence and mortality due to rearing at Site 1 over the study period.

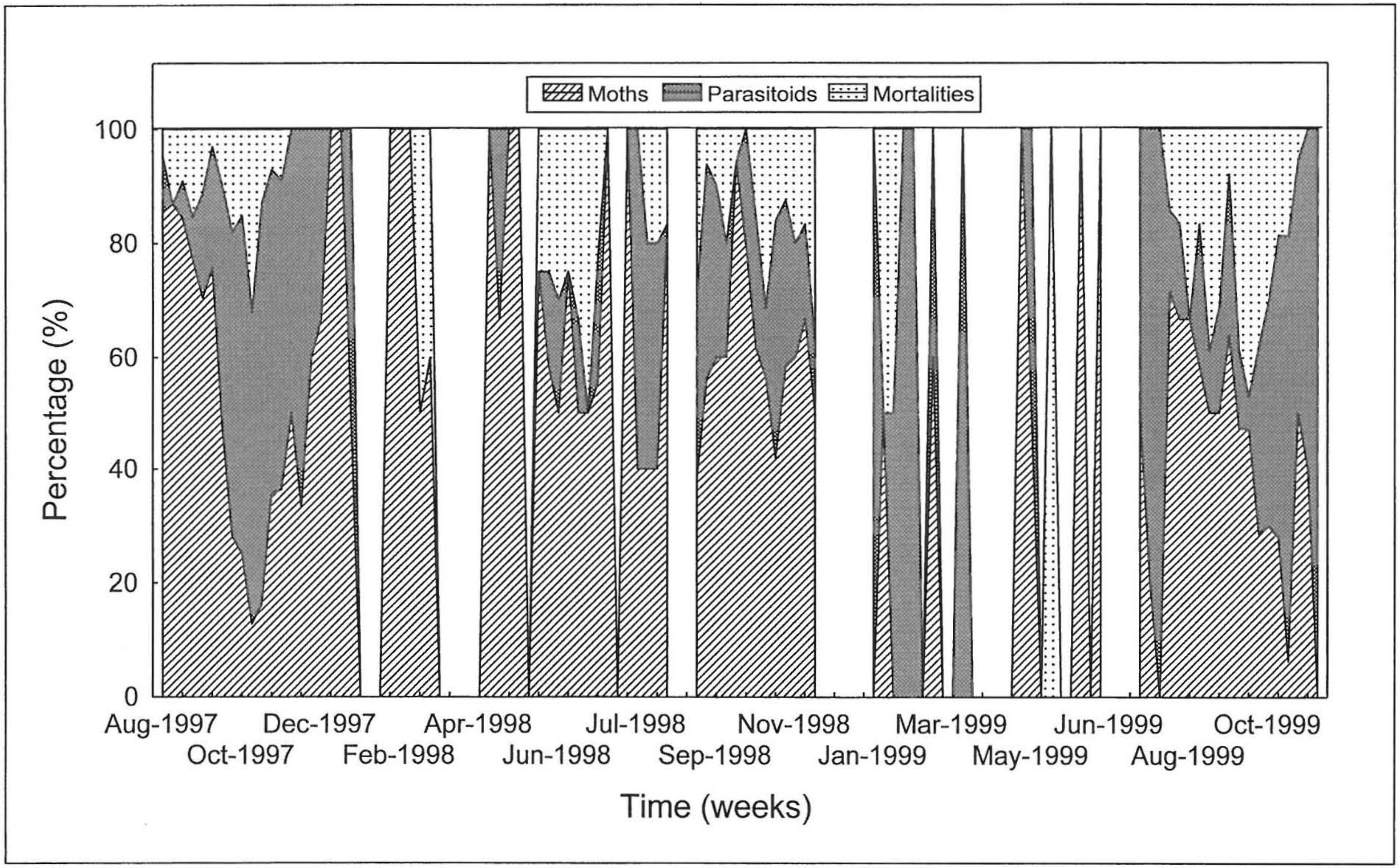

Figure 8.2. Moth eclosion, parasitoid emergence and mortality due to rearing at Site 2 over the study period.

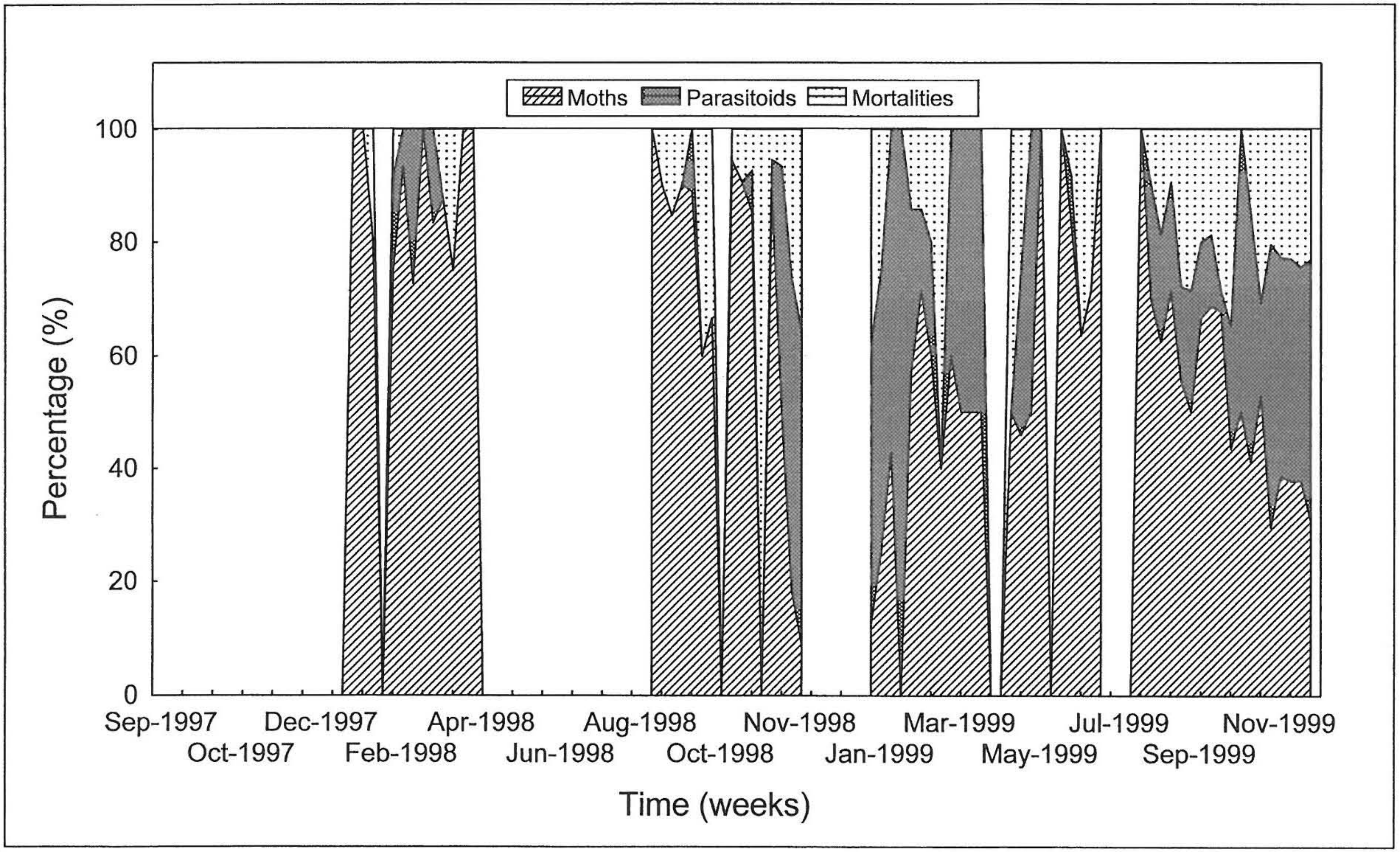

Figure 8.3. Moth eclosion, parasitoid emergence and mortality due to rearing at Site 3 over the study period.

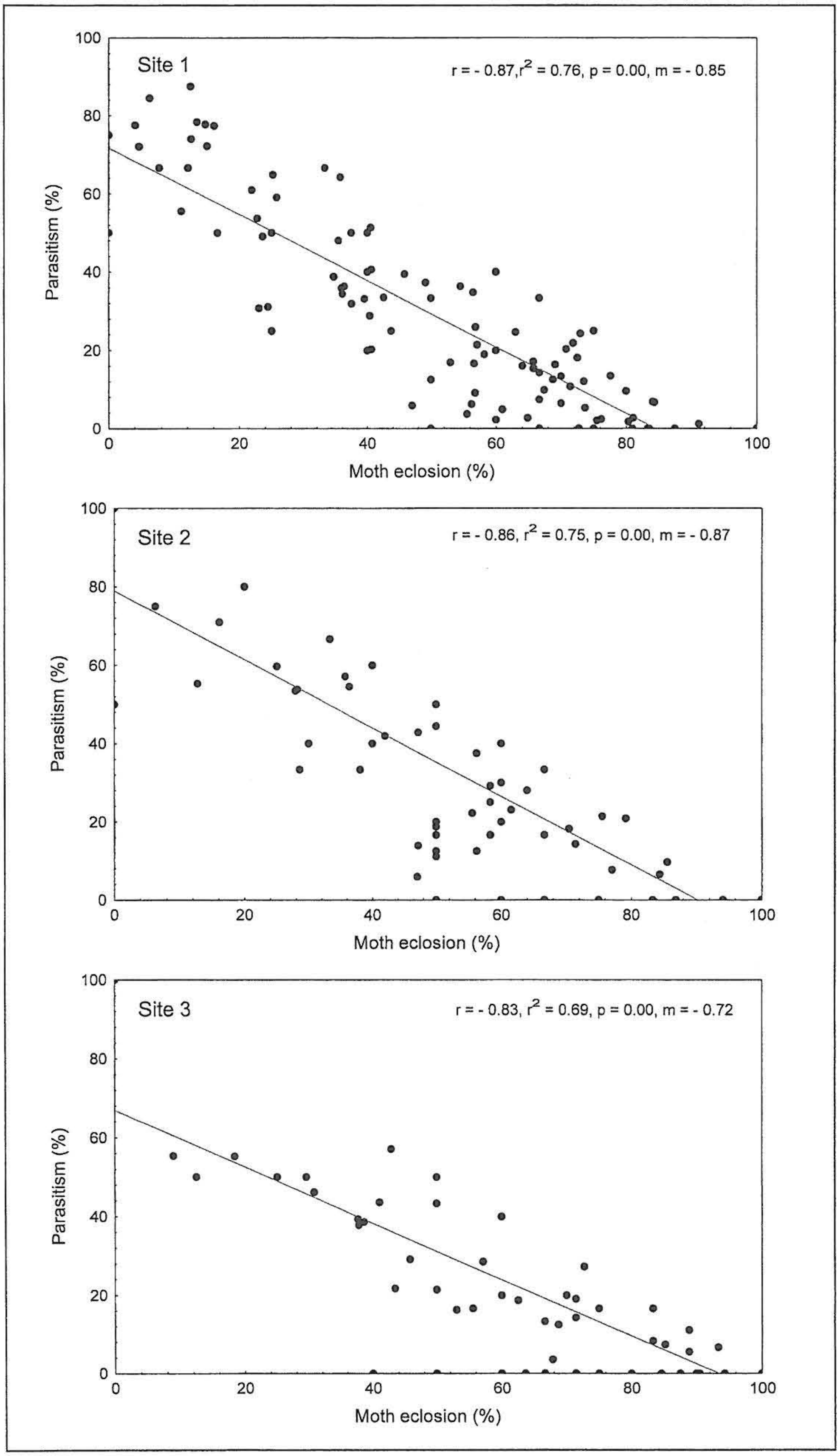

Figure 8.4. Relationship between moth eclosion and parasitism at each site.

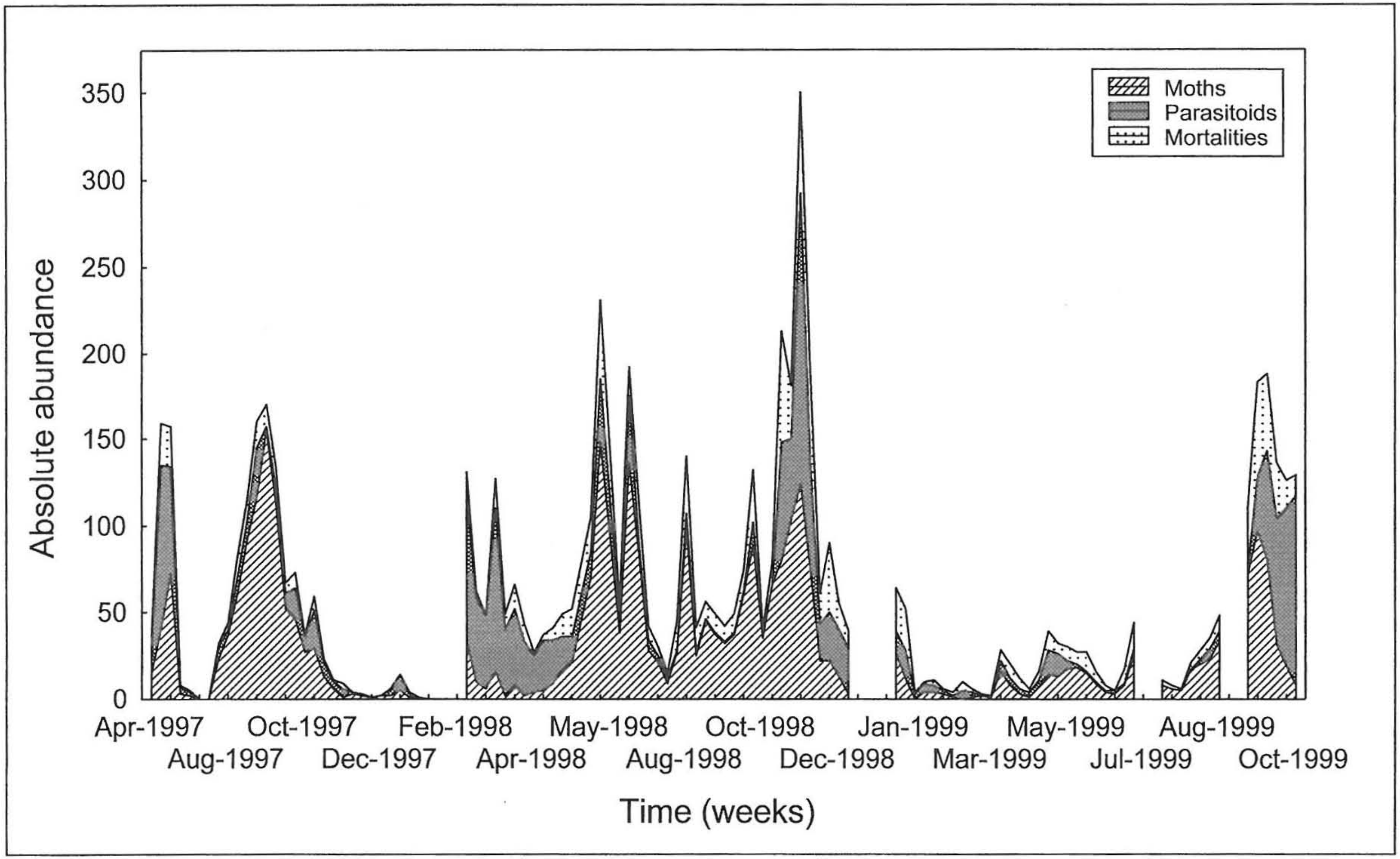

Figure 8.5. Absolute abundance of the emerged diamondback moth, its parasitoids and mortalities due to rearing at Site 1.

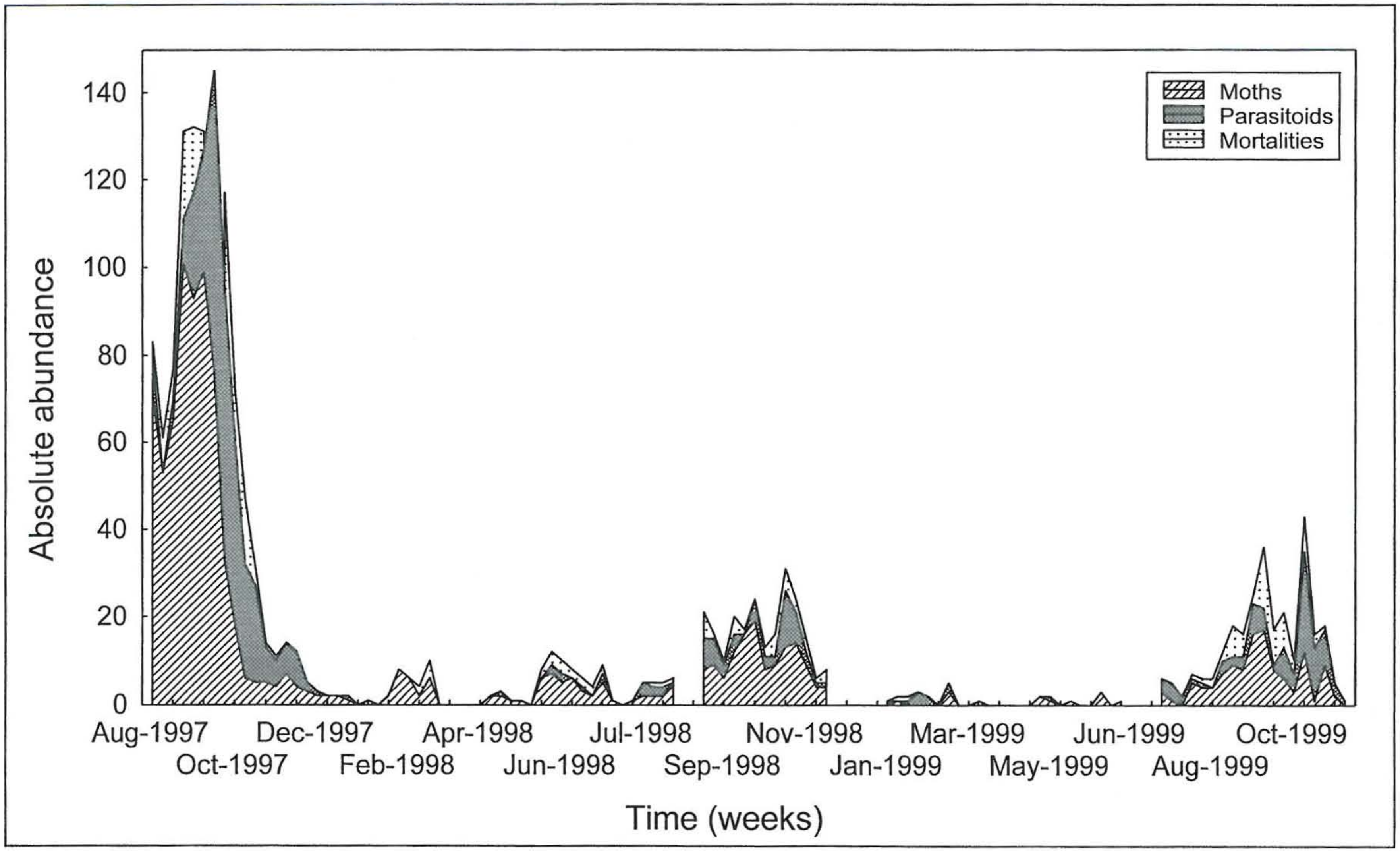

Figure 8.6. Absolute abundance of the emerged diamondback moth, its parasitoids and mortalities due to rearing at Site 2.

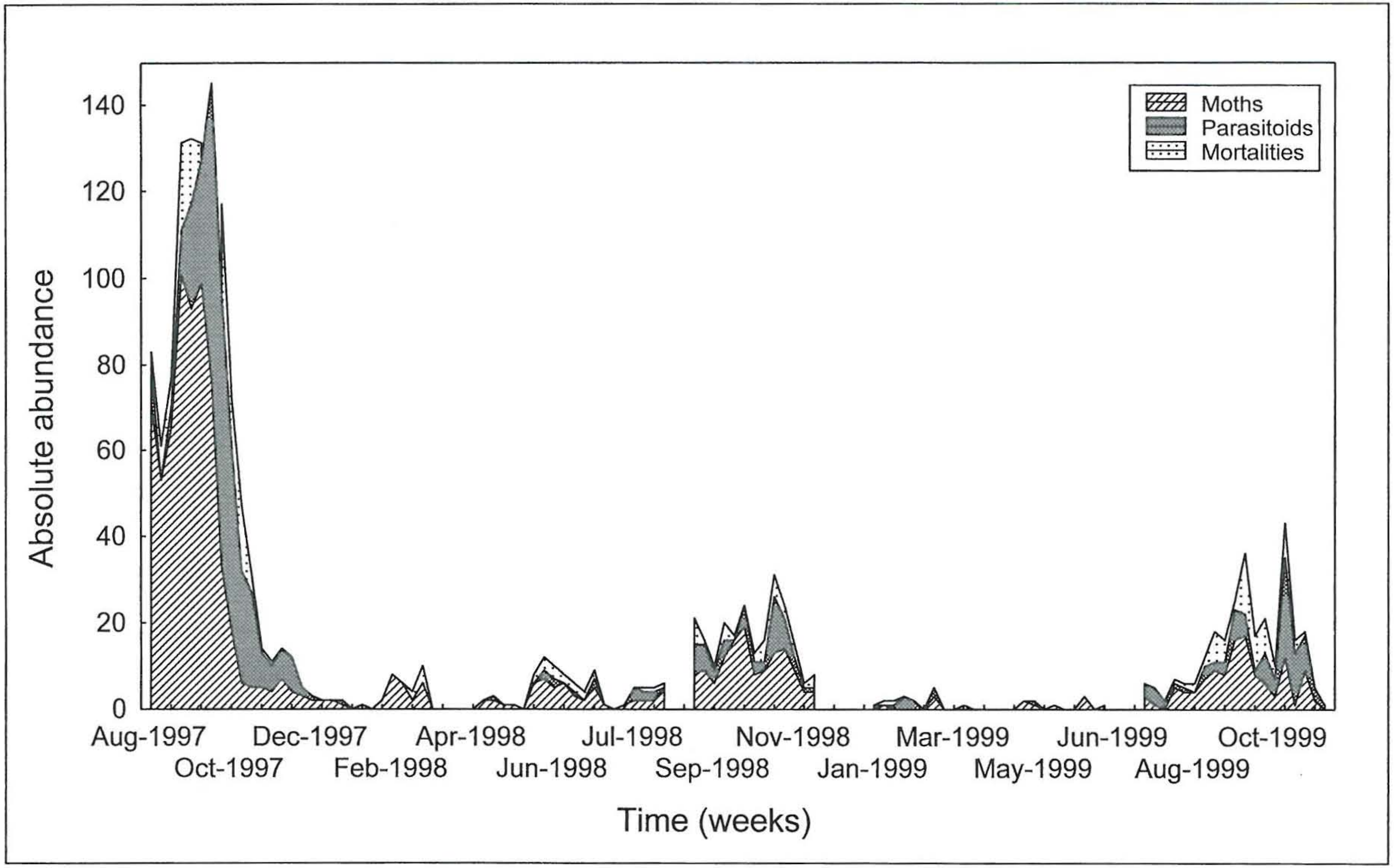

Figure 8.7. Absolute abundance of the emerged diamondback moth, its parasitoids and mortalities due to rearing at Site 3.

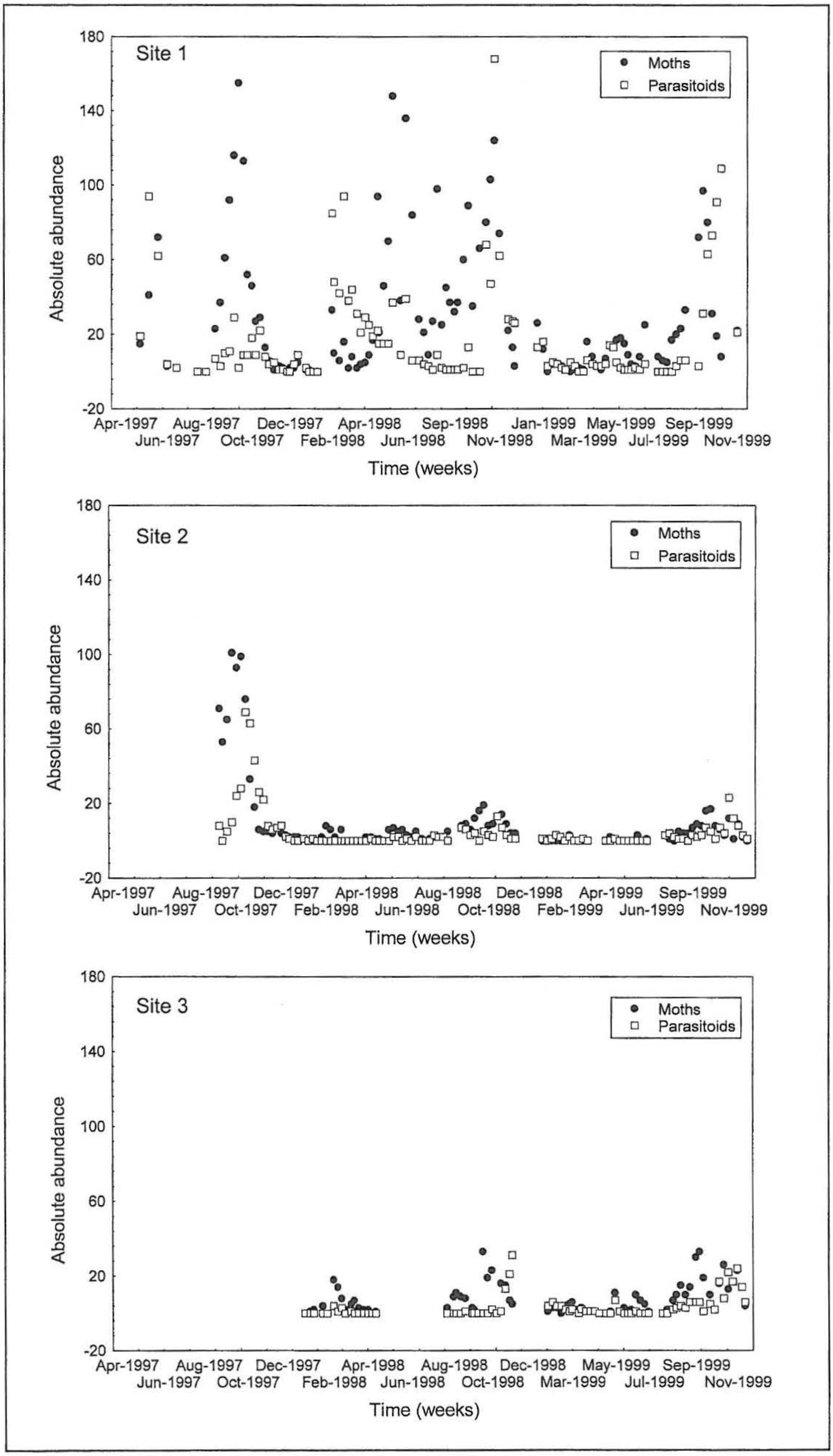

Figure 8.8. Absolute abundance of the diamondback moth and its parasitoids at each site over the study period.

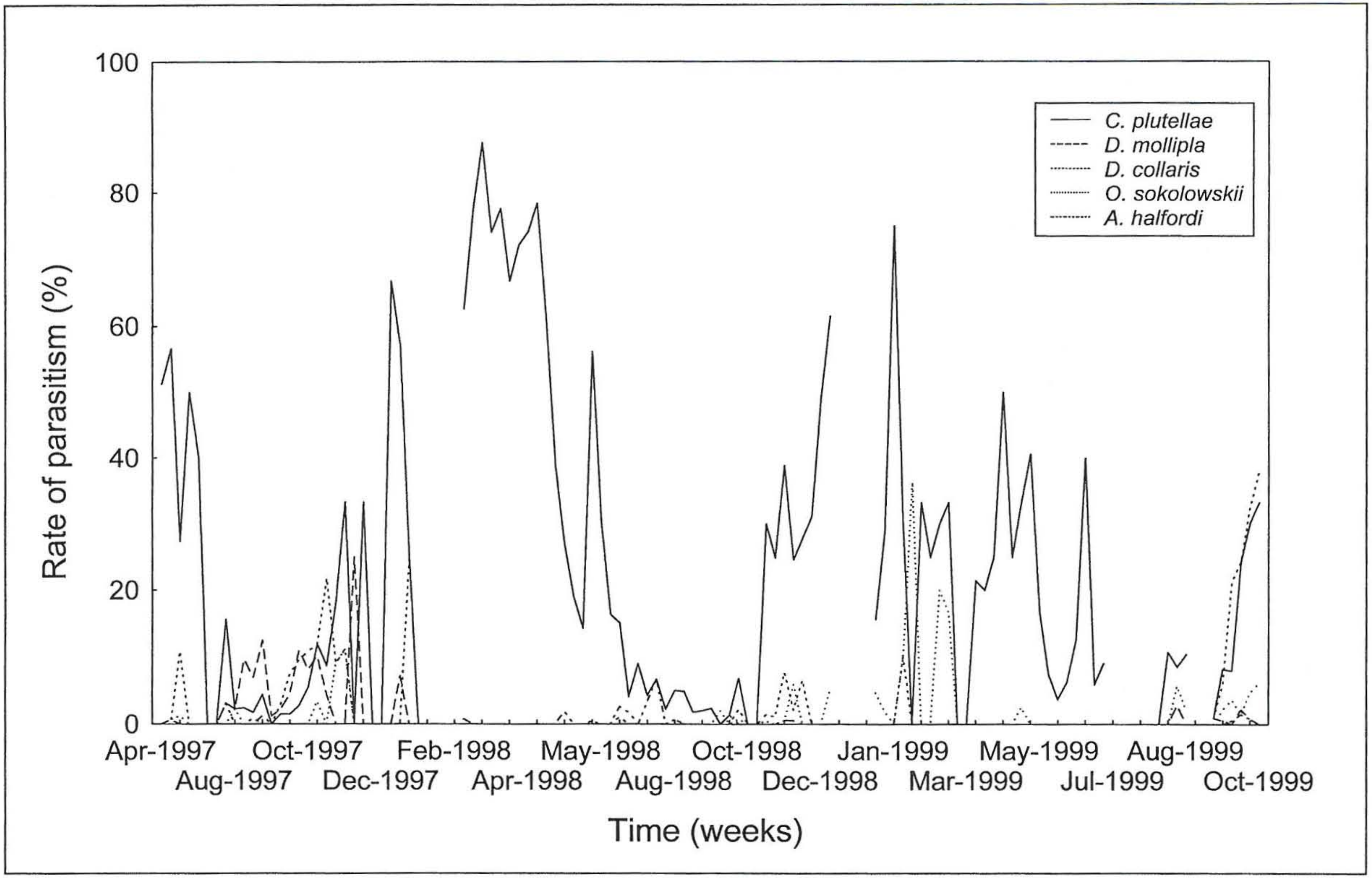

Figure 8.9. Rate of parasitism by the parasitoids associated with the diamondback moth at Site 1 from April 1997 to October 1999.

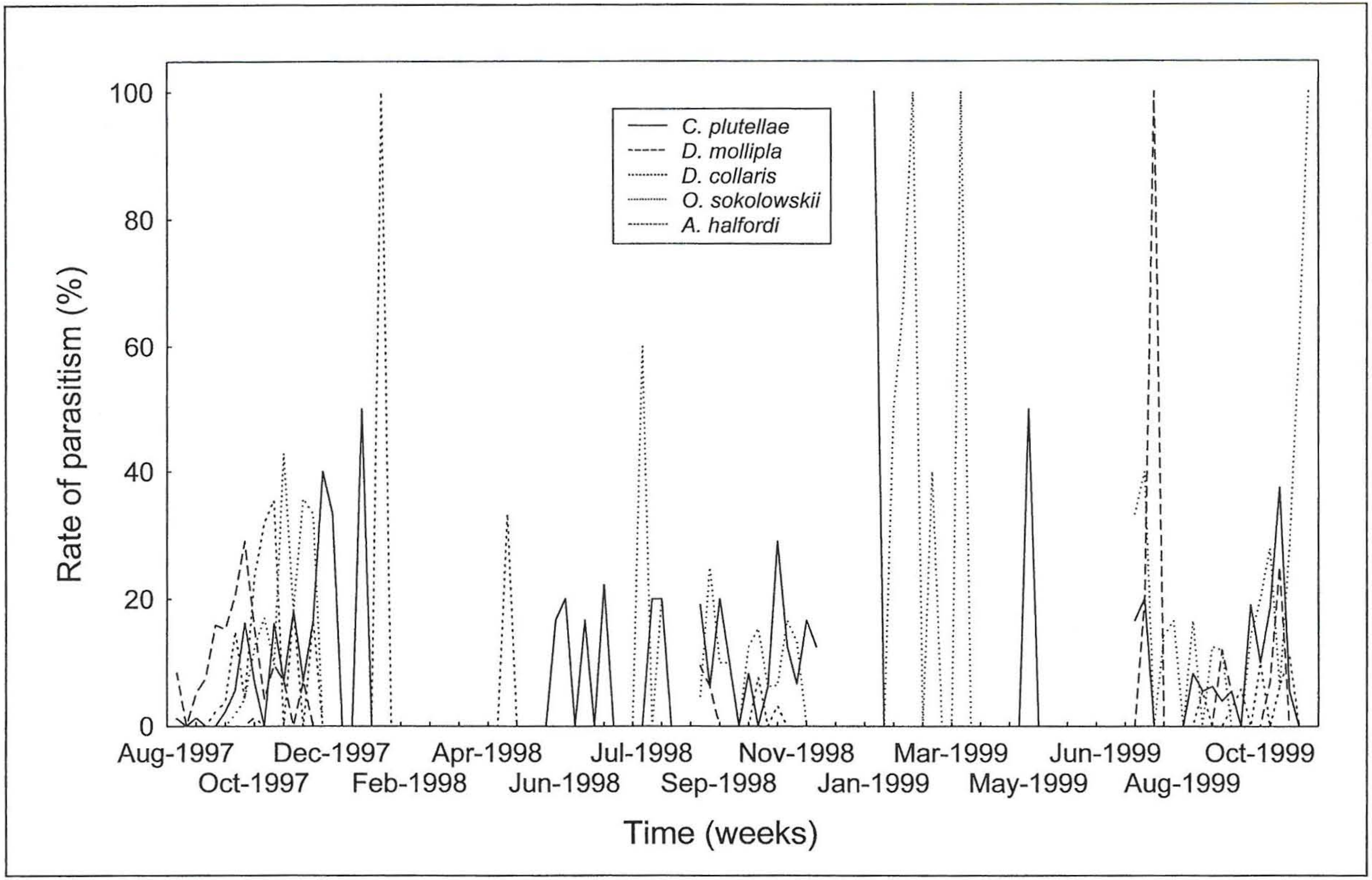

Figure 8.10. Rate of parasitism by the parasitoids associated with the diamondback moth at Site 2 from August 1997 to November 1999.

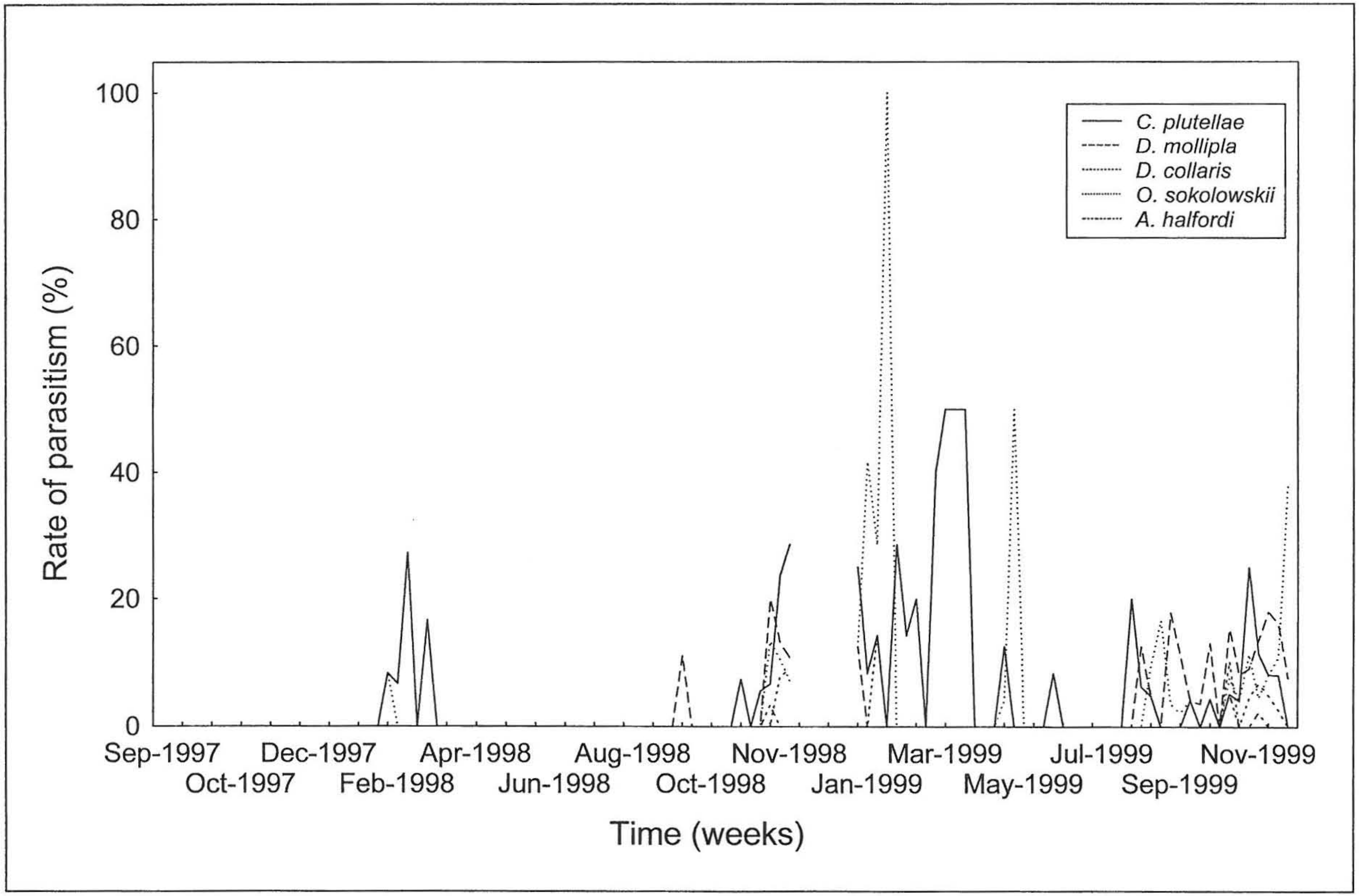

Figure 8.11. Rate of parasitism by the parasitoids associated with the diamondback moth at Site 3 from September 1997 to November 1999.

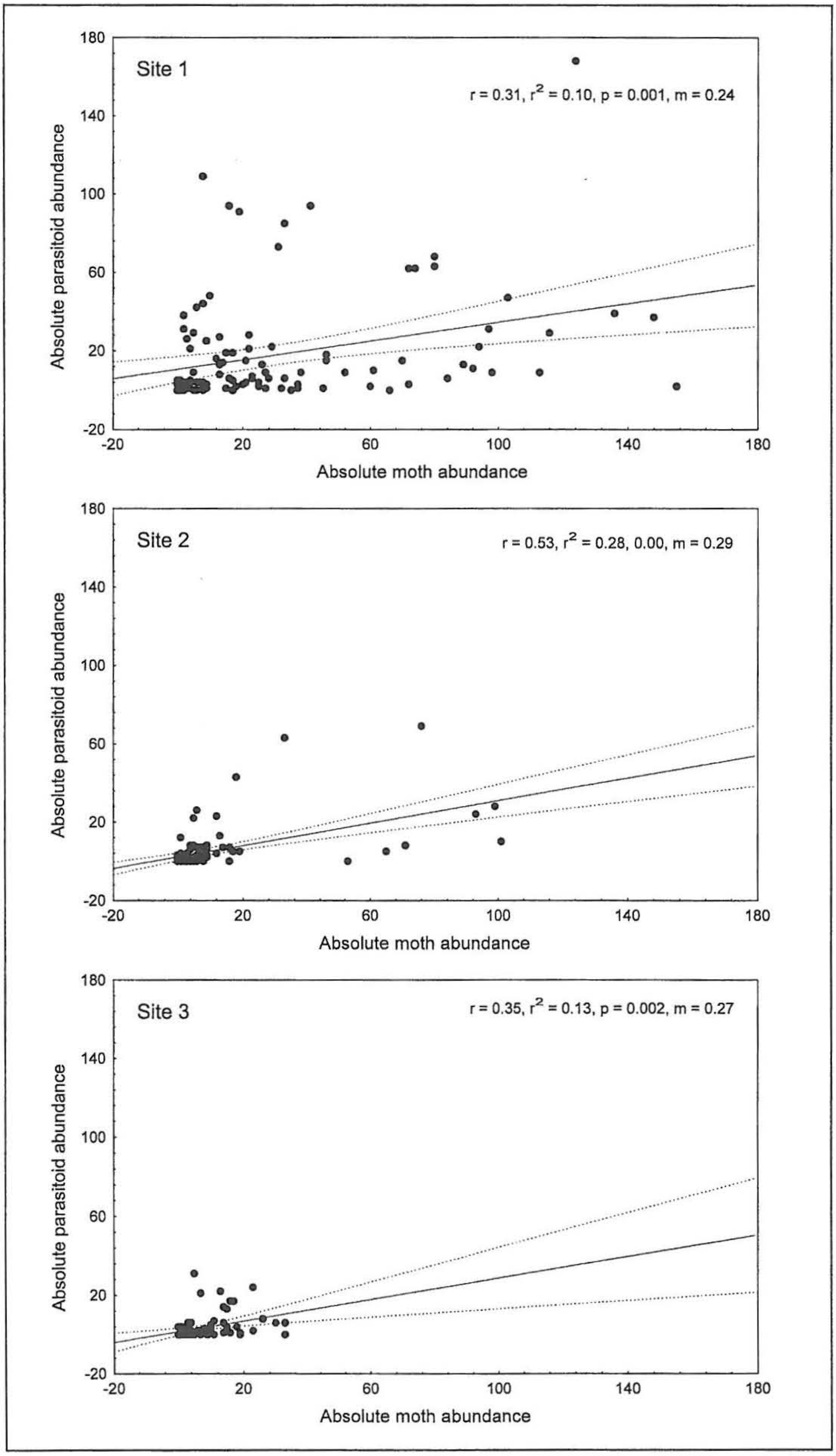

Figure 8.12. Relationship between diamondback moth and parasitoid absolute abundance at each site.

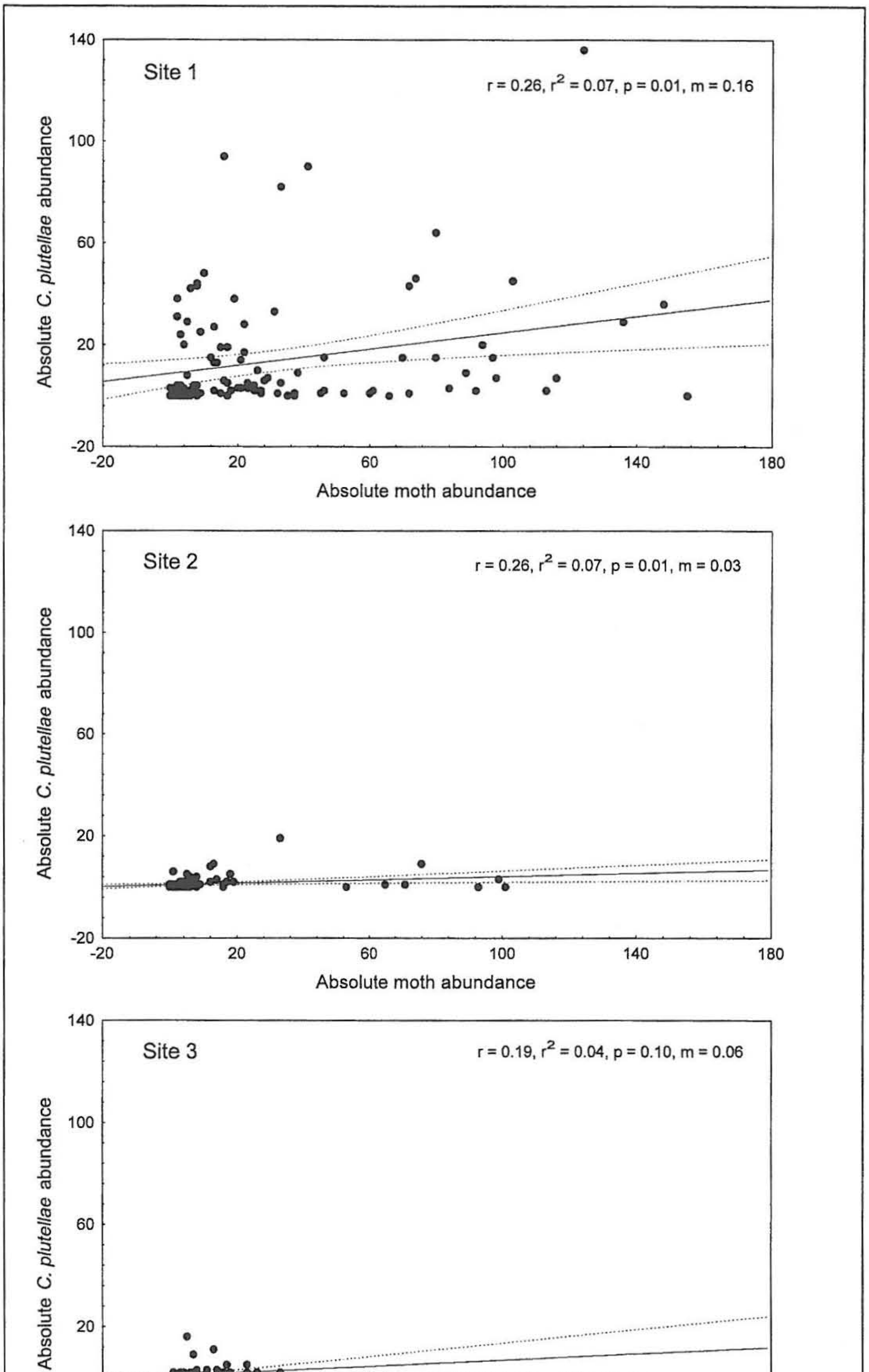

Figure 8.13. Relationship between diamondback moth and *Cotesia plutellae* absolute abundance at each site.

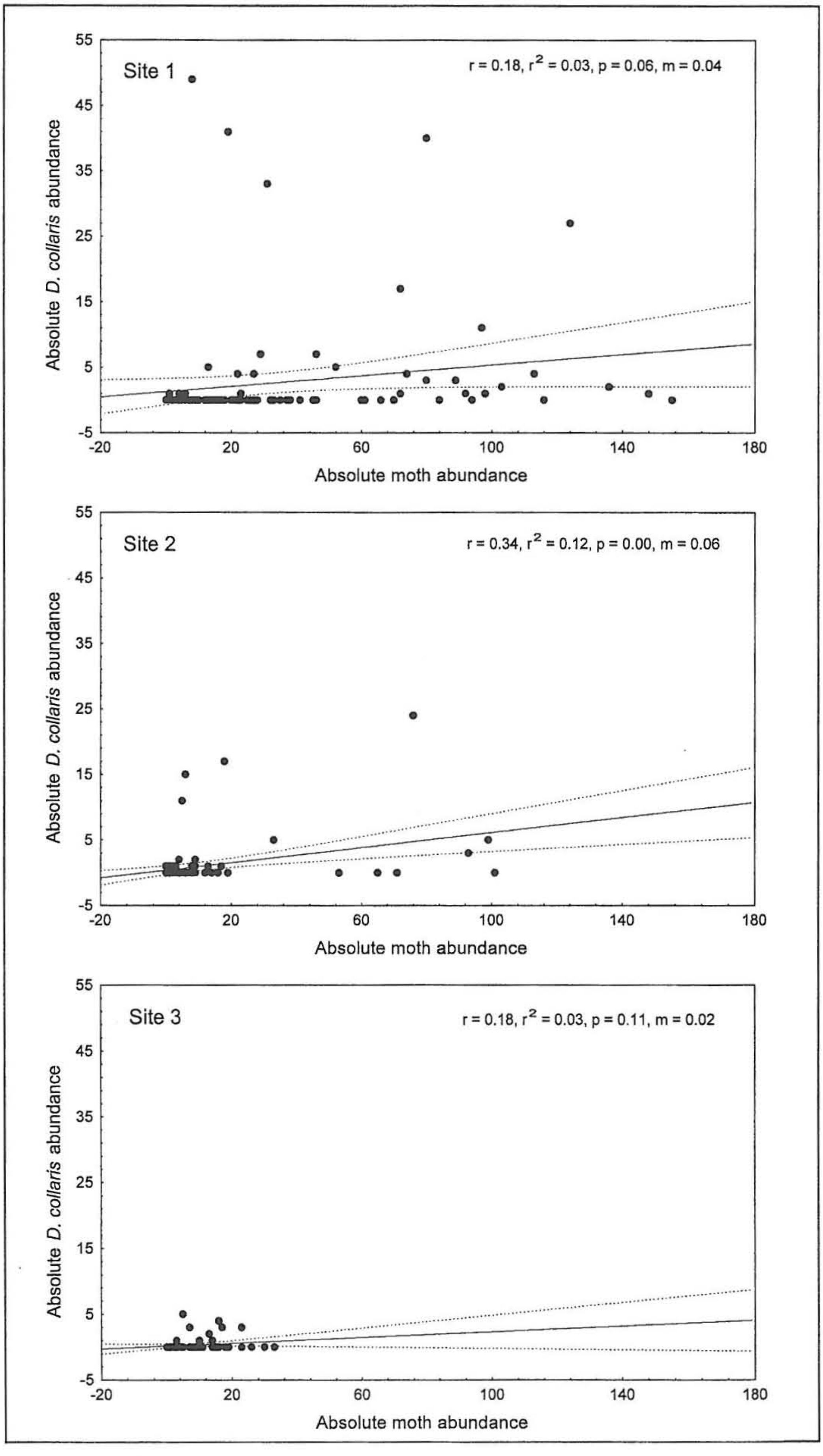

Figure 8.14. Relationship between diamondback moth and *Diadromus collaris* absolute abundance at each site.

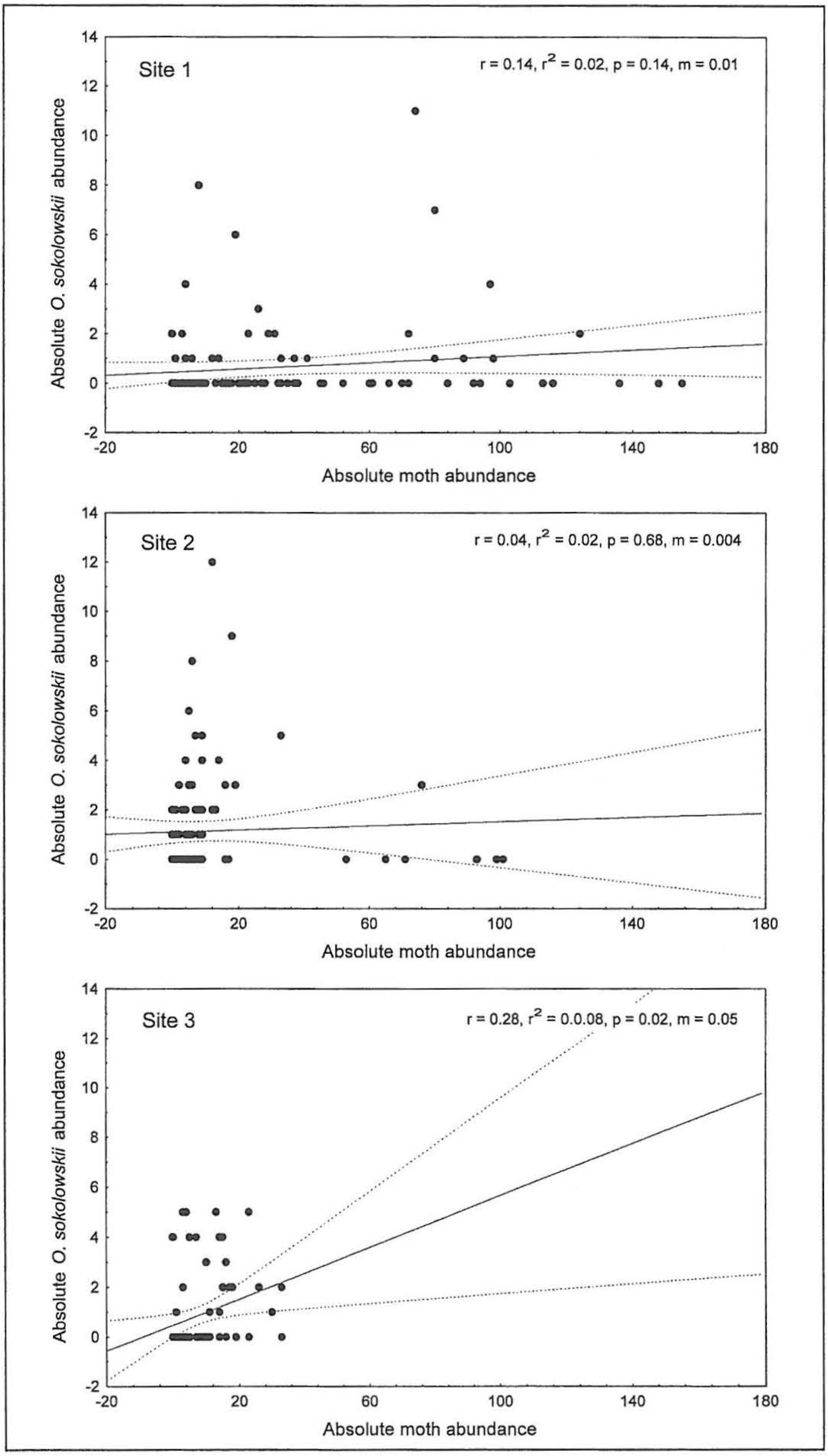

Figure 8.15. Relationship between diamondback moth and *Oomyzus sokolowskii* absolute abundance at each site.

Chapter 9:

Edge distributions in cabbage fields

9.1. Introduction

Determining the spatial distribution of a pest within a crop is difficult as remote sensing of insect populations is not possible and scouting the crop is very time-consuming (Murchie *et al.*, 1999). Edge distributions of pest insects within crops are common (Tahvanainen & Root, 1972; Price, 1976; Altieri & Letourneau, 1982; Russell, 1989; Weisz *et al.*, 1996; Hu *et al.*,1997; Murchie *et al.*, 1999; Landis *et al.*, 2000). Therefore dividing the crop into an edge and centre portion can offer an easy solution to determining spatial distributions of pests. This reduces the possibility of either underestimating or overestimating the pest population (Hu *et al.*,1997), which can be caused by scouting plants only in the centre or on the edge of the field. Often in crop pest sampling, the outer edges of the field are not sampled so as to avoid edge effects (Dempster, 1969). However, understanding this spatial variation results in targeting different areas of the crop for effective control, especially insecticide application (Weisz *et al.*, 1996; Hu *et al.*, 1997; Murchie *et al.*, 1999).

Edge distributions are a result of diffusion or migration of pests and or natural enemies from surrounding areas and are often associated with the vegetation found growing in the vicinity of the field. Outbreaks of pest populations occur more often in less diverse communities, such as in monocultures, as there is a greater concentration of food available for specialist insect pests (Pimentel, 1961b; Andow, 1991). The variety of plant species growing amongst the crop, on the margins of fields and in the general vicinity of the crop constitutes an increase in vegetational diversity within the agricultural environment. Vegetational diversity within the field has often been considered as a way to reduce insect herbivore populations and to increase those of natural enemies, for example parasitoids, in agricultural crops (Risch *et al.*, 1983; Andow, 1990; Schellhorn & Sork, 1997). In the past weeds within and around fields have been considered detrimental to commercial crops and removed through cultural and chemical control. However, many weed species play a beneficial role in the diversity and stability of insect populations found within these systems and can therefore be used as a form of habitat management to help conserve natural enemies (Altieri, *et al.*, 1977; Altieri & Letourneau, 1982; Powell, 1986; Landis, *et al.*, 2000).

In the past, agricultural research has generally focused only on the crop and not on the interaction between the crop and the surrounding landscape components. It is important to adopt a more holistic approach when trying to understand plant-pest interactions in an agro-ecosystem (Altieri *et al.*, 1983; Kemp & Barrett, 1989). This implies the need to take into account not only the crop, but also the surroundings of the field. Insect pests on crop host plants are affected by a number of factors including the size of the field, other vegetation, plant density, distance from other fields and their proximity to overwintering sites and alternate hosts (cited by Cromartie, 1975). This chapter examines the edge distribution of the diamondback moth and its parasitoids in three fields taking into consideration the conditions surrounding each field.

9.2. Material and methods

Three cabbage fields were sampled on the commercial farm, Lower Melrose (Site 1). The first field was sampled on the 3rd June, the second on the 6th September and the third on the 14th September 1999. Each field was sampled once and the crops were similar in age at the time of sampling. The presence of vegetation, crops, roads and ploughed land around each field was noted and the weeds identified. The number of cabbages in the outer vertical and horizontal rows of each field were counted and the field was divided into a geometric grid (Fig. 9.1) on the assumption that moths would spread through the field in a diffusion-like process. The cabbage plant at each point on the grid was sampled for each instar of diamondback moth larvae, diamondback moth pupae and parasitoid cocoons. All larvae, pupae and cocoons were counted, collected and reared through to adulthood in a constant environment room at 25°C, 16:8 hours light:dark. The number of moths and the number of each species of parasitoid eclosing were recorded. The data were plotted on contour maps using Statistica v.5. Least-squares interpolation was used as the survey results were only point estimations of the local population densities, and varied even between neighbouring cabbages. Each field was divided into an edge and a centre to determine whether there was a difference between diamondback moth abundance, parasitoid abundance, moth eclosion and parasitism. The edge included the cabbage plants within 2.5 meters from the outer row and the centre was the remaining area of the field.

9.3. Results

9.3.1. Conditions around the fields

Different conditions and a range of plant species were found surrounding each of the fields (Fig. 9.1). These species included other cruciferous plants, both exotic and indigenous, including *Rapistrum rugosum* (L.) All. (wild mustard), *Capsella bursa-pastoris* (L.) Medik (shepherd's purse) and *Lepidium* spp.(pepper weed). Generally there was a grassy verge around each field with one of the main species being kikuyu grass (*Pennisetum clandestinum* Chiov.). The other grass species were not identified. Other weeds included plants from the families Asteraceae, Fabaceae and Primulaceae. Most of the plant species grew with or amongst the grass along the verges. A large amount of natural bush grew on the farm, sometimes within 10 m of the cabbage crops. Crop species growing in adjacent fields included paprika, tomato and cabbage. Field 1 was separated from the other two fields by an unweeded paprika field (Fig. 9.1). Some adjacent fields, originally growing cabbage, had recently been ploughed over and others were lying fallow.

9.3.2. Field abundances of the diamondback moth

The absolute abundance of diamondback moth larvae (Fig. 9.2) and pupae (Fig. 9.3) collected at each field showed a general trend to increase towards the edges of the fields. T-tests showed that there was a significant difference ($p < 0.05$) between the abundance of larvae ($t = 1511.15$, 178.08 and 153.24 for Field 1,2 and 3 respectively) and pupae ($t = 1513.41$, 583.86 and 159.04 for Field 1, 2 and 3 respectively) around the edge and in the centre of the fields. At Fields 2 and 3, where there were fewer rows along two of the edges, an increase in absolute abundances was still found towards the edges. Higher abundances of larvae and pupae were generally found in the corners of each field. Field 1 had the lowest abundance of larvae, but abundances increased in the other fields (Field 2 and 3) as the season progressed.

In all three fields, some areas around the edges of each field showed a higher abundance of larvae and pupae than other areas. Generally, higher diamondback moth abundances were found along edges that were adjacent to grass verges that contained cruciferous and non-cruciferous weeds, the paprika field where weeds had been allowed to grow, and recently harvested or existing cabbage fields. Lower abundances of diamondback moth were found along edges near grass verges without weeds, fields that had been lying fallow for a period of time, areas of natural bushveld and fields of young cabbage seedlings (Figs. 9.2 and 9.3).

9.3.3. Field abundances of *Cotesia plutellae* (Kurdjumov) cocoons

Four parasitoid species were found but only one, *C. plutellae* , was easily detectable in the field due to its obvious cocoon. There was a significant difference ($p < 0.05$) between the abundance of cocoons found around the edges of the field and those found in the centre ($t = 1600.01$, 1168.03 and 496.42 for Fields 1, 2 and 3 respectively). The abundance of the cocoons increased towards the edge of the fields (Fig. 9.4). Highest abundance of cocoons was found adjacent to recently harvested cabbage fields, existing cabbage fields and the weed-filled paprika field. Lower abundance of cocoons was found adjacent to roads, natural bush, young cabbage fields and grassy verges. Generally, the corners of each field had the highest abundance of cocoons.

9.3.4. Eclosion of diamondback moth

There was a significant difference ($p < 0.05$) in rate of moth eclosion between the edges of each field and the centre ($t = 25.29$, 12.31 and 14.33 for Field 1, 2 and 3 respectively) (Fig. 9.5). In Field 1 the highest rate of moth eclosion was found in the northeast corner (>35%) and the southwest corner (25%). Eclosion reached 25% along parts of the south side.

In Field 2 the rate of moth eclosion reached between 65% along the east edge, 75% in the northeast corner and between 50 and 60% in the southeast and northwest corners.

In Field 3 the rate of moth eclosion was much higher than in the other two fields, reaching 100% along parts of the west and east edge. Eclosion reached greater than 65% on the north and south sides of the field. The entire field showed percentages greater than 50% but there was still an increase towards the edges of the field. At all three fields highest moth eclosion was found adjacent to weedy grass verges, existing cabbage fields or recently ploughed fields.

9.3.5. Rate of parasitism

Four species of parasitoid emerged from the diamondback moth larvae and pupae collected in the field including *C. plutellae*, *Diadegma mollipla* (Holmgren), *Diadromus collaris* Gravenhorst and *Oomyzus sokolowiskii* (Kurdjumov). *Cotesia plutellae* was the most common parasitoid and the percentage parasitism by *C. plutellae* therefore showed a very similar pattern to that of the total percentage parasitism in all three fields. In Field 1, *O. sokolowiskii* was the only other parasitoid found and from only one diamondback moth pupae. In Field 2, *O. sokolowiskii* became slightly more common and *D. mollipla* was found infrequently. In Field 3, *O. sokolowiskii*, *D. mollipla* and *D. collaris* were found.

There was a significant difference in parasitism between the edges of the field and the centre (t = 37.12, 47.03 and 38.75 for Fields 1, 2 and 3 respectively) (Fig. 9.6). At Field 1 the highest rate of parasitism was found along the east side of the field (25%) and the southwest corner (22%). At one of the central sampling points in the field 19% parasitism was found, probably as a result of the sampling design. In Field 2 higher rates of parasitism were found in the corners of the field with 35% parasitism in the northwest and 25% in the southeast corner. In Field 3 the highest parasitism rates were found in the four corners of the field with between 35 and 45% parasitism in the northeast and northwest of the field and between 20 and 30% in the southeast and the southwest corners. These areas of higher parasitism were adjacent to existing cabbage fields, cabbage fields that had just been harvested, weedy grass verges and the weed-filled paprika field. Low parasitism levels were found in areas adjacent to young cabbage plants, roads and natural bush.

9.3.6. Relationship between moth eclosion and parasitism

The rate of parasitism increased as the total abundance of diamondback moth larvae and pupae increased (Fig. 9.7). In Field 1, 2 and 3 significant ($p < 0.05$) positive correlations ($r = 0.20$, 0.39 and 0.22 respectively) were found between the rate of parasitism and abundance of the diamondback moth. However the coefficients of determination were small in each case ($r^2 = 0.04$ ($p = 0.01$), 0.16 ($p = 0.00$) and 0.04 ($p = 0.01$) for Field 1, 2 and 3 respectively). The slope of the line is greater than one in Field 1 and 2 ($m = 5.61$ and 1.14 respectively) which suggests that the parasitoids are density-dependent. In Field 1 the disparity between the line and the points is probably due to the zero values. In Field 3 the slope of the line is less than 1 ($m = 0.40$). The correlation between moth emergence and rate of parasitism (Fig. 9.8) in Field 1 was not significant ($r = -0.08$, $p = 0.26$) but in Field 2 and Field 3 they showed a significant negative relationship ($r = -0.19$ ($p = 0.03$) and $r = -0.48$ ($p = 0.00$) respectively).

The abundance of the diamondback moth and its parasitoids at each point of the sampling grid were plotted against the inverse of the distance that they moved into the field to determine the diffusion effect by the moths and parasitoids (Fig. 9.9). All of the gradients were significant ($p < 0.05$) except for the moths in Field 1 ($r = 0.13$, $r^2 = 0.01$, $p = 0.07$). The intercept for each line shows the population density at an infinite distance into each field. The intercept is highest for the moths than the parasitoids in each field, which shows that the moths move further into the fields than the parasitoids. A seasonal effect was found with the moths becoming more abundant as the season progressed. In the first field, which was sampled in winter, the moth and the parasitoid abundance was fairly uniform. In the second field , sampled in spring, the moth abundance started to increase and at the third field moth abundance was at its highest. A comparison of slopes in each graph (Zar, 1984) showed no significant difference between the moths and the parasitoids in Field 1 and 2 ($t = 0.37$, $p = 0.71$ and $t = 0.71$, $p = 0.48$, respectively), but in Field 3 they were significantly different ($t = 6.28$, $p = 0.000$) (Fig. 9.9).

9.4. Discussion

9.4.1. Edge distributions

In all three fields there was a general trend showing lower absolute abundances and percentage eclosion of both the diamondback moth and its parasitoids in the centre of the field (Figs. 9.2 - 9.6). The absolute abundances increased towards the edge of the fields. This suggests that there was a diffusion of moths and parasitoids into the fields from surrounding areas (Figure 9.9). The higher abundances of larvae and pupae, and the increase in rates of parasitism, in the corners suggested diffusion was happening from both edges. There was an indication that the variation along the edges of the field was related to the conditions surrounding the field. The variation in abundance needs to be taken into consideration when scouting for the diamondback moth and its parasitoids. Baker *et al.* (1982) found no difference between the numbers of larvae on the borders and the centre of the fields and stated that either area could be used to determine population trends. Their sampling design was different, it was a "V" shape and not a grid as was used in the Eastern Cape study.

9.4.2. Field abundance and eclosion of the diamondback moth

Ullyett (1947b) determined the distribution of diamondback moth in cabbage crops and stated that it could be one of three types. Firstly, migrational distribution which involves the infestation of moths from other cultivated areas or wild host plants and results in a higher abundance on the borders of the crop closest to the source. Secondly, directional distribution where there is a directional trend in the abundance of the moth but it has no relationship to the source of the infestation, and thirdly, attractional distribution where certain plants are more attractive than others. In the Eastern Cape the moths in the three fields studied showed a migrational distribution, with the moths moving from other areas to the edges of each field. Harcourt (1961) considered border effects in the diamondback moth and found no difference between the abundance of immature stages of the moth on the exterior or interior of the field. However, the plots he used were square with only 5000 plants in each one. The commercial fields in the Eastern Cape were much larger and they showed evidence that a distribution pattern existed.

Murchie *et al.* (1999) showed that in England the cabbage seed weevil, *Ceutorhynchus assimilus* (Paykull), a pest on oilseed rape, and its parasitoid, *Trichomalus perfectus* (Walker), congregated around the edges of the rape fields early in the season. They suggested that because the weevil used mainly olfactory cues to locate the crop, edge distributions were found as the edge is the first part of the crop that the pest reaches. Hu *et al.* (1997) showed that diamondback moth larvae on cabbage plants at the ends of rows were more abundant than in the interior of the field and that damage to the cabbage heads on the end of the rows was greater than those in the interior of the fields. Figures 9.2 and 9.3 suggest that the moths are moving into the fields from surrounding areas, mainly existing cabbage fields, cabbage fields that have just been harvested, and weedy areas. Koshihara (1986) found that diamondback moth population growth in cabbages was caused mainly by infestations of adults from crucifers around the fields, but it is unclear whether these were crucifer crops or non-crop crucifers.

A number of hypotheses have been developed to try to explain insect movement in agricultural environments. Two of these, the Resource Concentration Hypothesis and the Enemies Hypothesis, developed by Root in 1973, have formed the basis of a large number of studies (Risch, 1981; Letourneau, 1987; Russell, 1989; Andow, 1990; Schellhorn & Sork, 1997). The Resource Concentration Hypothesis postulates that herbivores are more likely to find and remain in areas where there are dense stands of a food source. The Enemies Hypothesis states that more predators and parasitoids are found in diverse vegetational habitats, leading to lower host populations (Root, 1973). These two hypotheses are not mutually exclusive (Sheehan, 1986; Andow, 1990). Finch and Collier (2000) decided that none of the hypotheses have been used to produce a general theory, which lead them to develop a theory know as "appropriate/inappropriate landings". This theory suggests that specialist insects looking for host plants tend to land on green objects, for example the leaves of the host plant, resulting in appropriate landings and the leaves of non-host plants resulting in inappropriate landings and avoid landing on brown objects like bare soil.

The high abundance of diamondback moth in the three fields indicated that the moths were moving to areas where there was a resource available to them in the form of the cabbage plants which provide suitable laying sites and food for the larvae. This suggests that Root's Resource Concentration Hypothesis applies. The "appropriate/inappropriate" theory may explain why a higher abundance of diamondback moth larvae and pupae were found around the edges of the fields. If they are moving in from other areas, the cabbages around the edge of the field would be the first green "appropriate landings" that the moths would find that were easily distinguishable from the surrounding brown bare soil. Even though diamondback moth are considered nocturnal and oviposit around dusk, they are able to distinguish between green and brown objects (Finch & Kienegger, 1997; Finch and Collier, 2000).

9.4.3. Rate of parasitism

Hu *et al.* (1997) found no significant difference in the rate of parasitism of diamondback larvae between the ends and interiors of fields. The species of parasitoids they found were not given. Mitchell *et al.* (1999) found that parasitoids released along the edges of fields showed an even dispersal throughout the fields. The rate of parasitism (Fig. 9.6) in this study was higher around the edges of the fields than in the interior. Field 1 was sampled during the winter and the presence of both diamondback moth and parasitoids indicates that they occur throughout the year in the Eastern Cape Province. The differences in occurrence of the different parasitoid species between the three fields is an indication of how the parasitoid suites change through the season. *Cotesia plutellae* was found in all three fields, but *D. mollipla* and *D. collaris* were only found in the spring samples, when the diamondback moth populations increased. Although *O. sokolowskii* was present in the winter sample, its abundance was very low and abundance increased in the spring samples.

Root's Enemies Hypothesis (1973) suggests that more predators and parasitoids are found in areas of higher vegetational diversity. More recently the Enemies Hypothesis has been considered to be true for generalist parasitoids and not specialist parasitoids. Specialist parasitoids probably find it easier to colonize simple agro-ecosystems than more diverse ones as there is an abundance of hosts available to them (Sheehan, 1986; Andow, 1991; Hawkins, 1994). Pimentel (1961b) found more parasitoids and predators in single-species plantings than in mixed-species plantings. Horn (1986) studied larval parasitism of diamondback moth in weedy and tilled fields and found that the specialist parasitoid, *Diadegma insulare*, parasitised higher numbers of diamondback moth in tilled fields while the generalist parasitoid, *Spilochalcis albifrons*, although rare, parasitised diamondback moth in the weedy fields. The parasitoid wasps associated with the diamondback moth are specialist parasitoids and are therefore unlikely to follow the Enemies Hypothesis and probably move to areas where there is a resource available to them in the form of diamondback moth larvae and pupae.

One of the main benefits of weedy species is that the flowers provide a source of nectar and pollen for parasitoids and predators (Altieri, *et al.*,1977; Altieri & Letourneau, 1982; Zandstra & Motooka, 1978; Powell, 1986; Zhao *et al.*, 1992; Bigger & Chaney, 1998; Baggen *et al.*, 1999). Idris & Grafius (1995,1996) have shown that, by growing wild brassicas near commercial cabbage crops, the field populations of diamondback moth can be reduced and there is an increase in the impact of parasitoids due to the presence of floral nectar which provides a food source for the adult wasps. These wildflowers also provide shade and shelter for the parasitoids (Idris & Grafius, 1995). It has been found that floral nectar from some species of wild brassica increased longevity and fecundity in parasitoid wasps (Yang *et al.*, 1993; Idris & Grafius, 1996,1997; Johanowicz & Mitchell, 2000a). It is important to determine which weeds are useful as a food source for these natural enemies and to encourage them to grow within the agro-ecosystem to improve pest management (Zandstra & Motooka, 1978). Other predators can play a role in reducing the numbers of diamondback moth larvae, for example, syrphid flies, the adults of which require nectar and pollen sources (Horn, 1981; White *et al.*, 1995).

9.4.4. Relationship between moth eclosion and parasitism

Studies of parasitoid searching behaviour have shown that paraitoids search for hosts in areas where there is a greater chance of finding a host and that parasitoids can discriminate between areas of high and low host density (Morrison & Strong, 1980). There was a significant positive correlation between the total abundance of diamondback moth larvae and pupae and rate of parasitism (Fig. 9.7). There were disproportionally more parasitoids in areas where there was a higher abundance of prey species. This suggests that the parasitoids are density-dependent. This density-dependance may be present only at certain times of the year as it was not found in Field 3. The small coefficients of determination calculated for each field suggest that the abundance of the diamondback moths is a poor indicator of parasitism. This implies that other undetermined factors are having an effect on the populations; these could included insecticide spraying and environmental factors, like temperature.

The significant negative correlation between moth eclosion and the rate of parasitism at Field 2 and 3 shows that in the areas where there was an increase in parasitism, there was a resulting decrease in moth eclosion (Fig. 9.8). This suggests that the parasitoids are influencing the diamondback moth populations. This effect was not seen in Field 1, possibly because this field was sampled during winter and there were not as many parasitoids present as during the second two samples in spring.

The highest abundances and eclosion of moths and parasitoids are generally found adjacent to existing cabbage fields or cabbage fields that have just been harvested, as both of these areas can harbour moths and parasitoids. There is an indication from the contour graphs (Figs. 9.2 , 9.3, 9.5 & 9.6) that the other vegetation found growing around the edges of the fields may also influence abundances of moths and parasitoids on cabbages growing in the border rows of a field. Hu *et al.* (1997) found that larval density was highest on cabbages growing on the edges adjacent to weed-filled ditches than those growing near woods and bushes. Zhao *et al.* (1992) showed that generally there were more diamondback moth larvae in broccoli that was interplanted with or adjacent to nectar-producing plants than in broccoli grown in a monoculture.

In the Eastern Cape study there were a variety of weeds growing in the vicinity of the fields including other cruciferous plants, both exotic and indigenous. Some of these plant species, for example, *Brassica juncea* (Indian mustard), *C. bursa-pastoris* (shepherd's purse) and *Lepidium* spp., act as alterative hosts for diamondback moth (cited by Talekar & Shelton, 1993), providing reservoirs or refuges for the diamondback moth adults or the parasitoids, or both. The surrounding vegetation can consist of both host plants and non-host plants. Having additional host plants around the field could provide a reservoir for diamondback moth, but at the same time it may also help in combatting resistance to insecticides by providing a refuge for susceptible diamondback moth (Idris & Grafius, 1996). Factors like soil fertility, drainage and moisture could all have affected the quality of the cabbage plants and therefore influence diamondback moth abundances, however this was beyond the scope of the study.

Hu *et al.* (1997) found that diamondback moth spread inwards to between 50 and 70 m. Field 1 is 58 m x 72 m which suggests that the moths can move to the centre. Larvae and pupae were found towards the centre of each field but at very low numbers (Figs. 9.2 & 9.3). Fields 2 and 3, although much longer (219 m) were much narrower (13 m and 31 m respectively) allowing moths to move throughout the fields. The shape of these two fields could also be the reason why higher percentages of moth emergence were found compared to Field 1. The number of *C. plutellae* cocoons and the percentage parasitism from the laboratory reared field collection show that the parasitoids do not move as far into the field as the moths (Fig. 9.9). This shows the importance of the size of the field in the control of the diamondback moth by parasitoids. It suggests that to obtain suitable control by parasitoids throughout the field the size of fields should be reduced. As the season progresses the gradient for the moths increases more than that for the parasitoids, possibly because of the build-up of moth numbers around the edges of each field rather than in the centre (Figs. 9.2 and 9.3).

9.5. Conclusion

Edge distributions of the diamondback moth within commercial cabbage fields are evident in the Eastern Cape Province. The diamondback moth, as with any crop pest, will move to areas where there is a resource available in the form of oviposition or feeding sites (Cromartie, 1975; Andow, 1991). Generally this movement was from areas of high diamondback moth abundance or areas where there was no longer a resource available, for example existing or recently harvested fields. It is impossible in this study to determine whether having host and non-host weedy species surrounding the fields had any impact on the abundances of diamondback moth and its parasitoids within the fields. No study was done to determine if the parasitoids were using the nectar-producing plants around the edges as a food source but other studies (Idris & Grafius, 1995, 1996) have suggested that this is possible. The increased parasitism levels around the edges of each field suggest that the parasitoids have moved into these areas because there is a resource available to them in the form of diamondback moth larvae and pupae.

Colonisation of fields by pests is much quicker than that by predators and parasitoids and it is important that the colonisation rates of natural enemies is increased so that an equilibrium can be reached. This can be done in a number of ways, by reducing the size of the fields, having uncultivated refuges and flowering plants to provide nectar and shelter to the natural enemies (Price, 1976). It is important that these factors are taken into consideration when designing management strategies for control of the diamondback moth.

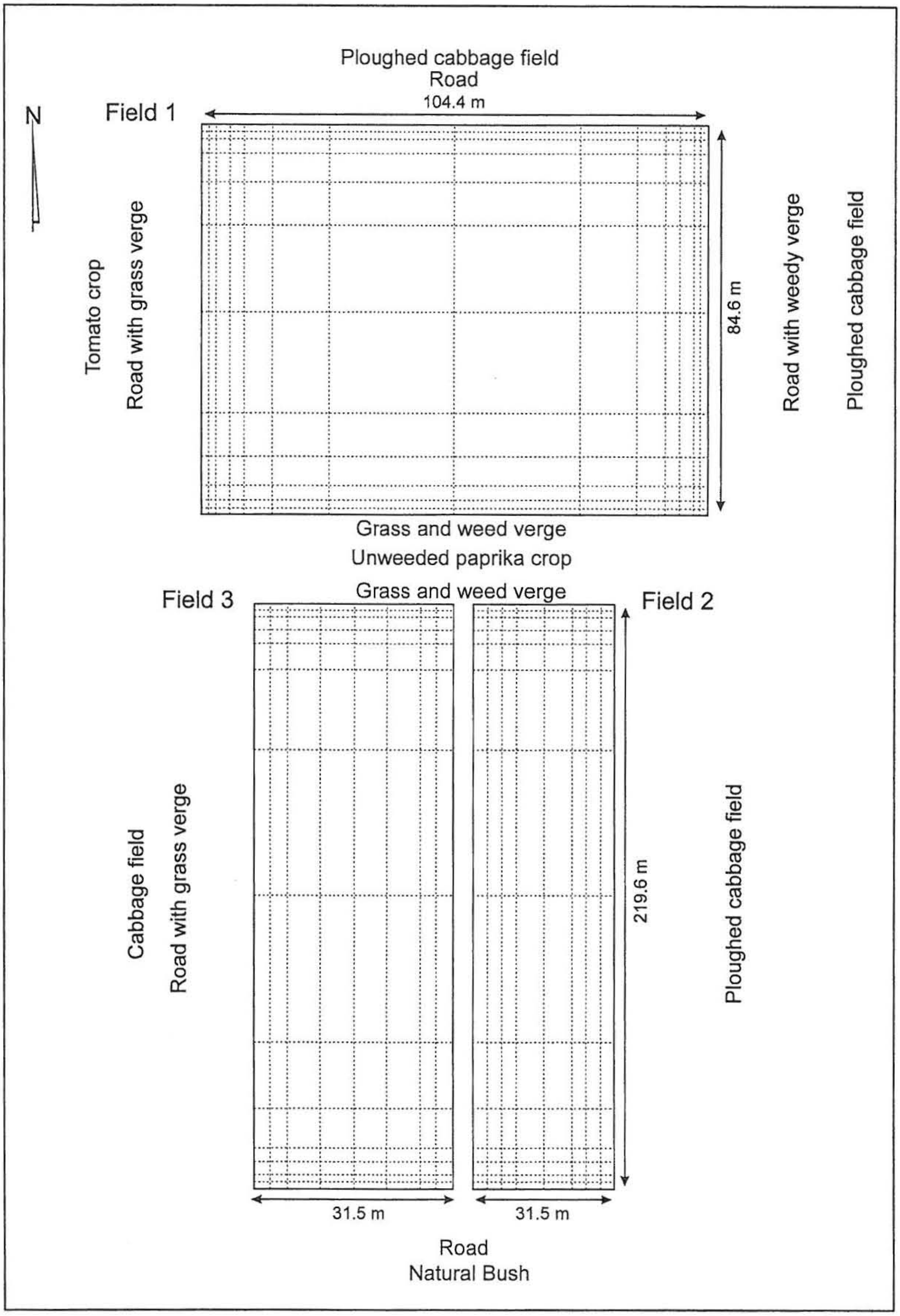

Figure 9.1. Layout of the three fields showing the conditions around and the size of each field. Note Field 1 and Field 2 and 3 were separated by a paprika crop.

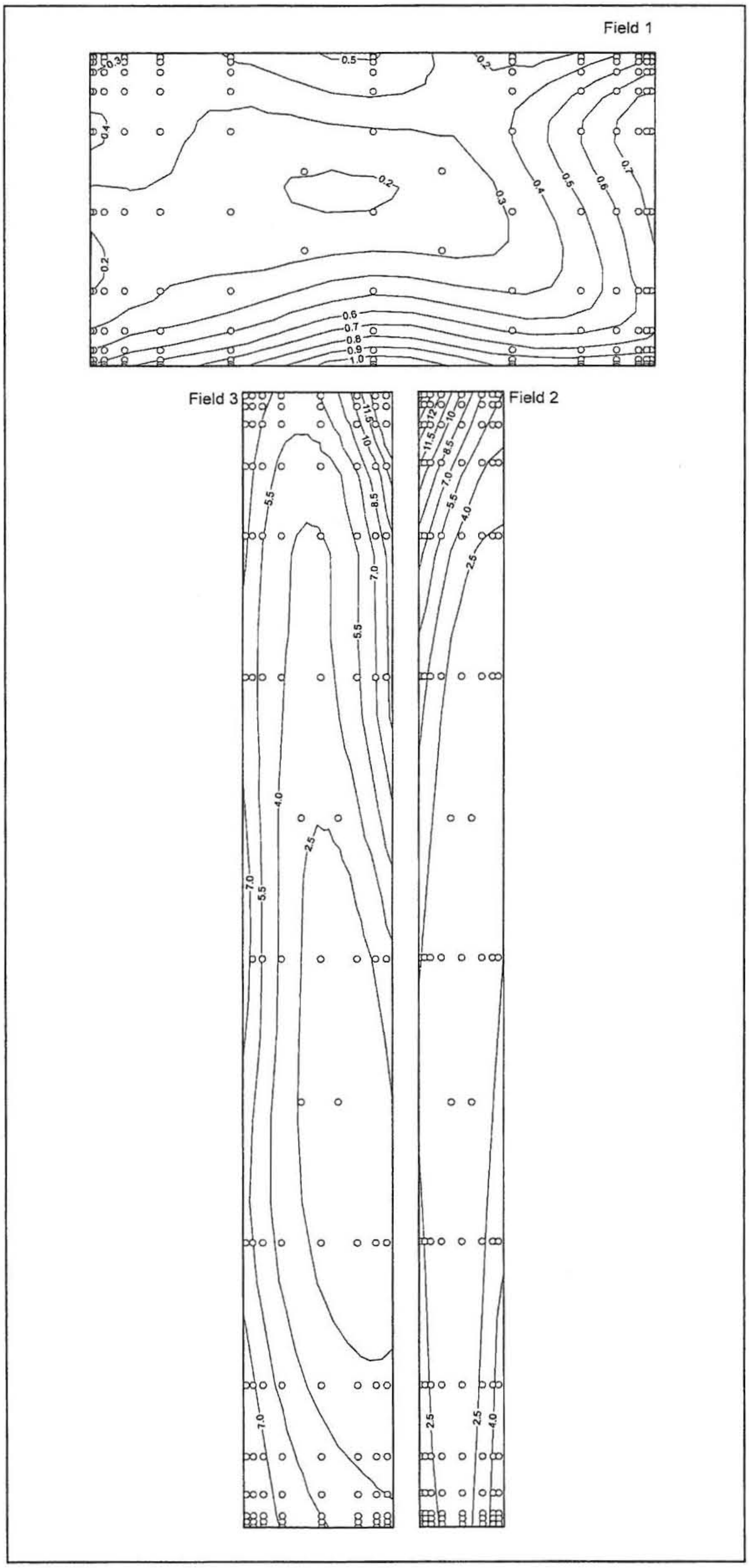

Figure 9.2. Distribution of diamondback moth larvae in three commercial fields. Mean number of larvae shown on contour lines. Open circles indicate cabbage plants sampled.

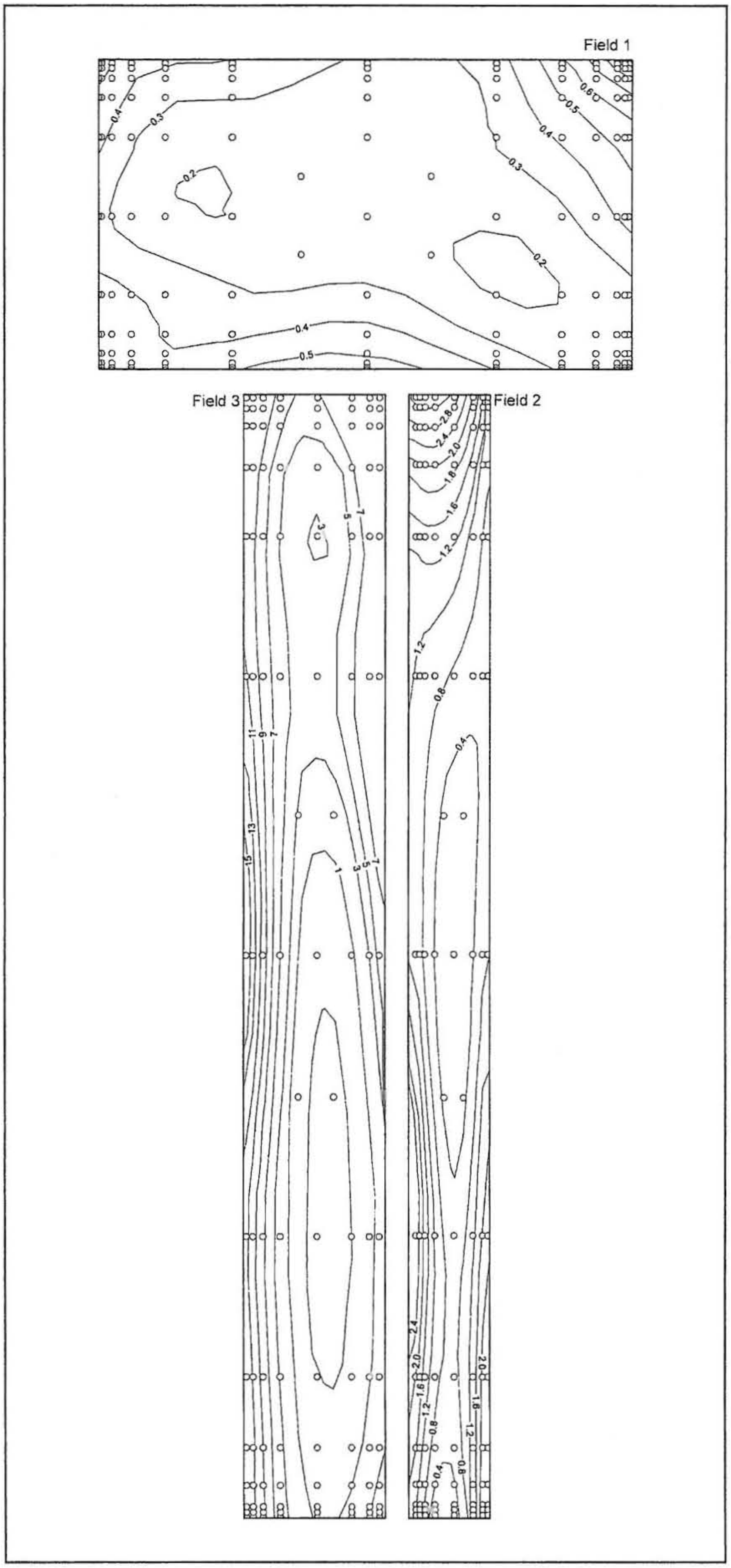

Figure 9.3. Distribution of diamondback moth pupae in three commercial fields. Mean number of pupae shown on contour lines. Open circles indicate cabbage plants sampled.

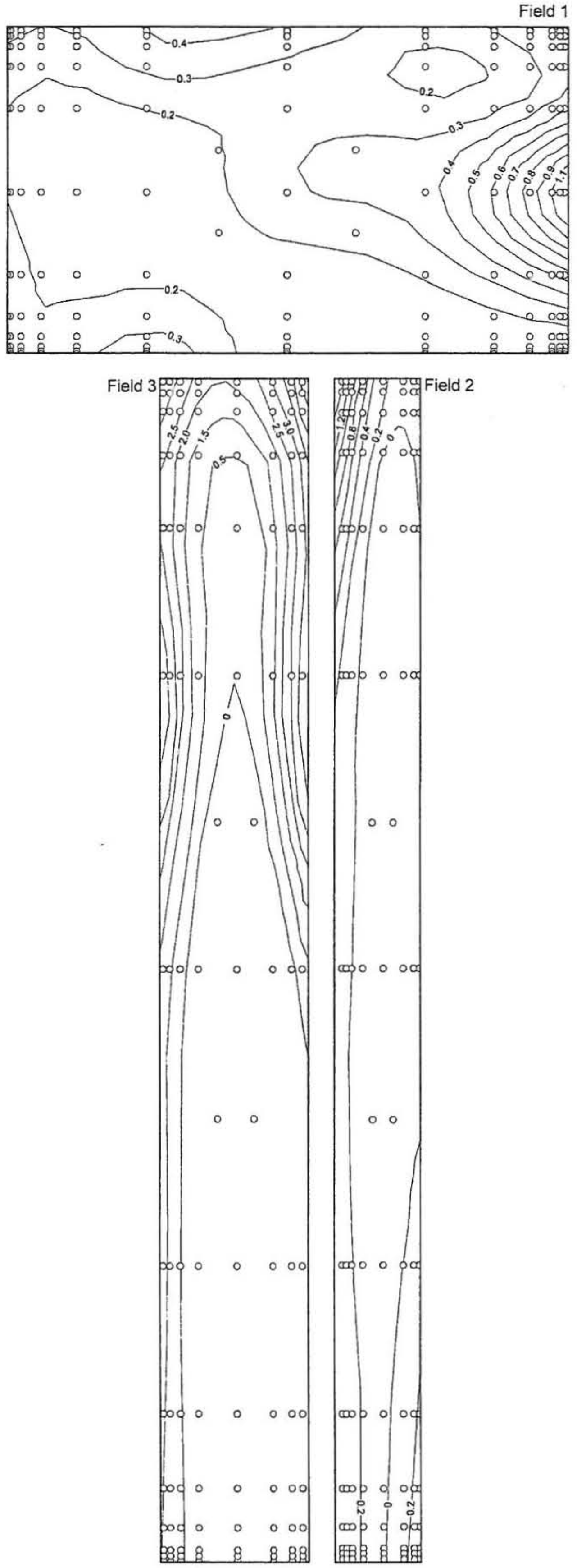

Figure 9.4. Distribution of *Cotesia plutellae* cocoons in three commercial fields. Mean number of coocoons shown on contour lines. Open circles indicate cabbage plants sampled.

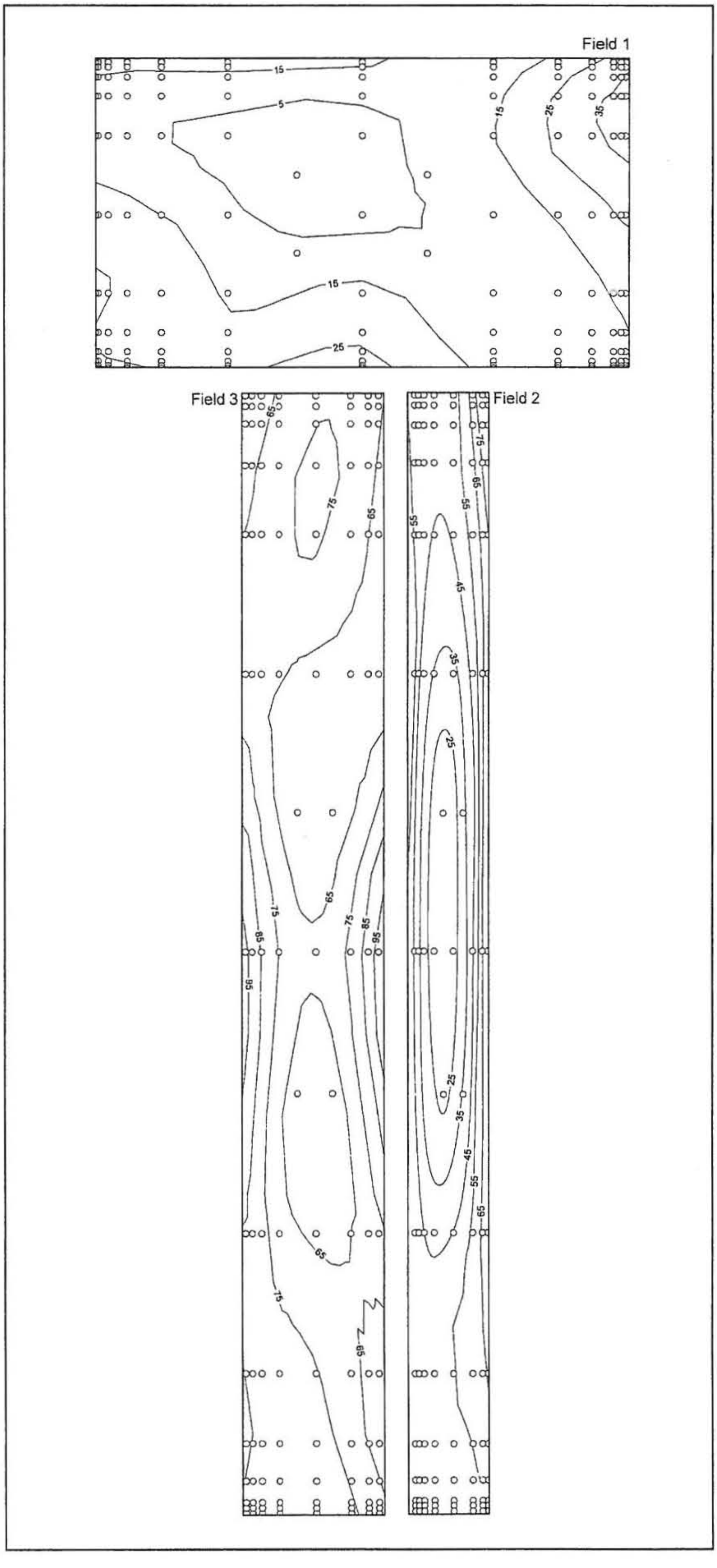

Figure 9.5. Distribution of moth eclosion in three commercial fields. Moth eclosion (%) shown on contour lines. Open circles indicate cabbage plants sampled.

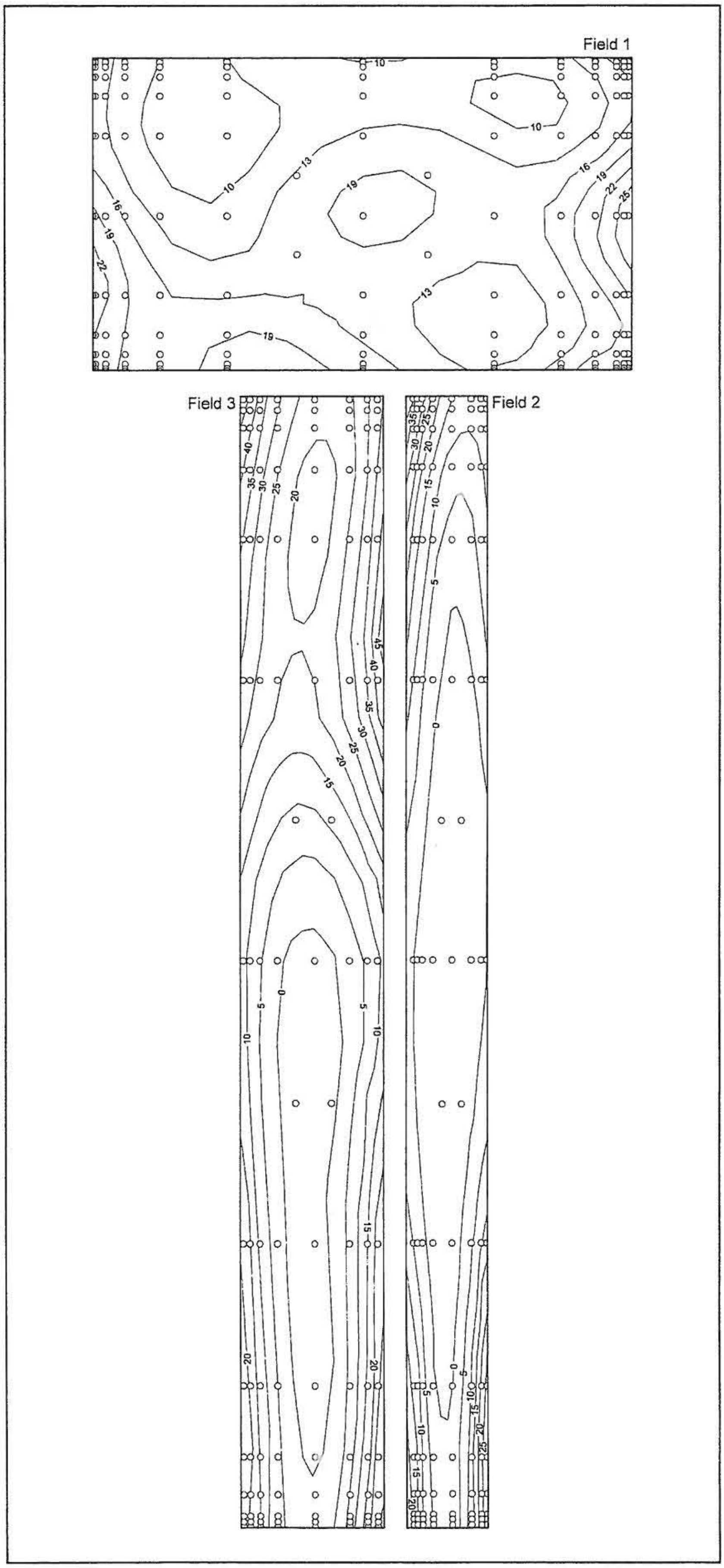

Figure 9.6. Distribution of parasitism in three commercial fields. Rate of parasitism (%) shown on contour lines. Open circles indicate cabbage plants sampled.

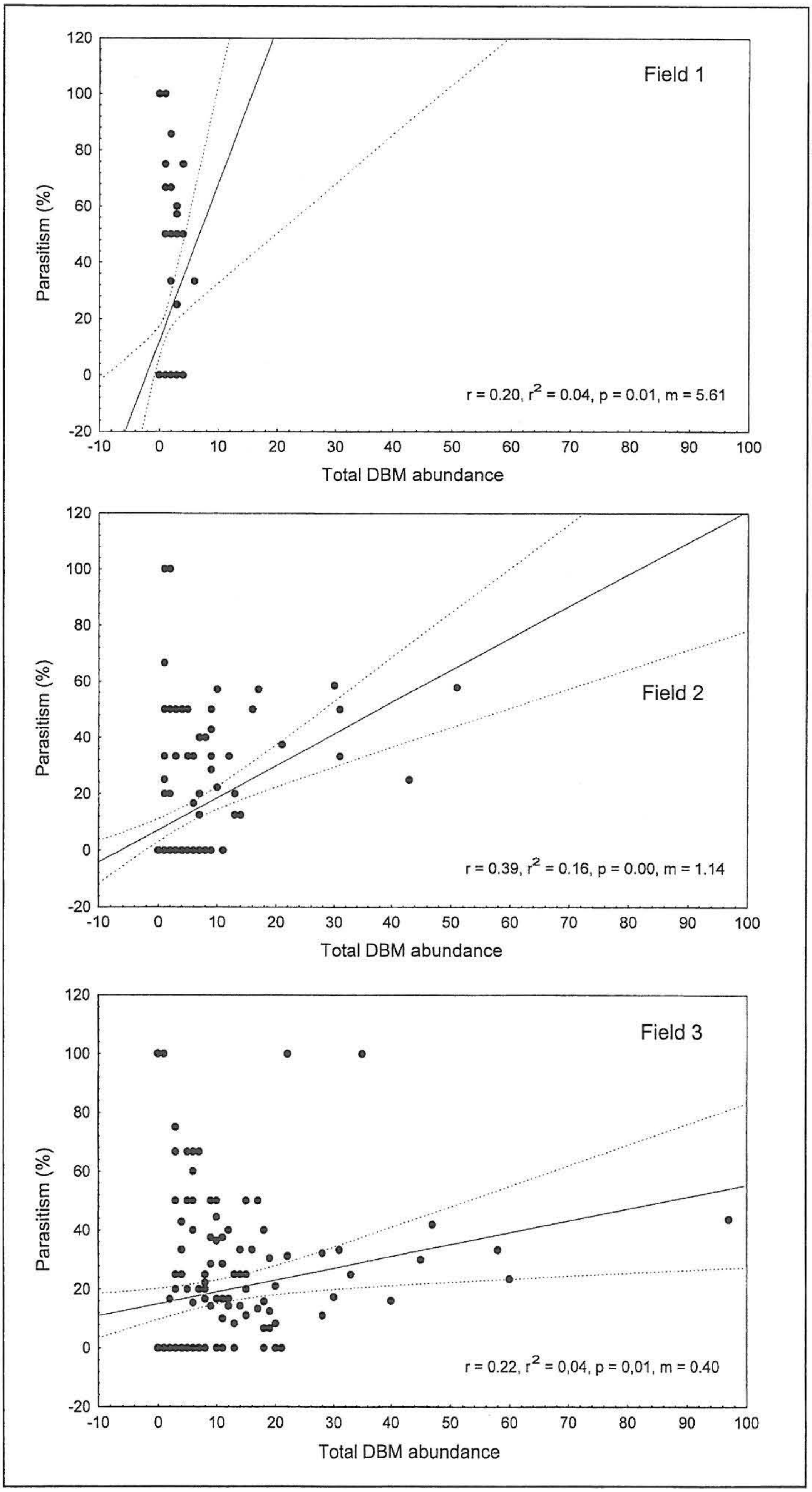

Figure 9.7. Relationship between rate of parasitism and total immature diamondback moth abundance in each field.

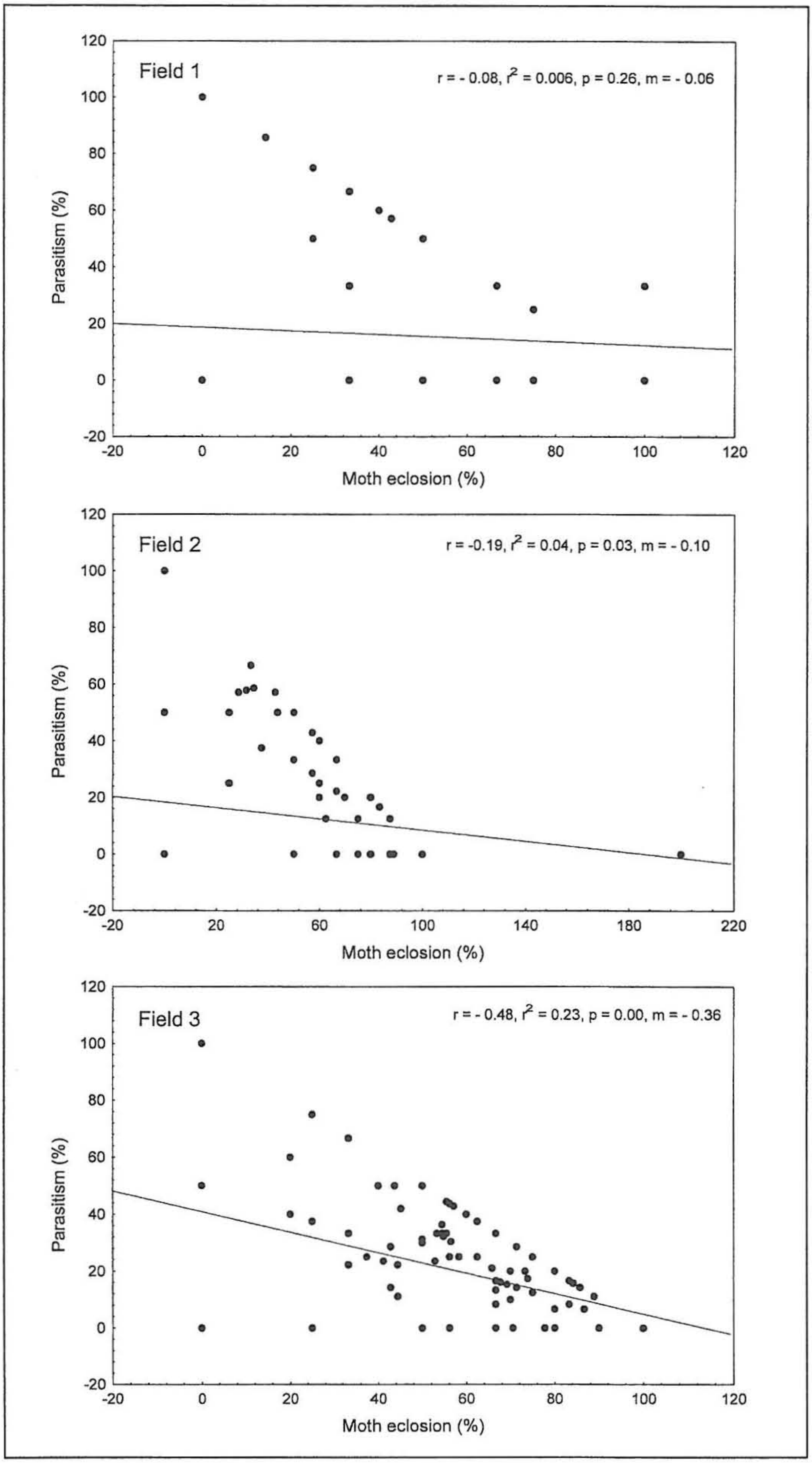

Figure 9.8. Relationship between parasitism and moth eclosion in each field.

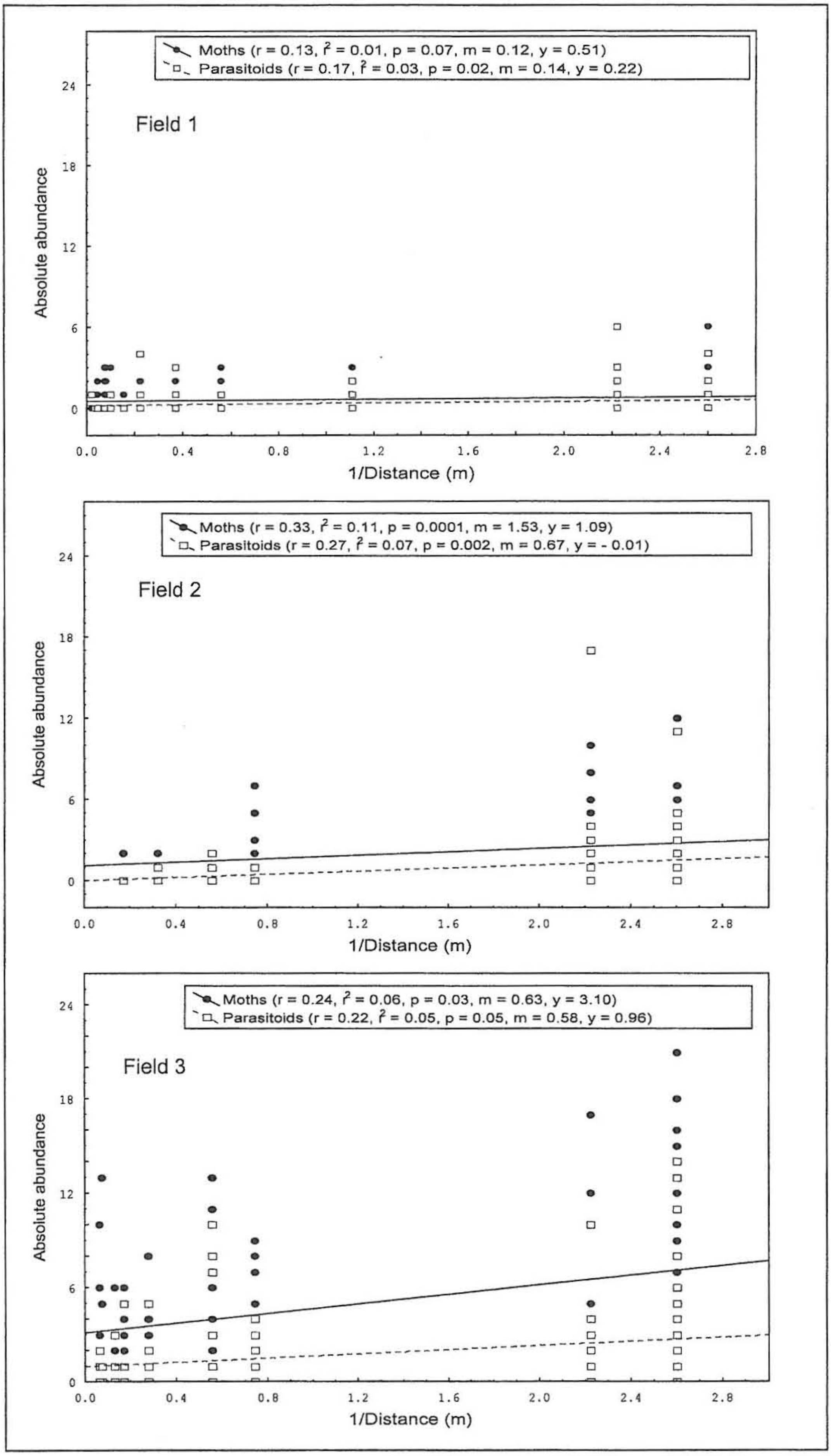

Figure 9.9. Distance moved by the diamondback moth and its parasitoids in each field.

Chapter 10:

Suitability of alternate host plants for the diamondback moth

10.1. Introduction

It is very important to understand the oviposition behaviour of pest insects as oviposition is the start of any pest infestation and therefore needs to be considered in management strategies and Integrated Pest Management programmes (Talekar *et al.*, 1994; Justus & Mitchell, 1996). The diamondback moth feeds only on plant species from the family Cruciferae and their host range is limited to plants that have glucosides or mustard oils (Gupta & Thorsteinson, 1960a; Muhamad *et al.*, 1994). There are a wide range of plant species that form part of this family, including cultivated crops and wild species, many of which are weedy (Muhamad *et al.*, 1994). Glucosinolates are known to stimulate feeding and oviposition in the diamondback moth (Gupta & Thorsteinson, 1960b; Reed *et al.*, 1989) but there are indications that these are not the only stimulants in crucifers that attract the diamondback moth (Hughes *et al.*, 1997).

Some of the wild crucifer species are able to maintain diamondback moth populations when crops are unavailable (Harcourt, 1986; Talekar & Shelton, 1993; Muhamed *et al.*, 1994; Begum *et al.*, 1996), particularly in regions where alternate hosts are needed during winter and early spring before crucifer crops are planted (Harcourt, 1986; Talekar & Shelton, 1993; Idris & Grafius, 1996). Alternative hosts provide a refuge for diamondback moth during preparation, planting and spraying of the land, which ensures that there is always a reservoir population present (Hu *et al.*, 1997). There is also evidence that these refugia delay the development of resistance of the moth to the bioinsecticide, *Bacillus thuringiensis* Berliner (*Bt*) (Liu & Tabashnik, 1997a) and to synthetic insecticides (Talekar *et al.*, 1994; Idris & Grafius, 1996).

Some of the weedy crucifers, for example yellow Kirby mustard, *Brassica hirta (author)*, (Kloen & Altieri, 1990), Indian mustard, *Brassica juncea* (L.) Czern, (Srinivasan & Krishna Moorthy, 1991, 1992; Luther *et al.*, 1996; Bender *et al.*, 1999; Charleston & Kfir, 2000) and collards (Mitchell *et al.*, 2000), have been studied as possible trap crops for diamondback moth. A trap crop is a stand of plants responsible for attracting insect pests away from the target crop (Hokkanen, 1991). These plants are usually not economically important but are preferred by the pest species

(Talekar & Shelton, 1993).This might result in associational resistance which is a reduction of herbivore attack on a specific plant that is associated with other genetically or taxonomically diverse plants (Tahvanainen & Root, 1972; Andow, 1991). These trap crops could either be planted in border belts of wild vegetation or in the field but separated from the crop by non-host barrier rows (Luther *et al.*, 1996).

Intercropping non-host plants that interfere with chemical or physical cues used by the pest to locate a host has also been used (Maguire, 1984; Talekar *et al.*, 1986). Sage, thyme and clover planted with brassicas have shown a reduction in moth oviposition (Dover, 1986; Finch & Kienegger, 1997) and the odour of tomato plants is known to repel diamondback moth (Chelliah & Srinivasan, 1986; Magallona, 1986; Talekar *et al.*, 1986; Bach & Tabashnik, 1990; Finch & Collier, 2000). This can lead to an increase in plant diversity and therefore a reduction in herbivores but only if the plant species are not related, do not attract other pests and do not compete with the crop (Latheef & Irwin, 1979; Shellhorn & Sork, 1997).

This chapter investigates oviposition of the diamondback moth on five non-crop crucifers that are found associated with, or in the vicinity of, cabbage fields in the Eastern Cape Province. The results will provide information on the relationship between the diamondback moth and alternate host plants in the Eastern Cape.

10.2. Materials and methods

Five species of brassica were grown from seeds collected from plants growing in the vicinity of cabbage fields. These included two species of *Lepidium* (pepperweed), *L. africana* (Burm.f.) and *L. ecklonii* Schrad., *Capsella bursa-pastoris* (L.) Medik. (shepherd's purse), *Sisymbrium thellungii* O.E. Schulz and *Alyssum minutum* Schlechtd. *Capsella bursa-pastoris* and *A. minutum* are introduced species and *A. minutum* is a commonly grown garden plant in South Africa. The two *Lepidium* species and *S. thellungii* are indigenous to South Africa. The seeds were germinated in trays under natural conditions.

The seedlings, together with cabbage (*Brassica oleracea* var. *capitata* L.), were transplanted into seed trays with individual blocks, the trays were 30 cm x 30 cm with 36 blocks in each (6 x 6). The seedlings were randomly placed in the blocks using a Latin Square design (Rao, 1998). There were two replicates as all the seeds did not germinate successfully. Each replicate was placed into a separate cage with diamondback moth pupae. Within 24 hours, 178 and 137 pupae eclosed in each tank respectively. The seed trays were left in the cages for a further 48 hours, after which they were removed and the number of eggs on the stems and the upper and lower surfaces of the leaves of each seedling were counted and recorded. The seed trays were kept in cages in a constant environment room at 25°C and 16:8 hours light:dark. The eggs were allowed to hatch and the 1st instars began mining. From the 2nd instar stage the larvae were placed in petri dishes and fed additional leaves from the relevant plant species until pupation. The number of moths that eclosed on each plant species was recorded. Categorized box-whisker plots were used to show the number of eggs oviposited, the preferred oviposition surface and moth eclosion on each plant species.

10.3. Results

10.3.1. Suitability of additional host plants as oviposition sites

A one-way ANOVA showed that there was no significant difference between the two trays regarding the total number of eggs laid ($F = 0.41$, $p = 0.52$). Ovipostion occurred on all of the plant species, but a one-way ANOVA showed that the numbers of eggs laid on each species were significantly different ($F = 3.89$, $p = 0,01$). A multiple range test showed significant differences between *Brassica oleracea* and the rest of the species except *L. africanum*, and between *C. bursa-pastoris* and *L. africanum* (Fig. 10.1).Very few eggs were oviposited on *C. bursa-pastoris* and the highest number of eggs was oviposited on *B. oleracea*. Of the two *Lepidium* spp, *L. africanum* had a higher number of eggs laid on its surfaces.

A two-way ANOVA showed that the preferred ovipostion surface varied significantly between the species (F = 3.58, p = 0.01) (Fig. 10.2). A multiple range test was done to determine significant differences in surface preference among the species. On *A. minutum* the diamondback moth preferred the upper leaf surface to the lower leaf surface or the stem. *Brassica oleracea* received the highest number of eggs, significantly more of which were oviposited on the stem than elsewhere. Both *Lepidium* species and *S. thellungii* had the smallest number of eggs oviposited on the stems. Generally the eggs were laid along the veins on *S. thellungii*, *A. minutum* and *L. africanum*.

10.3.2. Suitability of host plant for diamondback moth survivorship

A one-way ANOVA showed that there was no significant difference between the two trays regarding moth eclosion (F = 0.54, p = 0.48). A one-way ANOVA showed a significant difference between the species and moths eclosion (F = 7.76, p = 0.013). A multiple range test showed that there were significant differences in moth eclosion between *B. oleracea* and all the other species (Fig. 10.3). The highest moth survivorship was found on *B. oleracea*, followed by *A. minutum*. The other species showed very low survivorship. Moth survival was too low to continue and determine the fecundity of the 2nd generation of diamondback moth after feeding on different crucifer species.

10.4. Discussion

10.4.1. Suitability of additional host plants as oviposition sites

The reasons for higher oviposition by the diamondback moth on certain plants could include: different concentrations of glucosinolates, making some plants less attractive; oviposition deterrents or toxic substances; unsuitable host leaf morphology and leaf waxiness that affects pest movement and feeding (Talekar *et al.*, 1994; Justus *et al.*, 2000, Serizawa *et al.*, 2001). The diamondback moth does oviposit on a number of alternative crucifer species (Fig. 10.1), which are associated with commercial cabbage fields in the Eastern Cape Province. Idris & Grafius (1996) showed that diamondback moth preferred to lay on cultivated brassicas and that larval survival was greater than on wild brassicas. A similar result was found in this experiment where the highest number of eggs and the highest survivorship were found on *B. oleracea* (Figs. 10.1 & 10.3).

The seedlings in the laboratory were all of a similar age but the sizes of the leaves varied. *Capsella bursa-pastoris* had a very small leaf surface area in comparison with the other species, which may be a reason for the low numbers of eggs oviposited on these plants. Wakisaka *et al.* (1991) found that the development period and the emergence of diamondback moth was low on *C. bursa-pastoris* compared with cultivated crucifer crops. *Sisymbrium thellungii* had a large number of trichomes on the leaf surface but this did not seem to prevent the moths from laying on the leaves. It may have had an effect on larval feeding, as very few of the larvae reached adulthood. Talekar *et al.* (1994) found that the number of eggs laid on Chinese cabbage increased with trichome density and therefore suggested that plants with glabrous leaves are more resistant to oviposition. In the field diamondback moth larvae and pupae were found on *S. thellungii* and *A. minutum*, although none of these stages were seen on *Lepidium*, adults were found resting on these plants during the day (personal observation).

Differences in position of eggs oviposited on plants are due to differences in plant species and the specific position of the leaves on the plant (Talekar *et al.*, 1994). Talekar *et al.* (1994) found that eggs were mainly laid on the upper surface of outer leaves but on inner leaves they were on the lower surface. Wakisaka *et al.* (1992) found that in broccoli the highest percentage of eggs were ovipositied on the upper surface of the leaf, followed by the lower surface and then the stem. The upper surface of the leaf was also preferred as oviposition sites in studies done by Gunn (1917) and Harcourt (1957). In the Eastern Cape study the highest number of eggs were laid on the stems of *B. oleracea* seedlings which is probably an artifact of the experiment. Oviposition in the laboratory experiments was probably affected due to the large number of diamondback moths in each cage. Harcourt (1957) noted that when the diamondback moth was confined in the laboratory its laying behaviour changed and more eggs were laid on the stems of the plant.

10.4.2. Suitability of host plant for diamondback moth survivorship

Moth survivorship was very low, even on the cabbage seedlings (Figs. 10.3). This may be because the seedlings were left in the cage for too long, resulting in too many eggs being laid and overcrowding once the eggs hatched. Previous experiments have found that there was no significant difference in development time on cruciferous weeds, but Muhamed *et al.* (1994) found that development time in cabbage is slightly shorter than in other cruciferous weeds. Idris & Grafius (1996) found that the development time of the diamondback moth was longer on *Lepidium campestre* R. Br. than on crucifer crops and they suggested that *L. campestre* may have an antifeedent which prolonged development time and affected survival rate. Total development time of the diamondback moth was quicker on cabbage than on *A. minutum* and *L. africanum* (personal observation). There is a trend in other studies that diamondback moths feeding on cruciferous weeds have a lower fecundity than those feeding on crucifer crops (Wakisaka *et al.*, 1991; Muhamad *et al.*, 1994; Begum *et al.*, 1996). Unfortunately this could not be confirmed in this study as moth survival was too low.

Charleston & Kfir (2000) found that in laboratory experiments, diamondback moths preferred to lay on Indian mustard, *Brassica juncea*, but that larval survival was lower than on cabbage, broccoli or cauliflower. Srinivasan & Krishna Moorthy (1991,1992) showed that Indian mustard could be used as a successful trap crop in India but Bender *et al.* (1999) found that in Texas it had no increased economic effect. Luther *et al.* (1996) used Indian mustard and a second variety of cabbage as trap crop borders to determine if this had any influence on the pest numbers in the main crop. They found that the trap crops did harbour high numbers of diamondback moth and that there was a spill-over into the main crop. They suggested that these trap crops should be planted in island patches away from the main commercial crop, isolating these areas by border belts of wild vegetation or wind breaks which could then be easily managed. Mitchell *et al.* (2000) found that using collards as a trap crop reduced the number of insecticide applications, kept the action threshold below 0.3 larvae/plant and maintained the marketability of the cabbages. The results of the Eastern Cape study suggest that the only species investigated that might be suitable as a trap crop is *L.*

africanum

10.5. Conclusion

Cruciferous weeds are less suitable as host plants than cabbage, however, some of them are able to sustain a diamondback moth population if no crops are available. This indicates that non-crop crucifers found growing in the vicinity of the cabbage fields in the Eastern Cape may harbour diamondback moth. However, the results indicate that survivorship is low, which suggests that the cruciferous weeds are not having a detrimental effect on crop quality. It suggests that they may be useful in providing refugia which help to delay resistance to insecticides and in maintaining a population of moths to ensure that there are always moths available for the parasitoids. The cruciferous weeds also serve as refugia for the parasitoids associated with the diamondback moth and for other natural enemies. Some of these alternative host plants may also be suitable as trap crops but further work needs to be done before this can be determined.

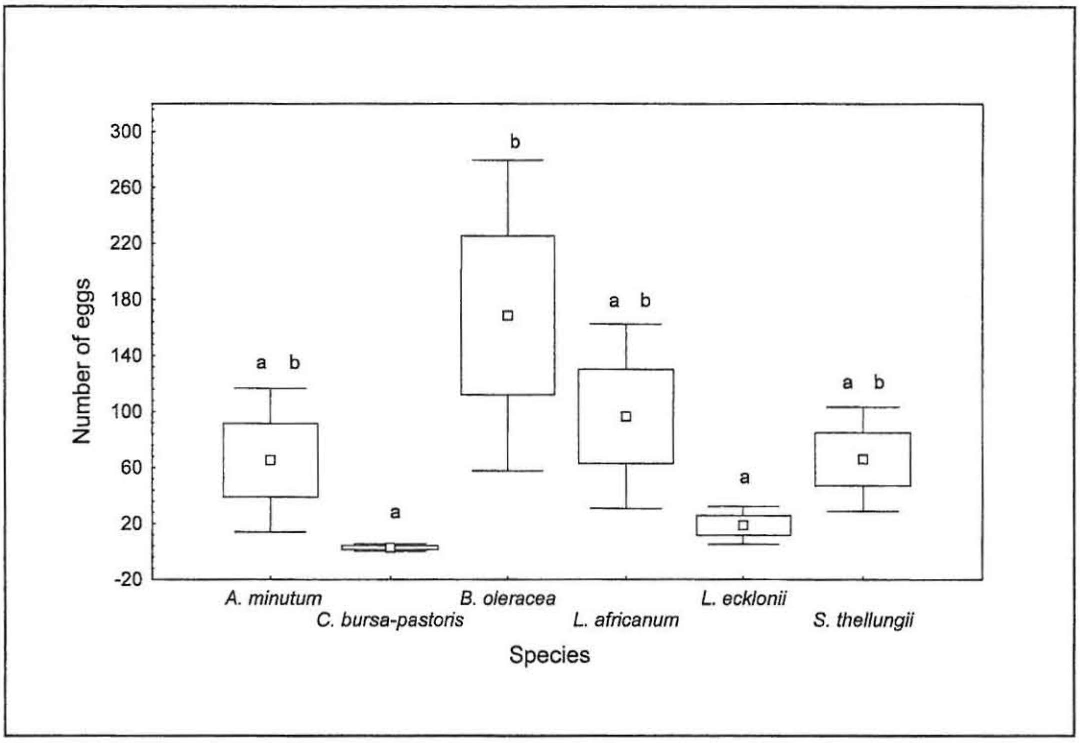

Figure 10.1. Number of eggs oviposited on each crucifer species. Species sharing a letter were not significantly different (p = 0.05) in an ANOVA. The small box represents the mean, the large box the standard error and the whisker is the 95% confidence limit. n = 72.

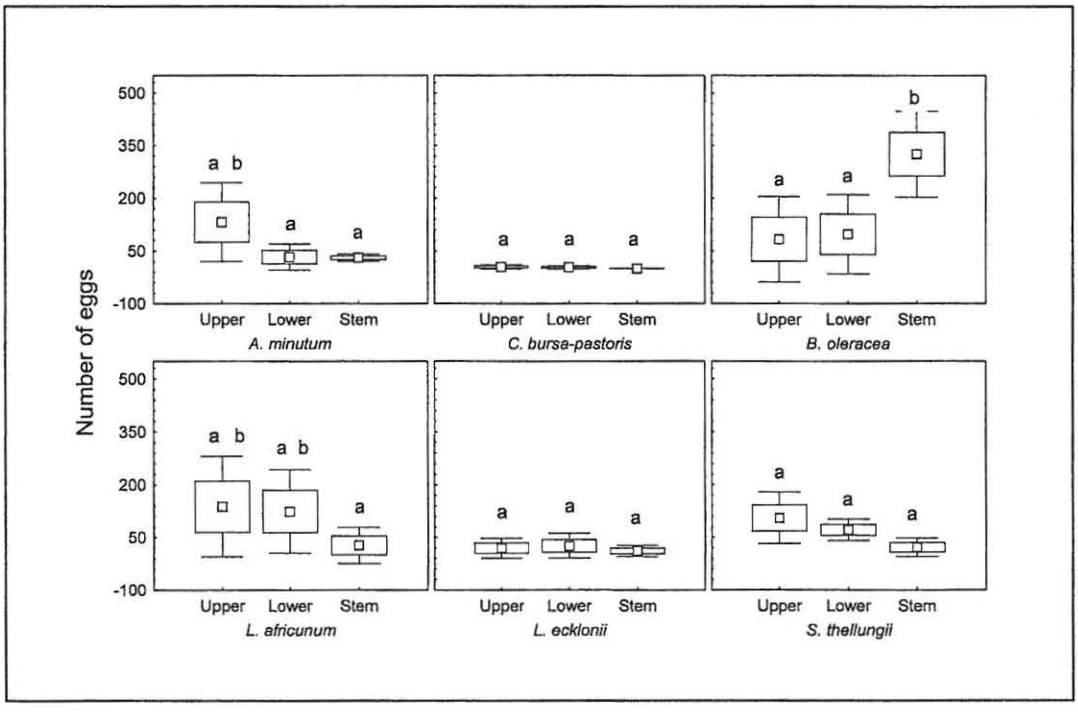

Figure 10.2. Crucifer species and surface preference of ovipositing moths. Species sharing a letter were not significantly different (p = 0.05) in an ANOVA testing for effects within and between species. The small box represents the mean, the large box the standard error and the whisker is the 95% confidence limit. n = 72.

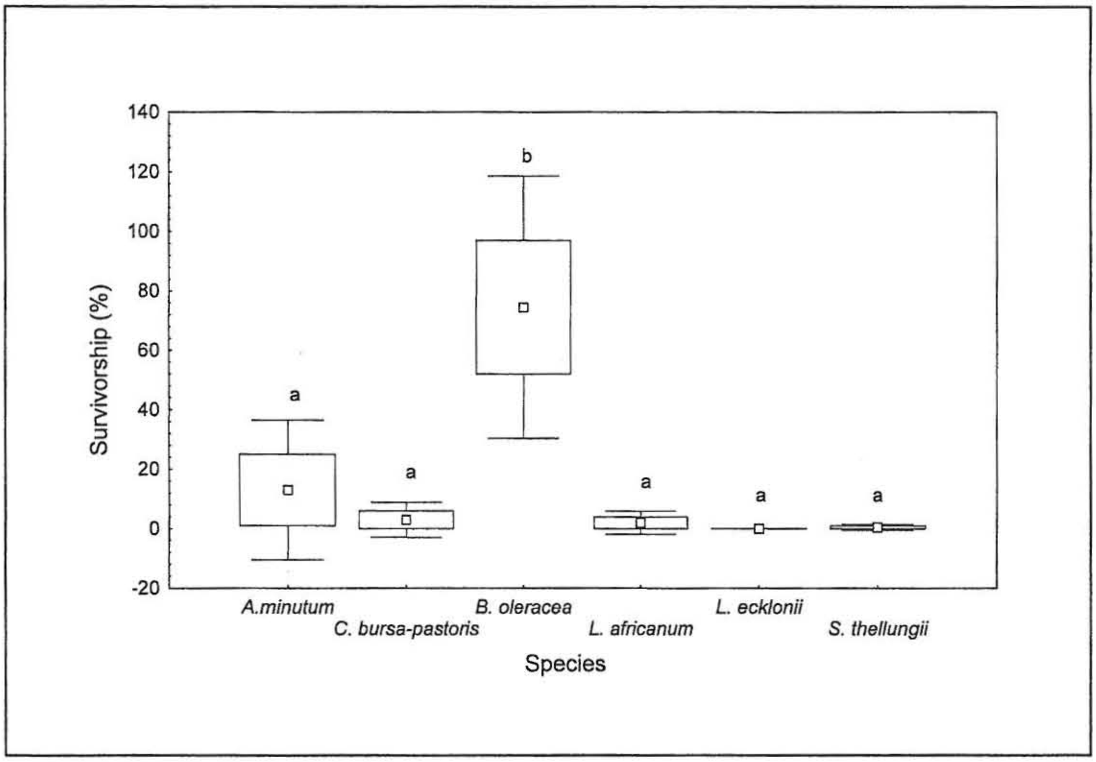

Figure 10.3. Survivorship of diamondback moth on different crucifer species. Species sharing a letter were not significantly different ($p = 0.05$) in an ANOVA. The small box represents the mean, the large box the standard error and the whisker is the 95% confidence limit. $n = 72$.

Chapter 11:

Contributions for Integrated Pest Management in the Eastern Cape

11.1. Introduction

Before the start of the insecticide era in the 1940's, vegetable growers relied on cultural practices and their knowledge of the pests to control pest problems (Kogan, 1998). With the introduction of insecticides, growers started relying on these chemicals for control because they were easy to use and effective, and many of the cultural control methods were forgotten. In many parts of the world, insecticides became the main form of control until the 1950's/60's (Matthews, 1997). By this stage insecticide resistance problems had started to develop in many pest insects, including the diamondback moth. This, together with public concern about residues and environmental pollution, led to the development of additional forms of pest control, including biological and cultural methods. It was soon discovered that, to be effective, these methods of control could not be used in isolation and that multiple strategies were needed (Shelton *et al.*, 1997). There was also a need to develop resistance management programs (Verkerk & Wright, 1994b, 1997; Shelton *et al.*, 1997; Tang *et al.*, 1997) to prevent rapid build-up of resistance to new chemicals in the future. The need to reduce insecticide applications and the introduction of additional forms of control led to the development of Integrated Pest Management (IPM).

Many definitions of Integrated Pest Management have been developed, most of which have an entomological bias. Integrated Pest Management not only covers management of insect pests species but also includes weeds, pathogens and other organisms (Kogan, 1998). Based on an analysis of definitions over 35 years, Kogan (1998) defined IPM as "a decision support system for the selection and use of pest control tactics, singly or harmoniously coordinated into a management strategy, based on cost/benefit analyses that take into account the interests of and impacts on producers, society, and the environment." There are a number of control methods that have been used in various parts of the world for IPM of the diamondback moth. Emphasis is placed on biological control, using natural enemies and pathogens; cultural methods, including intercropping, trap cropping, habitat management, and production breaks; plant resistance; and other non-polluting methods, for example selective and botanical insecticdes (Lim, 1992; Lim *et al.*, 1997). Insecticides should be used only when necessary and if there are no alternatives (Lim *et al.*, 1997).

Many of the ideas and methods that have been used in IPM programmes have been constructed and used successfully in developed countries, but they have often failed in developing countries. It is important to understand the differences between first- and third-world countries and to realise that IPM programmes from developed countries cannot be transferred without adapting them to meet the needs of growers in developing countries (Goodell, 1984; Rowell *et al.*, 1992; Waage, 1996). Many of the problems of IPM in third world countries are governmental and political (Goodell, 1984; Matteson *et al.*, 1984), socioeconomic (Andrews *et al.*, 1992), or a result of a lack of knowledge and training amongst the growers (Matteson *et al.*, 1984; Magallona, 1986). Unfortunately IPM in Africa has not had the same successes as in other parts of the world (Abate *et al.*, 2000). Generally, growers in Africa have not relied on insecticides because of economic and social concerns. As a result the development and implementation of IPM in Africa can evolve around traditional pest management strategies and not around reduction in insecticide use (Abate *et al.*, 2000).

Unfortunately, IPM programmes for commercial crucifers have not been used very often in the Eastern Cape Province. Generally, control of the diamondback moth is by calender spraying of broad-spectrum insecticides. Chapter 3 provides evidence to suggest that as a result of the continued use of insecticides, resistance has become a problem in the area. Because of this, additional methods of control and resistance management strategies need to become part of commercial crucifer growing in the Eastern Cape. In this chapter, results obtained from this study on the diamondback moth in the Grahamstown area of the Eastern Cape are considered with the development of an IPM programme in mind. Considerations include making predictions from thermal summation and weather records to determine generation times and therefore the expected production rates of the diamondback moth; determining the major mortality factors of the moth; and considering how cultural control methods, action thresholds and resistance management strategies should be introduced.

11.2. Prediction of field dynamics

Generation times can be useful in determining when control of the diamondback moth is most effective, and particularly when insecticide applications are necessary (Godin & Boivin, 1998b). The number of generations of the diamondback moth per year varies in different parts of the world. In Canada the diamondback moth cannot overwinter, but migrates from the United States in spring and as a result there are only 4 to 5 generations a year (Harcourt, 1986). In countries where the diamondback moth is present all year round, for example India and Japan, 13 or 14 and 10 to 12 generations are found per year respectively (Jayarathnam (1977) cited by Chelliah & Srinivason, 1986; Koshihara, 1986). In New Zealand the diamondback moth survives throughout the year, there are no migrations, and 6 to 7 generations have been found to occur during the year (Thomas & Ferguson, 1989). In the Eastern Cape a similar situation was observed, with the diamondback moth being present throughout the year and there was no indication of migration occurring.

The number of generations of diamondback moth in each year of the study period was determined using the thermal summations and developmental zero calculated in Chapter 4 and the actual temperature data for the study sites. During this study, five generations were possible in 1997 (April - December), nine in 1998 (January - December) and eight in 1999 (January to November). This shows that up to nine generations occur annually, with the generations being shorter (30 - 40 days) over the summer months from December to February and longer (52 - 68 days) over the winter months from June to August. Ullyett (1947b) found that in the Pretoria region of South Africa, development from egg to adult takes 14 days in summer and 18 to 21 days in winter. These generation times are much shorter than the corresponding periods in the Eastern Cape and this is probably due to the different climatic conditions in the two areas.

In New York, where the diamondback moth is not present all year round, the observed peaks in diamondback moth abundances were found to be within 1-6 days of the predicted peaks (Baker *et al.*, 1982). Butts & McEwen (1981) found a good correlation between thermal accumulations and the development of the moth, but they were working in Canada where the diamondback moth is only present over the summer months. In Quebec the observed and the predicted generations were similar but the discrepancy between the two increased with an increase in the number of generations (Godin & Boivin, 1998b).

In the Eastern Cape the generations overlap and as a result the populations did not show discrete increases as is found in more temperate climates. The number of generations is higher and this, together with the shortening of the generation times over the summer will be seen as an acceleration in population growth. This increase in the population growth of the moth (production rate) corresponded to the increase in the observed abundance of moths that was found at each site over spring (Figs. 11.1, 11.2 & 11.3). However, at all three sites a point was reached in early summer where the observed abundances fell, but the production rate continued to increase. This discrepancy must be due to mortality as a result of environmental conditions (for example temperature), parasitism or some other factor. At the sprayed site (Site 1, Fig. 11.1) the use of insecticides would affect the population fluctuations of the diamondback moth in the field.

These prediction methods are not without their drawbacks. Insects can develop at different rates in fluctuating field conditions compared to constant conditions within a growth chamber (Worner, 1992; Dent, 1997). When studies are done in a growth chamber, many of the factors that occur in the field are not considered, for example photoperiod (Higley *et al.*, 1986). Another assumption is that insects are unable to regulate their own temperature, but many in fact use behavioural and physiological mechanisms for thermoregulation (Higley *et al.*, 1986). The ambient temperature is used to make estimates, but the insect lives in a microclimate where the temperature may be very different (Dent, 1997; Higley & Haskell, 2001; Mohandass & Zalucki, 2001). In some cases weather station data have been related to the microclimate temperature and very few differences have been found, therefore weather station data have been considered adequate to predict insect development (Dent, 1997). Inaccuracies can also occur when deciding when to begin the accumulations (Pruess, 1983; Dent, 1997), but it is generally accepted that these can start once ambient temperatures exceed the developmental zero (Higley *et al.*, 1986).

11.3. Estimated diamondback moth mortality due to temperature

A number of studies have examined the effect of temperature on larval growth in the diamondback moth and the importance of temperature in population fluctuations (see Chapter 4 and 5). Generally, these studies have not always considered mortality due to thermal stress. The impact of mortality on diamondback moth populations in the Eastern Cape due to thermal stress was estimated using the rate of survival determined under laboratory conditions (Fig. 4.7, Chapter 4). The mortality determined at these various temperatures was used to convert recorded field temperatures during the study period (Fig. 5.10, Chapter 5) to instantaneous mortality rates shown in Fig. 11.1-11.3. This provided a more realistic estimate of the production rate for the diamondback moth, but there was still a discrepancy during the early summer at all the sites (Figs. 11.1 - 11.3). The estimated production rate, taking into account mortality due to thermal stress increased at this time of the year, but the actual abundances of the diamondback moth in the field decreased. This suggests that there is either a more important factor reducing the population of the diamondback moth at this time of year, or that the microhabitat of the cabbage leaf provides a refuge for the diamondback moth against thermal stress.

11.4. Diamondback moth mortality due to parasitism

Biological control using parasitoids is a central part of an IPM programme (Lim, 1986, 1992) and has been used in a number of countries (Chapters 6, 7, 8 and Appendix 1). It is crucial to be aware of the fact that using only parasitoids is unlikely to succeed in controlling the diamondback moth because both biotic and abiotic factors can disturb the balance between the moth population and its parasitoids (Chua & Ooi, 1986; Lim, 1986). In South Africa there are a large number of indigenous parasitoids associated with the diamondback moth (Kfir, 1997a, 1997b, 1998). In the Grahamstown region of the Eastern Cape, four parasitoid species were found regulating the diamondback moth population (Chapter 8). The indication that density-dependence is found between the diamondback moth and the parasitoid species (Chapter 8) further supports this suggestion.

During the summer months where there is a discrepancy between the estimated production rate of the moth and the actual abundances (Figs.11.1 - 11.3), the rate of parasitism at each site increased (Figs 11.4 - 11.6). This suggests that the parasitoids are reducing the populations at this time of year.

The effective use of parasitoids in an IPM programme relies on a number of important considerations, including selecting suitable species. Chua & Ooi (1986) found that in the Cameron Highlands different parasitoid species performed differently in laboratory trials and in field trials. *Cotesia plutellae* (Kurdjumov) provided the best control in the field, possibly because it had developed some form of resistance to the insecticides, had a higher proportion of female progeny, and had adapted to the environmental conditions. However, the introduced species, *Diadegma semiclausum* Hellèn, was superior in laboratory experiments. Different species of parasitoids also have different temperature requirements which make some more suitable for certain areas than others (Wang *et al.*, 1999).

Another factor to consider is the detrimental effect of insecticides on parasitoids. Insecticides will continue to be used and as a result it is important to know which ones will help in conserving the parasitoid species (Lim *et al.*, 1986). Growth regulators, sex pheromones, some botanical insecticides and *Bt* are generally harmless to parasitoids (Kao & Tzeng, 1992; Nemoto *et al.*, 1992; Idris & Grafius, 1993b; Muckenfuss & Shepard, 1994; Perera *et al.*, 2000).

Studies have shown that different parasitoid species parasitized larvae on different host plants at different rates. This is important for the introduction of parasitoids into areas where specific crucifer crops are grown (Talekar & Yang, 1991; Verkerk & Wright, 1997). Conservation methods are also needed to increase the impact of existing parasitoids (Verkerk & Wright, 1996b). These include providing suitable plants to provide a shelter and a food source for the parasitoids (Lim, 1986; Yang *et al.*, 1993; Idris & Grafius, 1995,1996 & 1997; Johanowicz & Mitchell, 2000a). Together with conserving parasitoids, suitable species need to be reared for release into areas where they are required (Morallo-Rejesus & Sayaboc, 1992). Rearing techniques should be easy, inexpensive and be able to produce large numbers of female parasitoids. A number of techniques have been tried and methods are continually being improved (Hu *et al.*, 1998; Okine *et al.*, 1998; Sieglaff *et al.*, 1998; Johanowicz & Mitchell, 2000b; Xu & Shelton, 2001).

11.5. Total mortality of the diamondback moth

The two most important factors found to affect the mortality of the diamondback moth in the Grahamstown area of the Eastern Cape were the estimated mortality due to temperature and the measured mortality due to parasitoids (Figs. 11.7 - 11.9). Mortality in the diamondback moth increased over the cooler winter months from June to August and decreased over the warmer months from October to January. However, as temperatures increase in late January and February, mortality due to temperature also increased (Figs. 11.1 - 11.3). Parasitism was found to be responsible for reductions in the diamondback moth over the summer months (Figs. 11.4 - 11.6). The remaining portion of the population survived or suffered mortality from other factors (which could include predators, diseases and insecticides, although these were not measured) and other environmental factors (Figs 11.7 -11.9). This suggests that in the Eastern Cape survival of the diamondback moth is generally below 40%, but in many cases these survivors are still able to cause serious damage. It also suggests that temperature and parasitoids complement one another fairly successfully.

11.6. Cultural control methods

Cultural control methods were not practised at any of the sites in this study but information collected during the study suggests that certain methods may be important in providing better control against the diamondback moth. These include promoting the efficacy of parasitoids by adapting field sizes and managing weeds.

The existence of an edge distribution (Chapter 9) in the diamondback moth and its parasitoids has implications in management strategies, including the use of insecticides. Insecticide application can be targeted to particular areas of a field which would help to reduce the costs of spraying. In a *Bt*-IPM programme set up by Biever (1997), scouting the fields resulted in only some fields or portions of a field requiring application of *Bt*. Weisz *et al.* (1996) found that spatial targeting of insecticides against the Colorado potato beetle reduced insecticide use by between 30 and 40 % but that the yield was unaffected..

The distance that the diamondback moth disperses into fields or between fields is important in resistance management strategies, for example rotational spraying (Shirai, 1991; Shirai, 1993; Shirai & Nakamura, 1994; Mo *et al.*, 2001). Shirai & Nakamura (1994) found that the moth moved further from the release sites into the surrounding fields in summer than they did in the autumn, probably as a result of lower temperatures. The optimal temperature for flight activity in male diamondback moths was 23°C (Shirai, 1991). In the Eastern Cape the diamondback moth moved further into the fields in the spring than the winter (Chapter 9) which agrees with Shirai (1991) that the diamondback moth has a higher flight capacity and ability in spring than in winter. The distance moved by parasitoids is also important as this would determine where additional plants, suitable as food sources, should be grown (Keller, 2001). Field size should then be considered when developing management strategies for the diamondback moth. In Chapter 9 three fields of different sizes were investigated and it was found that the moths moved further into the fields than the parasitoids. This suggests that smaller fields may allow increased control by parasitoids in the centre of fields. Price (1976) found that predators colonized a soybean crop from adjacent grassland but that they only moved in by about 30 m. He suggested that by reducing the size of the fields and by having uncultivated areas the colonization rates of the predators would increase.

Scouting and monitoring of the crop is very important and can result in reduced applications of insecticides and is important in determining which areas need more attention, for example the edges of the fields (Chapter 9). Monitoring the population is very important to determine which are the most important pest species, especially if these require specific control. Monitoring needs to be continued throughout the crop season as the system is continually changing and the methods of control may need to be adapted (Evans & Scarisbrick, 1994; Biever, 1997). It is also important that each field is monitored individually because there may be differences in the densities of the diamondback moth in different fields (Baker *et al.*, 1982), and even within single, large fields.

Smaller fields would result in more perimeter, which would increase the amount of weedy vegetation accessible to natural enemies. The presence of weeds in commercial fields is not always damaging because they can form a very useful part of the agro-ecosystem. Many of the suggestions made regarding the use of non-crop plants within agricultural environments are not used because of the risk of lower profits (Price, 1976) or because of the traditional belief that weeds are unfavourable. Kemp & Barrett (1989) examined the possibility of using uncultivated areas between soyabean crops to help control insect pests and improve crop yield by increasing the abundance of natural enemies within the crop. They suggested that these uncultivated corridors could provided an alternative to insecticide pest control in soybeans.

Most of the work involving other plant species in the control of the diamondback moth has included growing other plants amongst the cabbage plants. This could result in competition between the crop and the additional plants (Dempster, 1969). It may be more beneficial to let non-host plants grow around the edges of the fields. Encouraging weeds and flowering plants to grow along roadsides, in ditches, and along fence rows would help to attract parasitoids (Zandstra & Motooka, 1978; Poelking, 1992). It is important to know which plant species will benefit the parasitoids (Zandstra & Motooka, 1978) and encourage species that are going to improve parasitoid abundance. The plants chosen should not provide food to the pest species (Baggen *et al.*,1999). In the Eastern Cape alternative host plants were found associated with cabbage fields. Although diamondback moth oviposited on these plants under laboratory conditions (Chapter 10), survival was low. This suggests that these plants are probably not harbouring large numbers of diamondback moth and may be useful in the field as refugia to slow down insecticide resistance.

Other cultural management strategies include crop rotation (Magallona, 1986; Lim, 1992; Poelking, 1992), crucifer-free periods (Sun,1992; Roush, 1997a; Shelton *et al.*, 1997; Díaz-Gomez *et al.*, 2000, Saucke *et al.*, 2000), removal of crop residues immediately after harvest to prevent build-up of populations (Chelliah & Srinivasan, 1986; Lim, 1992; Poelking, 1992; Leibee &

Capinera, 1995; Magallona, 1986; Saucke *et al.*, 2000) and monitoring of transplants arriving from either affected areas or areas of insecticide resistance (Shelton *et al.*, 1993b; Leibee & Capinera, 1995; Shelton *et al.*, 1996).

11.7. Action thresholds

Insecticides have been, and will continue to be, important in the control of the diamondback moth, but because of their detrimental effect on biocontrol agents they should only be used when necessary. A method used to reduce the number of insecticide applications is to use thresholds rather than calender spraying (Hoy *et al.*, 1986; Andrews *et al.*, 1992; Cartwright *et al.*, 1992; Sun, 1992; Leibee & Capinera, 1995; Mumford & Knight, 1997) which helps to delay resistance and conserve parasitoids, especially if *Bt* is used. In the past it was accepted that insecticides were applied when the population reached an economic threshold, but more recently action thresholds are being used as they are considered more practical (Sastrosiswojo & Sastrodihardjo, 1986). Damage thresholds, where the number of holes per plant are used have also helped to reduce insecticide applications (Chalfant *et al.*, 1979; Workman *et al.*, 1980) but these often result in lower marketability (Workman *et al.*, 1980; Sears *et al.*, 1985). An action threshold considers the diamondback moth population per plant and Sastrosiswojo & Sastrodihardjo (1986) determined that in Indonesia this was 0.3 larvae per plant. Beck & Cameron (1992) and Hines & Hutchison (2001) developed action thresholds for the midwestern United States based on the percentage of plants infested (incidence-based action threshold). This system reduced insecticide use and resulted in a high level of marketability of the crop.

The successful use of action thresholds is dependent on monitoring of the crop and the pest populations. This requires scouting of the fields to determine the percentage of plants infested and the density of larvae per plant. Insecticides are only applied if the plants are infested or the larval density exceeds an action threshold. There are two important considerations if this approach is to work. Firstly, scouting needs to be simple, quick and effective and secondly, the action threshold must keep the quality of the product at the same level but reduce the number of insecticide applications (Beck & Cameron, 1992). In the Philippines, Palis (1983) found that monitoring the population of diamondback moth was as successful as bi-weekly spraying, but that monitoring was a time-consuming process. Scouting and monitoring cabbage crops to determine action thresholds is very rarely used in the Eastern Cape.

11.8. Resistance management strategies

A number of management strategies have been developed to slow down and prevent the build-up of resistance to insecticides. One of the management strategies used is rotational spraying, where different chemicals are sprayed on a rotation program to help slow down the evolution of resistance (Sakai, 1986; Hama, 1992; Miyata, 1992; Sun, 1992). Revolving doses of insecticides have also been used where low doses are used with a periodic high dose (Gardner *et al.*, 1998; Chilcutt & Tabashnik, 1999). Transgenic plants incorporating genes from *Bt* have also been used (Riggin-Bucci & Gould, 1997; Roush, 1997a, 1997b) and naturally occurring refugia of alternate hosts help delay resistance to insecticides, including *Bt* (Liu & Tabashnik, 1997a). It is also important to avoid mixing of insecticides (Sun, 1992; Roush, 1997a), to use economic thresholds (Chilcutt & Tabashnik, 1999) and to encourage grower education and participation (Cheng *et al.*, 1992). Again, in the Eastern Cape resistance management strategies are not used extensively.

11.9. Education of growers

Education of growers is very important (Matteson *et al.*, 1984; Ooi, 1986; Biever, 1997; Shelton *et al.*, 1997) and it is important to provide them with the knowledge to be able to develop and adapt an IPM programme into a way of life. In the past much of this knowledge has been provided through technology transfer or "top-down" information, where growers are taught in a classroom environment about problems and how to deal with them. In most cases this has not worked and the need to involve the grower, to use his expertise and to adapt the system to fit into the growers' farming practise has become important (Heisswolf *et al.*, 1997). This has been done with the introduction of Farmers Field Schools which provide "bottom-up" information and allow the growers, extension officers and scientists to share information (Lim, 1992; Lim *et al.*, 1997; Sastrosiswojo, 1996). This provides the farmers with an ecological approach and allows them to carry out their own experiments to determine the best control methods (Ooi, 1997). In Malaysia diamondback moth was successfully controlled by insecticides until the 1950's when resistance developed. IPM was put into practice with the release of natural enemies, but the growers were not involved and continued to use insecticides. As a result, the problems continued until *Bacillus thuringiensis* Berliner (*Bt*) was introduced. This allowed the natural enemies to establish which resulted in reductions in diamondback moth numbers (Ooi, 1997). IPM must involve all the people concerned including the growers, extension workers and scientists (Loke *et al.*, 1992; Waage, 1996).

IPM programmes involving diamondback moth have been set up in different countries using different methods but development of a full IPM process has been slow (Lim, 1992; Loke *et al.*, 1992). It is agreed that IPM needs to take an holistic approach to control diamondback moth (Lim, 1992; Loke *et al.*, 1992). Biological control is generally considered crucial in successful IPM (Ooi, 1986, 1992; Lim, 1992; Lim *et al.*, 1997). One of the most important aspects of biocontrol is conservation of natural enemies within the crop environment through habitat management, including food resources, shelter and alternative hosts (Waage ,1996; Baggen *et al.*, 1999; Landis *et al.*, 2000). It is also important to take into consideration that an IPM program for diamondback moth is not static but changes as new control methods and management strategies are developed (Loke *et al.*, 1992). We need to learn from mistakes made in the past and not let one "silver bullet" take over from IPM (Kogan, 1998).

11.10. IPM in other countries

Generally growers have been reluctant to adopt IPM programmes but IPM has been successful in a number of countries and has shown very favourable results for the control of diamondback moth. The following sections gives some of these programmes, how they were implemented and the results that were achieved.

Biever (1997) developed a Biological Control - Integrated Pest Management (BC-IPM) system where *Bt* applications were used rather than synthetic insecticides, resulting in a reduction of application by more than 50%. Augmentative releases of parasitoids were carried out which further reduced the need for *Bt* applications as the parasitoids increased and provided suitable control. This system has been successful in Rio Grande Valley, Texas, Guatemala, Mexico and more recently in Mauritius. Apart from using microbial sprays and releasing parasitoids, it is very important that population monitoring occurs as part of a BC-IPM system. This system reduced the application of chemicals from 20 applications to 6 applications of *Bt* over a growing season. Morallo-Rejesus *et al.* (1996) showed that using *C. plutellae* together with *Bt* and an economic threshold level resulted in 48% higher yields than in farmers' fields where a synthetic spraying program was being used. In Jamaica an IPM programme using *Bt* together with host plant resistance provided better control against the diamondback moth than the standard cabbage variety treated with pyrethroids (Ivey & Johnson, 1998).

In the Philippines an IPM programme was established using the introduced *Diadegma semiclausum* Hellén together with *Bt*, but the programme failed initially due to lack of grower knowledge. This lead to the establishment of Farmer Field Schools and the acceptance of these methods by the growers. Insecticide applications were reduced and most growers no longer use calender spraying. Yields either stayed the same or increased (Waage, 1996; Lim *et al.*, 1997). In the Cameron Highlands of Malaysia three major parasitoid species were found, including *C. plutellae*, and two introduced species, *D. semiclausum* and *D. collaris*. As a result of restrictions on some insecticides, farmers switched to *Bt*, allowing the parasitoids to build up. This programme worked well in the highlands but in the warmer lowlands the parasitoids were not suited to the higher temperatures (Ooi, 1992). In Indonesia biological control using *D. semiclausum* combined with applications of *Bt* resulted in reduced chemical applications, increased parasitism levels, increased marketable yield and increased profits (Sastrosiswojo, 1996). IPM has also been effective in Honduras and other Central American countries. These programmes have generally used *Bt* and cultural practices together with insecticides, as parasitoids have not become established. It has, however, still resulted in reduced applications of insecticides from 9 to 2 applications per crop

(Andrews *et al.*, 1992).

On a watercress farm in Hawaii, Nakahara *et al.* (1986) found that diamondback moth could be controlled effectively by the use of an overhead sprinkler system together with *C. plutellae*. This programme proved to be cost-effective, with production increasing by 93% and a reduction of chemical costs by 83%. Unfortunately, minor pests became a problem because of the change in the environment. Another consideration is the cost of overhead sprinkler systems and therefore this method of control is probably only feasible on smaller farms.

In developed countries IPM has also been successful. In Georgia (USA) on-farm management using *Bt* with occasional tank mixes of mevinphos has been used and has resulted in 85% or more marketable cabbage. This has not stopped the resistance problem but it has provided more time to find alternative control strategies (Adams, 1992). In North America resistance was a problem in the 1980's. *Bt* was used with late season applications of insecticides and it was found that parasitoids appeared and reduced diamondback moth numbers, increasing marketability to between 95 - 100% (Wyman,1992). In Queensland, Australia, resistance became a problem in the 1980's and a resistance management strategy was developed which included a summer production break, use of *Bt* and improved spray applications, insecticide rotation on farms and monitoring programs (Heisswolf *et al.*, 1997). This section shows that in those countries where IPM has been used to control the diamondback moth, the results have usually been favourable and yields and marketability have increased.

11.11. Conclusions

In the past much of the work on the diamondback moth has been considered on a ditrophic level but very little has been done on a tritrophic level which considers the host plant-pest-natural enemy relationships (Wright & Verkerk, 1995; Verkerk & Wright, 1996b; Lewis *et al.*, 1997, Verkerk *et al.*, 1998). In the past, control methods have often been used in isolation from one another, but with IPM this has changed. Biocontrol, plant resistance, cultural practices, physical or mechanical methods, and chemical control are all used in IPM strategies (Lim, 1992; Poelking, 1992; Lewis *et al.*, 1997). Due to the significance of parasitoids in IPM programmes, the following recommendations are also important and should become part of the process. Selective insecticides need to be encouraged; cost-effective mass-rearing techniques need to be developed; strains of parasitoids that are resistant to chemicals chould be bred; and more potential biocontrol agents need to be found and imported (Morallo-Rejesus & Sayaboc, 1992). All of these factors need to be considered as control of the diamondback moth moves towards what Lewis *et al.* (1997) call a "total systems approach" to sustainable pest management.

The results of this study suggest that IPM of diamondback moth might succeed in the Eastern Cape, especially if more use was made of bioinsecticides and parasitoids. Unfortunately the scope of this study did not allow for any of the ideas to be developed into an active programme and there were many other issues that were not investigated, including the social and economic aspects of such a programme. IPM should be considered as an on-going process and the following strategies are suggested for the development of a programme in the area. Because there was an indication that resistance to the insecticides used had developed, a reduction in the number of applications of broad-spectrum insecticides and the replacement of chemical applications by bioinsecticides like *Bt* should be considered. This would allow for the build-up of the indigenous parasitoids that are present in the fields. Suitable flowering plants should be planted to provide nectar sources for these parasitoids. This study showed that the populations of diamondback moth varied over time and among sites and therefore scouting would form a very important part of any programme. The size and shape of the field are also important as the moths tend to disperse further into the fields than the parasitoids. Therefore using smaller fields would allow for the saturation of parasitoids throughout the field. There is also a potential for the use of trap crops. The removal of cabbage refuse from recently harvested fields is crucial to prevent rapid build-up of diamondback moth populations and the implementation of resistance management strategies are needed to slow down the development of insecticide resistance.

Resistance to insecticides is a common theme in the Pretoria region and the Eastern Cape Province. There seems to be a trend that when the use of insecticides is minimal, the diamondback moth problem is greatly reduced. This information suggests that parasitoids together with softer insecticides should form the basis for any integrated management programme in South Africa. Very little work has been done in South Africa on the diamondback moth. There are some early papers by Gunn (1917) and Ullyett (1947a & b), while more recently there has been one published paper on resistance (Sereda *et al.*, 1997), one on trap cropping (Charleston & Kfir, 2000), a thesis on canola (Mosiane, 2001) and a handful of publications discussing parasitoids (Dennill & Pretorius, 1995; Kfir, 1996; Kfir 1997a; Kfir, 1997b; Kfir, 1998; Waladde *et al.*, 2001). This thesis, although broad, will act as a platform for more targeted studies in the future.

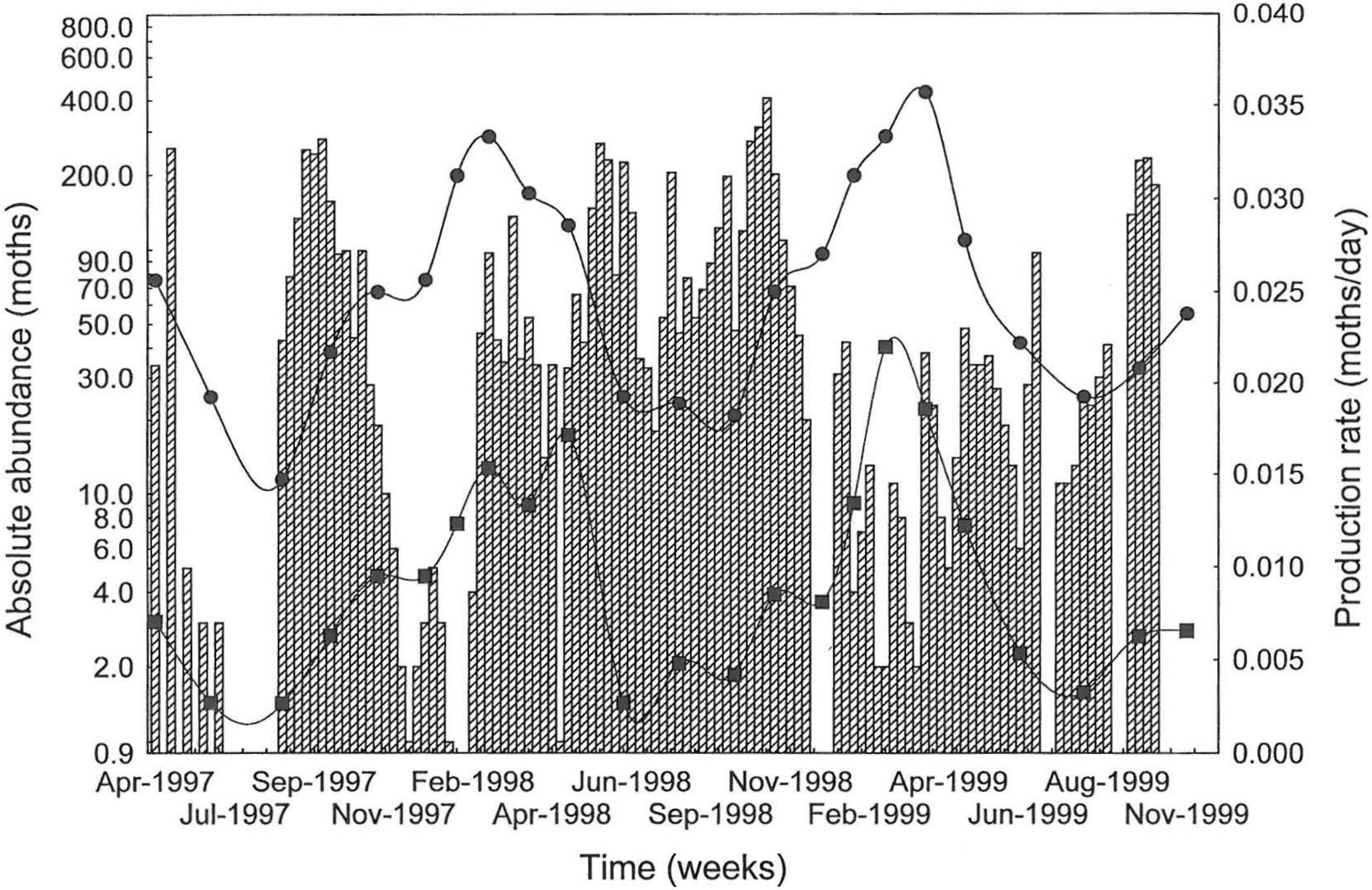

Figure 11.1. Histogram of the absolute abundance of diamondback moth (larvae and pupae) from field collections at Site 1, showing the expected production rate of the moth (●) and the calculated production rate taking into account mortality due to temperature (■).

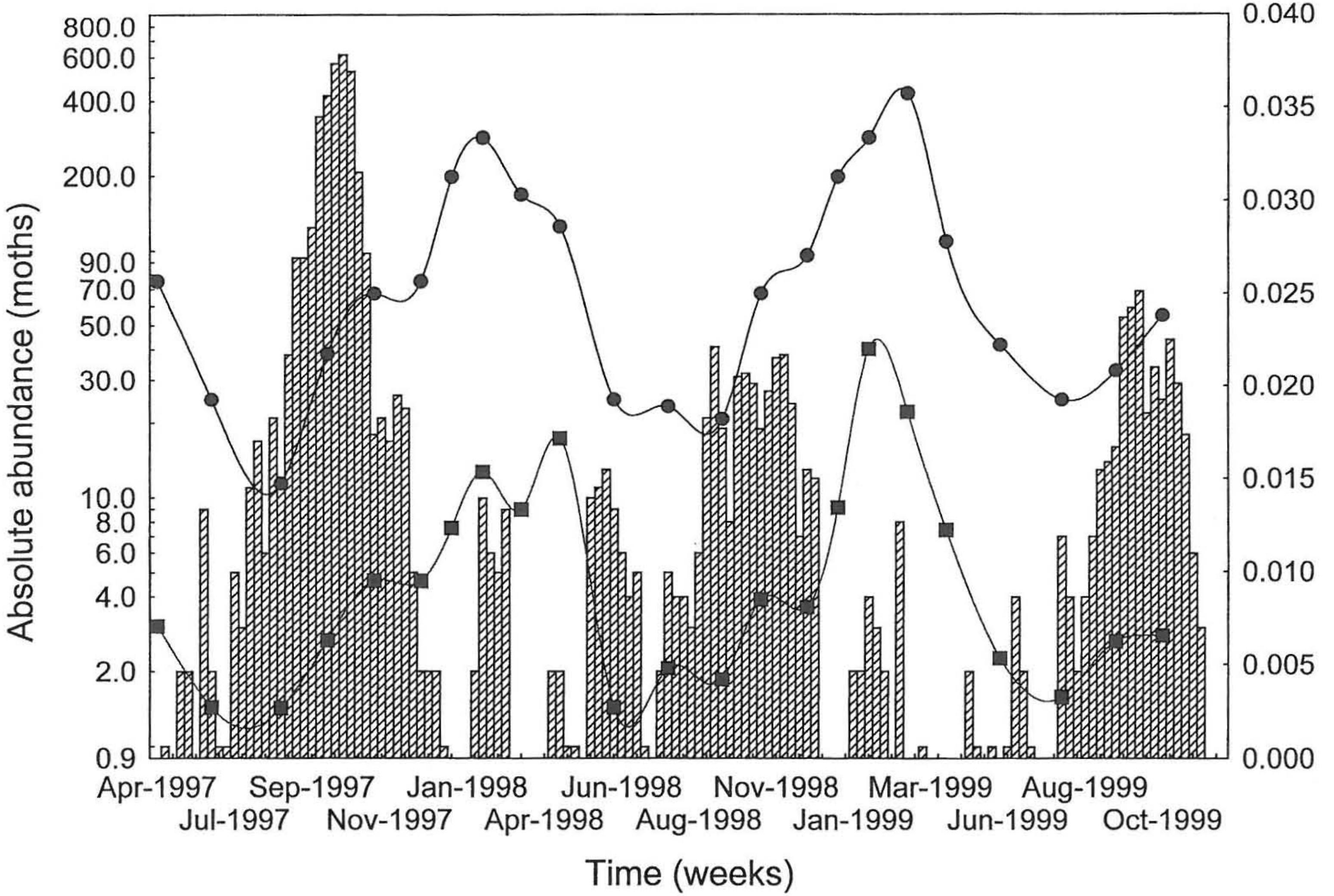

Figure 11.2. Histogram of the absolute abundance of diamondback moth (larvae and pupae) from field collections at Site 2, showing the expected production rate of the moth (●) and the calculated production rate taking into account mortality due to temperature (■).

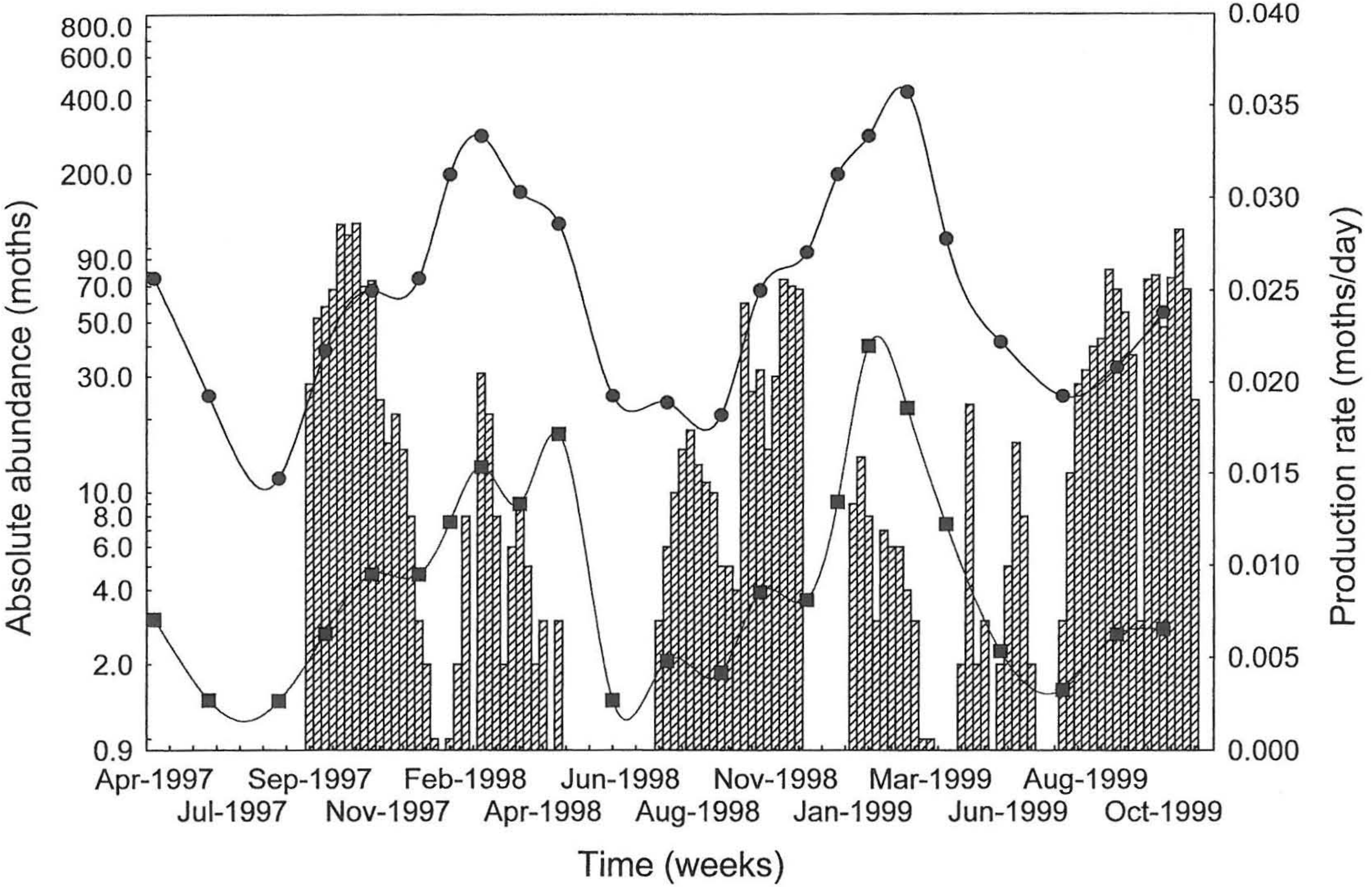

Figure 11.3. Histogram of the absolute abundance of diamondback moth (larvae and pupae) from field collections at Site 3, showing the expected production rate of the moth (●) and the calculated production rate taking into account mortality due to temperature (■).

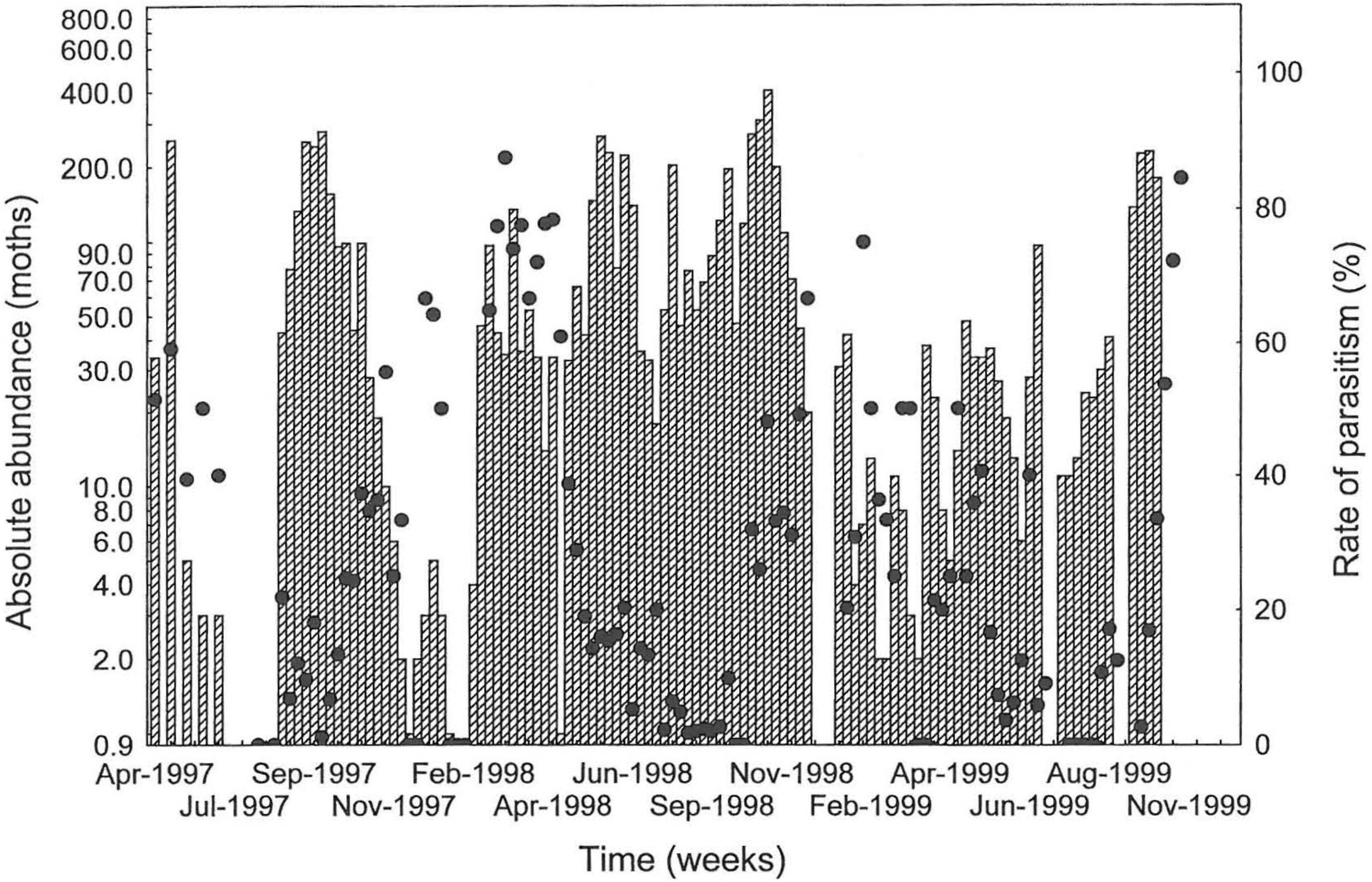

Figure 11.4. Histogram of the absolute abundance of the diamondback moth (larvae and pupae) at Site 1 showing the rate of parasitism in the field (●).

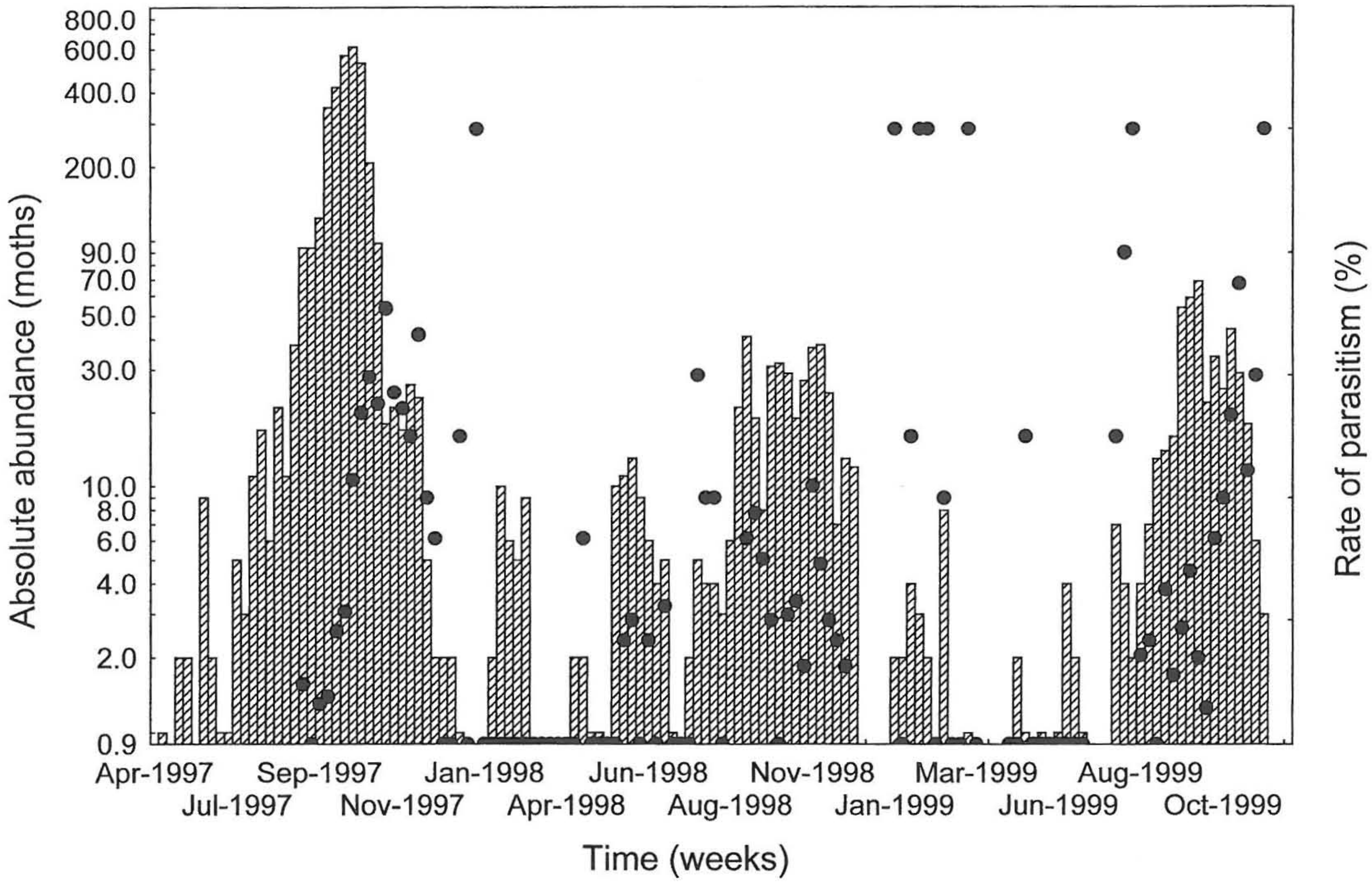

Figure 11.5. Histogram of the absolute abundance of the diamondback moth (larvae and pupae) at Site 2 showing the rate of parasitism in the field (●).

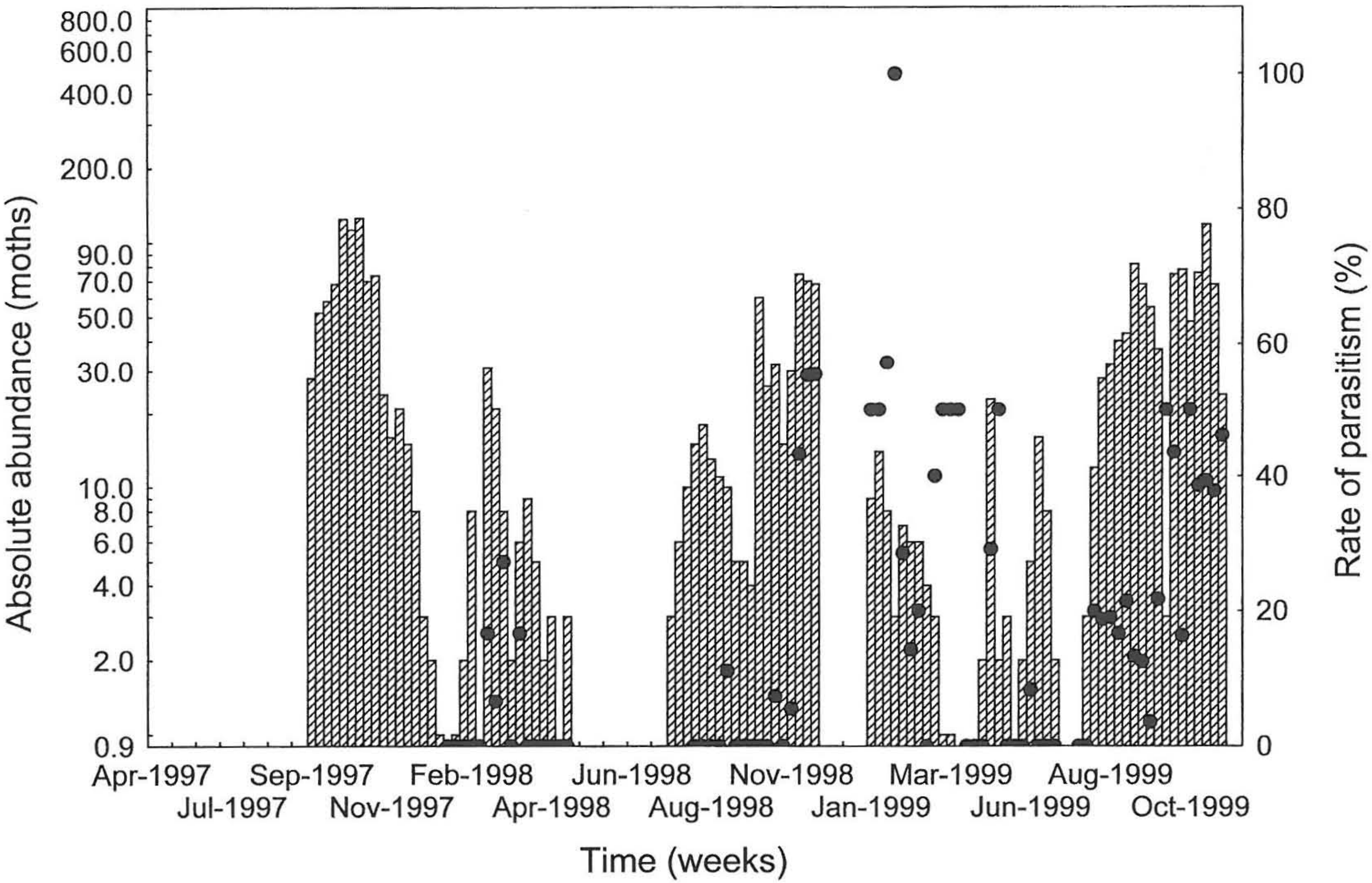

Figure 11.6. Histogram of the absolute abundance of the diamondback moth (larvae and pupae) at Site 3 showing the rate of parasitism in the field (●).

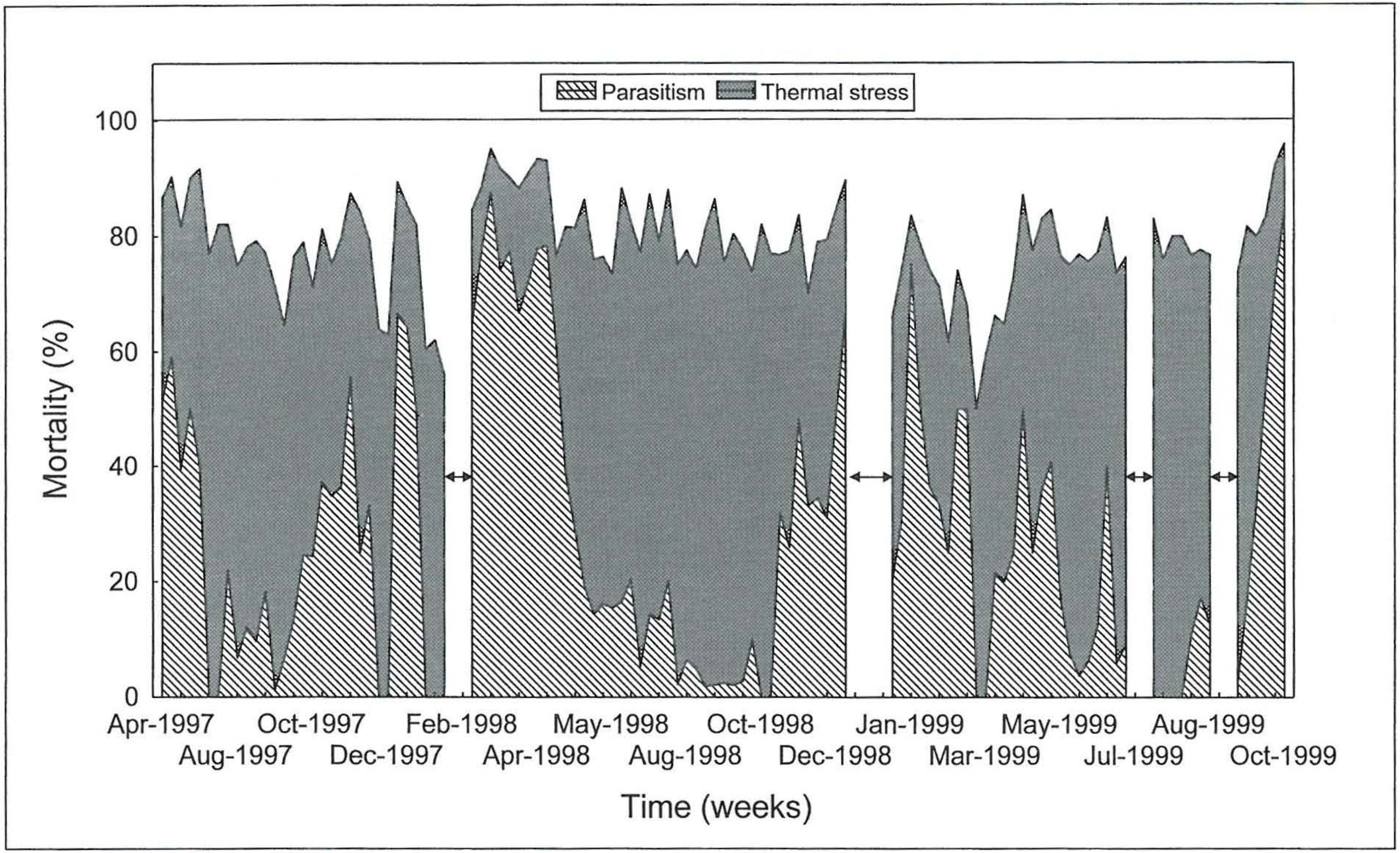

Figure 11.7. Proportion of the diamondback moth population effected by parasitoids (field data) and thermal stress (estimated from laboratory data and weather records) at Site 1. Arrows show periods of no sampling.

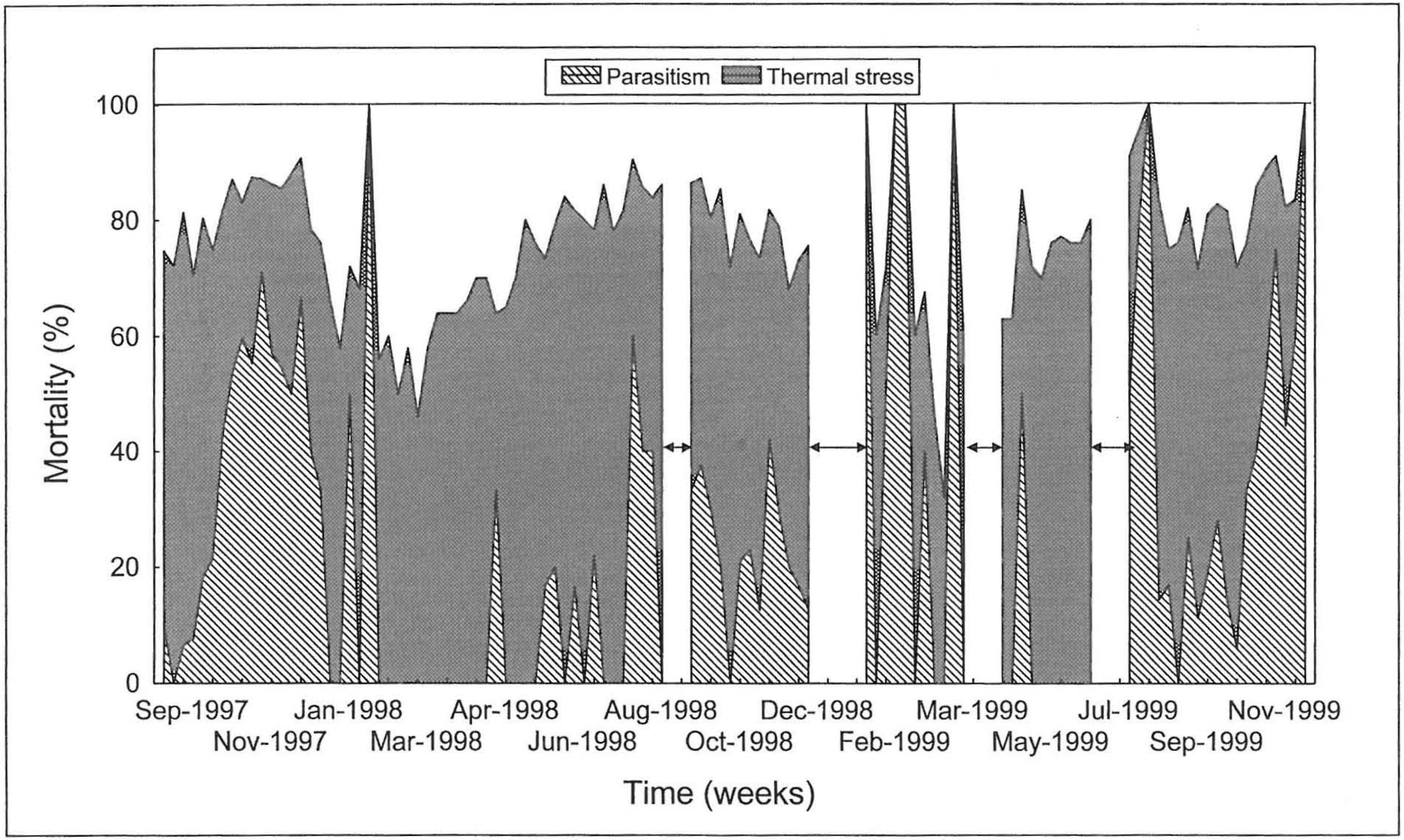

Figure 11.8. Proportion of the diamondback moth population effected by parasitoids (field data) and thermal stress (estimated from laboratory data and weather records) at Site 2. Arrows show periods of no sampling.

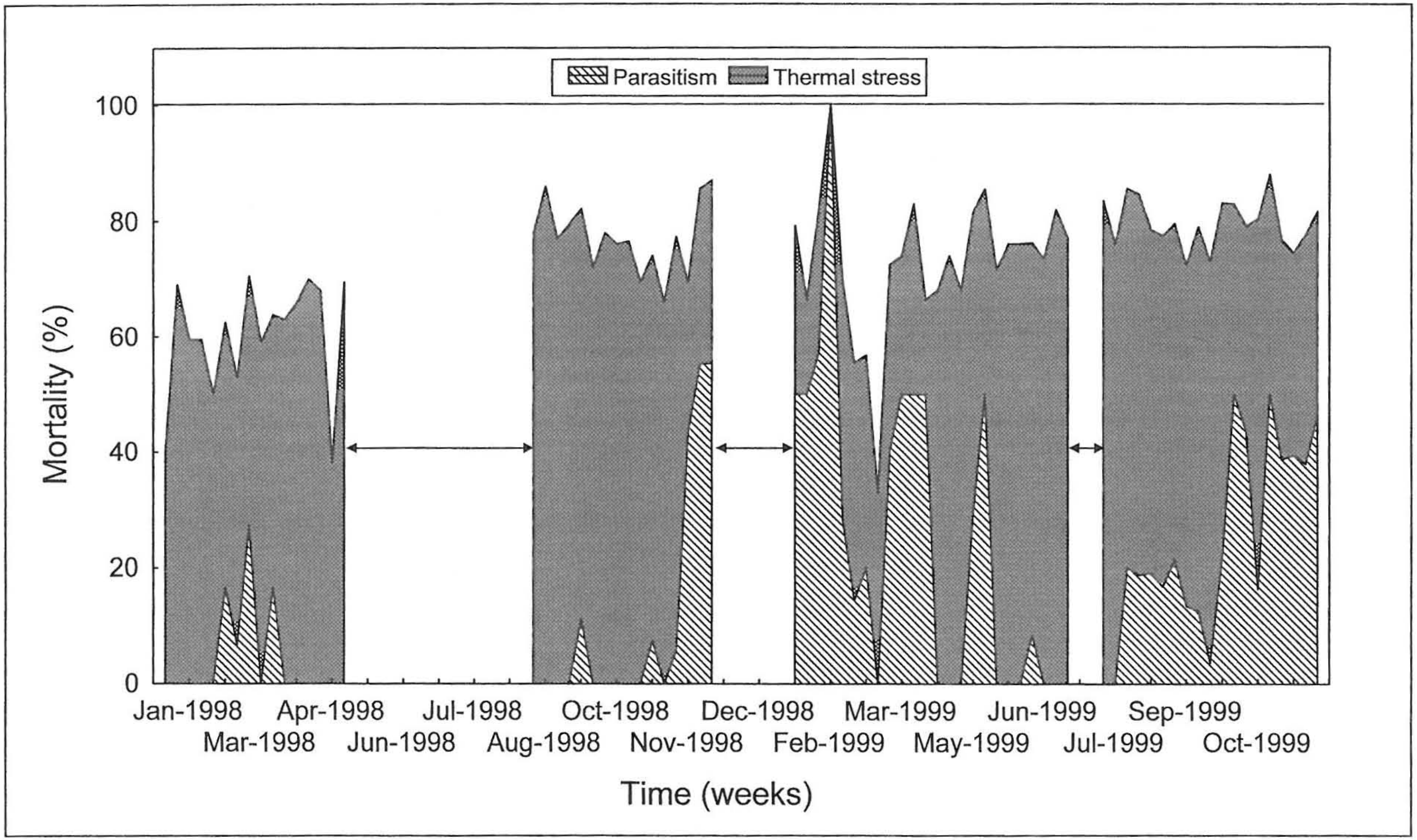

Figure 11.9. Proportion of the diamondback moth population effected by parasitoids (field data) and thermal stress (estimated from laboratory data and weather records) at Site 3. Arrows show periods of no sampling.

Appendix

Table 1. Indigenous and naturally introduced parasitoid species associated with the diamondback moth in other countries. Dashes indicate no available data.

Country	**Species**	**Parasitism levels**	**Authors**
Ontario, Canada	*Diadegma insularis* Cresson	36%	Harcourt (1960)
	Microplitis plutellae Meusbeck	-	
	Diadromus plutellae (Ashmead)	16%	
	Dibrachys cavus (Walker)	-	
	Habrocytus sp.	-	
	Oomyzus sokolowskii (Kurdjumov)	-	
	Spilochalcis albifrons (Walsh)	-	
Saskatchewan, Canada	*D. insulare* *M. plutellae*	35 - 81% (combined)	Putnam (1973)
England	*Diadegma fenestralis* Holmgren *Diadegma semiclausum* Hellén	90% (combined)	Hardy (1938)
Michigan, USA	*D. insulare*	68%	Zhao *et al.* (1992)
	M. plutellae	32%	
South Carolina, USA	*D. insulare*	90%	Muckenfuss *et al.* (1992)
Florida, USA	*D. insularis*	32%	Ru & Workman (1979)
	O. sokolowskii	10%	
Japan	*Cotesia plutellae* (Kurdjumov)	-	Koshihara (1986)
	Tetrastichus sp.	-	
	Diadromus collaris Gravenhorst	-	
	C. plutellae	50%	Wakisaka *et al.* (1992)
	O. sokolowskii *Diadromus subtilicornis*	16 - 95% (combined)	

Table 1 continued

Country	**Species**	**Parasitism levels**	**Authors**
Benin	*C. plutellae*	59%	Bordat & Goudegnon (1997)
Romania	28 species (Ichneumonidae and Braconidae)	60% (only a few effective)	Mustata (1992)
Taiwan	*C. plutellae* *D. collaris*	< 40% -	Talekar *et al.* (1992)
	C. plutellae, *D. collaris* and *Itoplectis naranyae* (Ashmead)	-	Talekar (1996)
Honduras - Central America	*D. insulare*	9 - 47%	Andrews *et al.* (1992)
Trinidad (West Indies)	*Apanteles aciculatus* (Ashmead) *Spilochalcis hirtifemora* (Ashmead) *Tricogramma brasiliensis* (Ashmead)	Not effective	Yaseen (1978)
Jamaica	*D. insulare* *O. sokolowskii* *C. plutellae* *Trichospilus diatraeae* Cherian and Margabandhu	0 - 76% < 30% < 5% rare	Alam (1992)
Northwestern Himalaya	*C. plutellae* *Diadegma fenestralis* Holmgren	31% 29%	Bhalla & Dubey (1986)
India	*C. plutellae* *O. sokolowskii*	0 -75% < 20%	Chelliah & Srinivasan (1986)

Table 1 continued

Country	**Species**	**Parasitism levels**	**Authors**
Thailand	*Trichgrammatoidea bactrae* Nagaraja	-	Rowell *et al.* (1992)
	Tricogramma confusum	-	
	C. plutellae	12 - 88%	
	D. collaris	9 - 31%	
	Macromalon orientale Kerrich	< 9%	
	Isotima sp.	rare	
	Brachymeria excarinata Gahan and *B. lasus* Walker	4 - 60%	
	T. bactrae	16 - 45%	Keinmeesuke *et al.* (1992)
Malaysia:	*C. plutellae* & *Tetrastichus ayyari* Rohw	-	Lim (1986)
	C. plutellae	12 - 19%	Ooi (1986)
Cameron Highlands	*C. plutellae*	low	Chua & Ooi (1986)
	C. plutellae	12 - 35%	Ooi (1992)
	C. plutellae	12 - 49%	Loke *et al.* (1992)
Philippines	*D. semiclausum*	4 - 24% (in laboratory)	Velasco (1983b)
	Microplitis sp.		
	C. plutellae	0 - 70%	Poelking (1992)
	C. plutellae	<17%	Morallo-Rejesus & Sayaboc (1992)

Table 1 continued

Country	Species	Parasitism levels	Authors
Zambia	*O. sokolowskii*	- -	Lim (1986) Yaseen (1978)
New Zealand	*Diadegma laterallis* Gravenhorst	< 7%	Lim (1986)

Table 2. Parasitoid species introduced into some countries for diamondback moth control. Dashes indicate unavailable data.

Country	**Year**	**Species**	**Effective**	**Established**	**Authors**
Northern Japan	1996 - 1999	*Diadegma semiclausum* Hellèn	29 - 53%	Yes	Noda *et al.* (2000)
Florida, USA	-	*Cotesia plutellae* (Kurdjumov)	3 - 11%	No	Mitchell *et al.* (1997b)
Hawaii	1972 - 1974	*C. plutellae*	No	No	Nakahara *et al.* (1986)
	1981 - 1982	*C. plutellae*	Yes	Yes	
Pakistan	-	*Oomyzus sokolowskii* (Kurdjumov)	1 - 72%	Yes	Mushtaque (1990)
		C. plutellae	0 - 34%	Yes	Mushtaque & Mohyuddin (1987)
Taiwan Highlands	1980's	*D. semiclausum*	65%	Yes	Talekar *et al.* (1992)
Lowlands	1992	*O. sokolowskii*	76 - 95%	Slow	Talekar (1996)
Central America	1990	*C. plutellae*	No	No	Andrews *et al.* (1992)
		Diadromus collaris Gravenhorst	No	Yes	
Jamaica	-	*C. plutellae* *O. sokolowskii*	5 - 86%	?	Alam (1992)

Table 2 continued

Country	**Year**	**Species**	**Effective**	**Established**	**Authors**
Lesser Antilles (West Indies)	-	*C. plutellae* *Apanteles vestalis* Haliday *Diadromus collaris* Gravenhorst	No No No	Yes No No	Lim (1986) Bennett & Yaseen (1972)
Trinidad (West Indies)	-	*C. plutellae* *O. sokolowskii*	5 - 56%	Yes	Lim (1986) Yaseen (1978)
Cape Verde Islands	1981 & 1982	*C. plutellae* *O. sokolowskii* *Microplitis plutellae* Meusbeck	Yes Yes No	Yes Yes No	Lim (1986)
Thailand	1965	*C. plutellae* *Brachymeria* sp *O. sokolowskii* *D. collaris* *D. semiclausum*	17 - 29% - - - -	?	Buranapanichpan *et al.* (1998)
Malaysia: Cameron Highlands	1970's	*D. semiclausum* *D. semiclausum* *D. collaris* *D. semiclausum* *D. collaris*	- 3 % < 9% - -	? Yes Yes Yes Yes	Ooi (1980) Lim (1986), Ooi (1986) and Chua & Ooi (1986) Loke *et al.* (1992) and Ooi (1992)

Table 2 continued

Country	**Year**	**Species**	**Effective**	**Established**	**Authors**
Indonesia	1950	*D. semiclausum*	80%	Yes	Sastrosiswojo & Sastrodihardjo (1986)
	1970's	*D. semiclausum*	64 - 100%	Yes	Lim (1986)
	1990's	*D. semiclausum*	36 - 90%	Yes	Sastrosiswojo (1996)
St Helena	1999	*C. plutellae*	27 - 80%	Yes	Kfir & Thomas (2001)
		D. collaris	0 - 55%		
Zambia		*C. plutellae & D. collaris*	Yes 80%	Yes	Lim (1986) Yaseen (1978)
New Zealand	1930's	*D. semiclausum*	Yes	Yes	Lim (1986)
		D. collaris *D. semiclausum*	Yes	Yes	Thomas & Ferguson (1989), Beck & Cameron (1992) and Waterhouse (1992)

Table 2 continued

Country	**Year**	**Species**	**Effective**	**Established**	**Authors**
Pacific Islands:	-				
Australia		*D. semiclausum, Diadegma rapi* Cameron and *D. collaris*	Yes - above 70%	Yes	Goodwin (1979) and Lim (1986)
		C. plutellae	Yes	Yes	Waterhouse (1992)
		D. semiclausum	Yes	Yes	
		D. collaris	Yes	Yes	
Cook Islands	1974 - 1975	*D. collaris*	Mostly	Unknown	Waterhouse (1992)
		Tricogramma spp.	No	No	
	1990	*D. semiclausum*	Yes	?	
Fiji	1943, 1971	*D. collaris*	?	?	
	1971, 1972,	*C. plutellae*	-	-	
	1983, 1984		Yes	-	
	1984	*O. sokolowskii*	Yes	-	
	1945,	*D. semiclausum*	No	No	
	1990		Yes	-	
Papua New Guinea	1983	*C. plutellae*	Yes	-	
	1993	*D. semiclausum*	53 - 85%	Yes	Saucke *et al.* (2000)
		C. plutellae	3 - 10%	Yes	
Tonga	1943	*D. collaris*	No	No	Waterhouse (1992)
Guam	1975	*D. collaris*	No	No	
		D. insulare	No	No	
		C. plutellae	No	No	
		O. sokolowskii	No	No	

References

Abate, T.; van Huis, A. and Ampofo, J.K.O. 2000. Pest management strategies in traditional agriculture: an African perspective. *Annual Review of Entomology*. 45: 631-659.

Adams, D.B. 1992. On-farm components of diamondback moth management in Georgia, USA. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 499-501.

Alam, M.M. 1992. The diamondback moth and its natural enemies in Jamaica and other Caribbean islands. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 233-243.

Altieri, M.A. and Letourneau, D.K. 1982. Vegetational management and biological control in agroecosystems. *Crop Protection*. 1: 405-430.

Altieri, M.A.; van Schoonhoven, A. and Doll, J. 1977. The ecological role of weeds in insect pest management systems: a review illustrated by bean (*Phaseolus vulgaris*) cropping systems. *PANS*. 23: 195-205.

Andow, D.A. 1990. Population dynamics of an insect herbivore in simple and diverse habitats. *Ecology*. 71: 1006-1017.

Andow, D.A. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology*. 36: 561-586.

Andrahennadi, R. and Gillot, C. 1998. Resistance of Brassica, especially *B. juncea* (L.) Czern, genotypes to the diamondback moth, *Plutella xylostella* (L.). *Crop Protection*. 17: 85-94.

Andrews, K.L.; Sanchez, R. and Cave, R.D. 1992. Management of diamondback moth in Central America. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 487-497.

Ankersmit, G.W. 1953. DDT resistance in *Plutella maculipennis* (Curt.) (Lepidoptera) in Java. *Bulletin of Entomological Research*. 44: 421-425.

Annecke, D.P. and Moran, V.C. 1982. Insects and Mites of Cultivated Plants in South Africa. Butterworth, Cape Town, South Africa.

Asayama, T. 1986. Pathology and morphogenesis of a granulosis virus of the diamondback moth. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 205-212.

Atwal, A.S. 1955. Influence of temperature, photoperiod, and food on the speed of development, longevity, fecundity, and other qualities of the diamondback moth *Plutella maculipennis* (Curtis) (Lepidoptera: Tineidae). *Australian Journal of Zoology*. 3: 185-221.

Azidah, A.A.; Fitton, M.G. and Quicke, D.L.J. 2000. Identification of the *Diadegma* species (Hymenoptera: Ichneumonidae, Campopleginae) attacking the diamondback moth, *Plutella xlostella* (Lepidoptera: Plutellidae). *Bulletin of Entomological Research*. 90: 375-389.

Bach, C.E. and Tabashnik, B.E. 1990. Effects of nonhost plant neighbors on population densities and parasitism rates of the diamondback moth (Lepidoptera: Plutellidae). *Environmental Entomology*. 19: 987-994.

Baggen, L.R.; Gurr, G.M. and Meats, A. 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. *Entomologia Experimentalis et Applicata*. 91: 155-161.

Bahari, I.B. 1994. Radiation-induced changes in reproductive ability of diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*. 87: 1190-1197.

Baker, G.J. and Kovaliski, J. 1999. Detection of insecticide resistance in *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) populations in South Australian crucifer crops. *Australian Journal of Entomology*. 38: 132-134.

Baker, P.B.; Shelton, A.M. and Andaloro, J.T. 1982. Monitoring of diamondback moth (Lepidoptera: Yponomeutidae) in cabbage with pheromones. *Journal of Economic Entomology*. 75: 1025-1028.

Banaag, A.; Honda, H. and Shono, T. 1997. Effects of alkaloids from Yam, *Dioscorea hispida* Schlussel, on feeding and development of larvae of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology*. 32: 119-126.

Banaag, A.B.; Honda, H. and Shono, T. 1998. Effects of non-alkaloid extracts from tropical yam, *Dioscorea hispida* against the diamondback moth, *Plutella xylostella* (Lepidoptera; Yponomeutidae). *Applied Entomology and Zoology*. 33: 369-373.

Baur, M.E.; Kaya, H.K. and Thurston, G.S. 1995. Factors affecting entomopathogenic nematode infection of *Plutella xylostella* on a leaf surface. *Entomologia Experimentalis et Applicata*. 77: 239-250.

Baur, M.E.; Kaya, H.K.; Gaugler, R. and Tabashnik, B. 1997. Effects of adjuvants on entomopathogenic nematode persistance and efficacy against *Plutella xylostella*. *Biocontrol Science and Technology*. 7: 513-525.

Baur, M.E.; Kaya, H.K.; Tabashnik, B.E. and Chilcutt, C.F. 1998. Suppression of diamondback moth (Lepidoptera: Plutellidae) with an entomopathogenic nematode (Rhabditida: Steinernematidae) and *Bacillus thuringiensis* Berliner. *Journal of Economic Entomology*. 91: 1089-1095.

Beck, N.G. and Cameron, P.J. 1992. Developing a reduced-spray program for brassicas in New Zealand. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second Internatioanl Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 341-350.

Becker, P. 1986. The potential use of CME 134 for the control of vegetable pests. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 257-263.

Begum, S.; Tsukuda, R.; Fujisaki, K. and Nakasuji, F. 1996. The effects of wild cruciferous host plants on morphology, reproductive performance and flight activity in the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae). *Researches on Population Ecology*. 38: 257-263.

Beirne, B.P. 1971. Pest insects of annual crop plants in Canada.*Memoirs of the Entomological Society of Canada*. 78: 1-123.

Bender, D.A.; Morrison, W.P. and Frisbie, R.E. 1999. Intercropping cabbage and Indian mustard for potential control of Lepidopterous and other insects. *HortScience*. 34: 275-279.

Bennett, F.D. and Yaseen, M. 1972. Parasite introductions for the biological control of three insect pests in the Lesser Antilles and British Honduras. *PANS*. 18: 468-474.

Bhalla, O.P. and Dubey, J.K. 1986. Bionomics of the diamondback moth in the northwestern Himalaya. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 55-61.

Biever, K.D. 1997. Development and use of a biological control-IPM system for insect pests of crucifers. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 257-261.

Biever, K.D. and Boldt, P.E. 1971. Continuous laboratory rearing of the diamondback moth and related biological data. *Annals of the Entomological Society of America*. 64: 651-655.

Bigger, D.S. and Chaney, W.E. 1998. Effects of *Iberis umbellata* (Brassicaceae) on insect pests of cabbage and on potential biological control agents. *Environmental Entomology*. 27: 161-167.

Bloem, S. and Carpenter, J.E. 2001. Evaluation of population suppression by irradiated Lepidoptera and their progeny. *Florida Entomologist*. 84: 165-171.

Bonnemaison, L. 1965. Insect pests of crucifers and their control. *Annual Review of Entomology*. 10: 233-256.

Bordat, D. and Goudegnon, A.E. 1997. The status of the diamondback moth and its natural enemies in the Porto Novo and Cotonou areas in Benin. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 312-313.

Brunner, E. and Stevens, P.F.E. 1986. The control of diamondback moth with Thuricide. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 213-217.

Buranapanichpan, S.; Ratanabhumma, S.; Hamasaki, S. and Kajita, H. 1998. Biology and efficacy of larval parasitoids, *Cotesia plutellae* (Kurdjumov) as a potential for diamondback moth management in Chiang Mai. In: Kameya, M. and Ratanabhumma, S. (Eds.), Joint Study of IPM on Cruciferous Pests in Thailand. Faculty of Agriculture, Yamaguchi University, Japan, pp. 52-60.

Butts, R.A. and McEwan, F.L. 1981. Seasonal populations of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in relation to day-degree accumulation. *The Canadian Entomologist*. 113: 127-131.

Byrne, M.J.; Currin, S. and Hill, M.P. 2002. The influence of climate on the establishment and success of the biocontrol agent *Gratiana spadicea*, released on *Solanum sisymbriifolium* in South Africa. *Biological Control.* 24: 128-134.

Caprio, M.A. and Tabashnik, B.E. 1992. Allozymes used to estimate gene flow among populations of diamondback moth (Lepidoptera; Plutellidae) in Hawaii. *Environmental Entomology.* 21: 808-816.

Cartwright, B.; Schatzer, R.J.; Morrison, W.P. and Chambers, C. 1992. Economics of managing lepidopterous cabbage pests in the southwestern United States. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 351-359.

Chalfant, R.B. 1992. Microbial and other insecticides to control lepidopteran pests of cole crops in Georgia. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 139-146.

Chalfant, R.B.; Denton, W.H.; Schuster, D.J. and Workman, R.B. 1979. Management of cabbage caterpillars in Florida and Georgia by using visual damage thresholds. *Journal of Economic Entomology.* 72: 411-413.

Chang, W.X.Z.; Tabashnick, B.E.; Artelt, B.; Malvar, T.; Ballester, V.; Ferré, J. and Roderick, G.K. 1997. Mitochondrial DNA sequence variation among geographic strains of diamondback moth (Lepidoptera: Plutellidae). *Entomological Society of America.* 90: 590-595.

Charleston, D.S. 1998. The tritrophic interactions of diamondback moth. *Plant Protection News.* 51: 8-9.

Charleston, D.S. and Kfir, R. 2000. The possibility of using Indian mustard, *Brassica juncea*, as a trap crop for the diamondback moth, *Plutella xylostella*, in South Africa. *Crop Protection.* 19: 455-460.

Charleston, D.S.; Dicke, M.; Vet, L.E.M. and Kfir, R. 2001. Integration of biological control and botanical pesticides - evaluation in a tritrophic context. In: Program and Abstracts for the Fourth International Workshop on the Management of Diamondback Moth and Other Crucifer Pests. Melbourne, Australia, 26th - 29th November 2001. p. 13.

Chelliah, S. and Srinivasan, K. 1986. Bioecology and management of diamondback moth in India. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 63-76.

Chen, C.C.; Chang, S.J.; Cheng, L.L. and Hou, R.F. 1996. Effects of chinaberry fruit extract on feeding, growth and fecundity of the diamondback moth, *Plutella xylostella* L. (Lep., Yponomeutidae). *Journal of Applied Entomology.* 120: 341-345.

Chen, C.N. and Su, W.Y. 1986. Ecology and control thresholds of the diamondback moth on crucifers in Taiwan. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 415-421.

Cheng, E.Y.; Kao, C.H. and Chin, C.S. 1992. Resistance, cross-resistance and chemical control of diamondback moth in Taiwan: recent developments. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 465-475.

Chilcutt, C. and Tabashnik, B.E. 1997a. Host-mediated competition between the pathogen *Bacillus thuringiensis* and the parasitoid *Cotesia plutellae* of the diamondback moth (Lepidoptera: Plutellidae). *Environmental Entomology*. 26: 38-45.

Chilcutt, C.F. and Tabashnik, B.E. 1997b. Independent and combined effects of *Bacillus thuringiensis* and the parasitoid *Cotesia plutellae* (Hymenoptera: Braconidae) on susceptible and resistant diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*. 90: 397-403.

Chilcutt, C. and Tabashnik, B.E. 1999. Effects of *Bacills thuringiensis* on adults of *Cotesia plutellae* (Hymenoptera: Braconidae), a parasitoid of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Biocontrol Science and Technology*. 9: 435-440.

Chow, Y.S. 1992. Disruption effect of the synthetic sex pheromone and its analogues on the diamondback moth. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 105-108.

Chown, S.L. and Avenant, N. 1992. Status of *Plutella xylostella* at Marion Island six years after its colonisation. *South African Journal of Antarctic Research*. 22: 37-40.

Chu, Y-I. 1986. The migration of the diamondback moth. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. The Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 77-81.

Chua, T.H. and Ooi, P.A.C. 1986. Evaluation of three parasites in the biological control of diamondback moth in the Cameron Highlands, Malaysia. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 173-184.

Crafford, J.E. and Chown, S.L. 1987. *Plutella xylostella* L. (Lepidoptera: Plutellidae) on Marion Island. *Journal of the Entomological Society of South Africa*. 50: 259-260.

Crafford, J.E. and Chown, S.L. 1990. The introduction and establishment of diamondback moth (*Plutella xylostella* (L)., Plutellidae) on Marion Island. In: Kerry, K.R. and Hemple, G. (Eds.), Antarctic Ecosystems: Ecological Change and Conservation. Springer-Verlag, Berlin, pp. 354-358.

Cromartie, W.J. 1975. The effects of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology*. 12: 517-533.

Davison, T.F. 1969. Changes in temperature tolerance during the lifecycle of *Calliphora erythrocephala*. *Journal of Insect Physiology*. 15: 977-988.

Day, W.H. 1994. Estimating mortality caused by parasites and diseases of Insects: comparisons of the dissection and rearing methods. *Environmental Entomology*. 23: 543-550.

Dempster, J.P. 1969. Some effects of weed control on the numbers of the small cabbage white (*Pieris rapae* L.). *Journal of Applied Ecology*. 6: 339-345.

Dennill, G.B. and Pretorius, W.L. 1995. The status of diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae), and its parasitoids on cabbages in South Africa. *African Entomology*. 3: 65-71.

Dent, D.R. 1997. Quantifying insect populations: estimates and parameters. In: Dent, D.R. and Walton, M.P. (Eds.), Methods in Ecological and Agricultural Entomology. CAB International, Wallingford, UK, pp. 57-109.

Díaz-Gomez, O.; Rodríguez, J.C.; Shelton, A.M.; Lagunes-T, A. and Bujanos-M, R. 2000. Susceptibility of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) populations in Mexico to commercial formulations of *Bacillus thuringiensis*. *Journal of Economic Entomology*. 93: 963-970.

Dickson, M.H.; Shelton, A.M.; Eigenbrode, S.D.; Vamosy, M.L. and Mora, M. 1990. Selection for resistance to diamondback moth (*Plutella xylostella*) in cabbage. *HortScience*. 25: 1643-1646.

Dosdall, L.M. 1994. Evidence for successful overwintering of diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), in Alberta. *The Canadian Entomologist*. 126: 183-185.

Dover, J.W. 1986. The effect of labiate herbs and white clover on *Plutella xylostella* oviposition. *Entomological Experimental Application*. 42: 243-247.

Eckenrode, C.J.; Dickson, M.H. and Lin, J. 1986. Resistance in crucifers to diamondback moth and other lepidopterous pests. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Developmental Center, Shanhua, Taiwan, pp. 129-136.

Eigenbrode, S.D. and Pillai, S.K. 1998. Neonate *Plutella xylostella* responses to surface wax components of a resistant cabbage (*Brassica oleracea*). *Journal of Chemical Ecology*. 24: 1611-1627.

Eigenbrode, S.D. and Shelton, A.M. 1992. Resistance to diamondback moth in *Brassica*: mechanisms and potential for resistant cultivars. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 65-74.

Eigenbrode, S.D.; Castagnola, T.; Roux, M-B. and Steljes, L. 1996. Mobility of three generalist predators is greater on cabbage with glossy leaf wax than on cabbage with a wax bloom. *Entomologia Experimentalis et Applicata*. 81: 335-343.

Evans, K.A. and Scarisbrick, D.H. 1994. Integrated insect pest management in oilseed rape crops in Europe. *Crop Protection*. 13: 403-412.

Finch, S. and Collier, R.H. 2000. Host-plant selection by insects - a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata*. 96: 91-102.

Finch, S. and Kieneggar, M. 1997. A behavioural study to help clarify how undersowing with clover affects host-plant selection by pet insects of brassica crops. *Entomologia Experimentalis et Applicata*. 84: 165-172.

Fitton, M. and Walker, A. 1992. Hymenopterous parasitoids associated with the diamondback moth in Moldavia, Romania. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second Internatioanl Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 225-232.

Fox, L.R.; Letourneau, D.K.; Eisenback, J. and Van Nouhuys, S. 1990. Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. *Oecologia*. 83: 414-419.

Furlong, M.J. and Wright, D.J. 1994. Examination of stability of resistance and cross-resistance patterns to acylurea insect growth regulators in field populations of the diamondback moth, *Plutella xylostella*, from Malaysia. *Pesticide Science*. 42: 315-326.

Furlong, M.J.; Pell, J.K. and Reddy, G.V.P. 1997. Premortality effects of *Zoophthora radicans* infection in *Plutella xylostella*. *Journal of Invertebrate Pathology*. 70: 214-220.

Gardner, S.N.; Gressel, J. and Mangel, M. 1998. A revolving dose strategy to delay the evolution of both quantitative vs major monogene resistances to pesticides and drugs. *International Journal of Pest Management*. 44: 161-180.

Godin, C. and Boivin, G. 1998a. Lepidopterous pests of *Brassica* crops and their parasitoids in southwestern Quebec. *Environmental Entomology*. 27: 1157-1165.

Godin, C. and Boivin, G. 1998b. Seasonal occurrence of Lepidopterous pests of cruciferous crops in southwestern Quebec in relation to degree-day accumulations. *The Canadian Entomologist*. 130: 173-185.

Goodell, G. 1984. Challenges to the international pest management research and extension in the Third World: Do we really want IPM to work? *Bulletin of the Entomological Society of America*. 30: 18-26.

Goodwin, S. 1979. Changes in the numbers in the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera) in Victoria. *Australian Journal of Zoology*. 27: 981-989.

Gu, H. and Dorn, S. 2001. How do wind velocity and light intensity influence host-location success in *Cotesia glomerata* (Hym., Braconidae)? *Journal of Applied Entomology*. 125: 115-120.

Gunn, D. 1917. The small cabbage moth (*Plutella maculipennis* Curtis). *Union of South Africa Department of Agriculture Bulletin*. 8: 3-10.

Gupta, P.D. and Thorsteinson, A.J. 1960a. Food plant relationship of diamondback moth (*Plutella maculipennis* (Curt.)). 1. Gustation and olfaction in relation to botanical specificity of larva. *Entomological Experimental Application*. 3: 241-250.

Gupta, P.D. and Thorsteinson, A.J. 1960b. Food plant relationship of diamondback moth (*Plutella maculipennis* (Curt.)). II. Sensory relationship of oviposition of the adult female. *Entomological Experimental Application*. 3: 305-314.

Gurr, G.M. and Wratten, S.D. 1999. "Integrated biological control": a proposal for enhancing success in biological control. *International Journal of Pest Management*. 45: 81-84.

Hama, H. 1992. Insecticide resistance characteristics of the diamondback moth. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 455-463.

Harcourt, D.G. 1957. Biology of diamondback moth, *Plutella maculipennis*(Curt.) (Lepidoptera: Plutellidae) in Eastern Ontario. 11. Life-history, behaviour and host relationship. *The Canadian Entomologist*. 89: 554-564.

Harcourt, D.G. 1960. Biology of the diamondback moth, Plutella maculipennis (Curt.) (Lepidoptera: Plutellidae), in Eastern Ontario 111. Natural enemies. *The Canadian Entomologist*. 92: 419-428.

Harcourt, D.G. 1961. Design of a sampling plan for studies on the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). The *Canadian Entomologist*. 93: 820-831.

Harcourt, D.G. 1986. Population dynamics of the diamondback moth in Southern Ontario. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 3-15.

Harcourt, D.G. and Cass, L.M. 1966. Photoperiodism and fecundity in *Plutella maculipennis* (Curt.). *Nature*. 210: 217-218.

Hardy, J.E. 1938. *Plutella maculipennis* Curt., its natural and biological control in England. *Bulletin of Entomolgical Research*. 29: 343-372.

Haseeb, M.; Amano, H. and Nemoto, H. 2000. Pesticidal effects on mortality and parasitism rates of *Diadegma semiclausum*, a parasitoid of the diamondback moth. *BioControl*. 45: 165-178.

Hawkins, B.A. 1994. Pattern and Process in Host-Parasitoid Interactions. Cambridge University Press, Cambridge, UK.

Heisswolf, S.; Houlding, B.J. and Deuter, P.L. 1997. A decade of integrated pest management (IPM) in brassica vegetable crops - the role of farmer participation in its development in Southern Queensland, Australia. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 228-232.

Higley, L.G. and Haskell, N.H. 2001. Insect development and forensic entomology. In: Byrd, J.H. and Castner, J.L. (Eds.), Forensic Entomology: The Utility of Arthropods in Legal Investigations. CRC Press LLC, Boca Raton, pp. 287-302.

Higley, L.G.; Pedigo, L.P. and Ostlie, K.R. 1986. DEGDAY: A program for calculating degree-days, and assumptions behind the degree day approach. *Environmental Entomology*. 15: 999-1016.

Hill, T.A. and Foster, R.E. 2000. Effect of insecticides on the diamondback moth (Lepidoptera: Plutellidae) and its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Journal of Economic Entomology*. 93: 763-768.

Hines, R.L. and Hutchison, W.D. 2001. Evaluation of action thresholds and Spinosad for lepidopteran pest management in Minnesota cabbage. *Journal of Economic Entomology*. 94: 190-196.

Ho, S.H.; Lee, B.H. and See, D. 1983. Toxicity of deltamethrin and cypermethrin to the larvae of the diamondback moth, *Plutella xylostella* L. *Toxicology Letters*. 19: 127-131.

Hokkanen, H.M.T. 1991. Trap cropping in pest management. *Annual Review of Entomology*. 36: 119-138.

Honda, K. 1992a. Hibernation and migration of the diamondback moth in north Japan. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 43-50.

Honda, K. 1992b. Seasonal abundance and the possibility of spring immigration of the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Yponomeutidae), in Morioka City, northern Japan. *Applied Entomology and Zoology*. 27: 517-525.

Horn, D.J. 1981. Effect of weedy backgrounds on colonization of collards by green peach aphid, *Myzus persicae*, and its major predators. *Environmental Entomology*. 10: 285-289.

Horn, D.J. 1986. Vegetational background and parasitism of larval diamondback moth on collards. *Entomologia Experimentalis et Applicata*. 43: 300-303.

Hoy, C.W., Shelton, A.M. and Andaloro, J.T. 1986. Action thresholds for processing cabbage, a short-term solution to a long-term problem. *Agriculture, Ecosystems and Environment*. 16: 45-54.

Hu, G.Y.; Mitchell, E.R. and Okine, J.S. 1997. Diamondback moth (Lepidoptera: Plutellidae) in Cabbage: influence of initial immigration sites on population distribution, density and larval parasitism. *Journal of Entomological Science*. 32: 56-71.

Hu, G.Y., Mitchell, E.R., Sieglaff, D.H. and Okine, J.S. 1998. Field production of two species of parasitoids of the diamondback moth (Lepidoptera: Plutellidae). *Florida Entomologist*. 81: 526-534.

Hughes, P.R.; Renwick, A.A. and Lopez, K.D. 1997. New oviposition stimulants for the diamondback moth in cabbage. *Entomologia Experimentalis et Applicata*. 85: 281-283.

Idris, A.B. and Grafius, E. 1993a. Differential toxicity of pesticides to *Diadegma insulare* (Hymenoptera: Ichneumonidae) and its host, the diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*. 86: 529-536.

Idris, A.B. and Grafius, E. 1993b. Field studies on the effect of pesticides on the diamondback mmoth (Lepidoptera: Plutellidae) and parasitism by *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Journal of Economic Entomology*. 86: 1196-1202.

Idris, A.B. and Grafius, E. 1993c. Pesticides affect immature stages of *Diadegma insulare* (Hymenoptera: Ichneumonidae) and its host, the diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*. 86: 1203-1212.

Idris, A.B. and Grafius, E. 1995. Wildflowers as nectar sources for *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). *Environmental Entomology*. 24: 1726-1735.

Idris, A.B. and Grafius, E. 1996. Effects of wild and cultivated host plants on oviposition, survival, and development of diamondback moth (Lepidoptera: Plutellidae) and its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Environmental Entomology*. 25: 825-833.

Idris, A.B. and Grafius, E. 1997. Nectar-collecting behaviour of *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Plutellidae). *Environmental Entomology*. 26: 114-120.

Idris, A.B. and Grafius, E. 1998. Diurnal flight activity of *Diadegma* insulare (Hymenoptera: Ichneumonidae), a parasitoid of the diamondback moth (Lepidoptera: Plutellidae), in the field. *Environmental Entomology*. 27: 406-414.

Ikemoto, T. and Takai, K. 2000. A new linearized formula for the law of total effective temperature and the evaluation of line-fitting methods with both variables subject to error. *Environmental Entomology*. 29: 671-682.

Iman, M.; Soekarna, D.; Situmorang, J.; Adiputra, I.M.G. and Manti, I. 1986. Effect of insecticides on various field strains of diamondback moth and its parasitoid in Indonesia. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. The Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 313-323.

Iqbal, M. and Wright, D.J. 1997. Evaluation of resistance, cross-resistance and synergism of abamectin and teflubenzzuron in a multi-resistant field population of *Plutella xylostella* (Lepidoptera: Plutellidae). *Bulletin of Entomological Research*. 87: 481-486.

Iqbal, M.; Ismail, F. and Wright, D.J. 1996. Loss of residual activity of abamectin on foliage against adult hymenopteran parasitoids. *Entomophaga*. 41: 117-124.

Ivey, P.W. and Johnson, S.J. 1997. Efficacy of *Bacillus thuringiensis* and cabbage cultivar resistance to diamondback moth (Lepidoptera: Yponomeutidae). *Florida Entomologist*. 80: 396-401.

Ivey, P.W. and Johnson, S.J. 1998. Integrating control tactics for managing cabbage looper (Lepidoptera: Noctuidae) and diamondback moth (Lepidoptera: Yponomeutidae) on cabbage. *Tropical Agriculture (Trinidad)*. 75: 369-374.

Jansson, R.K. 1992. Integration of an insect growth regulator for control of diamondback moth. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 147-156.

Johanowicz, D.L. and Mitchell, E.R. 2000a. Effects of sweet alyssum flowers on the longevity of the parasitoid wasps *Cotesia marginiventris* (Hymenoptera:Braconidae) and *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Florida Entomologist*. 83: 41-47.

Johanowicz, D.L. and Mitchell, E.R. 2000b. A novel method to rear *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of the diamondback moth (Lepidoptera: Plutellidae). *Florida Entomologist*. 83: 377-379.

Justus, K.A. and Mitchell, B.K. 1996. Oviposition site selection by the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). *Journal of Insect Behavior*. 9: 887-897.

Justus, K.A.; Dosdall, L.M. and Mitchell, B.K. 2000. Oviposition by *Plutella xylostella* (Lepidoptera: Plutellidae) and effects of phylloplane waxiness. *Journal of Economic Entomology*. 93: 1152-1159.

Kadir, H.A. 1992. Potential of several baculoviruses for control of diamondback moth and *Crocidolomia binotalis* on cabbages. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 185-192.

Kao, S.S. and Tzeng, C.C. 1992. Toxicity of insecticides to *Cotesia plutellae*, a parasitoid of diamondback moth. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 287-296.

Kawaguchi, M. and Tanaka, T. 1999. Biological characteristics of a larval endoparasitoid, *Cotesia plutellae* (Hymenoptera: Braconidae): Host stage preference, subsequent sex ratio of progeny and mate location of males. *Applied Entomology and Zoology*. 34: 213-221.

Keinmeesuke, P.; Vattanatangum, A.; Sarnthoy, O.; Sayampol, B.; Miyata, T.; Saito, T.; Nakasuji, F. and Sinchaisri, N. 1992. Life table of diamondback moth and its egg parasite *Tricogrammatoidea bactrae* in Thailand. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 309-315.

Keller, M. 2001. Improving the integration of pest management practices: theoretical and practical challenges. In: Program and Abstracts for the Fourth International Workshop on the Management of Diamondback Moth and Other Crucifer Pests. Melbourne, Australia, 26th - 29th November 2001. p. 4.

Kemp, J.C. and Barrett, G.W. 1989. Spatial patterning: impact of uncultivated corridors on arthropod populations within soybean agroecosystems. *Ecology*. 70: 114-128.

Kfir, R. 1996. Diamondback moth - natural enemies in South Africa. *Plant Protection News*. 43: 20-21.

Kfir, R. 1997a. Parasitoids of *Plutella xylostella* (Lep: Plutellidae) in South Africa: an annotated list. *Entomophaga*. 42: 517-523.

Kfir, R. 1997b. The diamondback moth with special reference to its parasitoids in South Africa. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 54-60

Kfir, R. 1998. Origin if the diamondback moth (Lepidoptera: Plutellidae). *Annals of the Entomological Society of America*. 91: 164-167.

Kfir, R. and Thomas, J. 2001. Biological control of diamondback moth on St. Helena Island with parasitoids supplies by ARC-PPRI. *Plant Protection News*. 59: 12-13.

Kim, Y.; Kim, K. and Kim, N. 1999. Genetic difference between two field populations of *Plutella xylostella* (Linne) based on four polymorphic allozymes. *Journal of the Asia-Pacific Entomologist.* 2: 1-5.

Kloen, H. and Altieri, M.A. 1990. Effect of mustard (*Brassica hirta*) as a non-crop plant on competition and insect pets in broccoli (*Brassica oleracea*). *Crop Protection.* 9: 90-96.

Kmec, P. and Weiss, M.J. 1997. Seasonal abundance of diamondback moth (Lepidoptera: Yponomeutidae) on *Crambe abyssinica. Environmental Entomology.* 26: 483-488.

Kobayashi, S.; Aida, S.; Kobayashi, M. and Nonoshita, K. 1992. Studies on resistance of diamondback moth to insect growth regulators. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 383-390.

Kogan, M. 1998. Integrated pest management: Historical perspectives and contemporary developments. *Annual Review of Entomology.* 43: 243-270.

Koshihara, T. 1986. Diamondback moth and its control in Japan. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First Internatioanl Workshop. The Asian Vegetable and Development Center, Shanhua, Taiwan, pp. 43-54.

Kuwahara, M.; Keinmeesuke, P. and Shirai, Y. 1995. Seasonal trend in population density and adult body size of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), in Central Thailand. *Applied Entomology and Zoology.* 30: 551-555.

Kuwahara, M.; Keinmeesuke, P. and Sinchaisri, N. 1995. Present status of resistance of the diamondback moth, *Plutella xylostella* L., to insecticides in Thailand. *Applied Entomology and Zoology.* 30: 557-566.

Lamb, R.J. 1992. Developmental rate of *Acyrthosiphon pisum* (Homoptera: Aphididae) at low temperatures: Implications for estimating rate parameters for insects. *Environmental Entomology.* 21: 10-19.

Landis, D.A.; Wratten, S.D. and Gurr, G.M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology.* 45: 175-201.

Lasota, J.A. and Kok, L.T. 1986. *Diadegma insularis* (Hymenoptera: Ichneumonidae) parasitism of the diamondback moth (Lepidoptera: Plutellidae) in southwest Virginia. *Journal of Entomological Science.* 21: 237-242.

Latheef, M.A. and Irwin, R.D. 1979. The effect of companionate planting on lepidopteran pests of cabbage. *The Canadian Entomologist.* 111: 863-864.

Lee, S-T.; Chu, Y-I. and Talekar, N.S. 1995. The mating behavior of diamondback moth (Lepidoptera: Plutellidae). *Chinese Journal of Entomology.* 15: 81-89.

Leibee, G.L. and Capinera, J.L. 1995. Pesticide resistance in Florida insects limits management options. *Florida Entomologist.* 78: 386-399.

Leibee, G.L. and Savage, K. 1992. Insecticide resistance in the diamondback moth in Florida. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 427-435.

Letourneau, D.K. 1987. The enemies hypothesis: Tritrophic interactions and vegetational diversity in tropical agroecosystems. *Ecology*. 68: 1616-1622.

Lewis, W.J.; Van Lenteren, J.C.; Phatak, S.C. and Tumlinson, J.H. 1997. A total system approach to sustainable pest management. *Proceedings of the National Academy of Sciences, USA*. 94: 12243-12248.

Lim, G.S. 1986. Biological control of diamondback moth. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 159-171.

Lim, G.S. 1992. Integrated Pest Management of diamondback moth: Practical realities. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 565-576.

Lim, G.S.; Sivapragasam, A. and Ruwaida, M. 1986. Impact assessment of *Apanteles plutellae* on diamondback moth using an insecticide-check method. In: Talekar, N.S. (Ed.), Diamondback Moth Management: Proceedings of the First Internatioanl Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 195-204.

Lim, G.S.; Sivapragasam, A. and Loke, W.H. 1997. Crucifer insect pest problems: trends, issues and management strategies. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifers: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 3-16.

Lin, J., Eckenrode, C.J. and Dickson, M.H. 1983. Variation in *Brassica oleracea* resistance to diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*. 76: 1423-1427.

Liu, S-S.; Wang, X-G.; Guo, S-J.; He, J-H. and Shi, Z-H. 2000. Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in Hangzhou, China. *Bulletin of Entomological Research*. 90: 221-231.

Liu, S-S.; Chen, F-Z. and Zalucki, M.P. 2002. Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. *Environmental Entomology*. 31: 221-231.

Liu, Y-B. and Tabashnik, B.E. 1997a. Experimental evidence that refuges delay insect adaptation to *Bacillus thuringiensis*. *Proceedings of the Royal Society of London. Series B Biological Sciences*. 264: 605-610.

Liu, Y-B. and Tabashnik, B.E. 1997b. Inheritance of resistance to the *Bacillus thuringiensis* toxin Cry1C in the diamondback moth. *Applied and Environmental Microbiology*. 63: 2218-2223.

Loke, W.H.; Lim, G.S.; Syed, A.R.; Abdulaziz, A.M.; Rani, M.Y.; Jusoh, M.M.; Cheah, U.B. and Fauziah, I. 1992. Management of diamondback moth in Malaysia, development, implementation and impact. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 529-539.

Luck, R.F.; Shepard, B.M. and Kenmore, P.E. 1988. Experimental methods for evaluating arthropod natural enemies. *Annual Review of Entomology*. 33: 367-391.

Luther, G.C.; Valenzuela, H.R. and Defrank, J. 1996. Impact of cruciferous trap crops on lepidopteran pests of cabbage in Hawaii. *Environmental Entomology*. 25: 39-47.

Magallona, E.D. 1986. Developments in diamondback moth management in the Philippines. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 423-435.

Maguire, L.A. 1984. Influence of surrounding plants on densities of *Pieris rapae* (L.) eggs and larvae (Lepidoptera: Pieridae) on collards. *Environmental Entomology*. 13: 464-468.

Maltais, P.M.; Nuckle, J.R. and LeBlanc, P.V. 1998. Seasonal occurrence of three Lepidoptera on broccoli and effectiveness of planting date as a pest management tool in southeastern New Brunswick. *Phytoprotection*. 79: 129-137.

Mani, M. and Krishnamoorthy, A. 1984. Toxicity of some insecticides to *Apanteles plutellae*, a parasite of the diamondback moth. *Tropical Pest Management*. 30: 130-132.

Mason, J.M. and Wright, D.J. 1997. Potential for the control of *Plutella xylostella* larvae with entomopathogenic nematodes. *Journal of Invertebrate Pathology*. 70: 234-242.

Matteson, P.C.; Altieri, M.A. and Gagne, W.C. 1984. Modification of small farmer practices for better pest management. *Annual Review of Entomology*. 29: 383-402.

Matthews, G.A. 1997. Techniques to evaluate insecticide efficacy. In: Dent, D.R. and Walton, M.P. (Eds.), Methods in Ecological and Agricultural Entomology. CAB International, Wallingford, UK, pp. 243-269.

McCully, J.E. and Salas Araiza, M.D. 1992. Seasonal variations in populations of the principle insects causing contamination in processing broccoli and cauliflower in central Mexico. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 51-56.

McGaughey, W.H. 1994. Problems of insect resistance to *Bacillus thuringiensis*. *Agricultural Ecosystems and Environment*. 49: 95-102.

McLaughlin, J.R.; Mitchell, E.R. and Kirsch, P. 1994. Mating disruption of diamondback moth (Lepidoptera: Plutellidae) in cabbage: reduction of mating and suppression of larval populations. *Journal of Economic Entomology*. 87: 1198-1204.

Mills, N. 1997. Techniques to evaluate the efficacy of natural enemies. In: Dent, D.R. and Walton, M.P. (Eds.), Methods in Ecological and Agricultural Entomology. CAB International, Wallingford, UK, pp. 271-291.

Mitchell, E.R.; Hu, G.Y. and Okine, J.S. 1997a. Diamondback moth (Lepidoptera: Plutellidae) infestation and parasitism by *Diadegma insulare* (Hymenoptera: Ichneumonidae) in collards and adjacent cabbage fields. *Florida Entomologist*. 80: 54-62.

Mitchell, E.R.; Tingle, F.C.; Navasero-Ward, R.C. and Kehat, M. 1997b. Diamondback moth (Lepidoptera: Plutellidae): parasitism by *Cotesia plutellae* (Hymenoptera: Braconidae) in cabbage. *Florida Entomologist*. 80: 477-489.

Mitchell, E.R.; Hu, G.Y.; Okine, J.S. and Carpenter, J.E. 1999. Parasitism of diamondback moth (Lepidoptera: Plutellidae) larvae by *Cotesia plutellae* (Hymenoptera: Braconidae) and *Diadegma insulare* (Hymenoptera: Ichneumonidae) in cabbage fields after inundative releases of *C. plutellae*. *Journal of Entomological Science*. 34: 101-112.

Mitchell, E.R.; Hu, G. and Johanowicz, D. 2000. Management of diamondback moth (Lepidoptera: Plutellidae) in cabbage using collard as a trap crop. *HortScience*. 35: 875-879.

Miyata, T.; Saito, T. and Noppun, V. 1986. Studies on the mechanism of diamondback moth resistance to insecticides. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 347-357.

Miyata, T.; Noppun, V. and Saito, T. 1992. Inheritance of resistance to phenthoate and fenvalerate in diamondback moth and management of insecticide resistance. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 477-484.

Mo, J.; Baker, G.; Keller, M. and Roush, R. 2001. Estimation of some characteristic dispersal ranges of diamondback moth (*Plutella xylostella*) (Lepidoptera: Plutellidae). In: Program and Abstracts for the Fourth International Workshop on the Management of Diamondback Moth and Other Crucifer Pests, Melbourne, Australia, 26-29 November 2001. p. 38.

Mohandass, S. and Zalucki, M.P. 2001. Development time of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) under varied microclimatic conditions: are we measuring the right temperatures? In: Program and Abstracts for the Forth International Workshop on the Management of Diamondback Moth and Other Cricifer Pests, Melbourne, Australia, 26th - 29th November 2001. p. 40.

Møller, J. 1988. Investigations on a laboratory culture of the diamondback moth, *Plutella maculipennis* (Curt.) (Lep., Tineidae). *Journal of Applied Entomology*. 105: 360-373.

Morallo-Rejesus, B. 1986. Botanical insecticides against the diamondback moth. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 241-255.

Morallo-Rejesus, B. and Sayaboc, A.S. 1992. Management of diamondback moth with *Cotesia plutellae*: prospects in the Philippines. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 279-286.

Morallo-Rejesus, B.; Inocencio, E.L. and Eusebio, J.E. 1996. Comparative effectiveness of IPM-DBM technology versus farmers control practice for diamondback moth, *Plutella xylostella* (L.) control. *The Philippine Entomologist*. 10: 57-65.

Morallo-Rejesus, B.; Inocencio, E.L.; Eusebio, J.E. and Barrago, S.F. 1997. Technology transfer of *Cotesia*-based IPM for diamondback moth on lowland crucifers in the Philippines. In: Sivapragasam, A.; Loke, W.H.; Husson, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 267-275.

Mori, H. 1992. Effectiveness of dead-spore *Bacillus thuringiensis* for control of diamondback moth. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 157-164.

Morrison, G. and Strong, D.R. 1980. Spatial variations in host density and the intensity of parasitism: Some empirical examples. *Environmental Entomology*. 9: 149-152.

Mosiane, M.S. 2001. Diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), and other insects of canola, *Brassica napus*, in Gauteng Province, South Africa. MSc Thesis, Rhodes University, Grahamstown, South Africa. 69 p.

Muckenfuss, A.E. and Shepard, B.M. 1994. Seasonal abundance and response of diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), and natural enemies to esfenvalerate and *Bacillus thuringiensis* subsp. *kurstaki* Berliner in coastal South Carolina. *Journal of Agricultural Entomology*. 11: 361-373.

Muckenfuss, A.E.; Shepard, B.M. and Ferrer, E.R. 1992. Natural mortality of diamondback moth in coastal South Carolina. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 27-36.

Muhamad, O.; Tsukuda, R.; Oki, Y.; Fujisaki, K. and Nakasuji, F. 1994. Influences of wild crucifers on the life history traits and flight ability of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae). *Researches on Population Ecology*. 36: 53-62.

Mumford, J.D. and Knight, J.D. 1997. Injury, damage and threshold concepts. In: Dent, D.R. and Walton, M.P. (Eds.), Methods in Ecological and Agricultural Entomology. CAB International, Wallingford, UK, pp. 203-220.

Murchie, A.K.; Williams, I.H. and Perry, J.N. 1999. Edge distribution of *Ceutorhynchus assimilis* and its parasitoid *Trichomalus perfectus* in a crop of winter oilseed rape (*Brassica napus*). *BioControl*. 44: 379-390.

Murdoch, W.W.; Chesson, J. and Chesson, P.L. 1985. Biological control in theory and practice. *The American Naturalist*. 125: 344-366.

Mushtaque, M. 1990. Some studies on *Tetrastichus sokolowskii* Kurd. (Eulophidae: Hymenoptera), a parasitoid of diamondback moth in Pakistan. *Pakistan Journal of Zoology*. 22: 37-43.

Mushtaque, M. and Mohyuddin, A.I. 1987. *Apanteles plutellae* Kurdj. (Braconidae: Hymenoptera), an effective parasite of diamondback moth, in Pakistan. *Pakistan Journal of Zoology*. 19: 341-348.

Mustata, G. 1992. Role of parasitoid complex in limiting the population of diamondback moth in Moldavia, Romania. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 203-211.

Nakahara, L.M.; McHugh, J.J., Jr.; Otsuka, C.L.; Funasaki, G.Y. and Lai, P-Y. 1986. Integrated control of the diamondback moth and other insect pests using an overhead sprinkler system, an insecticide, and biological control agents, on a watercress farm in Hawaii. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 403-413.

Nemoto, H.; Yano, E. and Kiritani, K. 1992. Pheromonal control of diamondback moth in the management of crucifer pests. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 91-97.

Ninsin, K.D.; Mo, J. and Miyata, T. 2000. Decreased susceptabilities of four field populations of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), to acetamiprid. *Applied Entomology and Zoology*. 35: 591-595.

Noda, T.; Miyai, S.; Takashino, K. and Nakamura, A. 2000. Density suppression of *Plutella xylostella* (Lepidoptera: Yponomeutidae) by multiple releases of *Diadegma semiclausum* (Hymenoptera: Ichneumonidae) in cabbage fields in Iwate, northern Japan. *Applied Entomology and Zoology*. 35: 557-563.

Noran, A.M. and Tang, P.Y. 1997. Allozymic polymorphism among three populations of *Plutella xylostella*. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 322-325.

Norris, K.R. 1987. *Plutella xylostella* (Linnaeus). In: Waterhouse, D.F. (Ed.), Biological Control, Pacific Prospects. ACIAR, Inkata Press, Melbourne, Australia, pp. 177-191.

Noyes, J.S. 1994. The reliability of published host-parasitoid records: a taxonomist's view. *Norwegian Journal of Agricultural Sciences*. 16: 59-69.

Ohbayashi, N.; Simizu, K. and Nagata, K. 1992. Control of diamondback moth by using synthetic sex pheromone. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 99-104.

Ohno, T.; Asayama, T. and Ichikawa, K. 1992. Evaluation of communication disruption method for suppressing diamondback moth infestations at two different areas using synthetic sex pheromone. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 109-114.

Okine, J.S.; Mitchell, E.R.; Carpenter, J. and Hu, G.Y. 1998. Oviposition response of *Cotesia plutellae* (Hymenoptera: Braconidae) to sterile and normal diamondback moth (Lepidoptera: Plutellidae) larvae. *Environmental Entomology*. 27: 1520-1524.

Okine, J.S.; Mitchell, E.R. and Hu, G.Y. 1996. Low temperature effect on viability of *Diadegma insulare* (Hymenoptera: Ichneumonidae) pupae and effect of this parasitoid on feeding rate of diamondback moth larvae (Lepidoptera: Plutellidae). *Florida Entomologist*. 79: 503-509.

Ooi, P.A.C. 1980. Laboratory studies of *Diadegma cerophagus* (Hym.: Ichneumonidae), a parasite introduced to control *Plutella xylostella* (Lep.: Hyponomeutidae) in Malaysia. *Entomophaga*. 25: 249-259.

Ooi, P.A.C. 1986. Diamondback moth in Malaysia. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. The Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 25-34.

Ooi, P.A.C. 1992. Role of parasitoids in managing diamondback moth in Cameron Highlands. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 255-262.

Ooi, P.A.C. 1997. Bringing science to farmers: experiences in integrated diamondback moth management. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 25-33.

Palis, F.G. 1983. Economic assessment of the monitoring and the calendar systems in the chemical control of the diamondback moth, *Plutella xylostella* (L.) on cabbage. *The Philippine Agriculturist*. 66: 65-74.

Pedigo, L.P. 2002. Entomology and Pest Management. Prentice Hall, New Jersey.

Perera, D.R.; Armstrong, G. and Senanayake, N. 2000. Effect of antifeedants on the diamondback moth (*Plutella xylostella*) and its parasitoid *Cotesia plutellae*. *Pest Management Science*. 56: 486-490.

Perez, C.J. and Shelton, A.M. 1997. Resistance of *Plutella xylostella* (Lepidoptera: Plutellidae) to *Bacillus thuringiensis* Berliner in Central America. *Journal of Economic Entomology*. 90: 87-93.

Pichon, A.; Bordat, D.; Bordat, A.; Arvanitakis, L. and Tertois, C. 2001. Biological and genetic differences between populations of diamondback moth from different geographic origins. In: Program and Abstracts for the Fourth International Workshop on the Management of Diamondback Moth and Other Crucifer Pests. Melbourne, Australia, 26th - 29th November 2001. p. 45.

Pimentel, D. 1961a. Natural control of caterpillar populations on cole crops. *Journal of Economic Entomology*. 54: 889-892.

Pimentel, D. 1961b. Species diversity and insect population outbreaks. *Annals of the Entomological Society of America*. 54: 76-86.

Plapp, F.W.; Magaro, J.J. and Edelson, J.V. 1992. Diamondback moth in south Texas: a technique for resistance monitoring in the field. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 443-446.

Poelking, A. 1992. Impact and release of *Diadegma semiclausum* for the control of diamondback moth in the Philippines. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 271-278.

Powell, W. 1986. Enhancing parasitoid activity in crops. In: Waage, J. and Greathead, D. (Eds.), Insect Parasitoids. Academic Press, London, UK, pp. 319-340.

Price, P.W. 1976. Colonization of crops by arthropods: non-equilibrium communities in soyabean fields. *Environmental Entomology*. 5: 605-611.

Prinsloo, G.L. 2002. The identity of *Apanteles halfordi* Ullyett (Hymenoptera: Braconidae), a parasitoid of the diamondback moth, *Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae). *African Entomology*. 10 (in press)

Pruess, K.P. 1983. Day-degree methods for pest management. *Environmental Entomology*. 12: 613-619.

Putnam, L.G. 1973. Effects of the larval parasites *Diadegma insularis* and *Microplitis plutellae* in Saskatchewan rape and mustard crops. *Canadian Journal of Plant Science*. 53: 911-914.

Radcliffe, E.B. and Chapman, R.K. 1966. Varietal resistance to insect attack in various cruciferous crops. *Journal of Economic Entomology*. 59: 120-125.

Ramachandran, S.; Buntin, G.D.; All, J.N. and Raymer, P.L. 1998a. Diamondback moth (Lepidoptera: Plutellidae) resistance of *Brassica napus* and *B.oleracea* lines with differing leaf characteristics. *Journal of Economic Entomology*. 91: 987-992.

Ramachandran, S.; Buntin, G.D.; All, J.N.; Raymer, P.L.and Stewart, C.N. 1998b. Greenhouse and field evaluations of transgenic canola against diamondback moth, *Plutella xylostella*, and the corn earworm, *Helicoverpa zea*. *Entomologia Experimentalis et Applicata*. 88: 17-24.

Rao, P.V. 1998. Statistical Research Methods in th Life Sciences. Duxbury Press, Pacific Grove.

Reed, D.W.; Pivnick, K.A. and Underhill, E.W. 1989. Identification of chemical oviposition stimulants for the diamondback moth, *Plutella xylostella* present in three species of Brassicaceae. *Entomological Experimental Application*. 53: 277-286.

Riethmacher, G.W.; Rombach, M.C. and Kranz, J. 1992. Epizootics of *Pandora blunckii* and *Zoophthora radicans* (Entomophthoraceae: Zygomycotina) in diamondback moth populations in the Philippines. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhau, Taiwan, pp. 193-199.

Riggin-Bucci, T.M. and Gould, F. 1997. Impact of intraplot mixtures of toxic and nontoxic plants on population dynamics of diamondback moth (Lepidoptera; Plutellidae) and its natural enemies. *Journal of Economic Entomology*. 90: 241-251.

Risch, S.J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology*. 62: 1325-1340.

Risch, S.J.; Andow, D. and Altieri, M.A. 1983. Agroecosystem diversity and pest control: data, tentative conclusions and new research directions. *Environmental Entomology*. 12: 625-629.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). *Ecological Monographs*. 43: 94-125.

Roush, R.T. 1997a. Bt-transgenic crops: just another pretty insecticide or a chance for a new start in resistance management? *Pesticide Science.* 51: 328-334.

Roush, R.T. 1997b. Insecticide resistance management in diamondback moth: quo vadis? In: Sivapragasam, A.; Loke, W.H.; Husson, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 21-24.

Roush, R.T. 1998. Two-toxin strategies for management of insecticidal transgenic crops: can pyramiding succeed where pesticide mixtures have not? *Philosophical Transactions of the Royal Society of London B.* 353: 1777-1786.

Rowell, B.; Jeerakan, A. and Wimol, S. 1992. Crucifer seed crop pests, parasites, and the potential for IPM in northern Thailand. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 551-563.

Ru, N. and Workman, R.B. 1979. Seasonal abundance and parasites of the imported cabbageworm, diamondback moth and cabbage webworm in northeast Florida. *Florida Entomologist.* 62: 68-69.

Rushtapakornchai, W. and Vattanatangum, A. 1986. Present status of insecticidal control of diamondback moth in Thailand. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 305-312.

Russell, E.P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. *Environmental Entomology.* 18: 590-599.

Sagenmueller, A. and Rose, E. 1986. Hoe 522 (CME 134), a new insect growth regulator for control of the diamondback moth. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 271-278.

Sakai, M. 1986. Chemical control of diamondback moth in Japan with special reference to cartap. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. The Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 297-306.

Salinas, P.J. 1986. Studies on diamondback moth in Venezuela with reference to other Latinamerican countries. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 17-24.

Sastrodihardjo, S. 1986. Diamondback moth in Indonesia. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable and Research Development Center, Shanhua, Taiwan, pp. 35-41.

Sastrosiswojo, S. 1996. Biological control of the diamondback moth in IPM systems: case study from Asia (Indonesia). *BCPS Symposium Proceedings: Biological Control Proceedings.* 67: 15-31.

Sastrosiswojo, S. and Sastrodihardjo, S. 1986. Status of biological control of diamondback moth by introduction of parasitoid *Diadegma eucerophaga* in Indonesia. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 185-194.

Saucke, H.; Dori, F. and Schmutterer, H. 2000. Biological and integrated control of *Plutella xylostella* (Lep., Yponomeutidae) and *Crocidolomia pavonana* (Lep., Pyralidae) in Brassica crops in Papua New Guinea. *Biocontrol Science and Technology*. 10: 595-606.

Schellhorn, N.A. and Sork, V.L. 1997. The impact of weed diversity on insect population dynamics and crop yield in collards, *Brassica oleraceae* (Brassicaceae). *Oecologia*. 111: 233-240.

Schmutterer, H. 1992. Control of diamondback moth by application of neem extracts. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 325-332.

Schroeder, P.C.; Shelton, A.M.; Ferguson, C.S.; Hoffman, M.P. and Petzoldt, C.H. 2000. Application of synthetic sex pheromone for management of diamondback moth, *Plutella xylostella*, in cabbage. *Entomologia Experimentalis et Applicata*. 94: 243-248.

Sears, M.K.; Shelton, A.M.; Quick, T.C.; Wyman, J.A. and Webb, S.E. 1985. Evaluation of partial plant sampling procedures and corresponding action thresholds for management of Lepidoptera on cabbage. *Journal of Economic Entomology*. 78: 913-916.

Sereda, B.; Basson, N.C.J. and Marais, P. 1997. Bioassay of insecticide resistance in *Plutella xylostella* (L.) in South Africa. *African Plant Protection*. 3: 67-72.

Serizawa, H.; Shinoda, T. and Kawai, A. 2001. Occurrence of a feeding deterrent in *Barbarea vulgaris* (Brassicales: Brassicaceae), a crucifer unacceptable to the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Applied Entomology and Zoology*. 36: 465-470.

Sharpe, P.J.H. and DeMichele, D.W. 1977. Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology*. 64: 649-670.

Sheehan, W. 1986. Response of specialist and generalist natural enemies to agroecosystem diversification: a selective review. *Environmental Entomology*. 15: 456-461.

Shelton, A.M. and Wyman, J.A. 1992. Insecticide resistance of diamondback moth in North America. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 447-454.

Shelton, A.M.; Robertson, J.L.; Tang, J.D.; Perez, C.; Eigenbrode, S.D.; Preisler, H.K.; Wilsey, W.T. and Cooley, R.J. 1993a. Resistance of diamondback moth (Lepidoptera: Plutellidae) to *Bacillus thuringiensis* subspecies in the field. *Journal of Economic Entomology*. 86: 697-705.

Shelton, A.M.; Wyman, J.A.; Cushing, N.L.; Apfelbeck, K.; Dennehy, T.J.; Mahr, S.E.R. and Eigenbrode, S.D. 1993b. Insecticide resistance of diamondback moth (Lepidoptera: Plutellidae) in North America. *Journal of Economic Entomology*. 86: 11-19.

Shelton, A.M.; Kroening, M.K.; Eigenbrode, S.D.; Petzold, C.; Hoffman, M.P.; Wyman, J.A.; Wilsey, W.T.; Cooley, R.J. and Pedersen, L.H. 1996. Diamondback moth (Lepidoptera: Plutellidae) contamination of cabbage transplants and the potential for insecticide resistance problems. *Journal of Entomological Science*. 31: 347-354.

Shelton, A.M.; Perez, C.J.; Tang, J.D. and Vandenberg, J.D. 1997. Prospects for novel approaches towards management of the diamondback moth. In: Sivapragasam, A.; Loke, W.H.; Hussan, A.K. and Lim, G.S. (Eds.), The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Third International Workshop. Malaysian Agricultural Research and Development Institute, Kuala Lumpar, Malaysia, pp. 17-20.

Shelton, A.M.; Vandenberg, J.D.; Ramos, M. and Wilsey, W.T. 1998. Efficacy and persistence of *Beauveria bassiana* and other fungi for control of diamondback moth (Lepidoptera: Plutellidae) on cabbage seedlings. *Journal of Entomological Science*. 33: 142-151.

Shelton, A.M.; Sances, F.V.; Hawley, J.; Tang, J.D.; Boune, M.; Jungers, D.; Collins, H.L. and Farias, J. 2000. Assessment of insecticide resistance after the outbreak of diamondback moth (Lepidoptera: Plutellidae) in California in 1997. *Journal of Economic Entomology*. 93: 931-936.

Shirai, Y. 1991. Seasonal changes and effects of temperature on flight ability of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology*. 26: 107-115.

Shirai, Y. 1993. Factors influencing flight ability of male adults of the diamondback moth, *Plutella xylostella*, with special reference to temperature conditions during larval stage. *Applied Entomology and Zoology*. 28: 291-301.

Shirai, Y. 2000. Temperature tolerance of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae) in tropical and temperate regions of Asia. *Bulletin of Entomolgical Research*. 90: 357-364.

Shirai, Y. and Nakamura, A. 1994. Dispersal movement of male adults of the diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae), on cruciferous vegetable fields, studied using the mark-recapture method. *Applied Entomology and Zoology*. 29: 339-348.

Shirai, Y. and Nakamura, A. 1995. Relationship between the number of wild males captured by sex pherome trap and the population density estimated from a mark-recapture study in the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae). *Applied Entomology and Zoology*. 30: 543-549.

Sieglaff, D.H.; Mitchell, E.R. and Hu, G.Y. 1998. Evaluation of rearing methods for *Diadegma insulare* (Hymenoptera: Ichneumonidae), an endoparasitoid of the diamondback moth (Lepidoptera: Plutellidae). *Florida Entomologist*. 81: 578-582.

Smith, D.B. and Sears, M.K. 1982. Evidence for dispersal of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), into southern Ontario. *Proceedings of the Entomological Society of Ontario*. 113: 21-28.

Soares, G.G. and Quick, T.C. 1992. MVP, a novel bioinsecticide, for the control of diamondback moth. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 129-137.

Speight, M.R., Hunter, M.D. and Watt, A.D. 1999. Ecology of Insects: Concepts and Applications. Blackwell Scientific Publications, Oxford.

Srinivasan, K. and Krishna Moorthy, P.N. 1991. Indian mustard as a trap crop for management of major lepidopterous pests on cabbage. *Tropical Pest Management*. 37: 26-32.

Srinivasan, K. and Krishna Moorthy, P.N. 1992. Development and adoption of integrated pest management for major pests of cabbage using Indian mustard as a trap crop. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 511-521.

StatSoft, Inc. 2001. Statistica v.5. Tulsa, Oklahoma.

Stern, V.M., Smith, R.F., van den Bosch, R., Hagen, K.S. 1959. The integrated control concept. *Hilgardia*. 29: 81-101.

Steÿl, L. 1998. Earn R50 000 per hectare with cabbages (Part 1). *Farmer's Weekly*. 6 March, pp. 14-18.

Stoner, K.A. 1992. Resistance and susceptibility to glossy genetic lines of Brassica oleracea in Connecticut. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 57-63.

Strand, M.R. and Obrycki, J.J. 1996. Host specificity of insect parasitoids and predators. *BioScience*. 46: 422-429.

Suenaga, H. and Hamamura, T. 1998. Laboratory evaluation of carabid beetles (Coleoptera: Carabidae) as predators of diamondback moth (Lepidoptera: Plutellidae) larvae. *Environmental Entomology*. 27: 767-772.

Suenaga, H. and Hamamura, T. 2001. Occurrence of carabid beetles (Coleoptera: Carabidae) in cabbage fields and their possible impact on lepidopteran pests. *Applied Entomology and Zoology*. 36: 151-160.

Sun, C.N. 1992. Insecticide resistance in diamondback moth. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 419-426.

Syed, A.R. 1992. Insecticide resistance in the diamondback moth in Malaysia. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 437-442.

Tabashnik, B.E. 1994. Evolution of resistance to *Bacillus thuringiensis*. *Annual Review of Entomology*. 39: 47-79.

Tabashnik, B.E. and Cushing, N.L. 1987. Leaf residue vs. topical bioassays for assessing insecticide resistance in the diamondback moth, *Plutella xylostella* L. *FAO Plant Protection Bulletin*. 35: 11-14.

Tabashnik, B.E. and Mau, R.F.L. 1986. Suppression of diamondback moth (Lepidoptera: Plutellidae) oviposition by overhead irrigation. *Journal of Economic Entomology*. 79: 189-191.

Tabashnik, B.E.; Cushing, N.L.; Finson, N. and Johnson, M.W. 1990. Field development of resistance to *Bacillus thuringiensis* in diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*. 83: 1671-1676.

Tabashnik, B.E.; Finson, N and Johnson, W. 1991. Managing resistance to *Bacillus thuringiensis*: lessons from the diamondback moth (Lepidoptera: Plutellidae). *Journal of Economic Entomology*. 84: 49-55.

Tabashnik, B.E.; Finson, N.; Schwartz, J.M.; Caprio, M.A. and Johnson, M.W. 1992. Diamondback moth resistance to *Bacillus thuringiensis* in Hawaii. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 175-183.

Tabashnik, B.E.; Liu, Y-B.; Malvar, T.; Heckel, D.G.; Masson, L.; Ballester, V.; Granero, F.; Mensua, J.L. and Ferré, J. 1997. Global variation in the genetic and biochemical basis of diamondback moth resistance to *Bacillus thuringiensis*. *Proceedings of the National Academy of Sciences, USA*. 94: 12780-12785.

Tabashnik, B.E.; Liu, Y-B.; Malvar, T.; Heckel, D.G.; Masson, L. and Ferre, J. 1998. Insect resistance to *Bacillus thuringiensis*: uniform or diverse? *Philosophical Transactions of the Royal Society of London B*. 353: 1751-1756.

Tahvanainen, J.O. and Root, R.B. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrsomelidae). *Oecologia*. 10: 321-346.

Talekar, N.S. 1996. Biological control of diamondback moth in Taiwan - a review. *Plant Protection Bulletin (Taiwan)*. 38: 167-189.

Talekar, N.S. 1992. Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Shanhua, Taiwan. Asian Vegetable Research and Development Center. 603pp.

Talekar, N.S. and Hu, W.J. 1996. Characteristics of parasitism of *Plutella xylostella* (Lep: Plutellidae) by *Oomyzus sokolowskii* (Hym: Eulophidae). *Entomophaga*. 41: 45-52.

Talekar, N.S. and Shelton, A.M. 1993. Biology, ecology, and management of the diamondback moth. *Annual Review of Entomology*. 38: 275-301.

Talekar, N.S. and Yang, J.C. 1991. Characteristics of parasitism of diamondback moth by two larval parasites. *Entomophaga*. 36: 95-104.

Talekar, N.S. and Yang, J.C. 1993. Influence of crucifer cropping system on the parasitism of *Plutella xylostella* (Lep: Yponomeutidae) by *Cotesia plutellae* (Hym: Braconidae) and *Diadegma semiclausum* (Hym: Ichneumonidae). *Entomophaga*. 38: 541-550.

Talekar, N.S.; Lee, S.T. and Huang, S.W. 1986. Intercropping and modification of irrigation method for the control of diamondback moth. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 145-155.

Talekar, N.S.; Yang, J.C. and Lee, S.T. 1992. Introduction of *Diadegma semiclausum* for the control of diamondback moth in Taiwan. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 263-270.

Talekar, N.S.; Liu, S-H.; Chen, C-L. and Yiin, Y-F. 1994. Characteristics of oviposition of diamondback moth (Lepidoptera: Yponomeutidae) on cabbage. *Zoological Studies*. 33: 72-77.

Tanaka, H. 1992. Occurrence of resistance to *Bacillus thuringiensis* in diamondback moth, and results of trials for integrated control in a watercress greenhouse. In: Talekar, N.S. (Ed.), Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 165-173.

Tang, J.D.; Gilboa, S.; Roush, R.T. and Shelton, A.M. 1997. Inheritance, stability, and lack-of-fitness costs of field-selected resistance to *Bacillus thuringiensis* in diamondback moth (Lepidoptera: Plutellidae) from Florida. *Journal of Economic Entomology*. 90: 732-741.

Thomas, W.P. and Ferguson, A.M. 1989. *Plutella xylostella* (L.), diamondback moth (Lepidoptera: Yponomeutidae). In: Technical Communications (Commonwealth Institute of Biological Control). pp. 135-142.

Ullyett, G.C. 1947a. Host adoption by hymenopterous parasites. *Journal of the Entomological Society of South Africa*. 9: 236-237.

Ullyett, G.C. 1947b. Mortality factors in populations of *Plutella maculipennis* Curtis (Tinedae: Lep.), and their relationship to the problem of control. *Entomology Memoirs, Department of Agriculture and Forestry, Union of South Africa*. 2: 77-202.

Vail, K.M.; Kok, L.T. and McAvoy, T.J. 1991. Cultivar preferences of lepidopterous pests of broccoli. *Crop Protection*. 10: 199-204.

Vandenberg, J.D.; Ramos, M. and Altre, J.A. 1998a. Dose-response and age- and temperature-related susceptibility of the diamondback moth (Lepidoptera: Plutellidae) to two isolates of *Beauveria bassiana* (Hyphomycetes: Moniliaceae). *Environmental Entomology*. 27: 1017-1021.

Vandenberg, J.D.; Shelton, A.M.; Wilsey, W.T. and Ramos, M. 1998b. Assessment of *Beauveria bassiana* sprays for control of diamondback moth (Lepidoptera: Plutellidae) on crucifers. *Journal of Economic Entomology*. 91: 624-630.

Van Driesche, R.G. 1983. Meaning of "Percent Parasitism" in studies of insect parasitoids. *Environmental Entomology*. 12: 1611-1622.

Velasco, L.R.I. 1983a. Field parasitism of *Apanteles plutellae* Kurdj. (Braconidae, Hymenoptera) on the diamondback moth of cabbage. *The Philippine Entomologist*. 6: 539-553.

Velasco, L.R.I 1983b. The life history of *Apanteles plutellae* Kurdj. (Braconidae), a parasitoid of the diamondback moth. *The Philippine Entomologist.* 5: 385-399.

Verkerk, R.H.J.; Leather, S. R. and Wright, D.J. 1998. The potential for manipulating crop-pest-natural enemy interactions for improved insect pest management. *Bulletin of Entomological Research.* 88: 493-501.

Verkerk, R.H.J. and Wright, D.J. 1994a. Interactions between the diamondback moth, *Plutella xylostella* L. and glasshouse and outdoor-grown cabbage cultivars. *Annals of Applied Biology.* 125: 477-488.

Verkerk, R.H.J. and Wright, D.J. 1994b. The potential for induced extrinsic host plant resistance in IRM strategies targeting the diamondback moth. *Brighton Crop Protection Conference - Pests and Diseases.* : 457-462 pp.

Verkerk, R.H.J. and Wright, D.J. 1996a. Common cabbage resistance mechanisms against the diamondback moth: still an open book. *Annals of Applied Biology.* 128: 571-577.

Verkerk, R.H.J. and Wright, D.J. 1996b. Multitrophic interactions and management of the diamondback moth: a review. *Bulletin of Entomological Research.* 86: 205-216.

Verkerk, R.H.J. and Wright, D.J. 1997. Field-based studies with the diamondback moth tritrophic system in Cameron Highlands of Malaysia: implications for pest management. *International Journal of Pest Management.* 43: 27-33.

Waage, J. 1996. "Yes, but does it work in the field?" The challenge of technology transfer in biological control. *Entomophaga.* 41: 315-332.

Waage, J. and Cherry, A. 1992. Quantifying the impact of parasitoids on diamondback moth. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 245-253.

Wagner, T.L.; Wu, H-I.; Sharpe, P.J.H.; Schoolfield, R.M. and Coulson, R.N. 1984. Modeling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America.* 77: 204-225.

Wakisaka, S.; Tsukuda, R. and Nakasuji, F. 1992. Effects of natural enemies, rainfall, temperature and host plants on survival and reproduction of the diamondback moth. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 15-26.

Waladde, S.M.; Leutle, M.F. and Villet, M.H. 2001. Parasitism of *Plutella xylostella* (Lepidoptera, Plutellidae): field and laboratory observations. *South African Journal of Plant Soil.* 18: 1-6.

Wang, X-G.; Liu, S-S.; Guo, S-J. and Lin, W-C. 1999. Effects of host stages and temperature on population parameters of *Oomyzus sokolowskii*, a larval-pupal parasitoid of *Plutella xylostella. BioControl.* 44: 391-402.

Waterhouse, D.F. 1992. Biological control of diamondback moth in the Pacific. In: Talekar, N.S. (Ed.), Diamondback Moth Management: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 213-224.

Weisz, R.; Fleischer, S. and Smilowitz, Z. 1996. Site-specific Integrated Pest Management for high-value crops: Impact on potato pest management. *Journal of Economic Entomology*. 89: 501-509.

White, A.J.; Wratten, S.D.; Berry, N.A. and Weigmann, U. 1995. Habitat manipulation to enhance biological control of Brassica pests by hover flies (Diptera: Syrphidae). *Journal of Economic Entomology*. 88: 1171-1176.

Wilding, N. 1986. The pathogens of diamondback moth and their potential for its control - a review. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 219-232.

Woods, T.L.; Bailey, W.C. and Puttler, B. 1999. A comparison of methods to determine parasitoids and parasitism rates of the alfalfa caterpillar, *Colias eurytheme* (Boisduval) (Lepidoptera: Pieridae). *Journal of the Kansas Entomological Society*. 72: 273-276.

Workman, R.B.; Chalfant, R.B. and Schuster, D.J. 1980. Management of the cabbage looper and diamondback moth on cabbage by using two damage thresholds and five insecticide treatments. *Journal of Economic Entomology*. 73: 757-758.

Worner, S.P. 1992. Performance of phenological models under variable temperature regimes: consequences of the Kaufmann or rate summation effect. *Environmental Entomology*. 21: 689-699.

Wright, D.J. and Verkerk, R.H.J. 1995. Integration of chemical and biological control systems for arthropods: evaluation in a multitrophic context. *Pesticide Science*. 44: 207-218

Wyman, J.A. 1992. Management approaches for cruciferous insect pests in central North America. In: Talekar, N.S. (Ed.), Diamondback Moth and Other Crucifer Pests: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 503-509.

Xu, J. and Shelton, A.M. 2001. A method for rearing *Diadegma insulare* (Hymenoptera: Ichneumonidae) in the greenhouse. *Journal of Entomological Science*. 36: 208-210.

Xu, J.; Shelton, A.M. and Cheng, X. 2001a. Comparison of *Diadegma insulare* (Hymenoptera: Ichneumonidae)and *Microplitis plutellae* (Hymenoptera: Braconidae): field parasitism, insecticide susceptibility, and host-searching. *Journal of Economic Entomology*. 94: 14-20.

Xu, J.; Shelton, A.M. and Cheng, X. 2001b. Variation in susceptibility of *Diadegma insulare* (Hymentoptera: Ichneumonidae) to permethrin. *Journal of Economic Entomology*. 94: 541-546.

Yang, J.C.; Chu, Y.I. and Talekar, N.S. 1993. Biological studies of *Diadegma semiclausum* (Hym: Ichneumonidae), a parasite of diamondback moth. *Entomophaga*. 38: 579-586.

Yang, J.C.; Chu, Y.I. and Talekar, N.S. 1994. Studies on the characeristics of parasitism of *Plutella xylostella* (Lep: Plutellidae) by a larval parasite *Diadegma semiclausum* (Hym: Ichneumonidae). *Entomophaga*. 39: 397-406.

Yaseen, M. 1978. The establishment of two parasites of the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) in Trinidad, W.I. *Entomophaga*. 23: 111-114.

Yasudomi, N.; Miyata, T.; Murai, K. and Umetsu, N. 1992. Use of benfuracarb in the integrated management of diamondback moth. In: Talekar, N.S. (Ed.), Diamondback Moth Management: Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 333-339.

Yeh, R.; Whipp, A. and Trijau, J-P. 1986. Diamondback moth resistance to synthetic pyrethroids: How to overcome the problem with deltamethrin. In: Talekar, N.S. and Griggs, T.D. (Eds.), Diamondback Moth Management: Proceedings of the First International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan, pp. 379-386.

Yu, S.J. and Nguyen, S.N. 1996. Insecticide susceptibility and detoxication enzyme activities in permethrin-selected diamondback moths. *Pesticide biochemistry and physiology*. 56: 69-77.

Zandstra, B.H. and Motooka, P.S. 1978. Beneficial effects of weeds in pest management - a review. *PANS*. 24: 333-338.

Zar, J. 1984. Biostatistical Analysis. 2nd Edition. Prentice Hall. New York. pp.294-295.

Zhao, J-Z.; Li, Y-X.; Collins, H.L.; Gusukuma-Minuto, L.; Mau, R.F.L.; Thompson, , G.D, and Shelton, A.M. 2002. Monitoring and Characterization of diamondback moth (Lepidoptera: Plutellidae) resistance to spinosad. *Journal of Economic Entomology*. 95: 430-436.

Zhao, J-Z.; Ayers, G.S.; Grafius, E.J. and Stehr, F.W. 1992. Effects of neighboring nectar-producing plants on populations of pest lepidoptera and their parasitoids in broccoli plantings. *The Great Lakes Entomologist*. 25: 253-258.