POTENTIAL OF PARASITOIDS FOR THE CONTROL OF CABBAGE MOTH IN AUGMENTATIVE RELEASES

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DECLARATION

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ABSTRACT

Cabbage moth (*Plutella xylostella* L.) is a serious insect pest on brassicas in many parts of the world. Studies of two larval parasitoids, *Cotesia plutellae* Kurdjumov and *Diadegma semiclausum* Hellen, were conducted to assess their potential for the control of this pest. In the laboratory, rates of parasitism by these parasitoids varied at various wasp densities for each host instar, where they preferred bigger hosts to lay eggs. Their searching efficiency decreased with increasing parasitoid densities, but their killing capacity and encounters increased at higher wasp densities for each instar. Within the temperature range of 15 ^{o}C to 35 ^{o}C, the lower the temperature, the longer was the developmental time and aging rate. Also, at low temperatures they developed slowly. The parasitoid *C. plutellae* was most active at the warmer temperature (range 20 ^{o}C to 35 ^{o}C), whereas *D. semiclausum* was most active at cooler temperatures (15 ^{o}C to 25 ^{o}C). Self-superparasitism by these wasps was the lowest at low temperatures and on the first instar. In glasshouse experiments, both parasitoids laid more eggs in the evening when released at a higher density. The temperature threshold of female *C. plutellae* was 3.6 ^{o}C. Field releases of 10 and 20 female *C. plutellae* produced the average of 23.4% and 43.7% parasitism, respectively. Superparasitism by this wasp occurred in very low rates, i.e. 0.9% and 2.27% for 10 and 20 released female wasp, respectively.

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CHAPTER 1

INTRODUCTION

The cabbage moth is an oligophagous species (Stanton, 1983) and mainly infests commercial or wild brassicas belonging to the family Brassicaceae. The caterpillars feed on leaves of crucifers from seedlings to mature plants, and their presence decreases the quantity and quality of yields (Talekar *et al.*, 1990). The heaviest damage caused by this insect occurs on young plants. On older plants, the caterpillars live on the outer leaves (Mustata, 1992). The moths are nocturnal and the females oviposit along the margins of sheltered leaves. The first instar or the youngest larvae are known as leaf miners, and they feed externally in the next larval stage. Older larvae feed on the undersides of leaves, producing small holes and often leave the upper epidermis (Hamilton and Toffolon, 1987).

Amongst the insect pests consuming plant parts of crucifers the cabbage moth (*Plutella xylostella* L.) is one of the most serious defoliators of these particular crop plants throughout the world, including subtropical and tropical countries (Talekar and Yang, 1991). It has a world-wide distribution, as it has the ability to adapt to different climatic conditions and to migrate over long distances (Salinas, 1986).

Cultivated cruciferous crops are important agricultural commodities from an economic point of view. They consist of several species which are harvested and marketed as edible roots (radish, *Raphanus sativus* L.; rutabaga or swede, *Brassica napus* L. var *napobrassica* and turnip, *Brassica rapa* L. var. *rapifera*), leaves (common cabbage, *Brassica oleracea* L. var *capitata*; brussels sprouts, *Brassica oleracea* L. var. *gemmifera*; kale or collard, *Brassica oleracea* L. var. *acephala*; Indian mustard, *Brassica juncea* L.; chinese cabbage, *Brassica campestris* ssp. *pekinensis* Lour.; Chinese kale, *Brassica albogabra* and charlock, *Brassica sinapsis* Vis. or *Sinapsis arvensis* L.), flowers (broccoli, *Brassica oleracea* L. var. *italica* and cauliflower, *Brassica oleracea* L. var.

botrytis), stems (kohlrabi, *Brassica oleracea* L. var. *gongylodes*), seeds (canola or rapeseed, *Brassica napus* L. and *B. campestris*; Indian mustard, *B. juncea*; black mustard, *Brassica nigra* L. and white mustard, *Brassica hirta* Moench. or *Sinapsis alba* L.), fodder (canola, *B. napus* and Indian mustard, *B. juncea*), fish food/cosmetics/margarine/industrial lubricants (canola, *B. napus*) or even for medicine (e.g. Indian mustard seeds produce a specific oil that is manufactured in the form of mustard plasters) (Gomez-Campo, 1980; Snogerup, 1980; Hartmann *et al.*, 1981; George, 1982; Murison, 1985; Sykes, 1989; Carmody, 1995).

The soft parts of these crops are subject to damage by agricultural tools, transportation, and insect pests and diseases. They are rich in glucosinolates, organic compounds that comprise sulphur and glucose whose products of enzymatic breakdown have biological activity in pest attraction, disease resistance, particular metabolic diseases in mammals and sharpness in flavour (Williams and Daxenbichler, 1981). Mustard oils in free form or in glucosidal combinations found in crucifers influence the egg laying and feeding habits of insects associated with this group of plants (Bonnemaison, 1965).

Growers currently depend on the use of large quantities of chemical insecticides to control insect pests like cabbage moth (Talekar and Yang, 1991). Since World War II, insect control by chemicals has been the dominant means of pest management in agriculture. This commenced with the production of DDT in the early 1940s, which was subsequently followed by other chlorinated hydrocarbons having a wide spectrum of insecticidal activity and persistence in the field. Later, these substances were replaced by carbamates and organophosphates with short residual effects, but notably higher toxicity than DDT and related compounds, and more recently by synthetic pyrethroids (DeBach and Rosen, 1991).

Continuous and unselective use of chemicals has led to the development of tolerance or resistance in cabbage moth to various types of insecticides. Consequently, the cost of crop production has increased (Talekar *et al.*, 1990), and other side effects such as

ecological, psychological and physiological problems have occurred. Over-dependency on insecticides has resulted in insecticide poisoning of farmers, elimination of natural enemies of pests (predators and parasitoids), adverse effects on non-target species (domestic animals, honey bees and pollinators, and wild life), outbreaks of secondary pests, pest resurgence, and presence of insecticidal residues in marketable crops (DeBach and Rosen, 1991; Dent, 1991; Metcalf, 1982; Ripper, 1956; Sudderudin and Kock, 1978;). In the environment, pollution from non-biodegradable insecticides is not only a danger but a reality that contaminates soils, food chains, and water systems. Frequently natural enemies are a major regulatory factor for insect pest populations in the absence of pesticide treatment has started. Unfortunately, pesticides may kill more natural enemies than pests or potential pests, because natural enemies are often more susceptible to pesticides than the herbivores on which they feed (Price, 1987). In the future, chemical insecticides will remain an essential and powerful tool in the management of the cabbage moth. However, their use should be integrated with various alternative pest management techniques to prevent environmental and agricultural disaster (Lim *et al.*, 1986).

An ecological approach to controlling the cabbage moth is to develop a biological control strategy. This potentially provides an alternative solution to the overuse of insecticides. Damage by destructive pests is lowered by the use of natural enemies at biologically and economically tolerable levels. Natural enemies combat living species by feeding on them or, in other words, regulating their population densities (Debach and Rosen 1991). From an ecological point of view, biological control is defined as the action of natural enemies, whether predators, parasitoids, or pathogens, in regulating the population density of an organism at lower levels than would take place in their absence. Natural control can be more broadly defined as the maintenance of the density of an organism within particular upper and lower limits over a period of time by the actions of abiotic and biotic environmental elements (DeBach, 1964; van den Bosch *et al.*, 1985). The abiotic factors such as food, space and shelter naturally control the number of insects.

Cold, heat, wind, drought or rain are other factors affecting their populations. Biotic factors comprise competition from themselves or from other organisms, including the existence of natural enemies i.e. predators, parasitoids and pathogens (van den Bosch and Messenger, 1973). When successful, the use of natural enemies is economical, safe, and permanently lowers a pest population below its economic injury level. In reality, the regulation of a pest population by biological control is complex. Therefore, studies of the biology, ecology, behaviour and systematics of pests and their natural enemies are crucial components in understanding and implementing biological control.

Natural enemies have been utilised to control pests for centuries, but a scientific approach to biological control was only developed late in the nineteenth century. This emerged from new concepts dealing with relationships among species, population pressures, evolution and the struggle for life. Also, the need for biological control emerged as new pest problems developed in conjunction with increased travel and transportation of goods around the world. These pests often colonised new areas without their native natural enemies. Hence, the role of predators, parasitoids, and pathogens in limiting numbers of insects was recognised, and practical utilisation of natural enemies was suggested as an effective way to interfere with imported pests. In 1883, the larval parasitoid *Cotesia glomerata* L. (= *Apanteles glomeratus* L; Hymenoptera: Braconidae) was imported into the United States from England to control the cabbage white butterfly, *Pieris rapae* L. (Lepidoptera: Pieridae) (Sweetman, 1958). The cottony cushion scale, *Icerya purchasi* Maskell invaded California (United States of America) from Australia around 1868, and within two decades it caused severe economic decline in the citrus industry of that state. After the introduction and establishment of its natural enemies from Australia in 1888, the vedalia beetle *Rodolia cardinalis* Mulsant, a coccinellid predator and the parasitic fly *Cryptochaetum iceryae* Williston, the cottony cushion scale was completely controlled (Stern *et al.*, 1959; Sweetman, 1958; Wilson and Huffaker, 1976).

Such a dramatic success stimulated further research into the manipulation of beneficial insects to reduce insect pest damage in agriculture.

Parasitic wasps are an important type of natural enemy. The diversity, abundance and biological characteristics make these insects attractive to study. For example, records from the British fauna indicate that 35.6 percent of the insects found are parasitic on animals and over 90 percent of these are parasitoids. The greatest number of wasps in Britain are in three families: Braconidae, Ichneumonidae, and Pteromalidae (Waage and Greathead, 1986). Reuter (1913) introduced the term 'parasitoid' to describe insect parasites that invariably kill the habitual host in the course of the parasitic interaction. Their larvae complete development on a single host insect that usually dies. Adult parasitoids live freely. They may feed on honey from flowers, sap flux, or other food sources, and many of them feed on potential hosts (host feeding). Female parasitic Hymenoptera possess characteristic ovipositors for laying eggs or stinging hosts. The effect of a sting may result in permanent paralysis, however in some species the stung host may recover (Godfray, 1994).

The adult female commonly oviposits in or on its host. Certain species lay eggs on the host's food plant. When a potential host starts feeding, the eggs hatch and parasitism takes place when the host starts feeding their eggs. Some also have free-living first instar larvae that actively search for hosts. Parasitoids may parasitise the eggs, larvae, pupae or adults of host insects. Therefore, host stages can be used to classify the parasitoids; egg parasitoids, larval parasitoids, pupal parasitoids and adult parasitoids. These may be holometabolous insects such as butterflies and moths, beetles, and flies. Hemimetabolous insects that do not have a pupal stage can be parasitised by egg parasitoids as well, but the difference between parasitoids attacking nymphs and adults is not significant. Parasitoids can also be classified according to their feeding habits. Endoparasitoids grow within the body of hosts, while ectoparasitoids develop externally. Parasitoids that develop alone on one host are called solitary parasitoids, and gregarious parasitoids develop in groups on a

host. If larvae of the second species feed on a parasitoid larvae not on the host, hyperparasitism takes place (Waage, 1986; van Alphen and Visser, 1990; Godfray, 1994). Koinophitic parasitoids, or koinobionts, are parasitoids that permit their hosts to continue growing after parasitism. These comprise most larval and adult endoparasitoids. By contrast, idiobionts or idiophitic parasitoids are individuals that prevent further host development. Egg, pupal and adult parasitoids commonly act as idiobionts (Askew and Shaw, 1986; Waage and Hassell, 1982).

In nature, the cabbage moth, as other insect pests, has natural enemies and these can be used to regulate the pest population at low population density so as not to reach the economic injury level. Investigations on parasitoids will undoubtedly contribute to solve problems of pest invasion in crucifer cultivation. Almost all stages of the cabbage moth have a particular parasitoid species. For example, *Trichogramma brasiliensis* Ashm. (Hymenoptera: Trichogrammatidae) parasitises eggs; *Cotesia plutellae* Kurdjumov (Hymenoptera: Braconidae), *Diadegma semiclausum* Hellën and *Diadegma rapi* Cameron (Hymenoptera: Ichneumonidae) are larval endoparasitoids; and *Diadromus collaris* Grav. (Hymenoptera : Ichneumonidae) is pupal parasitoid (Ooi, 1992). Evidence for the success of natural enemies in controlling cabbage moth is found in the investigation carried out by Putnam (1978) in Canada. The result indicated that with a combined action of the parasitoids *Diadegma insularis* Cress and *Microplitis plutellae* Muss., parasitism could reach 68% in the first generation of the cabbage moth. In Zambia, a combination of newly established *C. plutella* and *D. collaris*, along with the endemic *Tetrastichus sokolowskii* Kurdj. (Hymenoptera: Elophidae) resulted in 80 percent reduction of damage on cabbages infested by the cabbage moth (Yaseen, 1978). Morallo-Rejesus and Sayaboc (1992) imported the parasitoid *C. plutellae* from Taiwan into the Philippines. In the field, the indigenous strain of *C. plutellae* showed a low parasitism level (1.9-16.5%), while an imported strain when tested could parasitise the cabbage moth larvae at a higher rate than the indigenous species (17.4% and 36.5% in the first and second plantings respectively).

In the laboratory, the local strain also indicated lower parasitism (13.8-33%) compared with the introduced Taiwan strain (17.3-40%).

Establishment of parasitoids in the field for pest control can have variable results from time to time, depending on the abiotic and biotic circumstances. The abiotic factors are climates such as temperature, humidity, rainfal, wind, and sunlight, and also soil. Host plants for the pest, parasitoid hosts, other parasitoid becoming competitors, and maintenance of them by farmers or other people may become biotic ones. Thus, in the control of the cabbage moth, releases of the parasitic wasps should commence at the seedling stage to make an impact on the target pest. The objective of this research was to investigate the effect of releases of parasitic wasps to control the cabbage moth in crucifers. The wasps evaluated were the parasitoids *C. plutellae* and *D. semiclausum*. Firstly, these parasitoids were tested in the laboratory in terms of their rates of parasitism, killing capacity, searching efficiency, and numbers of encounters. Observations were also made on their development and size of offsprings. In the glasshouse, experiments were performed to detect the influence of parasitoid density and time of releases on the rate of parasitism. Finally, wasp releases at different densities were made to assess parasitism in the field.

CHAPTER 2

REVIEW OF LITERATURE

2.1. Introduction

The cabbage moth is a serious insect pest in cruciferous vegetable crops throughout the world. The caterpillars feed on the foliage of these plants from seedlings to harvest, greatly causing reduction in both quantity and quality of the produce. They also have alternate host plants, particularly wild brassicas that belong to the family of Brassicaceae (Cruciferae). Many methods of control can be applied to this pest, but farmers tend to use chemical insecticides with wide spectrum activities. Whereas dependence on chemicals requires additional costs and results in environmental disturbance in agro ecosystems (Ke *et al.*, 1991), the production of new types of insecticides such as insect-growth regulators (IGRs) and biological insecticides (containing active ingredients of certain insect pathogens) give promise to be alternatives for broad-spectrum chemical insecticides. These products specifically control the target pests. Insect growth regulators that act to disrupt chitin synthesis are expected to be an alternative to common synthetic insecticides and may reduce the incidence of insect resistance to chemicals.

In Thailand, Rushtapakornchai and Vattanatangum (1986) reported that insect growth regulators or IGRs (diflubenzuron, triflumuron, tefluron, and chlorfluazuron) which were introduced in early 1980s provided good controls on cabbage moth initially. However, triflumuron showed poor control after two years from 1982 to 1984. Furthermore, Perng *et al* (1988) indicated that a development of cabbage moth resistance to IGRs occurred only two to three years after use. Other research in terms of cabbage moth resistance to insecticides has been carried out, for examples in United States (Tabashnik *et al.*, 1987), Japan (Noppun *et al.*, 1983; Hama, 1986), Indonesia (Ankersmit, 1953), Malaysia (Sudderudin and Kok, 1978), and Taiwan (Sun *et al.*, 1978; Liu *et al.*, 1982). One of the biological agents, the microbial insecticide *Bacillus*

thuringiensis Berliner (BT) is commonly used against pests of lepidopterous larvae. This microorganism has been applied in pest control programs for more than 20 years and is shown to conserve natural enemies (Talekar and Shelton, 1993). But, McGaughey (1985) found that a lepidopteran pest of stored grain and grain products named the Indian meal moth, *Plodia interpunctella*, can develop resistance to *B. thuringiensis* ssp. *kurstaki* (BT) within a few generations. The strains collected from bins of BT-treated grain were more resistance than that of untreated ones. He explained that conditions in stored grain are ideal for resistance development due to the pathogen persisting undisturbed in this environment a for long time, allowing the insect pests to continuously breed in contact with the bacterial toxins and spores. Van Rie *et al.* (1990) concluded that resistance of this pest to BT is caused by an alteration in binding of the toxin to the gut membrane. In other words, resistance to this insecticidal crystal protein is related to reduction in the binding affinity of the protein's membrane receptor. Furthermore, research done by Kirsch and Schmutterer (1988) indicated low efficacy of *B. thuringiensis* for controlling the cabbage moth in the Philippines, and it was suspected that symptoms of genetic resistance to the toxin were the reasons. The presence of cabbage moth being resistance to high levels to *B. thuringiensis* was found in hydroponic glass houses by Hama (1992) in Osaka. It was a result of frequent usage, reaching 30-40 applications within three to four years to control the pest attacking watercress (*Nasturtium officinale* R. Br.) crops.

Development of integrated pest management strategies for controlling *P. xylostella* is an appropriate approach that is economically and ecologically sound. Since growers have used synthetic insecticides with broad spectrum activities for years, their applications have created numerous problems in agriculture and environment, and have led to pest resistance and the elimination of local natural enemies, especially parasitoids. Lack of suitable control methods and scarcity of new insecticides stimulate investigation of alternative. Utilisation of parasitoids provides a great opportunity as an alternative method to control cabbage moth in the field. According to DeBach (1964), regulation of

population densities of pests may need the use and manipulation of beneficial organisms through introduction, augmentation, or conservation. The cabbage moth has many parasitoids attacking it at various stages. Generally, predators such as spiders and birds consume adults of this pest. Goodwin (1979) concluded that there are more than 90 parasitoids attacking the cabbage moth, unfortunately not all the natural enemies are effective. However, Talekar and Shelton (1993) stated that only about 60 of them are likely to be important in biological control. Amongst the parasitoids found, larval parasitoids predominate and are effective. There are two major genera, *Cotesia* and *Diadegma*, which have performed effectively in controlling cabbage moth populations in some areas. The larval parasitoid, *Cotesia plutellae*, is effective in the low land areas of the tropics and subtropics at high temperatures. In the high lands, where temperatures are low, *Diadegma semiclausum* provides good control of this pest. Therefore, research on these parasitoids is necessary to formulate a successful integrated pest management program on the cabbage moth.

2.2. The cabbage moth (*Plutella xylostella* L.)

2.2.1. Introduction

It is generally believed that the cabbage moth is native to the Mediterranean region in Southern Europe. It is the source of most cruciferous crops. This pest is distributed world wide in areas where crucifers are cultivated. It is found in North and South America, most of Africa, China, India, Japan, New Zealand, South East Asia, Australia, and the Pacific islands (Bonnemaison, 1965; Fukaya and Takeuchi, 1995; Osmelak, 1990; Talekar *et al.*, 1990; Thomas and Ferguson, 1989 Wilson, 1960; Waterhouse and Norris, 1987).

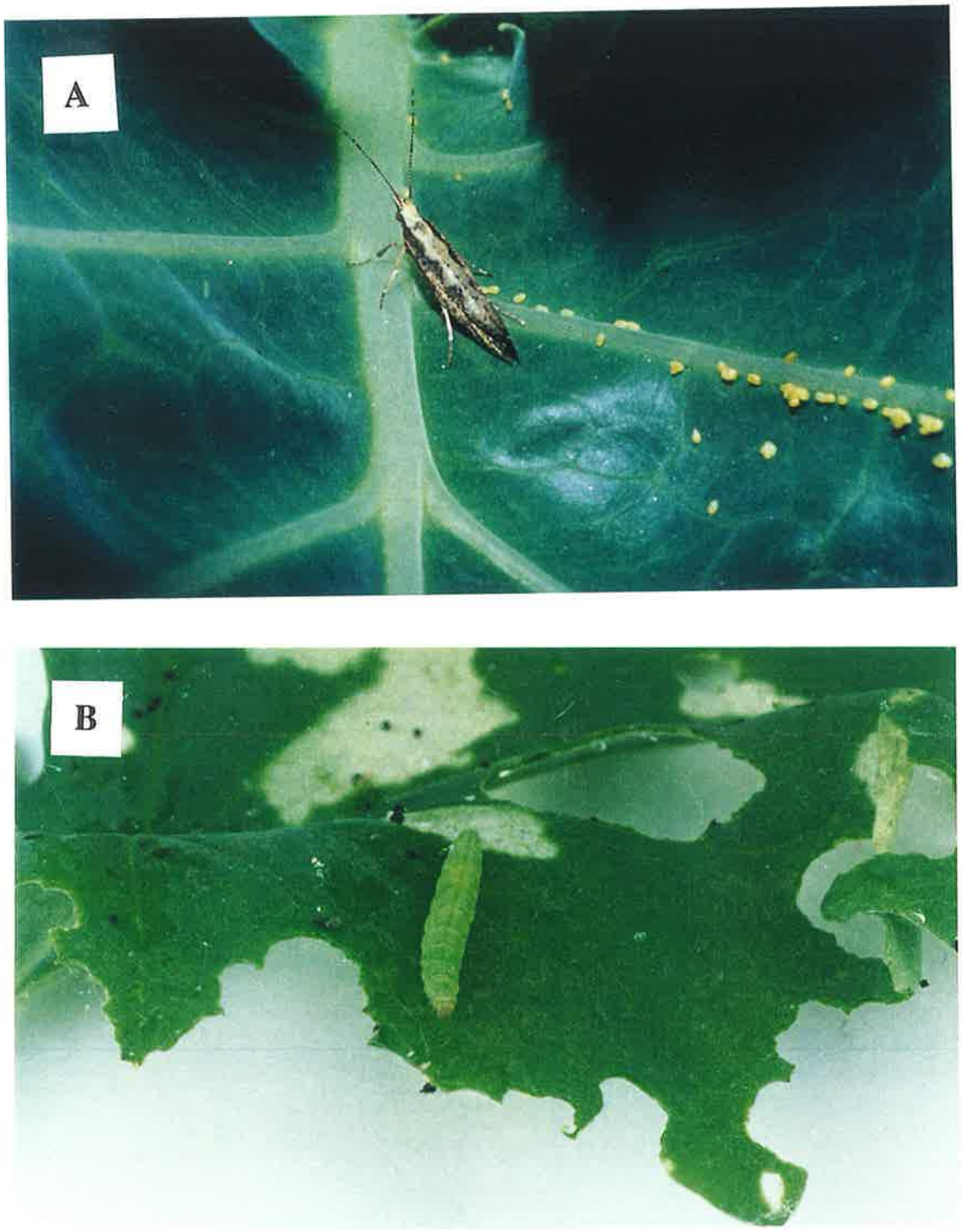

Plate 1. Cabbage moth (*Plutella xylostella*), a world wide pest on brassicas. A) The eggs and an adult moth resting on a cabbage leaf. B) A fourth instar larva on a damaged rapeseed leaf (enlarged).

In some cases, this pest has become a major limiting factor of crucifer production (Chu, 1986), due to its ability to survive in variable climatic conditions. In tropical regions, for instance in Indonesia, damage to crucifers caused by the cabbage moth and other pests may reduce the crop yield to zero (Sastrosiswojo and Sastrodihardjo, 1986). This pest is able to migrate long distances, however there is not any record of migration of its parasitoids (Talekar and Shelton, 1993). Lim (1986) explained that the absence of natural enemies, particularly parasitoids, causes the pest status of cabbage moth in many areas of the world. Nevertheless, in some countries it is generally not a major pest. According to Vos (1953), in England, Netherlands, and South Africa, for instance, a number of parasitoids control *P. xylostella* populations sufficiently.

2.2.2. Biology

Taxonomy

The cabbage moth has undergone several changes in the nomenclature after Linnaeus (1758) described it as *Plutella xylostella*. Moriuti (1986) listed synonyms of this pest, namely *Plutella Tinea xylostella* Linnaeus 1758; *Cerostoma maculipennis* Curtis 1832; *Plutella cruciferarum* Zeller 1843; *Plutella brassicella* Fitch 1856; *Plutella limbipennella* Clemens 1860; *Plutella mollipedella* Clements 1860; *Gelechia cicarella* Rondani 1876; *Tinea galeatella* Mabille 1888; and *Cerostoma dubiosella* Beutenmuller 1839. Then, in 1966, Bradley suggested replacement of the name *maculipennis* with *xylostella* which is now to be recognised to be valid. It belongs to the family Plutellidae and the order Lepidoptera (Harcourt, 1957; Harcourt, 1960; Chow *et al.*, 1976; Pivnick *et al.*, 1990).

Host plants

The cabbage moth feeds on various cultivated and wild crucifers. The cultivated crops are: common or white cabbage, brussels sprouts, collard or kale, Indian mustard,

Chinese cabbage, Chinese kale, charlock, broccoli, cauliflower, sweede or rutabaga, turnip, kohlrabi, canola or rapeseed, black mustard, white mustard, watercress, horse-radish (*Radicula armoracea*), sweet alyssum (*Koniga maritima*), and candytuft (*Iberis amara*). The pest also consumes weeds related to crucifers for alternate hosts. They are wild brassica (*Brassica elongata* Ehr.), twiggy turnip (*B. fruticulosa* Cirillo), smooth-stem turnip (*B. barrelieri* L.), mediteran turnip (*B. tournefortii* Gouan), wild watercress (*Roripa sinuata*), and hedge mustard (*Sisymbrium* sp.) (Marsh, 1917; Gomez-Campo, 1980; Snogerup, 1980; George, 1982; Hartmann *et al.*, 1981).

Egg

The egg of this insect is approximately 0.49 mm long and 0.26 mm wide. It has light yellow or greenish white colour (Plate 1A), is oval in shape and possesses a sculptured surface (Marsh, 1917; Hardy, 1938). In the field, the female lays eggs on the lower sides of cruciferous leaves, singly or in groups. They are along the veins and around the margins. Although it scarcely occurs, in cool weather sometimes eggs of the first and last broods may be placed on the upper sides of leaves. In the laboratory, where adults live in cages over young plants, females deposit eggs mainly on the stems of plants. The egg stage lasts for three to six days (Marsh, 1917; Vos, 1953). Biever and Boldt (1971) found that the egg stage was 3 days at 23±1 ^{o}C and 60±5% RH. The egg becomes much darker shortly before hatching and the young larva can be noticed coiled underneath the chorion. The anal segment and pigmented head are visible. At the head end the larva emerges from the egg shell by an opening in the chorion.

Larva

When the egg hatches, the larva breaks the chorion in front at the head region and progressively pulls its body through that hole. Immediately after hatching the first instar starts mining leaf tissue while feeding on it. Larvae emerge from the spongy mesophyll

for mining after they complete the first instar. They subsequently spin protective threads and moult inside the web. Newly second instar larvae become leaf feeders. At this stage, they do not normally mine leaf tissues, although some frequently feed with heads buried in the leaves. As the plants become older, the caterpillars consume the outer parts of leaves. They look very active, if interrupted they wriggle backward soon and even drop down to the ground or hang on their silken threads. Older larvae feed from the lower surface of leaves and usually leave the upper epidermis surface. Thus, they make window damage and puncture leaves. The mines persist with white markings on the leaves. This can be a specific marking for the attack of the species.

This pest has four larval instars, which can be distinguished microscopically by the width of head capsules, as the head is constant in size throughout any instar. Robertson (1939) in New Zealand, measured the head width of the first to fourth instar (average of 20 measurements) as follows: 0.163, 0.264, 0.378, and 0.628 mm. In Indonesia, Vos (1953) measured the head width of 10 larvae of each instar. The averages were 0.16, 0.24, 0.37, and 0.59 mm for the first to fourth instars respectively. Observations in Malaysia by Ooi and Kelderman (1979) showed that average head width of the first to four instar was 0.17, 0.28, 0.43, and 0.62 mm. Ratio between head widths of successive instars was 1.65 for second instar, 1.53 for the third instar, and 1.46 for the last instar. A fully grown larva is about 10 - 12 mm long (Abraham and Padmanaban, 1968; Hamilton and Toffolon, 1987).

The body of the first instar lacks pigmentation, and the head is very dark brown in colour. The second instar still possesses dark colour in its head, but the body shows a trace of pigmentation. In the third instar, pigmentation looks more apparent. Usually the colour of the head is almost colourless at the beginning of this instar. It gradually darkens, and finally is being very dark brown. Sometimes, the head may become dark very early or it may remain light in colour during this instar. The spots at the bases of setal body and on the prothorax are black or dark brown. The fourth instar is the largest size of the larval

stage. During this stage, a big increase in body size take places. The head is light in colour, but the pigment spots on the prothorax and setal bases are very dark brown or black. The newly moulted fourth instar is more or less colourless, although dark pigmentation may soon appear. The body becomes light green after a few days and the colour is compounded until the end of the instar. The green colour becomes visible (Plate 1B) caused by the green body fluid (Robertson, 1939).

The caterpillars cause serious injury on plants in the older instars. They may also feed on other parts of the plant. The duration of instars is different depending on temperature. Salinas (1986) in Venezuela observed the duration of the first to fourth instar at variable temperature (mean 18 ^{o}C) ranged as follows: 4-8, 3-8, 3-7, and 3-6 days. At constant temperature (20 ^{o}C) it was 2-6, 1-4, 3-4, and 3-4 days. In observations in Ontario, Canada, under field cage condition in 1955, the developmental times of first to fourth instars were 3-7, 2-7, 2-6, and 2-10 days (Harcourt, 1957). At 23 ± 1 ^{o}C and 60± 5% RH the larval stage was 11 days (Biever and Boldt, 1971). Climates influence the development of this insect; in warm weather it develops faster than in cool condition. Host plants are also reported to affect development (Talekar and Shelton, 1993). The duration of cabbage moth larvae varies from 14-21 days.

Prepupa

This stage is also called the propupa. Near the end of the larval stage, the larvae do not feed and normally wander from the host plant to dry or dead leaves lying on the ground (Robertson, 1939) or on the leaf surface (Talekar and Shelton, 1993). In the laboratory they accumulate on the frames of rearing cages. Then, after finding a suitable place for pupation, they start to spin their cocoons. This requires 24 hours and afterwards a period of quiescence representing the stage of prepupa commences. As this stage does not have any ecdysis or moulting to mark the beginning of the prepupa, an exact record of its duration is difficult. But, under laboratory conditions Robertson (1938) found that one

and a half to two days elapse for the completion of the cocoon and initiation of pupation is needed. During this phase the construction of head and its appendages change. Segmented, long antennae develop and coil below the larval skin on the dorsal surface of the head. Compared with the pupal antennae, they are thicker and irregular. Large eyes are present on the side of the head. The labrum or upper lip is visible, although minute. The mandible reduction to a pair of small lobes is next to the labrum. The maxillae and labium are more separated than in the larvae.

Pupa

When the prepupal stage is complete, the skin is split along the mid-dorsal line and slowly worked back along the body until it is sheded upon the anal segment. It immediately becomes shrunk at the anal end of the pupa, however it is within the cocoon. During this stage marked colour changes occur. It was previously light green or colourless, and as the pupae develop, a brown pigment appears on the two dorsal and two ventral bands. Shortly before emergence of the adult, the pupa is nearly black in colour. Depending on temperature, the duration of the pupa varies from 5 to 15 days (Biever and Boldt, 1971; Harcourt, 1957; Robertson, 1939; Waterhouse and Norris, 1987). Ooi and Kelderman (1979) mentioned that its length is about 4.5 to 7.0 mm, and in the laboratory it is usually smaller. The pupa is the obtected type, characteristic for certain group of Lepidoptera. The body is widest at the thorax and tapers gradually to the caudal segment.

Robertson (1939) explained that the labrum and mandibles are obviously separated, and maxillary palps are present. The maxillae are slender and long, curving around labial palps, subsequently going down to the fourth segment of the abdomen in the mid-ventral region. The wings extend up to the fifth abdominal segment. On each side of the maxillae, the femur of the prothoracic leg is present, while other legs are hidden. The anal opening is crack-like, and located on the ventral region next to the caudal edge. A number of spines are found along margins of the anal opening and caudal extremity.

An examination of genital openings can determine the sex of the pupa of this insect. In the male, the genital aperture is located on the ninth abdominal sternum, the eighth abdominal segment is rather uniform. The opening is seen as a longitudinal crack, with a semi-circular structure on each side. In the female, a genital aperture is situated in the mid-ventral area of the eighth abdominal sternum. The segment here is considerably narrowed, the aperture appears as a longitudinal split stretching from close the anterior to the posterior margin of the segment. The mid-ventral region of the ninth abdominal sternum is prolonged cephalad to the genital slit. The junction of the ninth and tenth abdominal segments is ventrally attributed indifferently.

Adult

The moth is greyish-brown and slender. At rest, the forewings cover the body, displaying three constrictions on the dorsal portion. These look like diamond-like shapes and therefore it is called the diamondback moth, the other common name besides the cabbage moth (Plate 1A). The emergence of the cabbage moth adult occurs primarily in the afternoon between 1:00 and 4:00 pm and reaches a peak at 2:00 pm (Pivnick *et al.*, 1990; Talekar and Shelton, 1993). During the daytime emergence, the adult moths are inactive until nightfall. The moths are nocturnal and in the field they rest on the underside surfaces of leaves in daytime. Their activity reaches a peak before midnight. When they are disturbed, they fly spiraling up above the plant in circles; or sometimes they may crawl and fly a short distance. In search of hiding places, they can move fast from the host plant. Wing movements are hardly seen, producing the next motion like a series of short hops. The moths are weak fliers and move around 3 - 4 m in a horizontal direction, they rarely rise more than 2 m vertically. However, the moths are readily carried by wind for long distances. They are active at dusk looking for food or nectar from the blossoms of crucifers.

Females mate just once at dusk on the day of emergence. It occurs on the plant while resting and the pair couple in opposite directions. The fertilised females do not attempt to mate again, and are less attractive to males. On the other hand, virgin females attract males. When they are disrupted during copulation, normally the female draws the male to a more hidden locality. Mating lasts approximately one hour. Shortly after mating, females lay eggs singly or in groups on the lower surfaces of leaves. But, small females oviposit on stems or petioles. Other preferred places are on feeding-sites of the larvae and yellow patches on leaves if the plant is young. In rearing conditions, the moths prefer to feed on sugar solution rather than honey, because the latter is stickier and trap moths when feeding (Harcourt, 1957; Os, 1953). In the laboratory, the adult cabbage moth lives for 6 to 14 days (Abraham and Padmanaban, 1968; Marsh 1917). But Robertson (1939) noted that their longevity is 25 - 30 days. It was said that nearly natural laboratory conditions presumably enable the adults to live longer. The sex ratio of this insect has been observed by Harcourt (1957) in Ontario, Canada. The ratio of males to females among 2,480 individuals was 52.9 : 47.1. The life span of males averaged 12.1 days, whereas females lived 16.2 days.

Migration

Insects move from one place to another in distinct ways resulting in particular patterns of dispersal which can characterise the species within a given habitat. For instance, the adults congregate temporarily to feed, rest, mate, deposit eggs, or overwinter. In insects, Dingle (1972) pointed out that migration is recognised as a distinct physiological and behavioural syndrome resulting in an adaptive spread. It involves an interaction between flight, feeding, and larval placement. This term includes active and passive migration (by wind) that is considered distinct by some entomologists. The latter type of movement needs active flight to achieve certain altitudes allowing wind displacement with less wing beating to keep airborne. Generally speaking, ecological and

physiological studies of migratory insects are consistent. Those are as follows: 1) migration commonly happens in pre-reproductive stages of adult insects, named as an oogenesis-flight syndrome. 2) Because these individuals are generally pre-reproductive, their reproductive value and colonising aptitudes are close or at maximum. 3) Migratory species usually inhabit temporary habitats. 4) Migrants have a potential for being colonisers which are potentially effective for population increase. 5) During migration, vegetative functions like feeding and reproduction are suppressed and locomotory functions are predominant. In addition, Sappington and Showers (1992) investigated that a delay in suppression of reproductive behaviour and oogenesis are not indication for the initiation of long-duration flight by *Agrotis ipsilon*.

Migration in the world of insects always deals with the dispersal of the females. All of them have a similar function: to ensure that the offspring are located in appropriate habitat. So far, as Johnson (1963) stated, the males are only required to fertilise the females. Moreover, mating can be performed at the emergence site without migration, while migrating, or at the final destination. Therefore, male migration is more complicated from species to species than female migration physiologically. Migratory flight can be prolonged by a prolonged pre-oviposition period. Thus, some factors that lengthen immaturity are likely to prolong and increase female migration. These factors, such as lack of food, wrong kind of food available, crowding, short days and high temperature influence the action of endocrine tissues and the corpus allatum. Conversely, low temperature, lengthened photoperiod, sufficient supply of the right food, and little crowding influence insects to suppress or shorten migratory flight activities. According to Johnson (1966), crowding produces sexual immaturity in some insects. Many migrants delay their ovarial development as a result of food deficiency. Crowding is related to food shortage, and in temperate regions, short autumn days signal preparation for the next generation.

It is known that the cabbage moth is one of the widest spread-insects throughout the world, for it has the ability to disperse and migrate over long distances (Talekar and Shelton, 1993). In Japan cabbage moths migrate from southwestern islands with warm subtropical weather, to the cooler temperate climate of Honshu and Hokaido. Between spring and autumn numerous adults are caught every year in areas where hibernation of this insect does not occur (Honda, 1992; Shirai, 1993). In 1854 this insect was first reported in Illinois, North America. By 1883, it had spread as far west as the Rocky Mountains and as far south as Florida. In 1885 it was reported from western Canada, from Brazil in 1892, and from Argentina by 1923 (Waterhouse and Norris, 1987). Harcourt (1986) reported that the adult moths migrate annually from the Southern United State to Eastern Canada. List in 1937 found that numerous cabbage moths came from somewhere into Colorado on all wild and cultivated cruciferous plants. In northeastern England and eastern Scotland the incidence of a cabbage moth outbreak was observed in 1958 by French and White (1960). They suspected that an easterly wind blew swarms of this species from central Russia to England and other Europen countries. Johnson (1966) noted that this invasion entailed continuous flights of about 3,200 km for several days.

Diapause

The occurrence of diapause of the cabbage moth to survive extreme conditions is controversial. In temperate regions where growers do not plant cruciferous vegetables throughout the year, the cabbage moth pupae and/or adults are believed to hibernate or to diapause in host plant debris through the winter season. In tropical and subtropical regions where host plants are available throughout the year, the cabbage moth is found anytime. Talekar and Shelton (1993) presumed that in temperate regions, where the cabbage moth becomes an insect pest, overwintering does not occur. Immigration can take place by adult movements by wind flows or other stages of the pest on transported plant materials. Harcourt (1957) noticed that during the winter months in southern areas

of North America, *P. xylostella* propagates continuously, but in northern regions the adults hibernate looking for shelter on crop remnants in the field.

Marsh (1917) observed a seasonal history of this insect at Rocky Ford, Colorado. It had seven generation in a year. The adults sought protection throughout winter to hibernate among crop debris or dead cabbage plant leaves. In the spring after a snowy winter the moths were more numerous than after a dry winter. Consequently, snow gave protection to the cabbage moth in hibernation. In concealment, they commonly stayed motionless, except on warm winter days when the moths initiated short flights especially when disrupted. They emerged from hibernation in May, flying to crucifer blossoms, usually wild watercress.

2.2.3 Control Measures

Insecticides

The cabbage moth is one of the major defoliators of crucifers. Since the caterpillars frequently feed on leaves of the vegetables, which commonly need a highly marketable standard, an effective control tactic is urgent and crucial. Most growers depend on utilisation of synthetic insecticides to produce the demanded quality of produce.

The desire for fast and easy methods of killing unwanted insects on cultivated plants has lastly given rise to overuse of chemicals. The use of chemicals to combat insect pests is still prevalent. Metcalf (1980) described the different phases of the successful applications of insecticides to limitations of their employment. In the USA, those are the era of optimism 1946-1962, the era of doubt 1962-1976, and the era of integrated pest management since 1976.

Era of optimism

During the era of optimism insecticides, particularly DDT, became powerful weapons to control insect pests in agriculture and in the house hold. For example, in New York and Wisconsin potato production rose 56 to 68 percent over the best harvests

previously achieved by spraying arsenate and Bordeaux mixture. Then, DDT became the successful chemical to control the codling moth *Laspeyresia pomonella,* invading deciduous fruits and the pink bollworm *Pectinophora gossypiella* on cotton plantation. For household use, DDT was also used to control insect pests on flowers and garden plant, carpet beetles, cloth moths, flies and mosquitoes (Metcalf, 1980).

Era of doubt

The accomplishments of insecticide usage for pest control on one side created criticism on the other side in response to negative effects that have arisen from excessive applications of chemicals. Carson in 1962 with her publication, "Silent Spring", described the presence of pollution in the whole environment as results of spraying poisonous chemicals for insect controls. This created conflicts between the social values of the public and the economic value of the chemical industry, and led to the era of doubt. Looking at the efficacy of insecticides in the age of pesticides, in the United States, production of insecticides dramatically increased from the 1920s to the 1970s. This coincided with the increased requirements due to the inclined crop damage. Higher crop injury during the pesticide age has been characterised by increased cultivation of more vulnerable cultivars, destruction of beneficial insects, decreased crop rotation, development of insect pest resistance, reduced tillage, lack of crop sanitation, and increased cosmetic values for crop quality (Metcalf, 1980).

Insect-pest resistance or tolerance to insecticides has been recognised for 80 years since it was originally observed in 1908 (Melander, 1914) in the San Jose scale (*Aspidiotus perniciosus*) selected by sprays of lime sulphur. Black scale *Saissetia oleae* and California red scale (*Aonidiella auranti*) were resistant to hydrogen cyanide in 1916 (Metcalf, 1955; Brown, 1971). By 1928 insecticide resistance was present in 5 species.

Growth of insect resistance to insecticides has then been documented: 7 species by 1938, 11 by 1946, 14 by 1948, 16 by 1951, 25 by 1954, 76 by 1957, 137 by 1960, 159 by

1963, 185 by 1965, 224 by 1967, 364 by 1975 (Georghiou and Taylor, 1977; Metcalf,

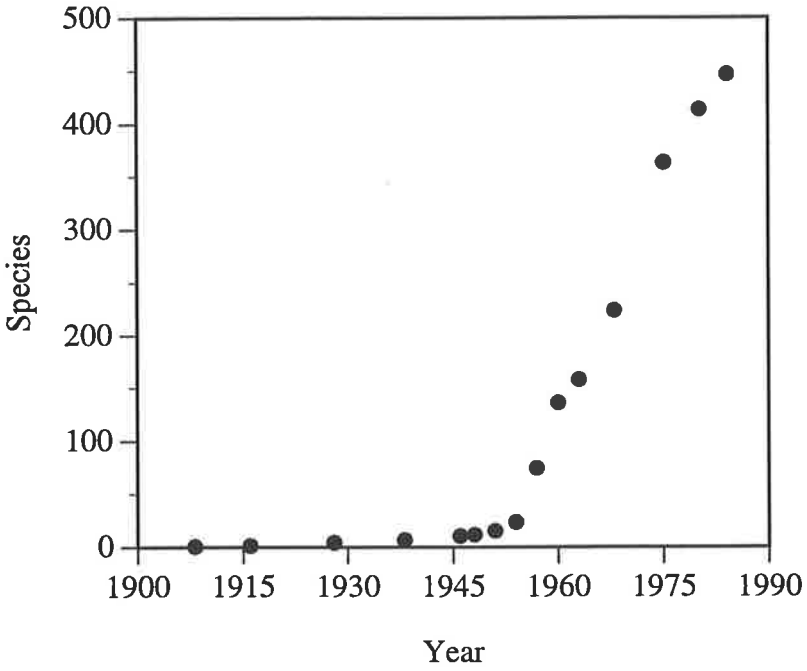

Figure 2.1. Increase in the number of insect species resistant to insecticides (after Davies and Doon, 1987; Georghiou and Taylor, 1977; Lever, 1990; Melander, 1914; Metcalf, 1980; Roush and McKenzie, 1987).

1980; Lever, 1990), 414 by 1980 (Davies and Doon, 1987), and still continued to incline to a level of 447 by 1984 (Roush and McKenzie, 1987). From around the 1940s, the incidence of insect pests resistant to insecticides appears to incline linearly (Figure 2.1). This shows that insecticide resistance in insect pests became a concern of scientific attention with the utilisation of organochlorine insecticides, particularly DDT. Studies in different countries indicated that this insecticide did not control resistant strains of the house fly (*Musca domestica*) in Denmark and Sweden in 1946, the mosquitoes *Aedes sollicitans* in Florida and *Culex pipiens* in Italy, and the human body louse *Pediculus corporis* in Japan and Korea in 1951 (Brown, 1971; Metcalf, 1955).

In fact, the illustration above does not sufficiently represent the impact of resistance. Cross resistance could take place in resistant species (Georghiou and Taylor, 1977). This makes the resistant individuals able to survive exposure to related insecticides. For instance, parathion-resistant species are not vulnerable to malathion, and lindane-resistant species are not vulnerable to dieldrin. Cross resistance is an outcome from target site insensitivity such as to acetylcholinesterase, or from a metabolic detoxification system. Furthermore, multiple resistance is likely to be more serious, due to many important insect pests becoming resistant to various groups of insecticides having distinctive modes of action and dissimilar detoxification pathways. Multiple resistant species are widely distributed in 43 families of nine orders (Metcalf, 1980). Georghiou (1972) noted that cross resistance limits the options for use of available insecticides, whereas multiple resistance mirrors the past history of insecticides selection and precludes a return to those chemicals applied previously.

The cabbage moth has a long history of becoming resistant to insecticides it was exposed extensively. In vegetable areas of Lembang (West Java), Indonesia, Ankersmit (1953) recorded the development of resistance in this pest to DDT, followed by its resistant to most other main classes of insecticides. In Malaysia, the cabbage moth has been resistant to all classes of conventional insecticides (Sudderuddin and Kok, 1978; Syed, 1992). Several authors have also noted the insecticide resistance of this pest from different countries such as the Philippines (Talekar and Shelton, 1992), Japan (Hama, 1992), Taiwan (Cheng *et al.*, 1992; Sun *et al.*, 1978), North America (Magaro and Edelson, 1990; Shelton and Wyman, 1992), South Australia (Keller, 1994) and another part of Australia (Talekar and Shelton, 1993). Multiple resistance has been documented by Georghiou and Taylor (1977).

Era of integrated pest management

Dependence on broad spectrum insecticides for insect pest control in the past did not result in an effective strategy. The economic impact of chemical pest control, comprising the increasing costs of insecticides due to dramatic increases in the expenses of developing new chemical insecticides, makes it crucial to go back from extensive routine uses to a policy of judicious application when necessary (Metcalf, 1982; Ruscoe, 1977). Besides the combined effects of pest resistance, pest resurgence, and outbreaks of secondary pests require pest control strategies that are dominated by chemicals (Luck *et al.* 1977). And lastly, short-term and long term damage as a result of careless application of persistent insecticides and the negative influence of insecticide usage can be only resolved by dramatic alterations in both quality and quantity of insecticides applied in agriculture (Davies and Doon, 1987; Metcalf, 1982).

The overuse, misuse, and unnecessary use of chemical insecticides have become important factors in the quick emergence of interest in insect pest management strategies or IPM as an ecological approach. This concept does not tolerate the exclusive use of broad spectrum and insecticides. Instead, in practice the use of chemicals as a component of IPM must be selective and wise. In other words, insecticides should be managed economically, safely, and efficiently from manufacture to utilisation and disposal. (Metcalf, 1982). Therefore, practical management of insecticide use is necessary. To counter or prevent pesticide resistance, Denholm and Rowland (1992) suggest a rational use of existing products, developing and optimally using new products, and generally reducing dependence on pesticides.

Cultural control

These methods have become alternative strategies where the use of insecticides failed to control the cabbage moth. Trap cropping, rotation, sprinkler irrigation, intercropping, and clean planting have been used as control measures for this pest.

Trap cropping

Plants grown outside of the main crops to attract insects or other organisms are trap crops. This technique aims to prevent pests from coming into the area of main crops or they concentrate in certain parts of the field where they can be economically destroyed (Hokkanen, 1991). Planting strips of a less important plant highly susceptible to the cabbage moth was a common practice in the past before the coming of modern synthetic insecticides. The preferred plants, particularly Indian mustard and white mustard, attracted the pest and protected commercial crops (cabbage, cauliflowers, broccoli, and others) from its invasion. This practice that became obsolete with the production of modern insecticides, recently has become a more acceptable alternative particularly in developing countries (Talekar and Shelton, 1993), as the cabbage moth becomes resistance to all types of insecticides (Denholm and Rowland, 1992).

Rotation

Routine cultivation of crucifers causes continuous propagation of cabbage moths. This ultimately leads to frequent use of insecticides and the emergence of insecticide resistance. In such conditions, crop rotation may provide interruption of pest proliferation. However, it is scarcely applied for the control of the pest population in the intensive crucifer growing areas of the tropics and subtropics due to practical requirements involving high cost (Talekar and Shelton, 1993).

Sprinkler irrigation

Abiotic factors, for example rain fall, can affect the mortality of cabbage moth larvae of all instars except the first instar on crucifer leaves, which is why the pest is troublesome in dry seasons. Sprinkler irrigation for five minutes at dusk on alternate days over the first three to four weeks, and every day afterwards, significantly decreased

cabbage moth infestation (Talekar *et al.*, 1986). The treatment probably disturbed the flying activity and oviposition, and washed the larvae off on leaves.

Intercropping

The practice of planting two or more crops together in the same area is known as intercropping. In the tropics growers commonly use this method, especially in small scale farming and where land is intensively cultivated every season. Plant diversity in intercropping acts as a physical hindrance for pest movements (Risch, 1981; Sheehan, 1986). Disruption of chemical or visual stimuli between pests and their host plants, or/and abundance of natural enemies may result in reduction of pest populations. The earliest success was reported from Russia where intercropping cabbage with tomato decreased the yield loss of cabbage by some destructive pests including the cabbage moth (Talekar and Shelton, 1993). But, it just gave small improvement in other countries such as the Philippines, India, and Taiwan (Chelliah and Srinivasan, 1986; The Asian Vegetable Research and Development Center. 1987; Magallona, 1986).

Clean planting

Talekar and Shelton (1993) suggested that an easy and efficient management practice is planting seedbeds before transplanting away from production areas, and plowing crop residues in production areas and seedlings.

Sex pheromones

The unwanted side effects of insecticide usage make sex pheromones another alternative for the management of the cabbage moth. Chow *et al.* (1974) initially isolated the female sex pheromone of the cabbage moth in Taiwan. Components of the pheromone are (Z)-11-hexadecenal (Z-11-16:Ald), (Z)-11-hexadecenyl acetate (Z-11-16:OAc), and (Z)-11-hecadecenyl alcohol (Z-11-16:OH) (Chisholm *et al.*, 1979; Tamaki *et al.*, 1977;

Maa, 1986). To date sex pheromones have been produced synthetically for commercial use to suppress pest populations through either communication disturbance between the sexes or adult male-trapping (Nemoto *et al.*, 1992). Chow (1992) tested the synthetic sex pheromone and its analogues on the cabbage moth. The results indicated that five mg and 50 mg of sex pheromone (Z-11-16:Ald, Z-11-16: Ac, and Z-11-16: OH in the ratio of 5:5:0.1), five mg and 10 mg of Z-9-14: Ac, and one mg and 10 mg of Z-11-16: disrupted the pest in the field. Cabbage moth males are actively attracted to pheromone traps at a distance between zero and 6.3 m. Baker *et al.* (1982) studied the potential of pheromone traps to monitor the cabbage moth in the field condition in New York during 1979 to 1980. They noted that adult catches related to the subsequent larval population occurring 11 to 21 days later. Japan now produces a commercial sex pheromone trap for the cabbage moth. Its name is Konaga-Con and is baited with a 1:1 mixture of Z-11-16:Ald and Z-11-16:OAc (Ohbayashi, 1992). Talekar and Shelton (1992) suggested that the use of sex pheromone may provide a good promise when applied in combination with augmentation and conservation of natural enemies.

Plant Resistance

One of the important components of an insect pest management program is the use of resistant or tolerant varieties. Some researchers have studied varietal resistance to insect attack including the cabbage moth in crucifers (Pimentel, 1961; Radcliffe and Chapman, 1966; Shelton *et al.*, 1988). By screening 43 cruciferous varieties, Pimentel (1961) found that one variety of kohlrabi, three varieties of turnip, and one variety of mustard proved more resistant to larval *P. xylostella* than the others.

A glossy-leaved cauliflower from Australia, P1234599, is reported to be resistant to the cabbage moth in the field. Most resistant plants possess glossy leaves and this glossy leaf feature is inherited as a simple recessive character. The heritability of resistance to damage by lepidopterous pests was as high as much as 85% of the total variance resulted

in genetic effect. Selected cauliflower and cabbage lines from P1234599 were highly resistant to the cabbage moth and other lepidopterous pests when they were tested at the New York State Agricultural Experiment Station, Geneva (Dickson *et al.*, 1986). At the same station, Eigenbrode *et al.* (1990) identified two types of resistance to this pest in cabbage: 1) antibiosis or nonpreference due to extractable polar ethanol-soluble compounds existing in normal bloom resistant cabbage lines, 2503 and 2535; and 2) possible nonpreference for glossy-leafed 2518 in neonate larvae. The resistant lines 2503 and 2535, which have active compounds polar that are extractable in ethanol, may produce toxins. Thus, they physiologically cause antibiosis, or as antifeedants reduce the feeding and survival of larvae. Neonate larvae of the cabbage moth move faster on a glossy line of cabbage derived from P1234599 than on host plants with normal wax.

The relationship between insect resistance and the glossiness of the leaf surface has been observed by Stone (1990). Only the four glossy lines were found to have consistent low numbers of *P. xylostella* larvae at different localities. Astonishingly, a glossy line of kale with allelic genes for glossiness from P11234599 displayed poor resistance to this insect pest.

Biological Control

Biological control takes place when natural enemies such as predators, parasitoids, or pathogens continually or temporarily regulate a prey or host population at densities below what they would be in their absence. In nature, biological control occurs without manipulation by man and this is termed naturally biological control. If man acts to manipulate the natural enemies, the pest population, or others within the environment to accomplish reduction of pest population numbers, this is referred to as applied biological control (Huffaker and Smith, 1980). Smith (1919) first used the term biological control to describe the introduction of exotic natural enemies for the suppression of insect pests. Nevertheless, it was first applied long before its definition (Waage and Greathead, 1988).

In broader meaning, there are other biological methods or non-chemical approaches to pest management, namely the use of plant resistance to pests, cultural methods or habitat modification (cultivation, planting time, harvesting, sanitation, irrigation and water management, and rotation), genetic methods (autocidal control or sterile male technique), and the use of pheromones (DeBach and Rosen, 1991). Here, however, the term biological control is restricted to the utilisation of natural enemies with emphasis on parasitoids and predators.

In practice, biological control to date includes several methods such as introduction, augmentation and conservation of natural enemies (DeBach, 1964; Dent, 1991; Waage and Greathead, 1988).

Natural enemies, especially many parasitoids and predators, attack cabbage moth in all stages. The adults are often eaten by polyphagous predators such as spiders and birds. Other predators include staphylinid beetles, *Polistes* wasps, syrphid fly larvae, chrysopid and hemerobiid larvae, and an anthocorid bug (Talekar and Shelton, 1993). The hoverfly larvae, *Melanostoma fasciatum* Macquart and *Melangyna novae-zelandiae* Macquart (Diptera: Syrphidae), prey on the early-instars of *Plutella* (Wratten *et al.*, 1995). Parasitoids generally attack egg, larval and pupal stages of this pest. The majority of parasitoid species have originated from Europe where the pest, cabbage moth, is believed to have evolved. Among them, numerous larval parasitoids are the most predominant and effective (Waterhouse and Norris, 1987).

Use of microoraganisms

Work on the application of microorganisms for the control of cabbage moth has been undertaken in some countries too. In practice the bacterium *Bacillus thuringiensis* is effective against the pest in India, Malaysia, Indonesia, Thailand, Canada, Western Samoa and Australia (Brunner and Stevens, 1986; Waterhouse and Norris, 1987). The fungus *Beauveria bassiana* (produced in the USSR with the trade name 'Boverin') was

effective against the cabbage moth on brassicaceous vegetables in USA (Ignoffo *et al.*, 1979) and *Beauveria brongniartii* is used in France (Fargues *et al.*, 1979; Robert and Marchal, 1980). Other fungi such as *Entomophthora sphaerosperma* (=*radicans*), *Metarhizium anisopliae*, *Paecilomyces fumoso-roseus*, *Erynia blunckii* and *Zoophthora radicans* are infective pathogens for cabbage moth in experimental tests or in the field as the humidity increases and showers of rain are apparent (Muggeridge, 1930; Robertson, 1939; Robert and Marchal, 1980; Tomiyama and Aoki, 1982; Ullyet and Schonken, 1940). Polyhedrosis, nucleopolyhedrosis and granulosis viruses also infect cabbage moth larvae (Wilding, 1986).

Use of parasitoids

High rates of parasitism by parasitoids maintain low populations of the cabbage moth in Holland, South Africa (Vos, 1953), New Zealand (Todd, 1959), parts of Australia (Wilson, 1960), England (Hardy, 1938), California (Oatman and Platner, 1969) and Cape Verde Islands (Cock, 1983).

In many European countries the wasps *Diadegma semiclausum* and *D. fenestralis* are dominant and parasitise up to 80% of cabbage moth caterpillars (Hardy, 1938). *Protomicroplitis claritibia* attacks this insect pest in Hungary. In Belgrade, the most abundant parasitoid is *Diadegma semiclausum*, followed by *Pimpla* (=*Itoplectis*) *alternans*, *Diadromus collaris* and *D. subtilicornis*. Parasitoids affecting cabbage moth populations in the Turgai region, USSR, are *Diadegma fenestralis*, *D. semiclausum*, *Cotesia plutellae* and *Diadromus subtilicornis*. The first two are the most important, killing up to 30% of the pest population. The principal parasitoid in the Moskow area is *Diadegma semiclausum*. In eastern USSR the major parasitoids are *Diadegma semiclausum* and *Diadromus* sp., which actively parasitise the hosts in the early part of summer and cause mortality up to 90% (Waterhouse and Norris, 1987). In Moldavia, Romania, 25 parasitoids are found and parasitism reaches 80-90% (Mustata, 1992).

The cabbage moth population in South Africa is maintained for most of the time under natural control, although outbreaks may occasionally be more or less seriously damaging. There are at least 14 larval and pupal parasitoids, including the wasps and a tachinid fly, and hyperparasitoids are also present (Waterhouse and Norris, 1987).

The most important parasitoid recorded in Eastern Ontario, Canada, is *Diadegma insulare* which causes an average of 33% mortality on host larvae and 21% mortality on prepupae. The parasitoid *Diadromus subtilicornis* parasitises 19% of pupae. The braconid *Lissogaster* (=*Microgaster*) *plutellae* kills 10% of all final instar larvae. Less important parasitoids of the cabbage moth are the ichneumonids *Gelis tenellus* and *Campoletis* sp., the chalcidid *Spilochalcis albifrons*, and the pteromalids *Dibrachys cavus* and *Pteromalus* (=*Habrocytus*) *phycidis,* and the eulophid *Tetrastichus* (=*Oomyzus*) *sokolowskii*. The pteromalid *Trichomalopsis* (=*Eupteromalus*) *viridescens* is a hyperparasitoid that attacks *Diadegma insulare* (Harcourt, 1986; Waterhouse and Norris, 1987).

In Florida 32% of the larval cabbage moth sampled was parasitised by *D. insulare* and *T. sokolowskii* (Ru and Workman, 1979). The parasitoids *Diadegma insulare* and *Lissogaster plutellae* are dominant in Georgia, USA. The braconid *Cotesia plutellae* was introduced to Trinidad from Barbados and within six months it parasitised over 50% of *P. xylostella* larvae. And in Hawaii, *D. insulare* is common and effectively controls the pest in cooler weather (Waterhouse and Norris, 1987).

In 1970, the parasitoid *C. plutellae* was introduced from India to the Caribbean countries of Grenada, St. Vincent, St. Lucia, Dominica, Antigua, Montserrat, St. Kitts-Nevis, Belize, Trinidad, Barbados and Jamaica. The parasitoid has been recovered at some of those release sites, but it did not control cabbage moth. Another species, *Apanteles vestalis* Haliday was obtained from Netherlands in 1971 but no recovery survey was conducted after release. Other introduced wasps are *Diadegma* spp. and *Diadromus* (=*Thyraeella*) *collaris* (Bennett and Yaseen, 1972). Reintroduction of *C. plutellae* in early 1989 in Jamaica resulted in its establishment; it increasingly parasitised from 5.4% in the

first generation after introduction to 88.7% by March 1990. As a result, plant damage reduced from 75% before introduction to 38% in 1990 (Alam, 1992).

In Gujarat, India, five parasitoids were reared from cabbage moth larvae, of which *Bracon* sp., *B. gelechiae* and *Mesochorus* sp. revealed maximum parasitism rates of 11. 4, 13.8 and 8.3% respectively. However, the major parasitoid was *C. plutellae* reaching up to 71.7% parasitism (Yadav *et al.*, 1979).

The cabbage moth has been a serious pest of crucifers in Taiwan since the 1960s (Chen and Su, 1986). The parasitoid *C. plutellae*, reported to parasitise cabbage moth caterpillars since 1972, only provided a little control. Then, *Diadegma semiclausum* was imported from Indonesia and liberated in the low land crucifer-growing regions in 1985; but, it was not established (Talekar and Shelton, 1993; The Asian Vegetable Research and Development Center, 1986). As broad-spectrum insecticides were replaced by a microbial insecticide, *Bacillus thuringiensis* or BT, *C. plutellae* became effective in controlling the pest; yet *D. semiclausum* did not give an adequate control (Talekar, 1988). However, when *D. semiclausum* was released in the highlands, it parasitised more than 70% in one season (The Asian Vegetable Research and Development Center, 1988). By now, this parasitoid is widespread throughout the highland areas of Central Taiwan (Talekar, 1992; Talekar *et al.*, 1990).

The cabbage moth is a major pest of crucifers in the Cameron Highlands of Malaysia, where the crops are grown all year round. In this country the pest has been recorded since 1925. The first reported parasitoid, *Cotesia plutellae*, was commonly encountered in 1970s. The second one is *Tetrastichus ayyari* Rohw (Hymenoptera: Eulophidae) attacking cabbage moth pupae. An unidentified chalcid and the fungus *Entomopthora sphaerosperma* Fres. also parasitise it. Syrphid larvae feed on the caterpillars (Ooi and Kelderman, 1977; Ooi, 1979a). Due to inadequate control level of cabbage moth, four parasitoids were introduced, the ichneumonids *Diadegma semiclausum*, *Diadromus collaris* and *Macromalon orientale* and the eulophid

Tetrastichus sokolowskii. In 1977-1978 cabbage moth parasitoids were evaluated in the field, *C. plutellae*: 11.7%, *D. collaris*: 8.9%, *D. semiclausum*: 3.0% and *T. sokolowskii*: 0.03%. However, in 1984 rates of parasitism reduced, the values being 4.80, 0.07, 0.04 and 0.00%, respectively (Chua and Ooi, 1986). Since insecticides were still effective, growers carried on using them intensively. The excessive use of chemicals and the presence of hyperparasitoids kept parasitoid populations very low (Lim, 1986). Toward the end of 1980s, cabbage moths developed resistance to practically all synthetic insecticides. Officials in Singapore, the main market for vegetables grown in Cameron Highlands, refused cabbage containing high insecticide residues. This forced farmers to begin employing *Bacillus thuringiensis*, resulting in an increase of parasitoid populations and decreased cabbage moth invasion (Ooi, 1992).

Cabbage moth is a destructive pest on brassicas in all mountain areas in Indonesia (Sastrosiswojo and Sastrodihardjo, 1986). Attempts to implement biological control of this pest by introduction of exotic natural enemies were begun in the 1920s. In 1928, Leefmans imported the ichneumonid *Diadegma* (=*Angitia*) *fenestralis* Holmg. from Netherlands to Indonesia, but it was not established in labratory rearing. In 1950, Vos introduced another ichneumonid parasitoid *Diadegma semiclausum* (=*Angitia cerophaga* Grav.), closely related to the previous wasp, from New Zealand to Indonesia. This was more successful and the parasitoid became established as a biological agent (Vos, 1953). Surveys in West Java and other locations showed that this wasp gave very high parasitism (up to about 80%). But, in some areas where people sprayed insecticides frequently, the cabbage moth population was still abundant (Sastrosiswojo and Sastrodihardjo, 1986; Sudarwohadi and Eveleens, 1977).

In the highland areas of northern Philipinnes, the release of *Diadegma semiclausum* early in the growing season in 1989 gave 64% parasitism of cabbage moth larvae (Poelking, 1992). *Cotesia plutellae* in this country has a hyperparasitoid *Trichomalopsis*

sp. and two other unidentified parasitoids of cabbage moth larvae are also found (Waterhouse and Norris, 1987).

Two egg parasitoids of cabbage moth, *Trichogramma japonicum* and *T. chilonis*, are encountered in Vietnam. They parasitised up to 45.5% of their hosts (Waterhouse and Norris, 1987).

The Commonwealth Institute of Biological Control (CIBC) Indian Station shipped several parasitoids of cabbage moth to Hong Kong during 1968. They were larval parasitoids *C. plutellae*, *Macromalon orientale* Kerr. and *Nytobia* sp., and pupal parasitoids *Tetrastichus sokolowskii* Kurjumov and *Diadromus collaris*. There was no indication of establishment of *M. orientale* and *T. sokolowskii* after field release (Rao *et al.*, 1971).

In 1965, Thailand introduced *C. plutellae*, *M. orientale*, *D. collaris* and the chalcidid *Brachimeria* sp. from India by CIBC Indian Station. However, these wasps could not be bred in the laboratory and seemingly no field releases were carried out (Rao *et al.*, 1971).

An ichneumonid *D. collaris*, recognised as a larval-pupal parasitoid of cabbage moth, was introduced into Ceylon (Sri Lanka) from India during 1965. Unfortunately breeding of the wasp in the laboratory was difficult (Rao *et al.*, 1971; Oatman, 1978).

Three native parasitoids were found in New Zealand during field collection of the cabbage moth from 1934 to 1937; namely *Diadegma* (=*Angitia*) sp., *Eupteromalus* sp. and *Diadromus* sp., and *Diadegma* was very common, but rates of parasitism were low (Robertson, 1939). So, efforts to introduce other cabbage moth parasitoids were made from 1936 to 1941. Among them, importations of *Diadegma semiclausum* from England in 1936-1937 and *Diadromus collaris* from Holland in 1937-1939 into New Zealand resulted in the establishment of these wasps (Hardy, 1938; Thomas and Ferguson, 1989).

In each Australian state *P. xylostella* has been a serious pest since late last century. Biological control of this insect pest has been attempted by introduction of unidentified

parasitoids into Western Australia in the early years in this century. One of these was probably *Diadegma* (=*Hymenobosmina*) *rapi* Cam. introduced from New South Wales, that is now commonly found in both Western and Eastern Australia (Table 2.1). In 1928 *Trichogramma minutum* released against *Cydia pomonella* L. by the Queensland Department of Agriculture and Stock was reported also to parasitise the cabbage moth in the laboratory; however no recovery from the cabbage moth in the field was observed. *Diadegma fenestralis* was released in New South Wales, Victoria and South Australia, whereas the others were released in large numbers in all states (Wilson, 1960).

Diadromus collaris is at least established in New South Wales, Queensland, Victoria and Tasmania. The wasp *Cotesia plutellae* has been established in Queensland, New South Wales and the Australian Capital Territory (Wilson, 1960).

In New South Wales *Plutella xylostella* grows well in dry and hot areas and is more important inland than on the coast. The host density generally increases in late summer and obviously decreases in winter. *Cotesia plutellae*, *Diadegma rapi*, *D. semiclausum* and *Diadromus collaris* have become established (Helly *et al.*, 1982). Observations in 1971 and 1972 close to Sydney showed that *Diadegma semiclausum* and *D. rapi* parasitised the hosts up to 41%, *Diadromus collaris* 25% and *Apanteles ippeus* 12%. In

Table 2.1. Introductions of parasitoids for biological control of cabbage moth in Australia (Wilson, 1960).

State and species	Introduced	Released	Source	Result
Western Australia				
2 parasitoids				
(1 probably				
Diadegma rapi)	1902	1902	New South Wales	Established
2 parasitoids	1903	1903	Spain	Established
1 parasitoid	1907	1907	Sri Lanka	Not established
1 parasitoid	1908	1908	India	Established
1 parasitoid	1909	1909	China	Not established
Many states				
*Diadegma fenestralis**	1936	No release	England	-
	1938	1938-39	New Zealand	Not established
Diadegma semiclausum	1946-47	1947-51	New Zealand	Established
*Diadegma tibialis**	1951	1951-52	Italy	?
Diadromus collaris	1947	1947-51	New Zealand	Established
	1951	1951-52	Italy	Established
Cotesia plutellae	1951	1951-55	Italy	Established
Tasmania				
Diadegma semiclausum	1947	1947	New Zealand	Established
Diadromus collaris	1947	1947	New Zealand	Established

* There is some uncertainty regarding the identification of these species and perhaps the wasps have been *Diadegma semiclausum*.

rearing, a small number of the chalcidid *Brachymeria phya* and an unidentified chalcidid were found as well (Waterhouse and Norris, 1987).

Nine species of parasitoids attacking the cabbage moth were recorded near Melbourne, Victoria, between 1972 and 1974 (Goodwin, 1979). *Diadegma semiclausum*, *D. rapi* and *Diadromus collaris* were the most important wasps, whereas the less important ones were *Apanteles* sp., *Spinolia* ap., *Stictopisthus* sp., *Antrocephalus* sp., *Eupteromalus* sp. and *Brachymeria* sp. There was also a hyperparasitoid *Trichomalopsis* sp. As the density of hosts was high, *D. semiclausum* seemed to be the most effective in reducing the pest population. At low host density, the mortality of the pest caused by each of three main parasitoids was somewhat equivalent and constituted 75 - 87% of the total mortality. Subsequently *Diadromus collaris* and *D. rapi* were in the second and third ranks, respectively. *Apanteles* sp and *Stictopisthus* sp caused 2.5% and 1.4% parasitism, however, they were still important on some occasions. A record was also made of the native chalcidid *Brachymeria phya* parasitising *P. xylostella* in Victoria (Cordingley and Danthanarayana, 1976).

The major parasitoids in Queensland are *Diadegma semiclausum* and *Diadromus collaris*, resulting in an average of parasitism of 29.0% and 2.4% respectively. Other parasitoids, *Brachymeria phya*, *B. sidnica* and *Apanteles ippeus* are less important, together causing approximately 2.5% parasitism. Three hyperparasitoids are recorded as well, *Aphanogmus fijiensis*, *Lienella* sp. and *Trichomalopsis* sp. (Yarrow, 1970).

Four wasps are recorded to encourage biological control of *P. xylostella* in Tasmania. These species are *D. semiclausum* and *D. rapi* which in late summer achieved 48% of parasitism, *Diadromus collaris* and *Cotesia plutellae*. Early in the season the existing parasitoids are able to reduce cabbage moth density. But, late in the season they fail to control the pest, especially when insecticides are intensively applied at the field. In this state the pest rarely causes serious damage in rapeseed crops (Russell, 1980).

Other parts of the world also have cabbage moth parasitoids either native or introduced, wherever crufiers are grown. However, only a few of them are reported as becoming established depending on the localitiy. At least four species of parasitoids are most important in reduction of pest populations, namely *Cotesia plutellae*, *Diadegma semiclausum*, *Diadromus collaris* and *Tetrastichus sokolowskii* (Waterhouse and Norris, 1987).

Integrated pest management

Integrated pest management (IPM) is defined as a combination of compatible control techniques and all available ecologically sound agricultural management strategies into a unified program to maintain pest populations below an economically damaging level (Hassan, 1986), whilst adverse side effects on humans, animals, plants and the environment are minimised (Luckmann and Metcalf, 1982).

Many recent products of synthetic organic insecticides available in markets have given good control of some formerly damaging pests. However, a heavy dependence on chemicals has led to repeated applications causing secondary problems such as resistance of insect pests to insecticides, emergence of pest populations, outbreaks of secondary pests, hazards to beneficial insects and non target organisms, and environmental contamination. Incidences of resistance are a serious problem, although these have been overcome so far by the use of new products (Hassan, 1986; Metcalf, 1982). Integrated pest management does not attempt to eliminate the use of insecticides, for they are an important tool in crop protection, particularly when other techniques are ineffective. The major interest of IPM is to develop pest control measures maximising the advantages of insecticides and minimising their disadvantages. In other words, IPM is a method which amalgamates chemicals, cultural, biological and any other means that will assure ecological, economical and social benefits.

Growers have intensively used insecticides for the control of cabbage moth for the past 30 years or more (Talekar and Shelton, 1993). The emergence of resistance to recently available insecticides and lack of new ones has stimulated investigations of alternative pest controls. Since parasitoids are important agents for biological control of *P. xylostella*, release and conservation of parasitoids will become essential to any sustainable IPM program. Coordination amongst farmers is crucial to implement IPM, since the practices done of one of them affects others. A successful attempt through such coordination was the establishment of *D. semiclausum* in the highlands of Taiwan, the Philipinnes, and Indonesia and the conservation of the parasitoid with *B. thuringiensis* (Poelking, 1992; Sastrosiswojo and Sastrodihardjo, 1986; Talekar, 1992). Another cabbage moth parasitoid, *C. plutellae*, is mainly established in lowland areas in Taiwan as reported by Talekar and Yang (1991).

Monitoring by sampling pest populations and treatment if the economic threshold is surpassed is basic to IPM. This has been promoted in many developing countries in the tropics (Chelliah and Srinivasan, 1986; Chen and Su, 1986; Loke *et al.*, 1992; Rushtapakornchai *et al.*, 1992) and in developed countries (Cartwright *et al.*, 1987; Hoy *et al.*, 1983; Sears *et al.*, 1985; Shelton *et al.*, 1982). Talekar and Shelton (1993) stated a skilled person is needed toeffectively carry out regular scouting of insects in the field. In developing countries, adoption of IPM is deterred since many growers cannot differentiate destructive and beneficial insects, and resistance to multiple insecticides caused these chemical applications to be useless. Therefore, the release and establishment of parasitoids and the use of cultural practices are very important to the success of IPM in the tropics and subtropics.

2.3. Role of parasitoids in insect pest management

2.3.1. Introduction

All insect pests have natural enemies that attack their various life stages (Stehr, 1982). One group of natural enemies is the parasitoids which may feed on their hosts externally (ectoparasitoids) or internally (endoparasitoids). The impact of parasitoids ranges from a temporary effect to paralysis or most often death of the host. They may parasitise a host at any stage. Parasitoids that find the host in early developmental stages are usually better biological control agents than those which parasitise later, because the host may be killed, or because parasitised larvae often feed less than healthy ones so that crop damage is less as well. However, in some cases parasitisation gives an adverse effect on the parasitised host. One parasitoid of the cabbage looper, *Trichoplusia ni* causes its host larvae to consume more food than unparasitised larvae Hunter and Stoner (1975). Such a parasitoid would not be a good candidate for mass releases of any sort, since greater damage may be the result. This confirms the requirement of knowing about as many of the interactions as possible to design a successful insect pest management strategy.

Parasitoids that directly attack the host are called primary parasitoids. These are regarded as beneficial organisms, with the exception being parasitoids of phytophagous insects applied for the biological control of weeds. In biological control of weeds everything is reversed; the plant is the pest and the phytophagous insect is beneficial. Parasitoids also possess natural enemies; they are secondary parasitoids or 'hyperparasitoids' if they attack primary parasitoids, and tertiary if they attack secondary parasitoids. Secondary parasitoids are generally categorised as harmful in IPM as they reduce the efficacy of primary parasitoids. Tertiary parasitoids are unusual, but they could be beneficial to control hyperparasitoids (Askew, 1971).

Hyperparasitoids seem to be able to detect the odour left by a primary parasitoids. Some insects are 'facultative' hyperparasitoids, attacking a healthy host or another parasitoid with equal readiness (Hassell and Godfray, 1992), whereas others are 'obligate' attacking only primary parasitoids (Gullan and Cranston, 1994). Many parasitoid species of the family Aphelinidae have females that develop as normal endoparasitoids of scale insects, while the males develop as hyperparasitoids of females; these are known as 'heteronomous' hyperparasitoids (Hassell and Godfray, 1992).

Interactions between insect pests and their natural enemies including parasitoids are fundamental ecological processes that furnish the regulation of some insect populations. Populations of insects may blow up when introduced into new geographic areas without having natural enemies or when insecticides destroy natural enemies (Dent, 1991; Price, 1987). The dissociation between insects and their parasitoids can cause the insects to become pests, because a habitat modification such as a monoculture favours the pest. Thus, the use of parasitoids in a pest management program is mainly aimed at remedying the imbalance which has taken place through the dissociation of the two species, either by releasing parasitoids into the system or by creating conditions to conserve and enhance an association.

2.3.2. Utilisation of parasitoids

The use of biological agents, either parasitoids, predators, or pathogens for pest control, has several advantages over other control methods.Biological control can be relatively safe, economical and permanent. The disadvantage is that it requires a long time to set up a biological control program (Stehr, 1982).

The safe use of biological control is possible, because many natural enemies are host specific or limited to a few closely related species. Thus, it is unlikely that non target species will be influenced. Biological control is also economical, because once natural enemies (both native and introduced) are present, little additional work must be carried

out. Biological control is relatively permanent, since it only controls specific organisms and does not to eradicate any species. Once efficient natural enemies are established, they frequently continue to have an impact year after year with no or little assistance by man (Stehr, 1982).

Effective natural enemies are ones that possess 1) a high searching ability, 2) a high degree of host specifity, 3) a high reproductive rate, 4) a good synchronisation with the host and 5) a high degree of adaptability to a broad range of ecoclimatic conditions. Hence a parasitoid that has these characteristics would prevent the host from exceeding the economic injury level (Pschorn-Walcher, 1977). Stehr (1982) concluded that, from the view point of pest management, such a parasitoid is ideal, because additional management is unnecessary to maintain the pest below a damaging level. However, no such potential natural enemies have been found for many pest species; hence the integration of two or more management techniques are required to keep these pests below the economic injury level.

In the field of biological control, utilisation of parasitoids includes importation or introduction, augmentation, and conservation for the regulation of other organisms (DeBach, 1964). Basic studies are also crucial in biological control before the implementation of parasitoid releases. These studies comprise pure research into essential aspects of taxonomy, biology, physiology, genetics, ecology and demography, nutrition, culture methods, and behaviour.

2.3.3. Classical biological control

The term introduction is employed to cover all phases about importation and establishment of exotic parasitoids into a new environment. Many agricultural pests have been accidentally introduced intonew areas, while their natural enemies have been left behind (DeBach, 1964). The introduction of exotic natural enemies to reduce insect pest

populations to a level at which the pest no longer causes economical damage is often called classical biological control (Waage and Barlow, 1993).

Events in classical biological control

The execution of classical biological control involves 12 steps (Pschorn-Walcher, 1977). These are 1) planning and logistic aspects of the project, 2) evaluation of available information, 3) selection of suitable test areas, 4) inventory of natural enemies, 5) research on the role of biotic mortality factors, 6) research of the structure of the natural enemy complex, 7) bioecological studies of individual species, 8) establishment of priorities in importation of species for ultimate propagation, 9) choice of suitable release locations, 10) release and monitoring of population build-up and spread of the natural enemy, 11) colonisation over whole region of pest infestation, and 12) final evaluation of project.

Waage and Barlow (1993) emphasize the importance of quarantine for exotic natural enemies before releases. For parasitoids, this involve removals of any hyperparasitoids, plant pathogens and insect pathogens from the culture.

Once an insect has been identified as an exotic pest, a review of literature would be conducted to find out as much as possible about the pest, its origin and its indigenous natural enemies (van den Bosch and Messenger, 1973). Cosiderable information about pests and their natural enemies can be obtained through the literature and correspondence, but generally foreign exploration is needed and desirable in order to a thorough knowledge of the natural enemy complex (DeBach, 1974). First, it is necessary to find the location where the pest is endemic and verify it taxonomically to avoid misidentification. Secondly, an investigation of the natural enemy complex may commence. Field exploration is crucial in this context since the interaction between natural enemies and their host can be precisely evaluated under natural conditions. Competition between guilds of parasitoids may occur through an overlap in resource use, for example a larval

parasitoid emerging from a host pupa may interfere with a pupal parasitoid. It is only via field studies that one can gain an understanding of hierarchies within and among guilds (Pschorn-Walcher, 1977 The degree of synchronisation between the natural enemy and the host, physiological tolerance, host-specificity, as well as genetic variability of natural enemy species should be determined. Collecting natural enemies from different areas is important to obtained individuals with a broad range of physiological tolerances or adaptations, though there is always the risk that these may turn out to be host or biogeographical races (DeBach, 1974).

Culturing and mass production

Culturing and mass production of imported species are important aspects of every classical biocontrol program, since sufficient numbers of individuals are required to make release and establishment achievable (Morrison and King, 1977; Dent, 1991). It is, however, a complex task and every species will necessarily be reared for at least one generation to ensure hyperparasitoids are eliminated in a quarantine. Quarantine only restricts the number of sampled insects and it is seemingly impossible to examine and keep large numbers. Hence, the process tends to limit sample size and genetic variability. Sample sizes and genetic variability may also be restrained in other ways during the process of introduction (Messenger and van den Bosch, 1971). Culturing needs the simultaneous rearing of the host insect, its associated plant host and the natural enemy. A break in the sequence of rearing could lead to loss of the natural enemy species (Dent, 1991).

Release and establishment

Prior to release, it is necessary to ensure the target pest is present in sufficient numbers at different release sites at an appropriate life stages. Also, one must ensure that ensure that: conditions at each release site are optimal for establishment, an adequate

number of natural enemies is available for release; an appropriate number of such releases is made; and several release sites over the ecological and geographical range of the pest are utulised (van den Bosch and Messenger, 1973).

Establishment may beprecluded if insecticides are applied at the release site or in the surrounding areas. If these chemicals have to be sprayed in the vicinity, then pre-introduction studies should involve work on the insecticide selectivity and their application delayed in the immediate area and period after release. Other attributes of the site such as the presence of secondary hosts, if multivoltine parasitoids are liberated against a univoltine pest, and adult food availability may affect the success of establishment. The presence of hyperparasitoids may also reduce the effectiveness of natural enemies (Dent, 1991). The possibility of establishment may be influenced by the number of individuals liberated on a single occasion. By an analysis of failure and success of introductions in Canada, Beirne (1975) suggested that release of large numbers of individuals may favour successful establishment. Releases of a total 5,000 individuals or less only resulted in 10% successful introduction. When introductions involved totals between 5,000 and 31,200 individuals, there was 40% success. And 78% of introductions were successfully made where liberations involved over 31,200 individuals. A sequence of releases is important too where releases of more than 20 times improved the rate of establishment compared with releases of less than 10 times. But, the success or failure of early releases may affect the decision whether or not to proceed with a succession of releases.

A number of different release sites are generally chosen, not only for situations appropriate to establishment, but also to reflect the range of environments inhabited by the host pest. The climate and ecological conditions at some parts of the site should be favourable to allow establishment of the introduced natural enemy. Once they are established, selection will take place and those best adapted will survive. Further genetic

alterations will occur when a natural enemy is able to extend its range into the entire environments of its host (Dent, 1991).

2.3.4. Augmentation

Augmentation implies actions to increase the populations of beneficial natural enemies (Rabb *et al.*, 1976). In biological control of a pest it deals with the manipulation of natural enemies themselves in order to make the agents more efficient in the regulation of host populations (DeBach, 1964). In conditions where natural enemies are absent or present in low levels, an augmentation could be implemented by the release of laboratory reared ones. An augmentative control is generally used to suppress pest populations below an economically damaging level and multiple releases may be necessary since the control is only temporary. With inoculative releases, the control will be for the duration of the crop or season (Dent, 1991; van Lenteren, 1986).

Augmentative releases could be used as an option when it is apparent that alternatives such as classical biological controls and conservation techniques are inappropriate or insufficient (DeBach, 1974; Waage and Barlow, 1993). This is mainly due to the high cost ofdeveloping and applying augmentative control programs in terms of rearing, handling, distributing and releasing large numbers of insects, usually parasitoids, at an appropriate time. Therefore before developing augmentation, attention is required to identify good economical, biological and ecological reasons for conducting the work. DeBach and Hagen (1964) give conditions under which augmentative control could be justified: 1) the pest is not successfully or easily controlled, or is too expensive to control by other techniques; 2) the level of control desired may be so low as to be impractical by any other technique; 3) the natural enemies considered potentially effective are made ineffective by adverse environmental conditions that can not to be changed by use of conservation; 4) treatment is needed for only one or two specific pests in a fauna complex; and 5) other methods are undesirable for various reasons such as direct or

indirect injury to the crop or soil, the presence of residues from insecticide applications, the occurrence of insecticide resistant insects and of secondary outbreaks.

In the application of augmentation techniques, the use of parasitoids or predators that are highly host-specific will produce more effective and reliable results than the use of polyphagous agents. The use of host-specific agents would also reduce or avoid adverse effects on non-target organisms (Knipling, 1977).

Factors influencing efficiency of parasitoids

Attempts have been made to recognise and quantify the major influences on the relationships between parasitoids and their hosts, especially in assessing potential of parasitoids when augmented. The following are the main factors involved in parasitoid-host interactions and must be quantified to develop models simulating the relationship between a parasitoid and its host (Knipling, 1977):

1. Density of the parasitoid population per unit of area and time. The number of parasitoids present in a provided habitat determines the proportion of the habitat that can be searched. This, in turn determines the proportion or percentage of parasitisation in the habitat. But, the host density within the area searched also influences the number of parasitised hosts and thus the number of parasitoids that will be alive in the next generation.

2. Host density per unit of area and time. The density of host is judged to be the overriding factor controlling the ultimate efficiency of a parasitoid. This determines the number of hosts that can be attacked, which in turn, regulates the number of progeny that will be present to perpetuate the parasitoid population in the next generation.

3. Size and characteristics of the host environment. The efficiency of a parasitoid population is determined by the ratio of the number of parasitoids to the size of the host ecosystem. The variation in size of the host habitat is a major influence regulating the dynamics and efficiency of a parasitoid population.

4. Oviposition capability of the parasitoid. If the host density is low, the number of eggs laid by parasitoids is considered of little importance or even meaningless as a factor regulating parasitoid efficiency. This is because fewer hosts will be encountered under the best of situations compared to the reproductive potential of the parasitoid population. However for scales, aphids and certain other insects that occur in large numbers in a restricted area, the reproductive potential of parasites is considered a meaningful factor. In such conditions available parasitoids can be expected to encounter far more hosts than the number of eggs that they can deposit.

5. Host-guidance mechanism. While random search for hosts occurs in all host-parasitoid complexes, the presence of kairomones and other guidance cues is regarded as a crucial factor affecting the host-finding efficiency of parasitoids.

6. Natural hazards to survival of parasitoid populations. Parasitoids face many environmental hazards that restrict the number of progeny surviving to reproduce.

Mass rearing for release

The implementation of augmentation is limited by the use of only those natural enemies that can be mass-reared and for which suitable storage and packaging techniques are necessary (Dent, 1991). Most natural enemies are reared on their natural hosts which implies the development of a triple step program where 1) the host plant is grown; 2) the insect pest on the host plant; and 3) the natural enemy is subsequently bred on the pest. Such program poses a great challenge to the insectary specialist (van den Bosch and Messenger, 1973). Due to the risk of contamination with other insects or with diseases, mass rearing of some natural enemies is either too expensive or impossible. In these situations unnatural hosts or artificial host media may provide the only alternative (van Lenteren, 1986a). Artificial diets possess the advantage that they probably reduce production costs, and although an unnatural host is not normally attacked by the natural enemy,it might be able to serve as a host in the insectary. The disadvantage of using

artificial media is the possibility that the natural enemy's host preference will be changed, making it useless for augmentation purposes, though experiments to examine this phenomenon have failed so far to show any change in effectiveness when liberated against the natural host (Morrison and King, 1977).

In mass rearing, every attempt should be made to rear the parasitoid or predator on the target pest, and if possible the target pest itself should get food from the commodity that is to be protected (Morrison and King, 1977). The initial stock for mass rearing should not be less than 1,000 individuals and should contain genetically diverse material (van Lenteren and Woets, 1988; Zw"lfer *et al.*, 1976). This high level of initial stock is useful to lessen the 'founder influence', where the genetic make up of the isolated population depicts only a small fraction of the original genetic variability existent in the parent population (Mackauer, 1972). Once a colony has been established, it is important to ensure that inbreeding is kept to a minimum and where possible to preserve random mating between family lines. If the insectary environment is similar to natural conditions, the selection of insects can be hindered or at least decreased. But, rearing in insectaries typically involve humidity and temperature with a fixed photo period and light intensity. These conditions are not surprisingly incompatible with rearing insects typical to wild populations (Dent, 1991).

In practice, mass rearing of natural enemies poses some problems. For one thing, one of the main problems seems to be the difficulty of producing good quality of natural enemies at an economical cost. Another problem is the lack of effective methods for mass rearing of natural enemies on artificial diets (van Lenteren, 1986b). The third obstacle is the lack of methods that limit selection pressures leading to genetic deterioration of the mass-produced insects. Since the natural enemy can loose its effectiveness through such deterioration, genetic variation is important (Boller, 1972; Mackauer, 1972). Another technical obstacle is cannibalism among predators when they are reared at high densities (e.g. *Phytoseiulus* sp. and *Amblyseius* sp.) or individual rearing (e.g. *Chrysopa* sp.) and

which may cause high costs of rearing procedures (van Lenteren, 1986b). The same occurs for superparasitism in parasitoids, which may lead to production of small or no adults, and strongly male biased sex ratio's (Waage and Ming, 1984) in gregarious parasitoids. Other obstacles are behavioural changes as a result of rearing under unnatural conditions or on artificial media or on unnatural hosts/preys, although accurate data about the effects of these factors in the field are insufficient to judge their significance (van Lenteren, 1986b). Rearing entomophagous insects reared on unnatural hosts may alter their host preference which may affect their efficacy when liberated against natural hosts (National Academy of Sciences, 1969). For instance, Taylor and Stern (1971) found that the egg parasitoid *Trichogramma semifumatum* underwent a significant reversal of host preference; it preferred *Sitotroga cerealella* eggs over those of the cabbage looper *Trichoplusia ni* when reared for more than 100 generations on *S. cerealella*. However, in other cases long-term rearing on various hosts did not influence a change in host dependence or host preference (van Lenteren, 1986b). Rearing on unnatural hosts may also reduce vigour due to an inadequate supply of both quality and quantity of nutrition by unnatural hosts. Moreover, the same effect may take place when the host is fed an unnatural diet.

Pathogens may infect cultures. One of the obstacles often met in insect mass rearing is the occurrence of pathogens and microbial contaminants which cause high mortality, prolonged development, small adults, changes in the quality of insects and direct pathological effects. The most common micro organisms that contaminate insect rearing are fungi, followed by bacteria, viruses, protozoa and nematodes. A major source of microbial contaminants is the use of the field-collected insects for commencing a laboratory colony and dietary ingredients (van Lenteren, 1986b).

The role of insect behaviour and its effects under selection in the insectary is also a meaningful factor affecting the quality of the reared insect species, that is not normally taken into account (Boller, 1972). In general, the quality of insects in insectaries

comprises four components: host selection, adaptability, sexual activity and mobility. Whereas most routine measurements of attributes are oriented to production such as percentage of parasitism, egg production and success of emergence, other attributes more directly concerned with behavioural performance such as flight propensity, diurnal rhythmicity and genetic variation are rarely estimated (Dent, 1991).

Storage

Storage techniques and facilities are to the success of rearing natural enemies for augmentation (Dent, 1991; van Lenteren and Woets, 1988). Insect storage is necessary to allow some kind of buffer for variation in demand. Low temperatures that reduce development rates have been the most common techniques applied to facilitate storage, often without loss of insect viability and vigour (Dent, 1991; Morrison and King, 1977). Short-term techniques have been developed for many beneficial arthropods and natural enemies are commonly stored as immature stages at temperatures between 4 and 15 ^{o}C. The duration of storage normally lasts for a few days, but reduction in fitness is still a problem. Storage of the adult stage may result in an even faster and higher reduction in fitness than storage of immatures. For short-term storage, the pupal stage is apparently most suitable (Dent, 1991; Scopes *et al.*, 1973).

Data on long-term storage are restricted. Nevertheless, long-term storage techniques are fundamental for continuous rearing, rearing during the best period of the year and /or buildup of reserves (Stinner, 1977).

Shipment

Natural enemies of pests should be delivered to growers as soon as possible after production (van Lenteren and Woets, 1988). Various types of packaging have been used, from cut leaves in boxes to insect coated sticky pads, or loose insects in sealed plastic containers. No particular procedures of shipment are required, if the beneficial organism

delivery is done by the producer within 48 hours after their collection. When the natural enemies are delivered through postal services and the delivery takes longer time, then cooling of organisms, special containers (eg. to regulate relative humidity), and/or additional food (eg. honey for parasitoids or prey in the case of predators) may be needed. Poor shipping conditions have often caused the death or injury of natural enemies (Dent, 1991; van Lenteren and Woets, 1988).

Augmentative releases

Once a promising entomophagous species has been selected and the methods have been developed, releases may be conducted against the target pest (Ables and Ridgway, 1981). For this purpose, one of several types of augmentative releases may be chosen. "Inoculative releases" of a restricted number of individuals are implemented with the expectation that the parasitoids will establish and gradually reduce the pest densities during a single season. Hence the natural enemies are expected to survive for only a few generations after the release. Such an approach is called "seasonal colonisation" (Ables and Ridgway, 1981; Stinner, 1977). One of the best examples of this is inoculative release of the parasitoid *Pediobius foveolatus* Crawford for the control the Mexican bean beetle *Epilachna varivestis* Mulsant (Knipling, 1979). Releases of 6,000 parasitoids in each of six widely scattered soybean fields in the shore area of Maryland during late June and early July 1973 yielded 80 to 100% parasitism by season's end in October in all fields where releases were carried out. However, this wasp does not overwinter (Knipling, 1979; Stevens *et al.*, 1975).

Another type of augmentation is "inundative releases" that involve a large numbers of natural enemies in a series of programmed releases in order to obtain immediate suppression of the pest over a short period of time (Rabb *et al.*, 1976; Stinner, 1977). Many species of egg parasitoids in the genus *Trichogramma* have been released to control lepidopterous pests. For example *Trichogramma pretiosum* liberated in 19.4 ha of cotton

in Texas in three releases of 194,000-289,000 per ha per release, resulted in 61% average parasitisation of *Heliothis* spp. eggs and 67% reduction in the larval population to a level below the economic threshold. Higher release rates produced 95% egg parasitisation and an 80% decrease in larval densities (Stinner *et al.*, 1974). But similar releases in corn did not reduce damage or resultant populations of large larvae. A number of braconid parasitoids have also been liberated with varying results. Releases of *Chelonus blackburni* in Arizona cotton for control of the pink bollworm *Pectinophora gossypiella* had little effect on the pest, possibly because few were released (less than 6,000 per ha for 13 releases). In the same trials, releases of *Bracon kirpatricki* reduced the pink bollworm population and only one insecticide treatment was needed, compared to four applications in a nonrelease site (Stinner, 1977). The eulophid wasp, *Encarsia formosa*, is widely used throughout the world for control of the greenhouse whitefly, *Trialeurodes vaporariorum* Wests. This parasitoid has been extensively studied and used in western Europe, where it is liberated onto tomatoes, vegetables, and horticultural crops. This parasitoid is also reported to have been successfully released on flowering ornamentals in the USA (Ables and Ridgway, 1981).

Costs and benefits

The reduction in pest damage or suppression of pest populations by augmentative releases of natural enemies has frequently been mentioned, but the economic feasibility of using such an approach has scarcely been demonstrated (Dent, 1991). The very nature of the control method is part of the puzzle. It is protective rather than curative and as such the use of augmentation can only be justified economically when there is a high possibility that the problem will develop. The cost of a control program can be broken down into its constituent parts such as the cost of natural enemy production and the actual cost of augmentation. These expenses can then be compared with the costs of alternative forms of control, although real costs such as diminished risk to the environment as a

result of not applying chemical insecticides can seldom be approximated. For augmentation, the costs of natural enemies varies depending on the species (Starler and Ridgeway, 1977). The price also varies according to the vendor. The costs used must cover production of the natural enemy as well as the costs for research and development, including the maintenance of cultures throughout the year. Therefore, the economics of augmentation are very important to the viability of the control method (Dent, 1991).

The California Department of Food and Agriculture estimated that the cost of control for *Heliothis zea* in that state in 1974 was $22 million. Besides this high cost, losses due to the pest approximately valued $47 million (Knipling, 1977). A hypothetical model forecasts that effective management of *H. zea* in California can be attained by releasing 500 wasps of adult *Eucelatoria* spp (Hymenoptera: Tachinidae) per acre during each of the first three pest generations. A parasitoid like *Eucelatoria.* could be mass produced at a cost of $3 per thousand, or $3 million per billion parasitoids. Based on this rough estimate, a management program for the pest *H. zea* in California would cost $7.5 million per year. This would be just about one third the approximate cost of control by the use of insecticides. If the losses that were eluded are taken into account, $ 47 million would be saved (Knipling, 1977). The management of *Heliothis* spp. in cotton with *Trichogramma pretiosum* costs $ 7.68 per ha per application which is relatively cheaper than fenvalerate (a commonly used pyrethroid synthetic insecticide) at $16.18 per ha, with the exception that the utilisation of pyrethroid is only once for every two or three parasitoid releases (Dent, 1991).

2.3.5. Conservation

Another approach to enhance biological control would be to manipulate the environment in such a way that any adverse environmental effects would be reduced or eliminated, or simply making the environment better suited to natural enemies which were previously not optimal. This can be termed 'conservation', and the same approach

can also be used to improve the establishment of introduced parasitoids or predators in a classical biological control program (DeBach, 1964; Dent, 1991). The activity of natural enemies may be enhanced by the presence of alternative hosts or prey, cropping methods/cultural practices or behavioural modifying chemicals. Food sources such as flowers, rather than their prey, may also be needed (Dent, 1991).

Food sources for adult parasitoids

Crop monocultures, particularly annual crops, do not give an adequate supply of pollen and nectar as food for many adult parasitoids to complete their life cycle (Zandstra and Motooka, 1978). Although in some cases the cultivated plant may provide a restricted source of nectar and pollen, weeds within crops or in surrounding areas more commonly supply these food sources (Altieri and Whitcomb, 1979). The availability of such food is essential because they can influence the natural enemy distribution within a crop. The distribution affects the rate of parasitism, particularly if adult parasitoids are unable or unwilling to move long distances between host habitats and food sources (Dent, 1991). The necessity of food sources for adults is common and widespread among parasitoids and that such food is frequently associated with plants normally regarded as weeds (Altieri *et al.*, 1977; Leius, 1967).

Alternative hosts or prey

In the absence of host species, parasitoids that are not host-specific will seek alternative hosts (Dent, 1991). If these alternative sources are not found in the vicinity of the cropping system then there will be a tendency for them to disperse away from the crop. This may imply that when the pest population in the crop begins to increase the natural enemies that could effectively reduce the growth rate are not within the crop vicinity and a delayed return, possibly later in the season, may be too late for them to significantly influence the pest population. Generally speaking, most natural enemies

found on alternative plants, mostly weeds, tend to spread into crops. Therefore, weeding at an appropriate period of time could force movements of the natural enemies into the crop (Altieri and Whitcomb, 1979).

Ideally, alternative hosts or prey would occur as non-pest species on the same crop as the pest, but in sufficient numbers at an earlier growth stage or part of the season to allow the natural enemies to increase prior to the beginning of infestation by the pest. This condition rarely happens and more frequently the alternative host or prey is present on other crops or weeds. Management of weeds for the conservation of alternative prey will generally be easier than that of weeds which are food sources for parasitoids. The reason is that the former only acts as temporary habitats and do not have to be planted with the crop. Somewhat adequate supplies of natural enemies may be achieved letting weeds to grow in woods, along fences, road sides, and ditch banks or in related sites (Zandstra and Motooka, 1978). Problems with this approach will largely be associated with implementation and convincing growers who have been encouraged to produce clean crops and farmlands for many years to do the opposite. Therefore, any technique applied to promote alternative hosts or prey of natural enemies must at least be compatible with the grower's perception of pest problems and the cropping methods that are used (Dent, 1991).

Cropping methods

A specific cropping method may enhance the conservation of natural enemies or alternatively a modified or abandoned technique may improve the opportunities of increased natural enemy activity (Dent, 1991). The problem is, as usual, determining the which techniques significantly affect natural enemies and subsequently determining whether such techniques are compatible with farming practice. Although reduction in crop related or unrelated weeds has been specifically recommended as a pest control strategy (van Emden and Williams, 1974), growers will have the tendency of adopting the

opposite approach, even though this may only involve the weed maintenance in hedgerows or headlands (Dent, 1991). Changes in cultural practices such as planting date, row spacing, crop duration, irrigation or direct seed planting may alter the crop environment and have an effect in favour of natural enemies. As an example, planting soybean at higher densities results in a better canopy closure and a more appropriate microclimate for the development of insect pathogens such as the fungus *Nomuraea rileyi* Sampson. Predators and parasitoids which exhibited significant differences among treatments were in highest populations when captured in high density plantings (Mayse, 1978).

Behaviour-modifying chemicals

The behaviour of natural enemies can be modified by the use of semiochemicals as a means of enhancing activity in crop areas (Dent, 1991). Semiochemicals are defined as chemicals that mediate interactions between organisms. They are classified into two main groups, 'pheromones', which mediate intraspecific interactions and 'allelochemicals', which mediate interspecific interactions (Nordlund, 1981). Further, each of these groups have different subgroups, pheromones into sex pheromones, alarm pheromones and aggregation or epidetic pheromones; allelochemicals into allomones, kairomones, synomones and apneumones. An 'allomone' is a substance produced or acquired by an organism that, when it contacts an individual of another species in the natural situation, evokes in the receiver a behavioural or physiological reaction that is adaptively favourable to the emitter but not the receiver. A 'kairomone' is a substance produced or obtained by an organism that evokes in the receiver a behavioural or physiological reaction that is adaptively favourable to the receiver but not emitter. A 'synomone' is a substance produced or obtained by an organism that evokes in the receiver a behavioural or physiological reaction that is adaptively profitable to both receiver and emitter (Nordlund, 1981).

Among the allelochamicals, the kairomones have received most attention in conjunction with insect pest management, primarily as a means of attracting natural enemies to crops or of directly disturbing the finding and recognition of host plants by insect pests (Dent, 1991; Nordlund, 1981).

Kairomones originate from the insect or result from feeding activity on the plant, whereas synomones directly originate from the plant and natural enemies can harness or use these chemicals as a means of locating their hosts or prey (Dent, 1991). If these semiochemicals can be identified and synthesised, then they can be applied on crops in order to attract natural enemies and thereby increase the frequency of encounter with their hosts and subsequently enhance the natural enemy effectiveness. The maintenance of an effective number of natural enemies and a high search activity within a habitat will depend on encountering kairomones in sufficient amount and frequency to reveal a suitably high population of host individuals. The problem with this approach is that over-stimulation could make the natural enemies search intensively in restricted areas over long periods, consequently reducing the likelihood of encounters with patchily distributed hosts. In the long term, if kairomones are applied extensively by diverting search activity into crops where hosts are rare, there would be the possibility of detrimentally affecting wild natural enemy populations, hence lowering the overall reproductive rate of the population (Dent, 1991; Powell, 1986).

Kairomones utilised by larval parasitoids

Host-derived kairomones can be encountered in various parts or stages of the hosts or from trails left by them (Kainoh, 1990).

Parasitoids of larvae use cues derived from host larvae such as frass, larval cuticle, the mandibular gland, the silk gland, exuviae, hemolymph and other sources (Kainoh, 1990). The kairomones for the braconids *Bracon melitor*, *Orgilus lepidus*, *Microplitis croceipes* and *M. demolitor* were found in the frass of the host. Certain tachinids such as

Bonnetia comta, *Lixophaga diatraeae* and *Eucelatoria bryani* also use the host frass for finding the host (Kainoh, 1990). The larval parasitoid *Cotesia rubecula* apparently harnesses volatiles from frass and regurgitate of the host (*Pieris rapae*) when searching for plants damaged by its host (Agelopoulos and Keller, 1994). An aphid parasitoid, *Aphidius nigripes*, is attracted to the honey dew of the host stimulating searching behaviour of this wasp (Bouchard and Cloutier, 1985). Mandibular gland secretion of larvae of the flour moth, *Anagasta* (*Ephestia*) *kuehniella*, stimulated oviposition movements in an ichneumonid, *Venturia canescens* (Corbet, 1971). A series of 2,5-dialkyltetrahydrofurans act as kairomones for the braconid *Apanteles kariyai* Watanabe, detected in the exuviae of the common armyworm, *Pseudaletia separata* Walker (Takabayashi and Takahashi, 1986).

Synomones utilised by parasitoids

Plant-produced synomones are frequently cues for the host-habitat location of parasitoids (Kainoh, 1990). A braconid *Diaeretiella rapae* known as an aphid parasitoid, responds to a plant volatile allyl isothiocyanate (Read *et al.*, 1970). Besides volatiles from regurgitate and frass of the host (*P. rapae*), volatiles from cabbage caused by injury appears to guide the larval parasitoid *Cotesia rubecula* to plants attacked by its host (Agelopoulos and Keller, 1994). A tachinid, *Lixophaga diatraeae*, is attracted to sugarcane infested by the host (Roth *et al.*, 1982).

2.4. The parasitoid *Cotesia plutellae* Kurdjumov

2.4.1. Introduction

The solitary larval endoparasitoid, *Cotesia plutellae* (Hymenoptera: Braconidae: Microgastrinae) (Plate 2A) has been known for a long time as a parasitoid that attacks the cabbage moth, *Plutella xylostella*, and Kurdjumov in 1912 first identified this species as

Apanteles plutellae (Wilkinson, 1931). This species is native to the Palearctic Region (Wilkinson, 1940). The wasp has been introduced into many countries and contributes to the control of cabbage moth (Fitton and Walker, 1992).

2.4.2. Morphology and life history

A description of *C. plutellae* and characters that distinguish it from closely related species was given by Wilkinson (1940) and Nixon (1974).

Adult longevity ranges from three to 14 days in Malaysia (Lim, 1982), one to five days at Los Banos, Laguna, and two to 17 days at Baguio City, the Philipinnes (Velasco, 1982). The egg stage lasts one to two days, the average egg-larval period is nine days, and the pupal stage four to five days in Malaysia. The larva has three instars. Like many first-instar *Apanteles* larvae, this parasitoid has a 'caudal horn' or tail situated beneath the vesicle and the tail is reduced in the next instar (Clausen, 1940; Ooi, 1979a). When its development is complete, it emerges from the body of the host and forms a cocoon (Ooi, 1979a). The sex ratio in the field is 1:1, but in the laboratory more males are usually present (Lim, 1982). The females are active in searching for hosts and deposit eggs only during photophase, but are inactive in darkness. They are able to parasitise various larval instars of the host, especially those of the cabbage moth (Talekar and Yang, 1991).

2.4.3. Host range

Besides *P. xylostella*, this parasitoid is also reported to attack *Aglais urticae* L., *Agdistis benneti* Curtis, *Spilosoma urtica* Esper, *Anthocharis cardamines*, *Maniola jurtina*, *Malacosoma castrensis* L., *Thaumetopea herculeana* Rambur, *Ocnogyna baeticum meridionalis* Seits (Nixon, 1974), *Trichoplusia ni* (Joshi and Sharma, 1974), *Corcyra cephalonica* Stnt., *Ephestia cautella* Wlk. (Chiu *et al.*, 1974) and *Hyphantria cunea* (Waterhaouse and Norris, 1987). The parasitoid also attacks other cruciferous

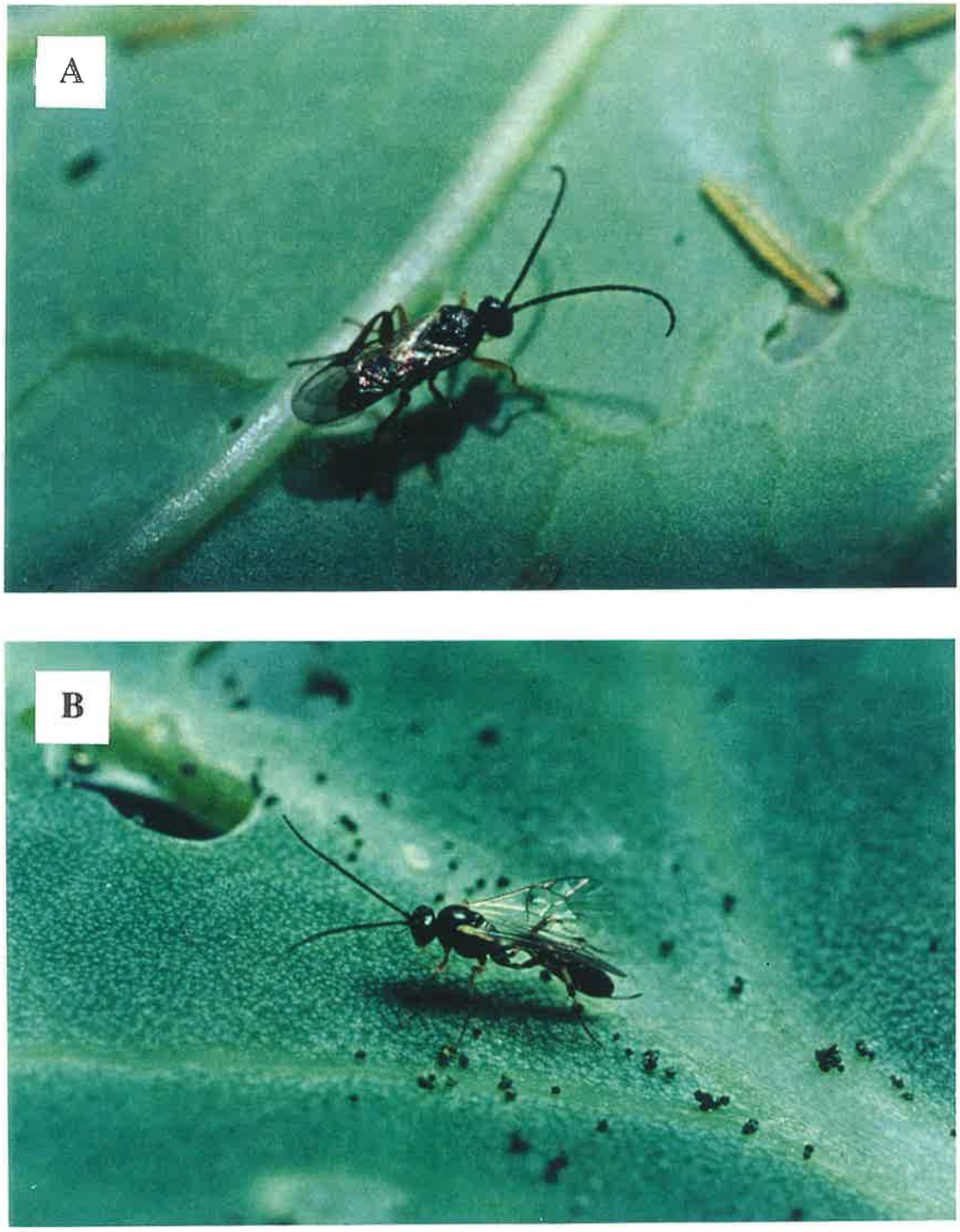

Plate 2. Parasitoids of larval cabbage moth. A) *Cotesia plutellae* searching for the host. B) *Diadegma semiclausum* attracted to frass produced by its host (enlarged).

pests, *Hellula hydralis* and *Crocidolomia binotalis* in the laboratory, although not in the field (Lim, 1982).

2.4.4. Hyperparasitoids

Some hyperparasitoids are known to attack *C. plutellae* and their activities adversely affect the efficiency of the parasitoid (Ooi, 1979b). In Malaysia, a total of 12 species of hymenopterous hyperparasitoids was collected from *C. plutellae* in fields (Ooi, 1979b; Sivapragasam and Rashid, 1994). In South Africa, four were found to attack braconid and ichneumonid parasitoids of the cabbage moth (Kfir, 1994).

2.5. The parasitoid *Diadegma semiclausum* Hellen

2.5.1. Introduction

Diadegma semiclausum (Hymenoptera: Ichneumonidae: Ichneumoninae) (Plate 2B) is native to Europe, but it is now distributed worldwide and has been introduced into many countries (Clausen, 1940; Waterhouse and Norris, 1987). The parasitoid has been used for biological control of cabbage moth and has been established in Barbados in America (Alam, 1974), Indonesia (Vos, 1953), Malaysia (Chua and Ooi, 1986), the Philipinnes (Poelking, 1992), Australia (Wilson, 1960), Fiji Island in the Pacific (Oatman, 1978) and New Zealand (Greathead, 1976).

2.5.2. Morphology and life history

This parasitoid has been referred to under the generic names *Horogenes*, *Nythobia* and *Angitia* (Robertson, 1939; Vetkatraman, 1964; Vos, 1953; Waterhouse and Norris, 1987). Synonims of the species are *tibialis*, *cerophaga* Gravenhorst, *cerophagus* Gravenhorst and *eucerophaga* Horstmann (Fitton and Walker, 1992; Hardy, 1938; Ooi, 1980).

In almost every area in which *P. xylostella* has been found, a number of parasitoids attacking this pest are recognised. And in many countries the same genera and even the same species of parasitoids have been found to parasitise it. The genus *Diadegma* is one of the most important parasitoids of this pest. The two parasitoids *D. fenestrale* Holmgren (=*fenestralis*) and *D. semiclausum* have a marked similarity in morphology and habit and this often makes it difficult to assign an individual to either species. Formerly they have frequently been reported from many countries as a single species, completely as *D. semiclausum*, or completely as *D. fenestrale*, or even under different names such as *Diadegma plutellae* Viereck and *Diadegma gracilis* Gravenhorst; further confusion has arisen from wrong homology and synonymy (Hardy, 1938), and also by records of *Diadegma* species from *Plutella* which are quite unusual or improbable, for example *Diadegma nana* (Morley and Smith, 1933). The diagnostic characters to distinguish these two species of *Diadegma* are given by Boyd (1934).

The wasp *D. semiclausum* is a solitary larval endoparasitoid (Venkatraman, 1964) and the female deposits eggs in all instars of the host and occasionally in the prepupal stage (Waterhouse and Norris, 1987). A larva when met by the wasp often reacts with lively movements or drops from the leaf but remains connected by a silken thread and escapes. The parasitoid normally attacks a wriggling larva, bends her abdomen in front, places the ovipositor and quickly inserts an egg. This process lasts only a few seconds and soon afterwards she may attack another larva. If the larva has dropped itself from the leaf by a silken thread, it is not followed by the parasitoid (Vos, 1953).

The parasitised larvae continue to live and feed as healthy ones and spin cocoons in the fourth instar. However, the parasitised caterpillars do not pupate. After sometime inside the cocoon the fullgrown larve of the parasitoid emerge from the host larvae. They spin their own cocoon inside the *Plutella* cocoon. The wasp cocoon is cylindrical, non-transparent and closed at both ends. The adult wasp emerges from the cocoon by biting a hole in one of the ends (Vos, 1953). The female parasitoid copulates soon after

emergence from the cocoon and subsequently searches for larvae amongst the leaves of the host plant to lay eggs (Hardy, 1938). The average life span of male and female wasps in the presence of hosts is 13 and 19 days, respectively. The average fecundity of a female is 193. The egg period ranges from 42 to 46 hours (Venkatraman, 1964). The development of *D. semiclausum* when oviposited in the third and fourth instar larvae varies from eight to 10 days in the pupal stage and the total development from egg to adult is completed in 17 to 20 days (Vos, 1953). In the English summer, the life cycle of *Diadegma* lasts about one month and, under favourable conditions, possibly as many as 2.5 to 3.0 generations of both host and parasitoid may be produced (Hardy, 1938).

2.5.3. Host range

Records indicate that some *Diadegma* species have wide host ranges. For instance, *D. fenestrale* is reported to attack 24 species of Lepidoptera and one coleopteran (Hardy, 1938). But, by looking at the patterns of host associations and the mechanism involved, it appears that most species of *Diadegma* are relatively host specific and the usual hosts are microlepidoptera (Dijkerman, 1990). The parasitoid *D. semiclausum* has some alternate hosts when the cabbage moth is absent or lacking. Those are *Depressaria atomella* How., *Enarmonia diniana* Gn., *Epischnia banksiella* Rich., *Euphyia bilineata* L., *Gelechia brahmiella* Heyd., *Gracilaria stigmatella* Fab., *Laverna fulvescens* How. and *Mompha fulvescens* How (Hardy, 1938).

2.5.4. Hyperparasitoids

In the course of work carried out in England to investigate the cabbage moth and its natural enemies, Hardy (1938) found six hyperparasitoids of *D. semiclausum* and *D. fenestrale*, namely *Eulophus* spp., *Habrocytus* spp., *Hemiteles* spp., *Hemiteles areator* Panz., *Itoplectis alternans* Grav. and *Mesochorus pectoralis* Ratz. Although the exposed position of the *Diadegma* cocoons would seem to make them ideal objectives for

hyperparasitoids, the actual number of such hyperparasitoids was very small, only in the case of *M. pectoralis* did parasitism by any one species increase above 0.1% (Hardy, 1938).

CHAPTER 3

EFFECTIVENESS OF PARASITOIDS AT VARIOUS PARASITOID DENSITIES AGAINST DIFFERENT HOST INSTARS

3.1. INTRODUCTION

In recent years, the production of cruciferous vegetables has been seriously influenced by a steady attack of insect pests, particularly the cabbage moth *P. xylostella.* Most growers still depend on the use of insecticides for the control of this pest. However, intensive and unselective use of chemicals, coupled with the quick turnover of generations in favourable climates, has caused the development of resistance in cabbage moth to practically all types of chemical insecticides (Talekar *et al.*, 1990). Hence, there is an increasing interest in the minimisation of the utilisation of insecticides through the development of integrated pest management (Yang *et al.*, 1994).

Before the introduction of modern chemical insecticides, the cabbage moth was not considered a destructive pest of brassicas, except for sporadic population outbreaks. Even around the Mediterranean, where the pest is originally believed to have originated, and in Central and Northern Europe, a natural enemy complex keeps the pest under control (Talekar *et al.*, 1990). For instance, in Moldavia, Romania, over 25 species of parasitic Braconidae and Ichneumonidae were found in brassica fields (Mustata, 1992). Since large numbers of parasitoids parasitise the cabbage moth (Lim, 1986), biological control could be important in the development and maintenance of a successful IPM strategy.

Among larval parasitoids, *C. plutellae* and *D. semiclausum* are two major species successfully introduced in many subtropical and tropical countries to regulate cabbage moth populations (Lim, 1986; Waterhouse and Norris, 1987). These parasitoids are able to parasitise each larval stage, but rates of parasitism vary depending on the instars of hosts (Talekar and Yang, 1991). Proportions of parasitism which are expressed as the

killing capacity increase with parasitoid density for these species. The efficiency of searching hosts by the parasitoids are low at high wasp densities (Chua and Ooi, 1986).

Experiments were conducted with the aim of investigating the effects of host instar and parasitoid density on rates of parasitism, killing capacity, searching efficiency and number of encounters by *C. plutellae* and *D. semiclausum*.

3.2. Materials and methods

3.2.1. Insect source

Plutella xylostella were obtained from field-collected larvae and were maintained in a continuous culture on potted cabbage plants (Figure A.1). The parasitoid *C. plutellae* was imported from Taiwan in 1990 by The Department of Crop Protection, The University of Adelaide, Waite Campus. It is established under laboratory conditions (24 ^{o}C) on cabbage moth caterpillars raised on potted cabbage plants (Figure A.2). In 1994 another parasitoid, *D. semiclausum*, was collected from crucifer growing areas in South Australia and was maintained on cabbage moth larvae in the laboratory. Procedures for rearing the pest and its parasitoids are described in Appendix 1.

3.2.2. Parasitoid effectiveness

The effectiveness of parasitoids was investigated by assessing rates of parasitism, killing capacity, searching efficiency and number of encounters.

Rate of parasitism

The parasitisation by female parasitoids of the cabbage moth larvae was studied in the laboratory. The temperature ranged from 22.7 to 26.5 ^{o}C and the relative humidity varied from 43 to 71%. The instar of cabbage moth was determined by the width of the

head capsule (Figure A.3; Table A.1) and two to five-day old mated female wasps were used for the test.

To determine the rate of parasitism, each treatment contained a potted cabbage plant infested with 30 host caterpillars (first, second, third or fourth instars) placed in a cage (23.5 x 23.5 x 32 cm). The cage was left overnight (≈ 16 hours) to allow the larvae to settle. On the next day, water in a container and honey were placed into the cage, and 1, 2, 4 or 8 mated female parasitoids were released into it for 24 hours. The experiment was designed in a factorial randomised complete block design. There were 16 treatment combinations and each was replicated three times. After the period of parasitisation, the treated larvae were removed to be dissected or reared until pupation of parasitoids. It was hypothesised that wasp density and host instar influenced the rate of parasitism of the cabbage moth larvae by the parasitoids. The percentage parasitism (P) was calculated by using the model suggested by Hassell and Varley (1969): $P = 100(u_1 - u)/u_1$, where u_1 is the initial host density and u is the final density of parasitised hosts. The data obtained were transformed into Arc Sine $\sqrt{x}$, where x is proportion of parasitised hosts, and subjected to an analysis of variance in a Genstat 5 (Giles *et al.*, 1994; Lane *et al.*, 1987). A Duncan's multiple range test at $P = 0.05$ was used to test differences among treatments (Duncan, 1955; Gomez and Gomez, 1984).

Another equation to transform the rate of parasitism was applied as well by the model: % parasitism = $100 - K_1e^{-K_2\rho}$ where K_1 and K_2 are constant, and ρ is number of parasitoids in a cage. The equation was then rearranged by using a logarithmic transformation to produce a linear function. So, $\log K_1e^{-K_2\rho} = \log$ (100-% parasitism), or $\log K_1 + K_2\rho = \log$ (100 - % parasitism). Since $\log K_1$ is a constant and is called K_1^*, therefore $K_1^* + K_2\rho = \log$ (100 - % parasitism) and this equation was used to regress the data. The transformed data were subjected to an analysis of variance in a SAS program (Joyner, Ed., 1985)

Killing capacity and searching efficiency

The proportion of hosts parasitised at the various densities of parasitoids per cage can be expressed using a K-value, which is a measure of the *killing capacity* (Varley and Gradwell, 1960). Using such a logarithmic expression for the proportional mortality where the K-value equals log initial host density minus log unparasitised host density, has the advantage that the relationship can be plotted linearly (Hassell, 1971; Hassell and Varley, 1969). This value is simply calculated from the model: $K = \log_e (u_1/u)$ where u_1 is the initial host density and u is the hosts surviving parasitism.

The efficiency of searching by a parasitoid species in utilising and finding out the hosts under given conditions is measured by its 'area of discovery' as a constant (Nicholson, 1933). Hence, efforts were carried out to know the efficiency of *C. plutellae* and *D. semiclausum* in the laboratory. The searching efficiency (A) can be determined if the parasitoid density (p), the initial host density (u_1) and the final (unparasitised) host density (u) are known (Hassell, 1971; Hassell, 1985). The value of area of discovery is obtained from the model: $A = (1/p) \log_e (u_1/u)$. The hypothesis was that the killing capacity and searching efficiency of the parasitoid varried between different wasp densities and host instars. Data obtained were analysed by analysis of variance in Genstat 5 (Lane *et al.*, 1987)

Number of Encounters

It is known that the searching capacity of parasitoids is limited, they are only able to search a proportion of the total host area during their life times (Rogers, 1972). Therefore, Rogers assumed that the total number of parasitoid encounters with hosts (Enc) can be determined if the parasitoid density (p), the efficiency of searching or proportion of the total host area measured by the area of discovery (A) and the total number of hosts present (N) are known. The number of encounters can be calculated by using the model:

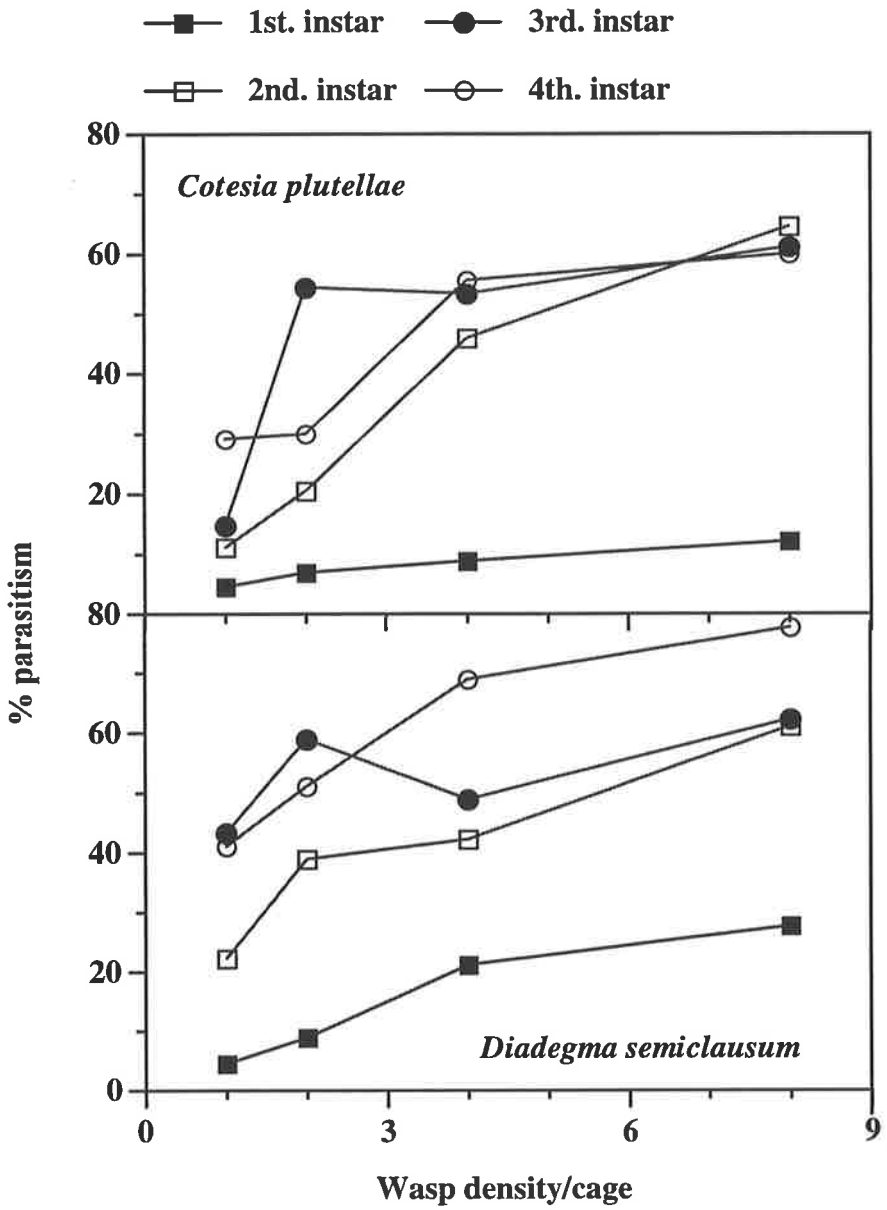

Figure 3.1. Parasitism of cabbage moth larvae by *C. plutellae* and *D. semiclausum* at various densities of wasps for each instar of their host. Thirty hosts were presented to wasps on a cabbage plant in a cage.

Enc = p.A.N. The hypothesis was that the wasps in high densities encountered more big host larvae. Data were subsequently analysed by the analysis of variance in the Genstat 5 (Lane *et al.*, 1987; Giles *et al.*, 1994) to established effects of host instar and parasitoid density on the number of parasitoid encounters.

3.3. Results and Discussion

3.3.1. Rate of parasitism

Based on results of regression analyses, there was a strong interaction between number of released wasps and various host instars on the rate of parasitism of cabbage moth larvae by *C. plutellae* ($P < 0.002$) (Table A.2). The percentage of cabbage moth larvae parasitised varied greatly from 4.6 to 64.6% (Figure 3.1; Table A.3). Releases of different wasp densities into cages of first instar larvae of the host gave low rates of parasitism compared to those of other instars. This could have been due to the behaviour of the first instar larvae of *P. xylostella* which mine leaf tissues (Vos, 1953; Waterhouse and Norris, 1987). As a result, the wasp deposited fewer eggs on this instar. Releases of a single female parasitoid produced the highest parasitism on the fourth instar hosts. But it changed considerably as wasp densities increased on different instars, where parasitism increased in the third, the fourth and the second instars with releases of 2, 4 and 8 wasps. Significant differences of parasitism are more obvious at high numbers of wasps (Figure 3.1). The highest rates of parasitism occurred in the second, third and four host instars after they wereexposed to 4 and 8 *C. plutellae*. However, there was no significant difference of parasitism among these instars. Possibly superparasitism occurred where the wasps increasingly deposited eggs in already parasitised hosts that they encountered.

These results agree with investigations by Talekar and Yang (1991) who found that each instar of the cabbage moth could be parasitised by *C. plutellae*. But, a slight distinction is seen in trends of parasitism. They reported the highest and lowest parasitism

occurring on the second and fourth instars respectively. Probably different wasp and host densities, insect ages or experimental conditions cause variations in parasitism by this parasitoid.

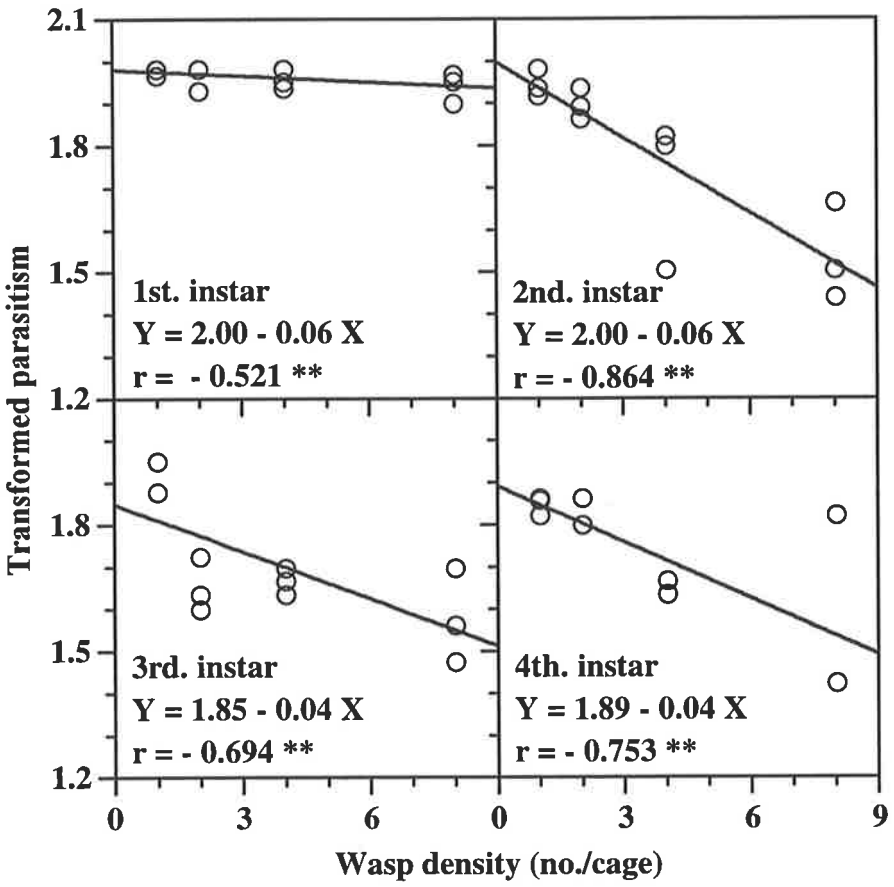

Figure 3.2. Parasitism of larval cabbage moth by *C. plutellae* at different densities of wasps for each instar of their host. ** indicates $P < 0.01$. Transformed parasitism = log (% unparasitised host).

There was a strong relationship between wasp density and host instar on parasitism by *C. plutellae* which was regressed by a logarithmic transformation into log (100 - %parasitism) (Table A.2b). Correlations between various densities of wasps and transformed parasitism in each instar were very strong (Figure 3.2). These imply that

larger densities of wasps produced larger numbers of parasitised larvae expressed by the lower transformed parasitism.

Densities of wasps and host instars both affected parasitism by *D. semiclausum* ($P < 0.01$ and $P < 0.01$) on the cabbage moth larvae. High densities of wasps resulted in high rates of parasitism and this parasitoid deposited more eggs on big hosts. However, there was no interaction between wasp density and host instar ($P = 0.068$) (Table A.4). The parasitism averaged from 4.4 to 77.8% and the lowest parasitism occurred on the first instar (Figure 3.1; Table A.5). Releases of single female wasps produced the highest levels of parasitism in third and fourth instars. The parasitisation of cabbage moth by *D.*

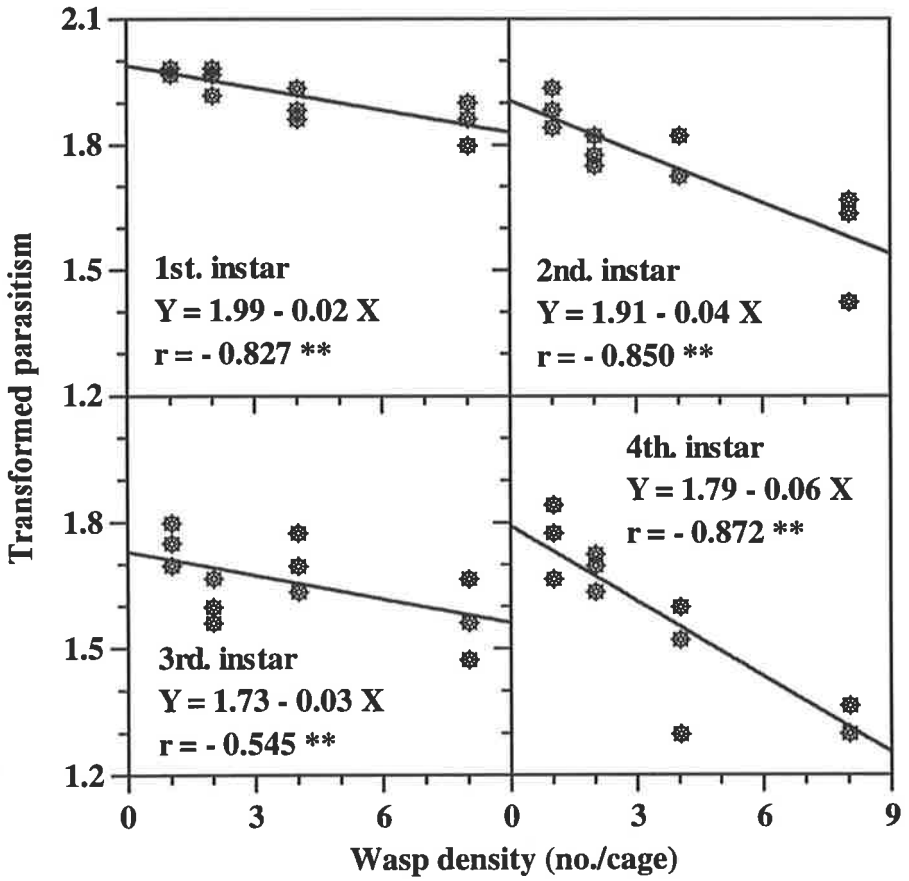

Figure 3.3. Parasitism of larval cabbage moth by *D. semiclausum* at various densities of wasps for each of their host. ** indicates $P < 0.01$. Transformed parasitism = log (% unparasitised hosts).

semiclausum in this study is slightly different from the findings of Talekar and Yang (1991) who found the lowest rate in the fourth instar. Vos (1953) carried out a laboratory experiment at Pacet (Indonesia) to liberate this parasitoid for 24 hours on various instarsof cabbage moth larvae in cages. It also oviposited on all instars where the egg laying average was higher in the second and the third instar larvae than in the first and fourth.

There was a strong linear relationship between wasp density and host instar on parasitism by *D. semiclausum* which was regressed by transforming rates of parasitism into log (100 - %parasitism) (Table A.4b). Correlations between numbers of wasps and each instar were very strong, where the highest densities of wasps produced the largest numbers of parasitised larvae expressed by the low rate of transformed parasitism (Figure 3.3).

3.3.2. Killing capacity

There was a strong relationship between wasp density and host instar on the killing capacity (K) of *C. plutellae* ($P = 0.01$) (Table A.6). The increase of wasp density made the K-value higher and therefore a typical functional response (Hassell and Varley, 1969) was obtained. A significant positive correlation could be found between the parasitoid density and the killing capacity in the first, second and fourth instars (Figure 3.4). The positive correlation was not significant only in the third instar.

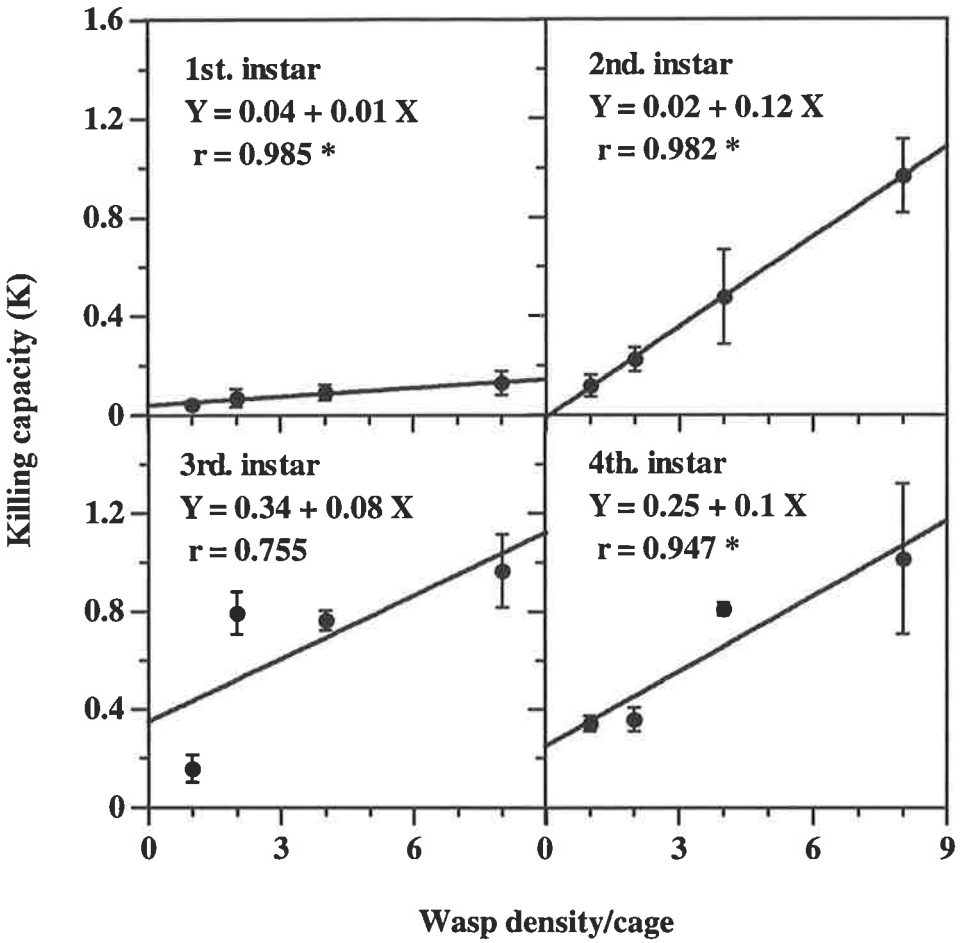

Figure 3.4. The relationship between the proportion of parasitism (expressed as K-values) and the density of female *C. plutellae* averaged over three replicates (± S.E.M.).

These results indicated a similar trend as Chua and Ooi (1986) achieved, where high wasp densities increased K-values. But they did not characterise the host instar used for the evaluation. Releases of two, four and eight wasps obviously enhanced the K-values. The ranges of killing capacity values for this parasitoid averaged from 0.046 to 1.016 (Table A.7). Interestingly, differences in the killing capacity values among host instars were statistically not significant when only one female parasitoid was used.

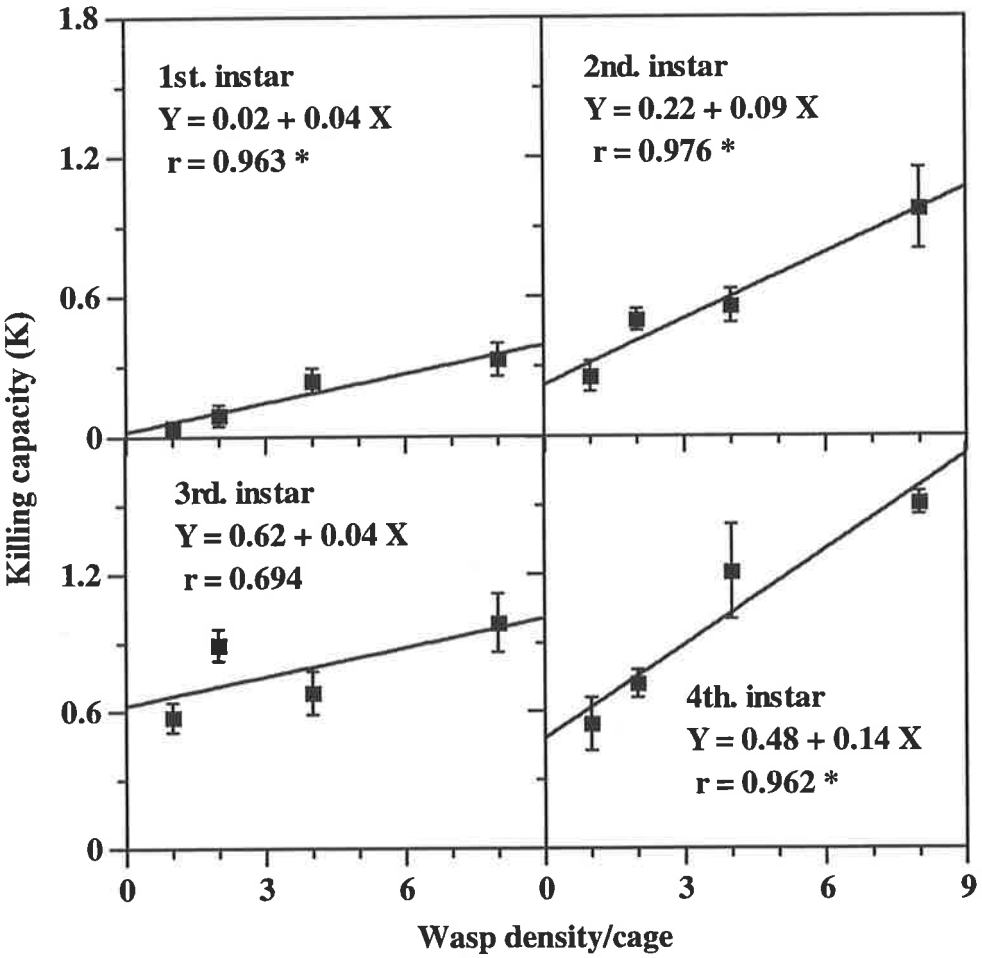

Figure 3.5. The relationship between the proportion of parasitism (expressed as K values) and the density of female *D. semiclausum* averaged over three replicates (± S.E.M.).

The wasp density and host instar significantly affected the killing capacity of *D. semiclausum* on cabbage moth larvae (P = 0.009) (Table A.8). The K-values rose when the number of parasitoids increased (Figure 3.5). Significant positive correlations between the wasp density and the killing capacity are found in the first, second and fourth instar larvae of the host and no significant in the third instar. The average K-values are from 0.046 to 1.506 (Table A.9; Figure 3.5). Ooi (1980) obtained killing capacity values in four levels of this parasitoid averaged from 0.38 to 1.41, but the trends were similar

where high wasp densities made the K-value high as well. Chua and Ooi (1986) also found a strong positive correlation between wasp densities and K-values for this parasitoid. These results differ from the experiments conducted by Yang *et al.* (1994) in which the killing capacity of *D. semiclausum* remained relatively unchanging with increasing parasitoid density and the correlation was negative.

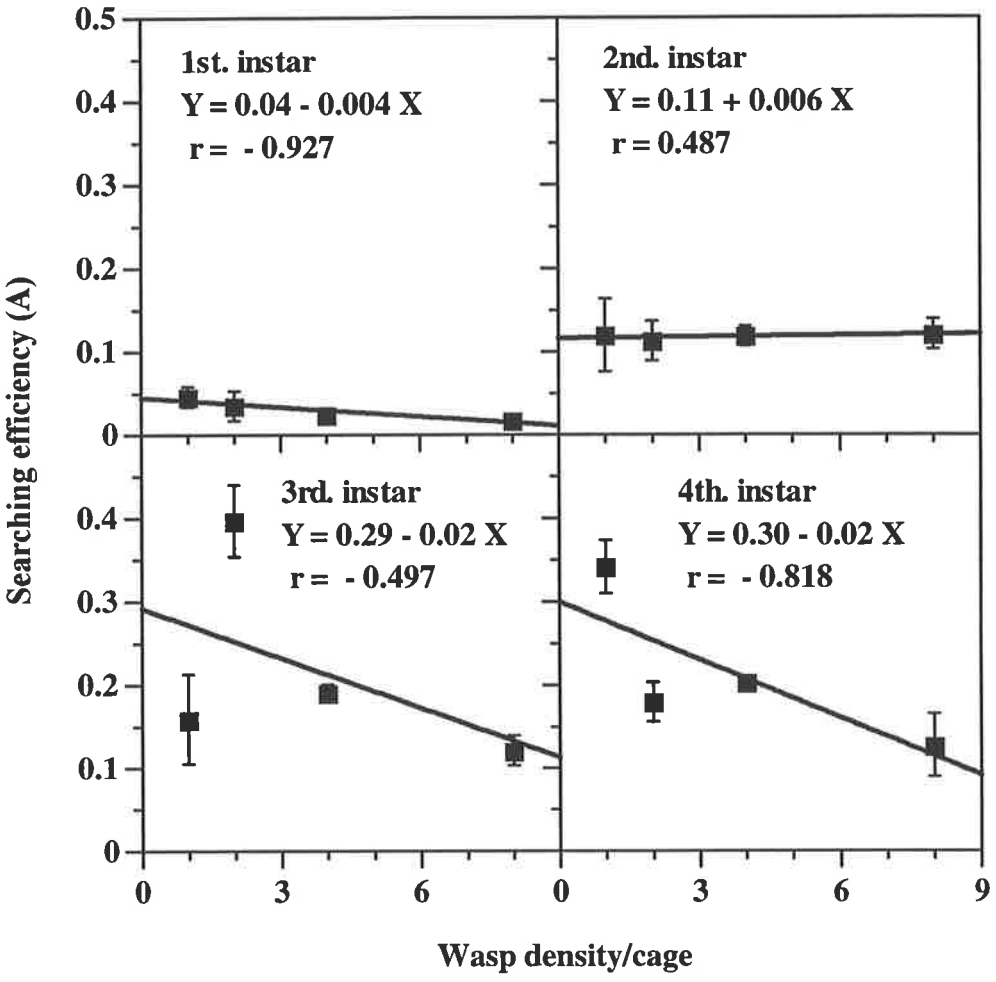

Figure 3.6. The relationship between searching efficiency and the density of female *C. plutellae* averaged over three replicates (± S.E.M.).

3.3.3. Searching efficiency

The searching efficiency of *C. plutellae* decreased as the density of wasps increased, especially in the first, third and fourth instars (Figure 3.6). The parasitoid searched more efficiently for larger host larvae, which is indicated by larger values of A compared to those of small ones. There was a strong relationship between the wasp density and host instar in producing the value of searching efficiency by this parasitoid ($P < 0.001$) (Table A.10). The average A-values for this wasp ranged from 0.017 to 0.397. Regardless of the host instars high wasp density reduced the A-value (Figure 3.4; Table A.11). By releasing one female wasp in a cage, Chua and Ooi (1986) found that the searching efficiency value was 0.18 and the values decreased as they doubled the wasp density. Hassell (1971) summarised that increasing densities of female *Nemeritis canescens* Grav., a parasitoid of the almond moth (*Ephestia cautella* Walk.) larvae, can cause a decrease in the searching efficiency per individual parasitoid. After repeated contacts the parasitoids walked or flew away from the area.

The wasp density and host instar significantly affected the searching efficiency of *D. semiclausum* (Table A.12). The results showed that increased wasp density at various host instars reduced the efficiency of searching by this parasitoid (Table A.13). This trend agrees with findings by Ooi (1980) and Yang *et al.* (1994). The average A-values varied from 0.041 to 0.573 (Figure 3.7) and these appear to be higher than that of *C. plutellae*. Chua and Ooi (1986) have compared the values of searching efficiency among three parasitoid species attacking the cabbage moth. It was reported that *Diadegma semiclausum* has much higher A-values than *Diadromus collaris* and *C. plutellae*.

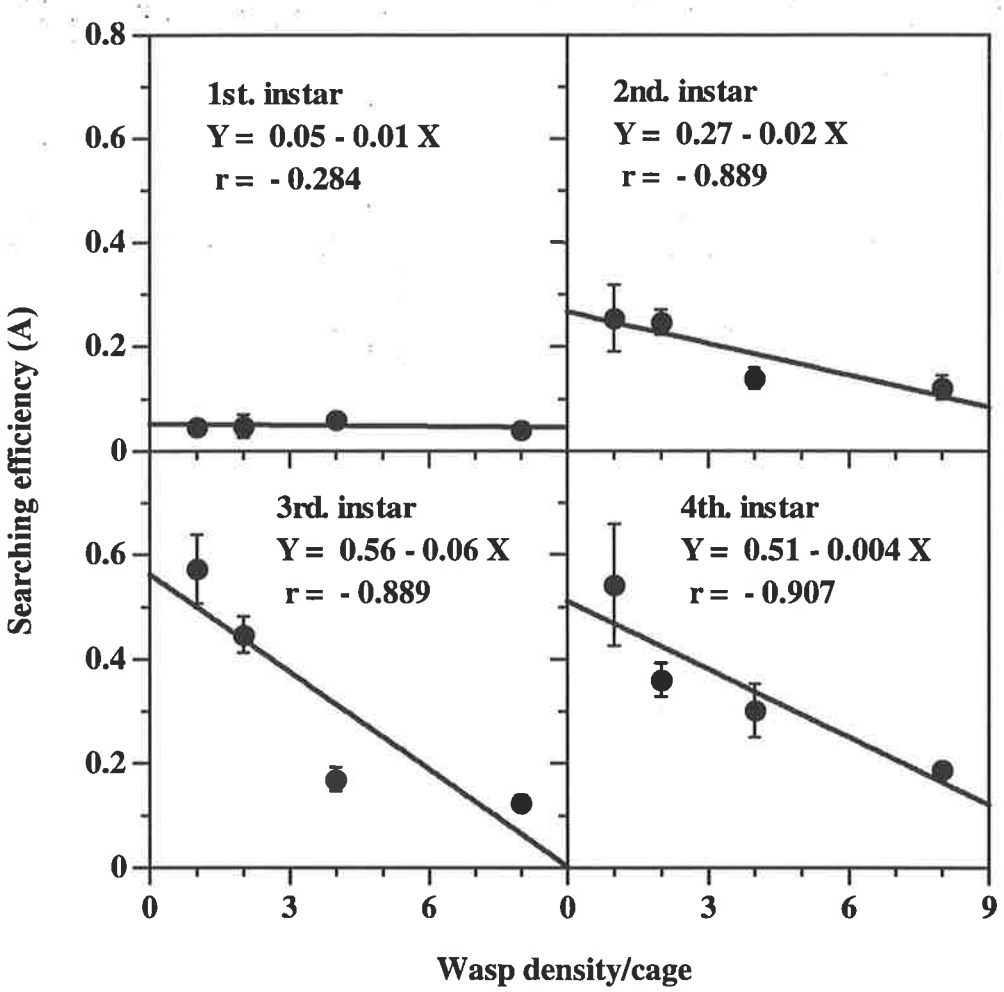

Figure 3.7. The relationship between searching efficiency and the density of female *D. semiclausum* averaged over three replicates (± S.E.M.).

3.3.4. Number of encounters

The wasp density and host instar influenced the number of encounters of *C. plutellae* with its host which was expressed by a strong interaction between treatments (P = 0.011) (Table A.14; Figure 3.8). Ranges of encounters averaged from 1.37 to 30.48 (Table A.15). Because the first instar of cabbage moth mines inside leaves, the wasp has difficulty in finding the host. Thus the number of encounters was low even at high wasp densities. There was no significant difference in the number of encounters among instars

in single releases of the parasitoid. When the wasp density was increased a significant difference of encounters occurred in the larger instars (Table A.15). High wasp densities increased the frequency of encounters (Figure 3.8).

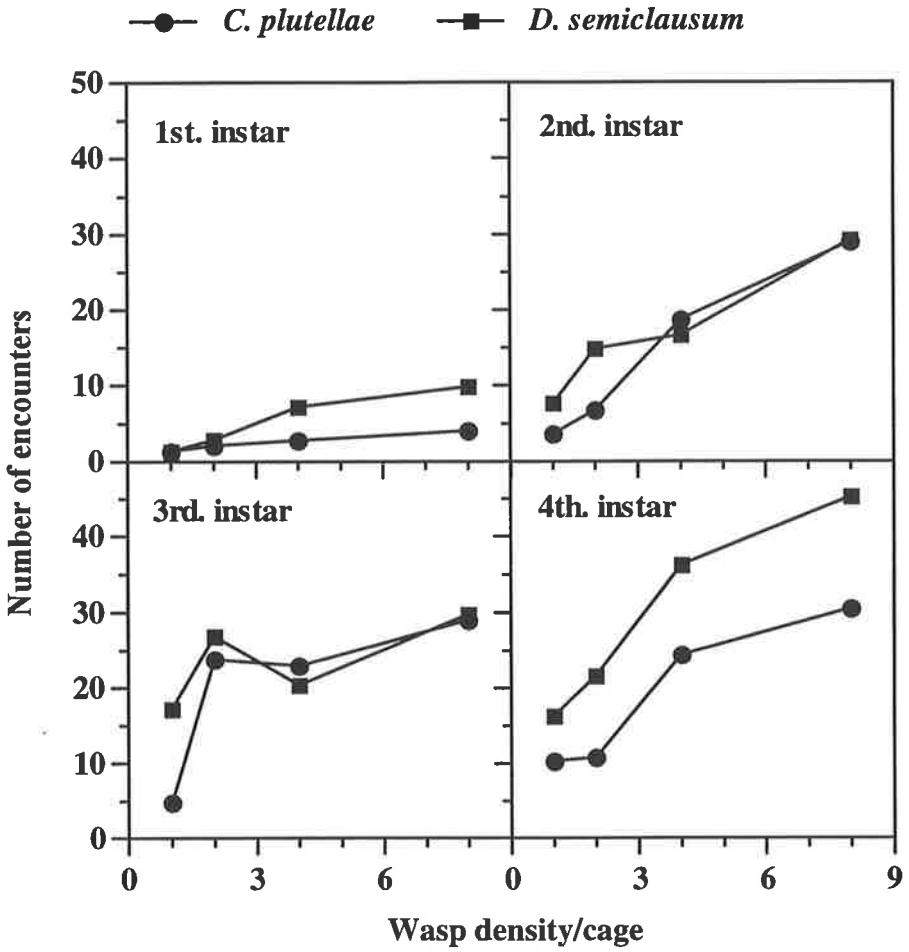

Figure 3.8. Parasitoid encounters on the various host instars averaged over three replicates.

The wasp density and host instar also affected total encounters by *D. semiclausum* with the host. There was a strong correlation between treatments (P = 0.009), where an increase of the wasp density increased the total number of encounters of the parasitoid on hosts (Table A.16; Table A.17). In the limited area of search, waps appeared to find more

hosts of bigger sizes (Figure 3.6). Releases at the high density of parasitoids onto the fourth instar of *P. xylostella* larvae produced the largest total number of encounters. In similar conditions, *D. semiclausum* seemingly possess a higher activity than *C. plutellae* as expressed by greater encounters with hosts. Rogers (1972) explained that many parts of the host area will be visited, if more than one wasp searches, and each host may have a similar chance of being encountered.

CHAPTER 4

EFFECT OF CONSTANT TEMPERATURES ON PARASITISATION, DEVELOPMENT, SIZE AND FECUNDITY OF PARASITOIDS

4.1. INTRODUCTION

Populations of cabbage moth and its habitual parasitoids fluctuate from season to season depending on factors such as temperature, wind velocity, rainfall and host plant availability (Harcourt, 1986).

Under natural conditions, climate and the weather influence the physiology and behaviour of insects (Varley *et al.*, 1973). They affect insect populations, by changing the survival, development, reproduction and endocrine activity. For instance, Ullyett (1947) monitored the population size and mortality of the cabbage moth in South Africa. With the rains the environment became favourable for the quick spread of fungal diseases of the larvae and the pathogen caused high mortality. The wet weather also inhibited for the activities of parasitoids so that the percentage of parasitised larvae fell. In Indonesia, the life-cycle of *P. xylostella* varies according to temperature (Vos, 1953). At Pacet (highland area) in West Java where temperature ranges from 16 to 25 ^{o}C, the average life-cycle is 21 days for cabbage moth and 18 to 20 days for the parasitoid *D. semiclausum*. Parasitism of this pest by *D. semiclausum* reached 86 to 89 %. In contrast, at Bogor (lowland area) with a temperature range from 25 ^{o} to 30 ^{o}C the life-cycle is only 15 days.

Temperature influences the development of insects (Campbell *et al.*, 1974; Liu *et al.*, 1995), and each stage may respond differently to temperature (Gordon, 1984). Since temperature seems to be fairly easily controlled and measured, it has been a routine procedure to study its effect upon species of economic importance (Howe, 1967). Under a controlled environment in the laboratory, Yang *et al.* (1993) observed that there were strongly negative correlation between temperatures and developmental times of the immature stages of the cabbage moth and its parasitoid, *D. semiclausum*. The parasitoid

developed slower at low temperatures and required less time at high temperatures. Temperature also affects the longevity or life span and reproduction of the potato tuber moth parasitoids, *Apanteles subandinus* Blanchard and *A. scutellaris* Muessbeck. Although variation occurred in response to different temperatures, these parasitoids in general lived shorter and produced fewer progeny at high temperatures (Cardona and Oatman, 1975). Temperature can also affect the size of insects. The rearing of *Orius sauteri* Poppius (Heteroptera: Anthocoridae) at different temperatures resulted in various adult body sizes. Both sexes were small when reared at high temperature (Nakata, 1995).

The inverse of the developmental time, whether estimated as mean, shortest period, or median, is frequently treated as the rate of development (Howe, 1967; Nakata, 1995). The median is favoured when estimating the developmental rate (Messenger and Flitters, 1974) because it is influenced much less by abnormal values as found in the mean, and, given that sufficient observations have been made, one does not have to decide whether or not to get rid of doubtful values. With homogenous results, it is even simpler to get the median though it is advisable to test the curve of distribution and to consider the effect of the experimental technique on raw data (Howe, 1967; Stanley, 1946).

The developmental rate curve at the lower thermal limit is asymptotically near the point of zero development, since insects frequently live for a long time at low temperatures without any development or they develop slowly. The rate of development becomes proportional to temperature as temperatures increase from a lower limit (Wagner *et al.*, 1984). Beyond the optimum or at high temperatures, more individuals die when temperatures are increased.

Superparasitism takes place when any individual host is parasitised by two or more primary parasitoids of the same species (Strand and Godfray, 1989). The second clutch of eggs (the clutch may consist of a single egg) may be laid by the same female and this is called self-superparasitism, or by other females from same species which is called conspecific superparasitism (van Dijken and Waage, 1987; Waage, 1986).

Multiparasitism occurs if a parasitoid oviposits on a host that has previously been parasitised by another parasitoid of a different species (Smith, 1916). Self-superparasitism will in many instances be a waste of either eggs or time (Waage, 1986). On the other hand, in solitary parasitoids, two eggs placed in a host may be advantageous against the host's defence system, or enhance the possibility that one of its own offspring beats a superparasitoid (Godfray, 1994).

The following experiments were carried out to investigate the effect of various constant temperatures on *C. plutellae* and *D. semiclausum* of the cabbage moth in terms of the parasitism and self-superparasitism, development, size and fecundity.

4.2. Materials and methods

4.2.1. Parasitisation at various constant temperatures

Rate of parasitism

An experiment to detect the rate of parasitism of cabbage moth larvae by parasitoids at different constant temperatures was conducted in the laboratory. The relative humidity was 75%. The stabilisation of relative humidity in each chamber was controlled by a cup of saturated sodium chloride solution (Rockland, 1960). This solution is commonly used in a variety of temperature ranges because it is cheap, convenient and harmless to insects (O'Brien, 1948). The third instar of cabbage moth and 2 - 5 day old gravid female wasps were used in this study.

The rate of parasitism was assessed by exposing the parasitoids to the cabbage moth larvae within containers at various constant temperatures. Each treatment consisted of a plastic cup (11.5 cm and 9.5 cm for top and bottom diameters, 6.5 cm high) containing 20 third instars which were feeding on a cabbage leaf. The cup was then left for 16 hours. On the next day, the female wasp was liberated into the cup and put into an incubator with adjusted temperature for 24 hours. Temperatures were 4 ^{o}, 8 ^{o}, 12 ^{o}, 15 ^{o}, 20 ^{o}, 25 ^{o}, 30 ^{o}

and 35 °C. Each was replicated four times. A randomised complete block design (Gomez and Gomez, 1984) was used in this experiment. After the incubation, the treated larvae were dissected under a binocular microscope to quantify the parasitisation. The hypothesis of this test was that different temperatures affected searching and oviposition activities of parasitoids. Rates of parasitism were calculated by the ratio of parasitised larvae to the total numbers of hosts (van Driesche, 1993).

Self-superparasitism

This experiment was conducted to detect the likelihood of parasitoids to superparasitise hosts at different constant temperatures. Two to four-day old female wasps and cabbage moth larvae from various instars were the subject of the experiment. Each treatment contained a female wasp and a cabbage moth caterpillar on a piece of cabbage leaf. They were subsequently placed in a small plastic cup (6.8 cm and 5.8 cm for top and bottom diameters; 5 cm high) with a lid. The cup was put in an incubator for 24 hours. Temperatures were 15 °, 20 °, 25 °, 30 ° and 35 °C. *Cotesia plutellae* and *D. semiclausum* were used in this experiment. A randomised complete block design was used and each had four replicates. After incubation, the treated larvae were dissected. It was hypothesised that self-superparasitism would vary according to temperature. Self-superparasitism was quantified by counting the number of parasitoid eggs in each host.

4.2.2. Parasitoid development

This experiment was done to investigate the developmental time and rate of completion of immature stages of *C. plutellae* and *D. semiclausum* and their life span of their adult stage. To obtain host larvae parasitised by *C. plutellae*, a gravid female wasp (two to five days old) was released into a plastic cup (11.5 cm and 9.5 cm for top and bottom diameters, cm high, or volume: 500 ml) with a ventilated lid containing a number of third instar larvae of the host. Before exposure, the larvae were released on a piece of

cabbage leaf and left for about three hours. Parasitised larvae were immediately collected and were put into small plastic cups (6.8 cm and 5.8 cm for top and bottom diameters, 5.0 cm high, or volume: 160 ml) with ventilated lids containing fresh leaf pieces. These cups were then placed into incubators (15 °, 20 °, 25 °, 30 ° and 35 °C). The food for parasitised hosts was checked daily and was changed if necessary. Variables observed in this study were time periods required from egg to pupation, pupal and adult stages. Emerging pupae were placed into vials (5.0 cm long, 1.3 or 1.7 cm diameter) with ventilated lids, and honey was smeared on the inner tops of vials. When adult wasps emerged, a drop of water was provided daily in each vial. In addition, pure honey was added if required.

To obtained host larvae parasitised by *D. semiclausum*, a different technique was used since this wasp did not lay as many eggs as *C. plutellae* using the cup as an oviposition arena. After the female *D. semiclausum* laid one egg in a host, she flew or walked away to the top or side of the cup. Within one hour of exposure, this method produced only 2 to 3 caterpillars by parasitised *D. semiclausum* compared to around 8 to 13, or more parasitised by *C. plutellae*. Therefore, another container, was chosen as an egg laying arena for *D. semiclausum*. A gravid female was placed in a glass vial (5.7 cm long and 1.8 cm diameter) and was offered a third instar larva of the host. When it was parasitised, the host was then placed into a cup with a ventilated lid which contained a piece of fresh cabbage leaf. Then another unparasitised host was exposed to the female wasp. A fine brush was used to transfer caterpillars from the plant to the oviposition vial. After a period of time the wasp was left to rest and it was fed a drop of honey and water inside the ventilated vial. Parasitised larvae in cups were subsequently incubated at various temperatures (15 °, 20 °, 25 °, 30 ° and 35 °C). The same data were collected as were gathered for *C. plutellae*.

Data dealing with developmental times were plotted after quantifying the means and confident intervals. For *C. plutellae*, five individuals were reared for each replicate,

and four replicates were used in the test. For *D. semiclausum*, 10 individuals were used as 10 replications to analyse the data. It was hypothesised that temperature would affect the development of cabbage moth parasitoids.

Life stages of *C. plutellae* and *D. semiclausum* from egg to pupation and pupae were converted to developmental rates by inverting their developmental times. Life spans of parasitoid adults were also converted to aging rates by taking their reciprocals. The relationship between developmental rates of parasitoid life stages and temperature was fitted to curves by the Pest Model Design System or PMDS (Logan, 1988). The best fit model was considered to be that with the highest adjusted coefficient of determination.

Three models were used to represent the relationship between temperature and rate of development:

Linear. The linear curve is given by,

$$r(T) = p(T - T_b) \tag{1}$$

where $r(T)$ is the developmental rate (1/days), and the x intercept (T_b) and the slope (p) are estimated with standard linear regression procedures.

Exponential. This type of curve is given by,

$$r(T) = \psi e^{pT} \tag{2}$$

Parameter estimation is achieved by first transforming the observed developmental rates to linear form by $r_i^T = \ln(r_i)$ for the observed rates of r_i, and transformed temperature (T^T) counted as $T^T = T_i - T_{min}$, where T_{min} is the minimum observed temperature. Parameters are subsequently regressed linearly by plotting r_i^T on T_i.

Stinner. This functional form is,

$$r(T) = \frac{C}{(1 + e^{k_1 + k_2(T)})} \qquad \text{for } T \leq T_0 \tag{3a}$$

$$r(T) = \frac{C}{(1 + e^{k_1 + k_2(2T_0 - T)})} \qquad \text{for } T > T_0 \tag{3b}$$

where T_0 is optimum temperature or temperature at which the maximum developmental rate take places, and C is the asymptote, k_1 and k_2 are empirical constants (Stinner *et al.*, 1974 and 1975).

4.2.3. Size and fecundity

The size and fecundity of adult *C. plutellae* and *D. semiclausum* were studied under laboratory conditions at various temperatures (15, 20, 25, 30 and 35 °C). Parasitised cabbage moth caterpillars (third instars) were placed in small cups containing cabbage leaves. They were then held at various temperatures until the adult emerged. The head width and length of hind tibia of the parasitoids of both sexes were measured. The egg load of female parasitoids was used to measure their fecundity by dissecting the abdomen. Then the ovary of the female was placed in a drop of methylene blue solution (0.03 % in 50 % ethanol) on glass slides. A few minutes later, it was opened to quantify the number of eggs stained by the methylene blue. All dissections and measurements were done under a binocular microscope.

Sample of sizes for each temperature were of 12 individuals of *C. plutellae* and 10 individuals of *D. semiclausum*. Data were processed by the analysis of variance in a randomised complete block design that were run in Genstat 5 (Lane *et al.*, 1987).

4.3. Results and Discussion

4.3.1. Parasitisation at various constant temperatures

Rate of parasitism

Different constant temperatures strongly affected the rate of parasitism of cabbage moth larvae by *C. plutellae* (Figure 4.1; Table A.18). Females only laid a few eggs when kept at low temperature. However, they were more active as the temperature increased.

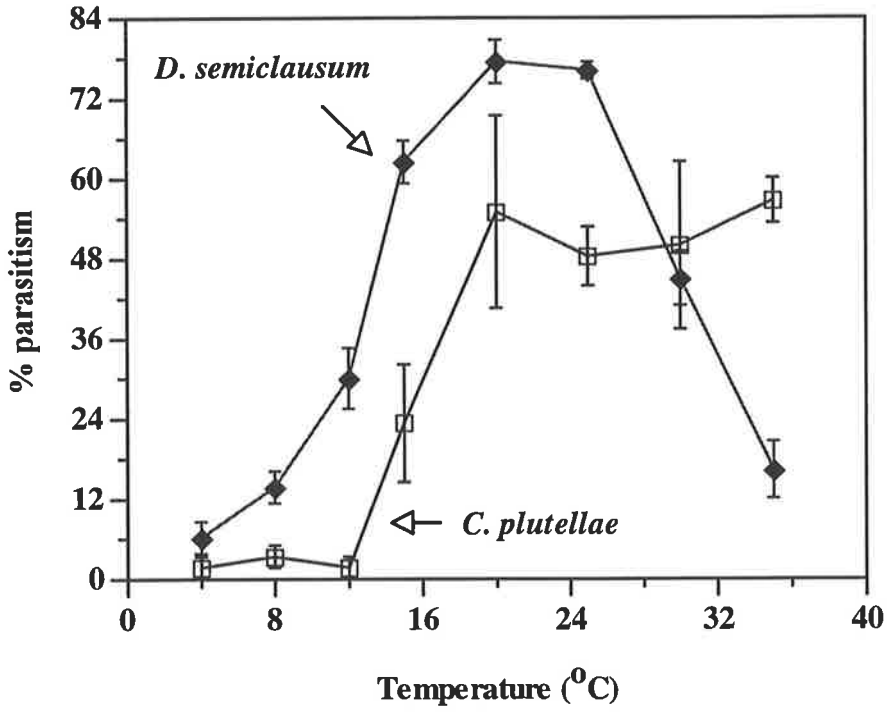

Figure 4.1. Rates of parasitism of cabbage moth larvae by *C. plutellae* and *D. semiclausum* at different constant temperatures over 4 replicates. Points indicate means ± S.E.M.

Parasitism was greatest at temperatures of 20 - 35 °C, and ranged from 1.2 - 56.2% overall (Table A.20). Parasitism by *D. semiclausum* also varied with temperature (Table A.19), but its response was different when compared to *C.plutellae*. Parasitism by *D. semiclausum* peaked at 20 °C, and ranged from 6.2 - 77.5 % (Table A.20).

It is crucial to note that this experiment provides an index of the activity of parasitoids over the range of temperatures that was tested. The data reflect both the searching activities of the parasitoids and the defensive behaviour of *P. xylostella*. Talekar and Yang (1991) found that the suitable range of temperature for the activity of *D. semiclausum* was 15 - 25 °C, whereas *C. plutellae* parasitised many hosts at a temperature range of 20 - 35 °C.

In the tropics, some brassicas such as common white cabbages, chinese cabbages and cauliflowers are grown in the highlands where temperatures are low throughout the

year. Other brassica species are planted in the lowlands where temperature is approximately 25 °C or more throughout the year (Talekar and Yang, 1991). In Taiwan, releases of *D. semiclausum* imported from Indonesia were not successful in the lowland brassica-growing areas in 1985 (Asian Vegetable Research and Development Center, 1986). But, when this ichneumonid was liberated in the highlands, it controlled cabbage moth, and up to 70% parasitism was recorded within one season (Asian Vegetable Research and Development Center, 1988). In Taiwan *C. plutellae* is mainly effective in the lowlands (Talekar and Yang, 1991). In Indonesia and Taiwan, *D. semiclausum* has currently been established in the highlands (Sastrosiswojo and Sastrodihardjo, 1986; Talekar and Yang, 1991; Vos, 1953). Furthermore, in tropical and subtropical regions, *C. plutellae* has established in hot lowlands where *D. semiclausum* has failed to establish. In contrast, *D. semiclausum* is established in cooler regions where *C. plutellae* is very rarely encountered (Wilson, 1960; Yang *et al.*, 1994). Based on the results of my experiment, *C. plutellae* is best suited for release in warm areas and *D. semiclausum* in cool areas.

Self-superparasitism

Both host instar and temperature influenced self-superparasitism by *C. plutellae* (Figure 4.2; Table A.21). The females laid fewer eggs on small hosts at temperatures of 15 ° - 35 °C. Larger host larvae were stung more frequently at temperatures of 25 ° - 30 °C. The maximum number of eggs laid averaged 45.5 on third instars at 25 °C and 46 on fourth instars at 30 °C (Table A.22). At all four instars, there was a sharp reduction in egg deposition by *C. plutellae* at 30 - 35 °C.

For the first instar, *Diadegma* laid slightly more eggs than *C. plutellae* did, particularly in the range of 20 - 30 °C. However, for the other instars, this ichneumonid laid fewer eggs than *Cotesia* at 20 - 30 °C.

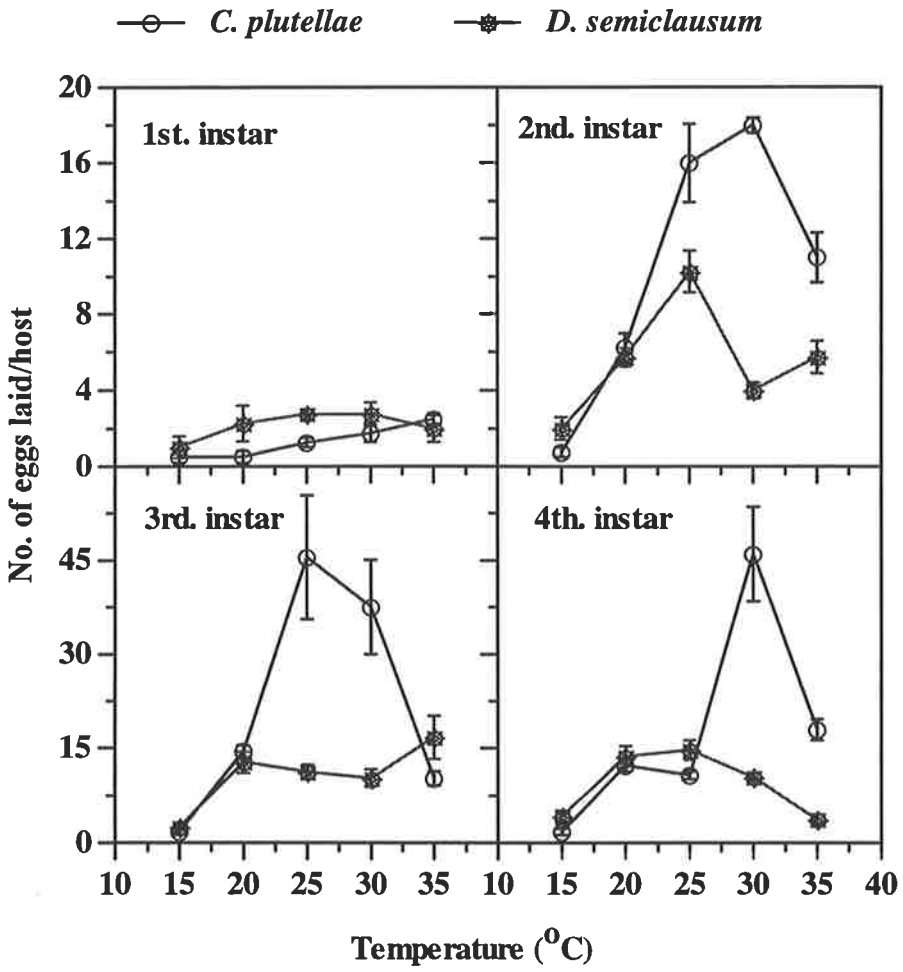

Figure 4.2. Influence of temperature on self-superparasitism of cabbage moth larvae by *C. plutellae* and *D. semiclausum*. Points show numbers of eggs laid over 4 replicates (mean ± S.E).

D. semiclausum is reported to discriminate between parasitised and unparasitised hosts (Hofsvang, 1990). In the laboratory, Legaspi (1986) studied host discrimination in two ichneumonid species, *Diadegma* spp., parasitising larval *P. xylostella*. The parasitoid *D. semiclausum* preferred to deposit eggs in unparasitised larvae and avoided patches containing parasitised larvae. Another wasp, *D. fenestralis*, showed no discrimination. In the extreme conditions of my experiment, this discrimination failed to prevent superparasitism by *D. semiclausum*.

4.3.2. Development and life span of parasitoids at various constant temperatures

Developmental time and life span

Variations in temperatures strongly influenced the developmental time of *C. plutellae* from egg to pupation and its pupal stage (Figure 4.3; Table A25).

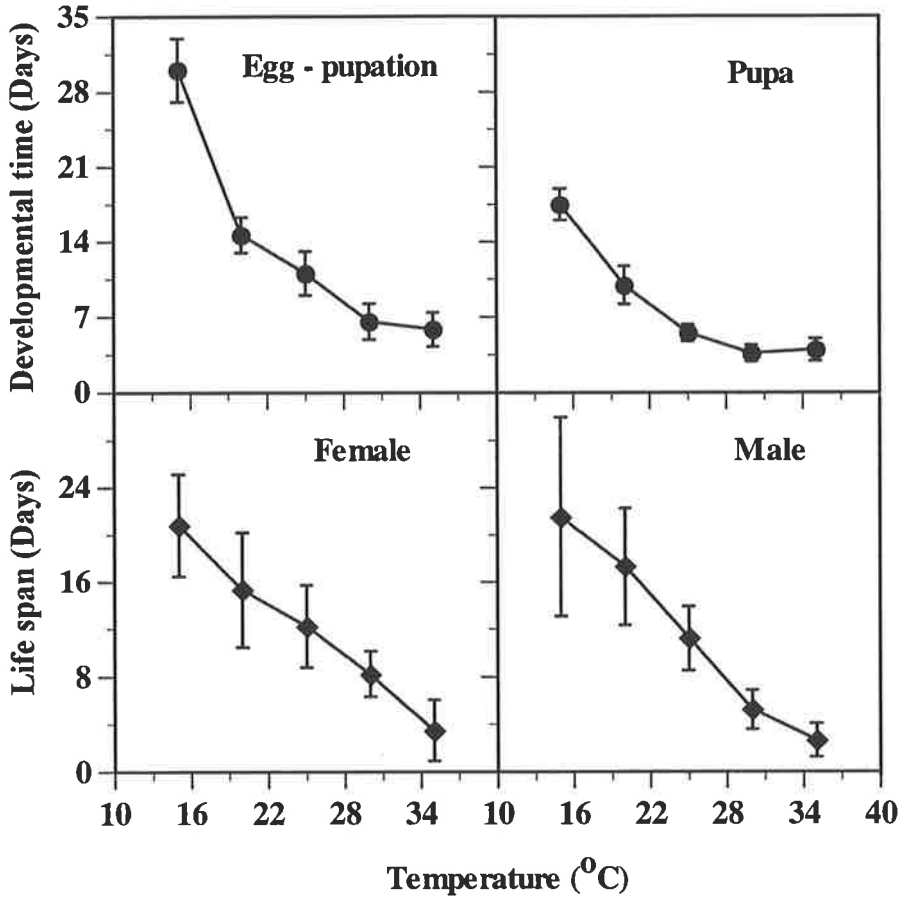

Figure 4.3. Influence of temperature on the developmental time and life span of *C. plutellae*. Points indicate the developmental time and the life span over 4 replicates ± C.I. (Confident Interval).

Temperature also strongly affected the life span of both sexes (Figure 4.3; Table A.26). The adult parasitoid lived longest at low temperatures and shortest at high temperatures. In addition, the longevity of males was shorter at high temperatures than

that of females. Similarly it was found that when temperature increased life duration of both immature stages and adults of *Apanteles subandinus* became shorter (Cardona and Oatman, 1975).

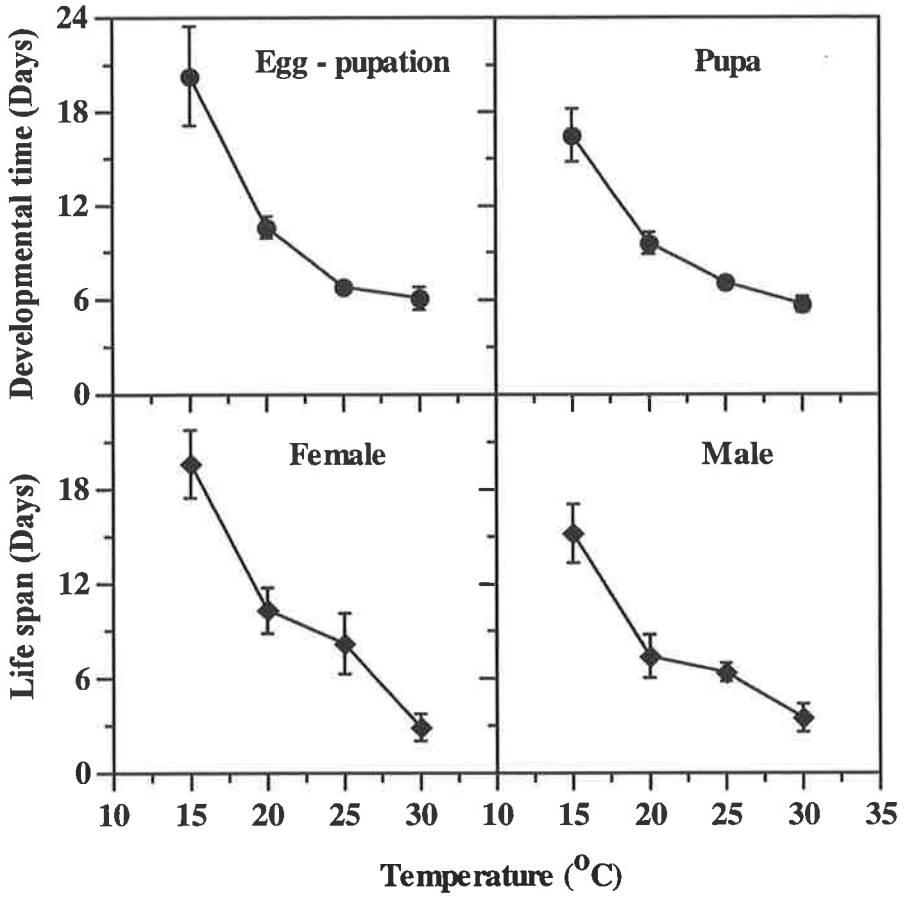

Figure 4.4. Influence of temperature on the developmental time and life span of *D. semiclausum*. Points indicate the developmental time and the life span over 10 replicates. Points indicate mean ± C.I.

Temperatures strongly influenced the developmental time of *D. semiclausum* from egg to pupation and its pupal stage (Figure 4.4; Table A.27). The life span of both sexes was also affected by different constant temperatures (Figure 4.4; Table A.28).

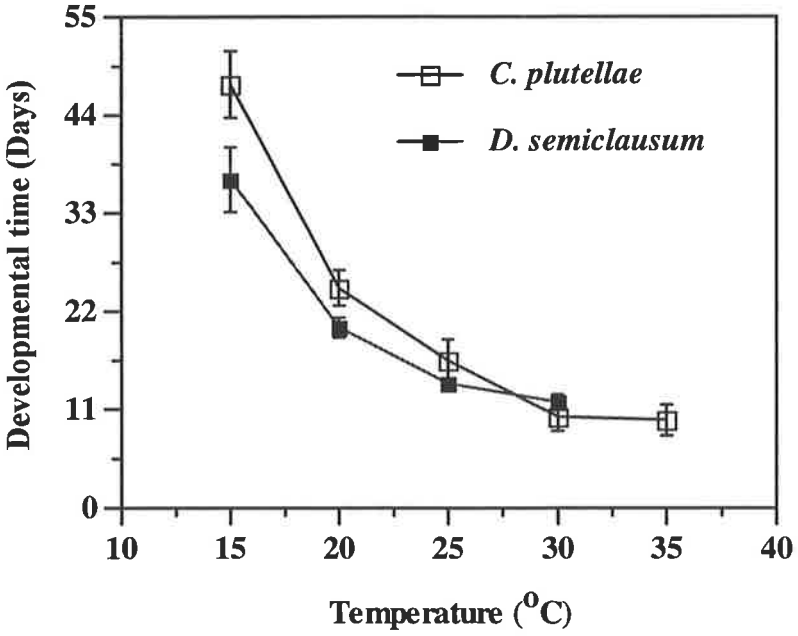

Figure 4.5. Influence of temperature on the developmental time of *C. plutellae* (4 replicates) and *D. semiclausum* (10 replicates) from oviposition to adult emergence. Points show the developmental time. Points indicate mean ± C.I.

The results of this experiment agree with the findings by Yang *et al.* (1993) that temperature affects the development of immature stages for *D. semiclausum*. In their study, they could observe the development of immature stages at 35 °C, where it did not occur in my experiment due to the death of most reared immatures at this temperature. When compared with the other parasitoid, the developmental time from egg to adult emergence for *D. semiclausum* is shorter than *C. plutellae* at 15 °C and a little bit longer at 30 °C (Figure 4.5; Table A.24).

Observations on the development of *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae), an egg parasitoid of *Podisus maculiventris* Say., have been made in the laboratory (Yeargan, 1980). At eight different temperatures, the wasps that developed from egg to adult were monitored in hosts over a temperature range of 15.5 ° - 32.2 °C. Males failed to emerge at 15.5 ° and 32.2 °, whereas females did not emerge from pupae at 32.2 °C. The reason why they did not emerge at those temperatures are not known.

Rate of development and aging

Cotesia plutellae

Data of medians and models of rates of development for *C. plutellae* are presented in Figure 4.6. The developmental rate of this parasitoid from egg to pupation over a temperature range of 15 - 35 ^{o}C was explained by the linear model : $r(T) = 0.007(T - 10.32)$, where the choice of model was based on adjusted coefficient of determination = 0.986. The median values ranged from 0.03 - 0.17 at 15 - 35 ^{o}C (Table A.39).

The development of pupae was fitted to the Stinner model, which was described by the equation:

$$r(T) = \frac{0.3}{(1+e^{4.71-0.21T})} \qquad \text{for } T \leq 32.2$$

$$r(T) = \frac{0.3}{(1+e^{4.71-0.21(2x32.2-T)})} \quad \text{for } T > 32.2.$$

The optimum temperature was approximately 32.2 ^{o}C to reach a maximum predicted rate of development (adjusted coefficient of determination = 0.952; Figure 4.6; Table A.39).

The developmental rate of *C. plutellae* from egg to adult emergence was described by the Stinner model (adjusted coefficient of determination = 0.989; Table A.39). The model was fitted by the equations:

$$r(T) = \frac{0.4}{(1+e^{4.48-0.11T})} \qquad \text{for } T \leq 32.5$$

$$r(T) = \frac{0.4}{(1+e^{4.71-0.21(2x32.5-T)})} \qquad \text{for } T > 32.5.$$

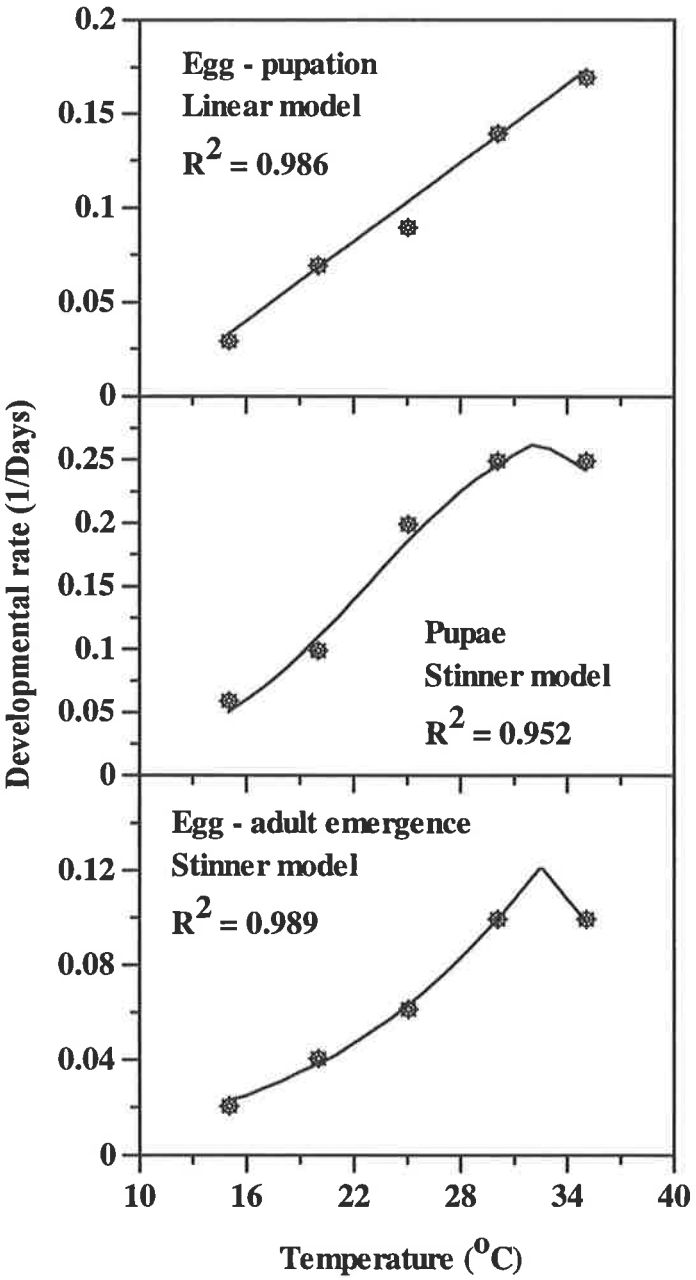

Figure 4.6. Relationship between temperature and rate of development of *C. plutellae* in immature stages. Points indicate medians of observed developmental rates, solid lines represent predicted rates.

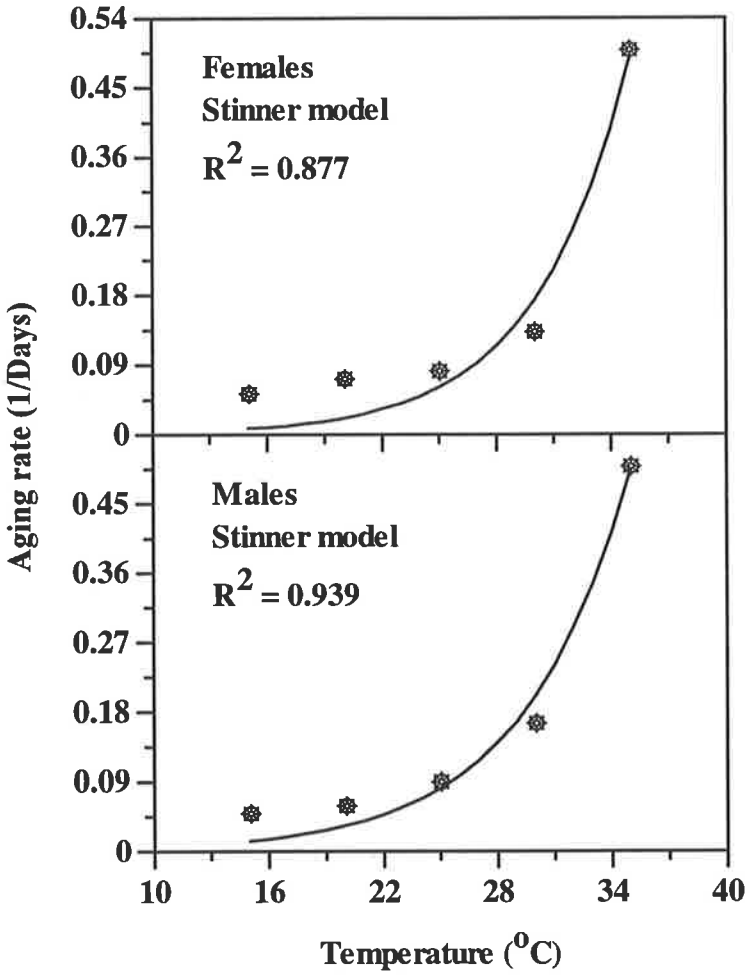

Figure 4.7. Relationship between temperature and aging rate of adult *C. plutellae*. Points are observed median rates and solid lines indicate predicted rates.

Aging rates of *C. plutellae* adults were fitted to the non-linear Stinner model. The predicted lines are similar for the sexes, the adjusted coefficient of determinations = 0.877 and 0.939 for females and males, respectively (Figure 4.7; Table A.40). The aging rate of the adults were explained by the following equations:

$$r(T) = \frac{39.8}{(1+e^{11.71-0.21T})} \qquad \text{for females}$$

$$r(T) = \frac{69.35}{(1+e^{11.27-0.18T})} \qquad \text{for males.}$$

Diadegma semiclausum

The development from egg to pupation in *D. semiclausum* was fitted to the non-linear Stinner model over 15 - 30 ^{o}C (adjusted coefficient of determination = 0.960; Figure 4.8; Table A. 41) by the equation:

$$r(T) = \frac{0.23}{(1+e^{4.17-0.20T})}.$$

Variation in the developmental rates of pupae were non-linear and the best fit was the Stinner model (adjusted coefficient of determination = 0.972; Figure 4.8; Table A. 41). The curve for this stage of was fitted by the equation:

$$r(T) = \frac{0.19}{(1+e^{3.59-0.19T})}.$$

The development from egg to adult emergence of *D. semiclusum* over 15 - 30 ^{o}C was fitted to the non linear Stinner equation model (adjusted coefficient of determination = 0.999; Figure 4.8; Table A.41). It was described by the equation:

$$r(T) = \frac{0.10}{(1+e^{3.36-0.17T})}.$$

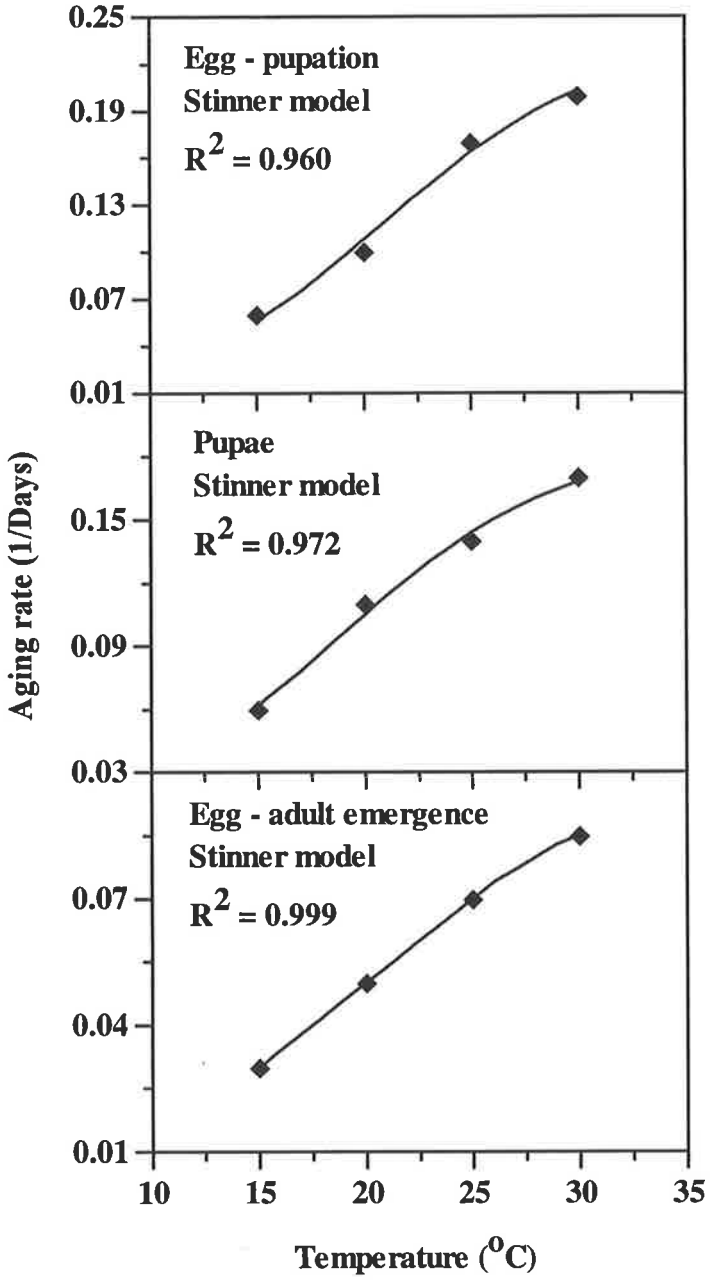

Figure 4.8. Relationship between temperature and developmental rates of *D. semiclausum*. Points are observed median rates and solid lines indicate predicted rates.

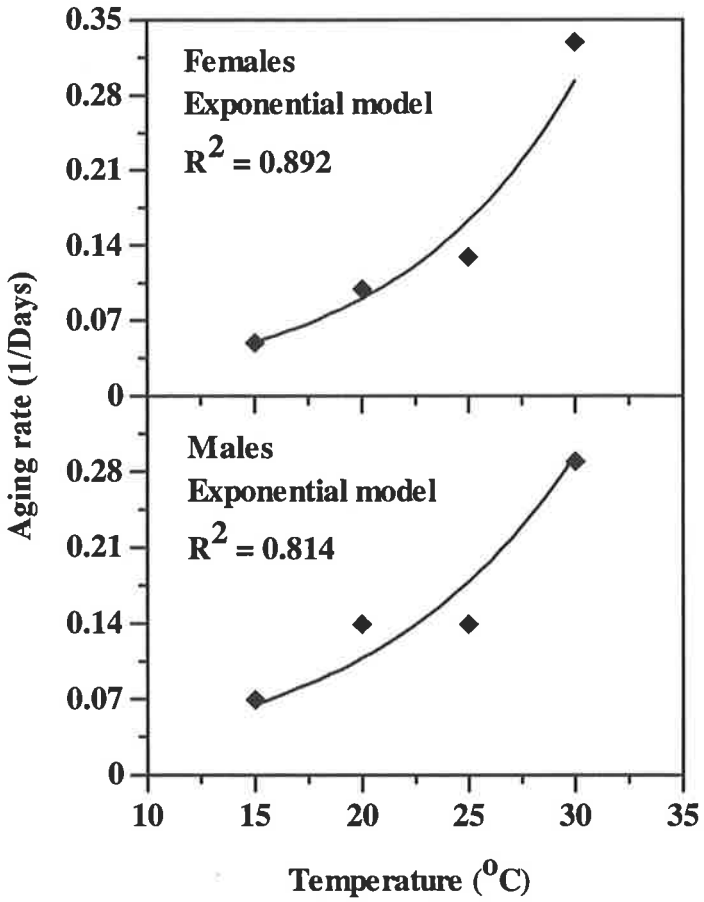

Figure 4.9. Relationship between temperature and aging rate of adult *D. semiclausum*. Points indicate observed rates and solid lines are predicted rates.

The aging rate of both sexes of *D.* were best fit by the exponential model over 15 - 30 ^{o}C (Figure 4.9; Table A.42). Aging was explained by equations: $r(T) = 0.05 \times e^{(0.12T)}$ for females (adjusted coefficient of determination = 0.892), and $r(T) = 0.07 \times e^{(0.08T)}$ for males (adjusted coefficient of determination = 0.814).

Variations in development of the immature stages of *C. plutellae* and *D. semiclausum* were mostly non-linear, except the egg to pupation rate of the first wasp fitted a linear model. A regression analysis of the developmental rate from egg to adult emergence of *Apanteles subandinus*, a potato tuber moth parasitoid, was reported for a

temperature range of 60 - 90 ^{o}F (15.5 - 32.2 ^{o}C) and a linear model was obtained in this case (Cardona and Oatman, 1975). By quantifying the inverse of developmental period, within the temperature range of 15 - 35 ^{o}C immature stages (eggs - pupae) of *D. semiclausum* showed a slow rate of development at low temperature and a faster at high temperature (Yang *et al.*, 1993).

4.3.3. Size and fecundity

Cotesia plutellae

Temperature affected the size of females and males. Head widths were larger at cool temperatures than at higher temperatures, and ranged from 0.602 - 0.647 mm for males and 0.603 - 0.660 mm for females. The influence of temperature on the size of hind tibia of the parasitoid was also very strong. Variation in the size of hind tibia of females was more pronounced than in males. The hind tibia was smaller when wasps were reared at high temperatures. The length of hind tibia averaged from 0.774 - 0.852 mm for females and 0.705 - 0.835 mm for males (Table 4.1; Table A.29, A.30, A.31, A.32). There was no detectable influence of temperature on the egg load of this wasp (Table A.33). Within the range of 15 - 35 ^{o}C the egg load averaged 208.6 - 326.3 (Table 4.2).

Table 4.1. Means for sizes of *C. plutellae* maintained at different constant temperatures.

Temperature (°C)	Sizes (mm ± SEM)			
	Head width		Length of hind tibia	
	Males	Females	Males	Females
15	0.647 ± 0.008	0.660 ± 0.013	0.835 ± 0.024	0.852 ± 0.023
20	0.621 ± 0.009	0.628 ± 0.012	0.806 ± 0.020	0.851 ± 0.020
25	0.621 ± 0.011	0.650 ± 0.006	0.809 ± 0.015	0.837 ± 0.013
30	0.607 ± 0.013	0.603 ± 0.015	0.775 ± 0.024	0.785 ± 0.021
35	0.602 ± 0.002	0.603 ± 0.009	0.705 ± 0.010	0.774 ± 0.003

However, there was a strong correlation between length of hind tibia and egg load (Figure 4.10). Individuals which had a long hind tibia produced a greater number of eggs. Fecundity in most insects varies with the body size of the females, as measured by dry weight or length of a part of the body (e.g. head, thorax and tibia) (Honek, 1993). Individuals which possess a long hind tibia should also have a big body. Big female parasitoids can be expected to have a high fecundity and conversely small ones yield a lower egg load. Therefore it can be concluded that temperature does affect egg load since there is an effect of temperature on size. This effect was not detected statistically because there is large variation in egg load among females.

Diadegma semiclausum

Over the range 15 - 30 °C, temperature strongly affected the head width of *D. semiclausum* (Table A.35; Table A.36). Females had a range of head widths of 0.902 - 1.013 mm and the range for males was 0.875 - 0.965 mm (Table 4.3). Both females and

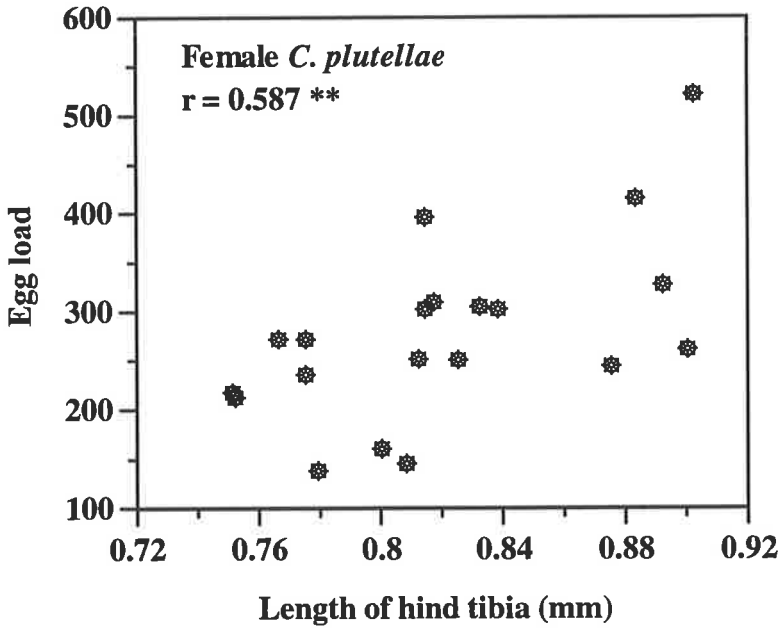

Figure 4.10. Relationship between hind tibia and egg load of *C. plutellae*. ** = $P < 0.01$ and n = 20.

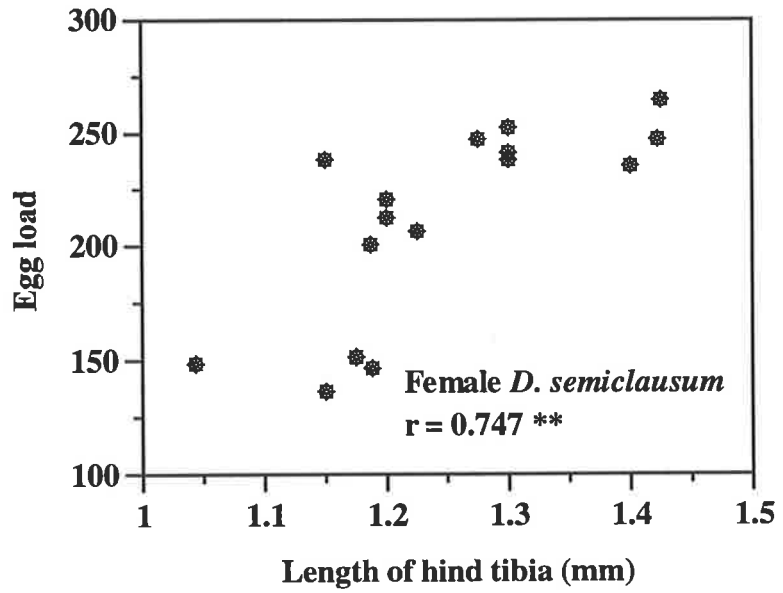

Figure 4.11. Relationship between hind tibia and egg load of *D. semiclausum*. ** = $P < 0.01$ and n = 16.

males had a significant variation in their length of hind tibia at various constant temperatures and their sizes ranged from 1.139 - 1.387 mm for females and 1.073 - 1.296 for males (Table A.37; Table A.38; Table A4.3). The egg load of *D. semiclausum* varied with temperature (Table A.34). In the range 15 - 30 ^{o}C, the egg load

Table 4.2 Means for egg loads of *C. plutellae* and *D. semiclausum* kept at various constant temperatures.

Temperature	Egg load ± S.E.M.	
(^{o}C)	*C. plutellae*	*D. semiclausum*
15	308.9 ± 37.6	247.0 ± 6.5
20	326.3 ± 77.0	245.5 ± 3.1
25	301.7 ± 35.2	210.5 ± 4.2
30	224.7 ± 29.3	146.2 ± 3.2
35	208.6 ± 29.3	*

* No development at 35 ^{o}C.

Table 4.3. Means for sizes of *D. semiclausum* maintained at different constant temperatures.

Temperature	Sizes (mm ± S.E.M.)			
(^{o}C)	Head width		Length of hind tibia	
	Males	Females	Males	Females
15	0.965 ± 0.013	1.013±0.024	1.296±0.033	1.387±0.029
20	0.951 ± 0.015	0.961±0.013	1.217±0.031	1.256±0.036
25	0.910 ± 0.014	0.925±0.010	1.170±0.033	1.203±0.008
30	0.875 ± 0.009	0.902±0.025	1.073±0.012	1.139±0.033

varied from 146.2 - 247.0 where the highest fecundity was observed at lowest temperature. (Table 4.2). There was a strong correlation between length of hind tibia and egg load of this parasitoid (Figure 4.11). This indicates that large females produces the largest numbers of eggs as a result of a environmental conditions during development. It appears that the female *D. semiclausum* has a lower fecundity than *C. plutellae*, even though they experienced a similar stress under unfavourable high temperatures (Table 4.2; Figure 4.10; Figure 4.11). At 35 ^{o}C *D. semiclausum* failed to survive, while *C. plutellae* developed rapidly at this temperature.

CHAPTER 5

RELEASES OF PARASITOIDS FOR THE CONTROL OF CABBAGE MOTH IN GLASSHOUSE

5.1. Introduction

Numerous parasitoids are reported to attack cabbage moth in various stages (Talekar and Yang, 1993). Among them, larval parasitoids predominate in nature. *Cotesia* and *Diadegma* are the two main genera that cause the highest levels of parasitism after releases in many areas of the world. The bulk of these species emanated from Europe in the Mediterranean area where *P. xylostella* is believed to have originated. In the country of origin, natural enemies maintain the pest at low densities. (Talekar, 1990). In Romania for instance, a large number of parasitoids was collected from cabbage fields in Moldavia and they parasitised 70 - 90% of cabbage moth (Mustata, 1992). In Jamaica, releases of *C. plutellae* in early 1989 were successful, and by March 1990 this parasitoid reduced crop damage to 38% from 75% before introduction (Alam, 1992). In Central Taiwan, *D. semiclausum* successfully controls cabbage moth in the highland areas (Talekar, 1992).

Studies of parasitisation of pests by their parasitoids under laboratory conditions indicate that rates of parasitism vary depending on factors such as host instar, host density, wasp density, host plant, photoperiod and ambient temperature (Hassell, 1971; Talekar and Yang, 1991; Vinson and Iwantsch, 1980). This research was conducted to investigate parasitism of larval cabbage moth by two parasitoids at different wasp densities and two times of release in the glasshouse.

5.2. Materials and Methods

It was hypothesised that the density of wasps and release time might affect parasitism by the parasitoids *C. plutellae* and *D. semiclausum*. Parasitisation of cabbage moths by parasitoids was assessed in the glasshouse under ambient conditions in which temperature ranged from 11.5 to 27 ^{o}C. The second or third instar of larval cabbage moth and gravid female wasps were used in these experiments.

Rape seed was grown in seedling trays in the glasshouse. Each tray containing 42 holes (5 x 5 cm) which were filled with fertilised soil, and two seeds were buried in each as deep as 1 cm. The tray was then placed in a cage (56 x 40 x 65 cm) equipped with a sliding door. Plants were watered every two days and fertiliser was added as necessary to stimulate plant growth. When the plants were approximately 30 - 35 days old, 2 pairs of cabbage moth adults were released into the cage for 48 hours. Eggs were allowed to hatch and larvae developed to the second or third instar. Each replicate consisted of 4 cages. The treatments were: density of wasp (1 or 2 pairs) and time of release (morning at 7 am or evening at 7 pm). The wasps were left to parasitise hosts for 24 hours. The experiment was designed in a factorial randomised complete block design and each treatment was replicated five times. After treatments, the larval cabbage moths were collected. Levels of parasitism were measured by dissection or rearing.

The percentage of parasitism (P) was quantified by the equation of Hassell and Varley (1969): $P = 100(u_1 - u)/u_1$, where u_1 is the initial host density and u is the final density of unparasitised hosts. The data were subjected to analysis of variance in Genstat 5 (Lane *et al.*, 1987).

3.3. Results and Discussion

Wasp density affected the rate of parasitism by *C. plutellae*, where higher wasp density increased parasitism (Figure 5.1; Table A.45). Time of release did not affect the level of parasitism, although more host larvae were parasitised when the wasps were

liberated in the evening. There was no significant interaction between wasp density and release time on the rate of parasitism by *C. plutellae* (Table A.43). Numbers of host larvae found ranged from 39.9 to 83.6, and the larvae parasitised by *C. plutellae* ranged 4.2 to 13.4 at various times of releases and wasp densities (Table 5.1).

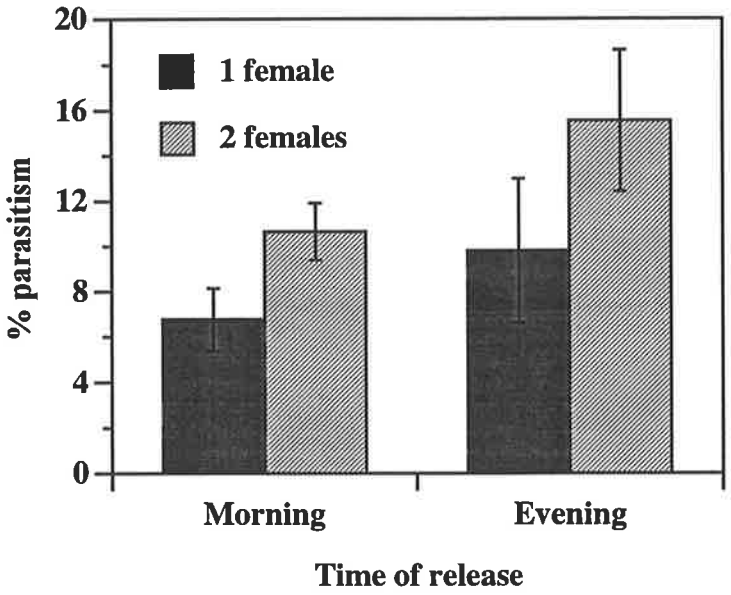

Figure 5.1. Parasitisation of larval cabbage moth by *C. plutellae* at various wasp densities and release times over five replicates in the glasshouse. Values are means ± S.E.M.

Table 5.1. Numbers of larval cabbage moth present in the cages after releases of *C. plutellae* in the glasshouse, averaged over five replicates

Time of release	Wasp density/cage	Total larvae/cage (Mean ± S.E.M.)	Parasitised larvae (Mean ± S.E.M.)
Morning (7 am)	1	55.6 ± 14.2	4.2 ± 1.6
Morning (7 am)	2	46.6 ± 15.2	6.2 ± 3.5
Evening (7 pm)	1	65.8 ± 12.2	6.8 ± 1.7
Evening (7 pm)	2	83.6 ± 33.6	13.4 ± 5.5

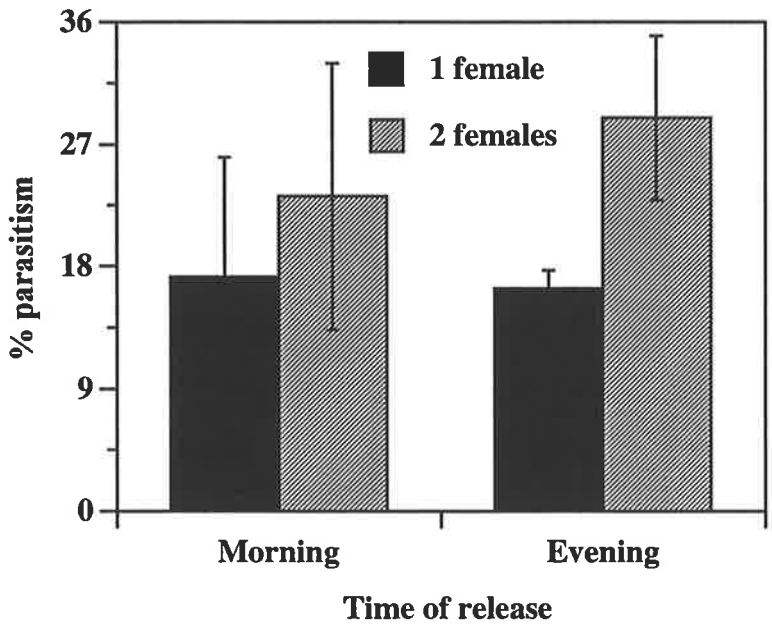

Figure 5.2. Parasitisation of larval cabbage moth by *D. semiclausum* at various wasp densities and release times over five replicates in the glasshouse. Values are means ± S.E.M.

Table 5.2. Numbers of larval cabbage moth present in the cages after releases of *D. semiclausum* in the glasshouse, averaged over five replicates

Time of release	Wasp density/cage	Total larvae/cage (Mean ± S.E.M.)	Parasitised larvae (Mean ± S.E.M.)
Morning (7 am)	1	161.2 ± 9.78	26.6 ± 12.11
Morning (7 am)	2	157.4 ± 11.95	36.2 ± 16.71
Evening (7 pm)	1	158.8 ± 45.43	24.2 ± 4.79
Evening (7 pm)	2	160.8 ± 19.68	44.2 ± 9.04

Neither the time of release nor the number of wasps released affected rate of parasitism by *D. semiclausum* (Figure 5.2; Table A.44). Host larvae found ranged from 157.4 to 161.2, and larvae parasitised by *D. semiclausum* ranged from 26.6 to 44.2 at different times of releases and wasp densities (Table 5.2). Based on the results of glasshouse experiments, parasitism by *D. semiclausum* was higher than *C. plutellae*. However, the experimental conditions differed so direct comparison of the two parasitoids is inappropriate.

Studies of the effect of day and night on parasitism (Chua and Ooi, 1986) indicated that both *D. semiclausum* and *C. plutellae* preferred to deposit eggs during photophase, releases in the darkness reduced the rate of parasitism. Note that both wasps experienced the same morning temperatures, whether released in the morning or in the evening.

It should be noted that there were high levels of variation among replicates in both experiments. Therefore, the lack of a statistically significant effect of increased number of *D. semiclausum* may be due to low statistical power. Also, there is a distinct trend toward higher levels of parasitism when *C. plutellae* was released in the evening. A more powerful experimental design may have detected this. When wasps are released in the evening, they may settle in the cage and initiate normal searching activities in the

morning. In contrast, those released in the morning have no period of inactivity, and thus may be more susceptible to disruption by handling. This could reduce initial searching activities.

CHAPTER 6

PARASITISATION OF CABBAGE MOTH BY *COTESIA PLUTELLAE* IN AUGMENTATIVE RELEASES

6.1. Introduction

Augmentation in biological control is implemented by the rearing and liberartion of natural enemies in conditions where they are absent or present in numbers (Dent, 1991). In developing augmentative control programs using parasitoids, it is important to determine biological, economical and ecological characteristics of the biological agent and procedures. Activities such as handling, rearing and transportation of parasitoids must be tested before release in the field (Ables and Ridgway, 1981).

Cotesia plutellae is one of the major larval endoparasitoids of the cabbage moth, and has been introduced in various subtropical and tropical countries (Lim, 1986). It is reported that this parasitoid is established and provides good control, particularly in lowland areas (Yang *et al.*, 1994). Under laboratory conditions parasitism of cabbage moth by *C. plutellae* is the greatest in the temperature range of 20 - 30 ^{o}C (Chapter 4); Talekar and Shelton, 1993). In Australia, the wasp is established in Australian Capital Territory, Queensland and New South Wales, resulting in a marked reduction of damage to brassicas (Wilson, 1960). In Taiwan, *C. plutellae* failed to provide adequate control of cabbage moth populations. But, when broad spectrum insecticides were replaced by *B. thuringiensis* (BT), this parasitoid became established and improved the level of control, particularly in lowland areas where the temperatures are optimal. In Malaysia, ambient temperatures in certain areas which have similar condition to Taiwan were also

Plate 3. Releases of the parasitoid *Cotesia plutellae* for the control of larval cabbage moth in the field at Lenswood area. A) Experimental plots at the upper site where daily temperatures were recorded by a data logger. B) Experimental plots at the lower site.

favourable for the establishment of *C. plutellae* (Talekar and Shelton, 1993; Talekar and Yang, 1991).

Field experiments were carried out to investigate the potential of laboratory-reared *C. plutellae* for the control of cabbage moth in augmentative releases. In this study, various densities of the parasitoid were released into artificially infested plots of kale.

6.2. Materials and Methods

Parasitisation by the parasitoid was assessed in small plots at the Lenswood Horticultural Research Centre, South Australia. Land was provided at two different widely-separated sites, the upper site (Plate 3A) and the lower site (Plate 3B). Experimental plots were made at each site. Each plot was 2 m wide and 5 m long, while plant spacings for the plot were 40 cm between rows and 20 cm within rows. Eighty young kale plants (≈ 30 days old) grown in a glasshouse were transplanted into the plots. A few days later when it was estimated that the plants had recovered from the stress of transplanting, third instar larvae of cabbage moth were released onto them.

Two hundred larvae were placed on the 80 plants in each plot at random by distributing them according to a Poison probability distribution with parameter $\lambda = 2.5$. The Poison random variable has a representative range of applications in diverse areas and is applicable in conditions where random events take place at certain points in time. Therefore, it might be used as an approximation for a binomial random variable, especially when n (number of samples) is large and the probability (p) is small, so that np or λ is of a moderate size (Ross, 1976; Sokal and Rohlf, 1987). The infestation of caterpillars onto host plants was randomised by using the Poison probability equation:

$$\text{Prob}\,(X = n) = \frac{e^{-\lambda}\,\lambda^{n}}{n!}$$

where e is the base of the natural logarithms (2.718). The expected number of larvae and plants were subsequently rounded to the actual numbers. The results indicated that in each plot containing 80 kale plants, 7 larvae of cabbage moth were placed on 1 plant, 6 larvae on 2 plants, 5 larvae on 5 plants, 4 larvae on 11 plants, 3 larvae on 18 plants, 2 larvae on 21 plants, 1 larva on 16 plants and no larvae on 6 plants.

The infested plants were allowed to stay for over night or ≈ 16 hours and the plot was covered by a white permeable cloth, and water was given to the experimental plots as needed. The next day, 10 or 20 gavid female *C. plutellae* were liberated in the centre of plots. During experiments, temperatures were recorded by a data logger every 10 minutes. After 48 hours, the larvae were collected with a fine brush and held in labelled vials (5 cm long and 1.2 cm diameter) filled with leaf pieces during transportation and storage. Each vial contained larvae found on from one plant. The larvae were then dissected to determine the frequency of parasitism.

The development and phenology of most organisms takes place on a time scale which is temperature-dependent (Allen, 1976). As temperature affects insect development, some researchers (Campbell *et al.*, 1974; Liu and Hughes, 1984) have suggested that developmental data collected in the laboratory at various constant temperatures can be used to predict the development of insects in the field. Many day-degree techniques have been proposed for predicting the development of insects (Taylor, 1981). Day-degree summation can be calculated using the mean of observed daily maximum and minimum temperature data, and a laboratory-obtained developmental threshold (Allen, 1976; Pruess, 1983; Bernal and Gonzalez, 1993; Sevacherian *et al.*, 1977; Pruess, 1983). To accomplish analyses of day degrees for *C. plutellae*, a linear function was fit to the aging rate of female wasps v.s. temperature (Chapter 4).

In this case, the accumulation of day-degrees was calculated by the equation:

$$r \sum_{\text{daylight}} (m - t)$$

where m is records of temperature taken every 10 minutes, t is the threshold temperature, and r is a constant to convert the result from minutes to days. Daylights were recorded from 30 minutes after sunsrise to 30 minutes before sunset.

6.3. Results and Discussion

The number of parasitised host larvae was greater when high densities of wasps were released (Figure 6.1). When 20 female wasps were released, parasitism

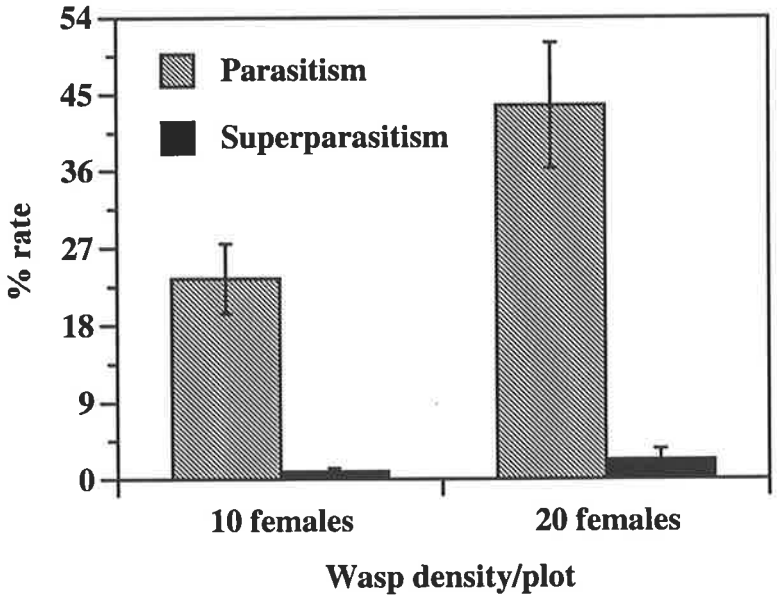

Figure 6.1. Rates of parasitism (including superparasitism) and superparasitism of cabbage moth by the parasitoid *C. plutellae* at Lenswood over 6 and 3 replicates (Mean ± S.E.M.) for releases of 10 and 20 wasps.

was 44%, whereas it was only 23% when 10 female wasps were released. There was a low incidence of superparasitism under field conditions. Rates of superparasitism in plots which were treated with liberations of 10 and 20 wasps averaged 0.9% and 2.3%, respectively (Table A.46).

The relationship between temperature and rate of aging is described by the linear regression equation: Y = - 0.02 + 0.005 X, where Y is the rate of aging for the female parasitoid and X is temperature (°C). The predicted threshold is 3.6 °C (Figure 6.2).

The difference between actual and predicted rates of aging was presented as a residual effect (Figure 6.3). At various constant temperatures, the residual points are dispersed between – 0.10 and 0.05. There was no systematic departure from the predicted rate of aging so the linear model was considered appropriate for calculation of day-degrees.

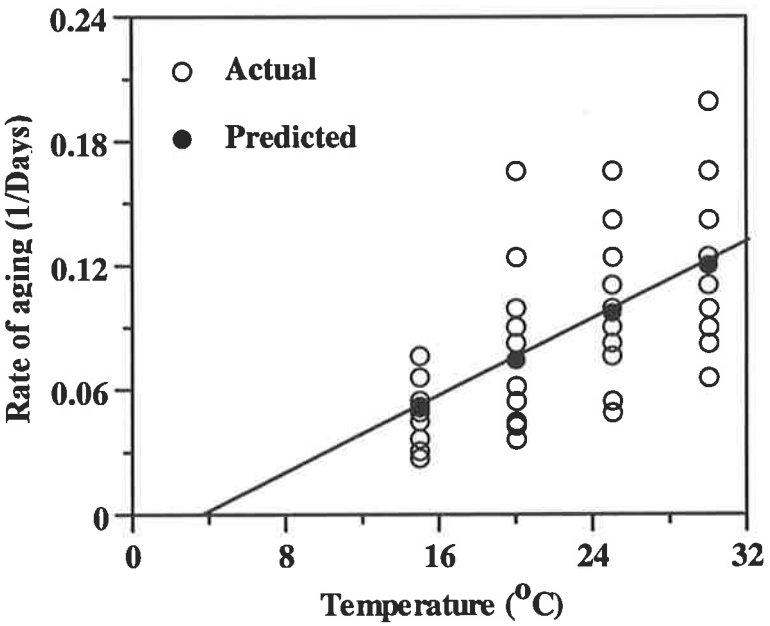

Figure 6.2. Relationship between temperature and aging rates of *C. plutellae* above the temperature threshold. Data were plotted over 20 replicates at each observed temperature.

Thresholds of *Aphelinus asychis* Walker, a parasitoid of Rusian wheat aphid (*Diuraphis noxia* Mordwilko), were estimated in experiments that were conducted under constant temperature conditions in the laboratory (Bernal and Gonzales, 1993). The lower developmental thresholds for the egg-mummy was 5.4 ^{o}C and the upper threshold was considered to be above 29.4 ^{o}C. Lower developmental thresholds from egg-larvae for *Cotesia urabae* Austin and Allen and *Dolichogenidea eucalypti* Austin and Allen (Hymenoptera: Braconidae), larval endoparasitoids of *Uraba lugens* Walker (Lepidoptera: Noctuidae), reared on small hosts had higher values than those reared on bigger hosts. The thresholds were 6.5 ^{o}C on small hosts and 11.5 ^{o}C on midsize hosts (Allen and Keller, 1991).

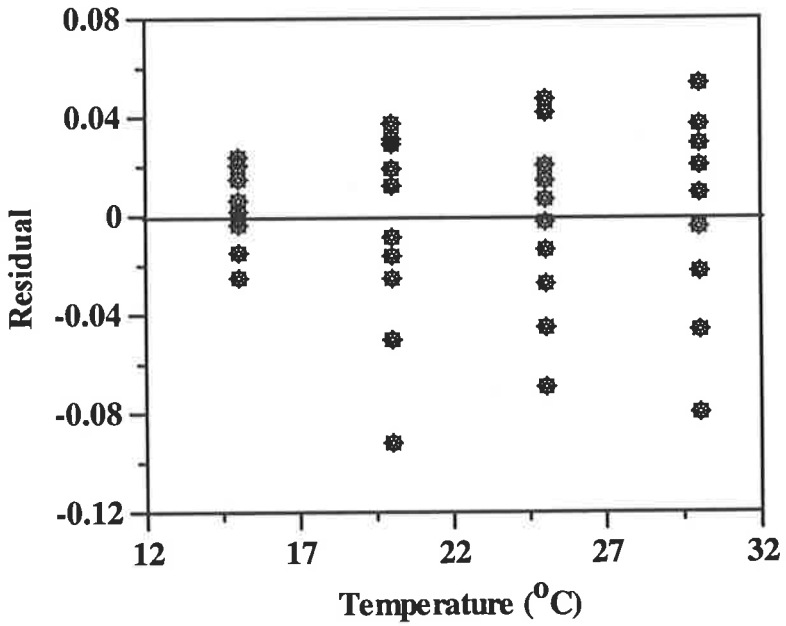

Figure 6.3. Residual rates of aging for *C. plutellae* at different constant temperatures over 20 replicates in each observed temperature.

Table 6.1. Parasitisation of larval cabbage moth by *C. plutellae* during experiments at Lenswood over 48 hours.

Dates	Wasp density (release site)	No. of hosts parasitised/ wasp	Accumulative day-degrees (Days) *	No. of hosts parasitised/ wasp/ day-degree
31/3 - 2/4/95	10 (upper site)	6.8	19.18	0.35
27 - 29/4/95	10 (upper site)	6.9	26.81	0.26
16 - 18/5/95	10 (upper site)	3.6		
16 - 18/5/95	10 (lower site)	2.8		
1 - 3/6/95	10 (upper site)	2.4	18.71	0.13
1 - 3/6/95	10 (lower site)	5.7	18.71	0.31
8 - 10/4/95	20 (lower site)	3.6		
23 - 25/4/95	20 (upper site)	5.8		
23 - 25/4/95	20 (lower site)	3.7		

* Observations were carried out during daylight.

Day-degrees were not analysed for some experiments, because the probe of the data logger was defective and consequently no temperature record was obtained.

The number of parasitised hosts per ranged from 2.4 to 6. (Table 6.1). The number of hosts parasitised per wasp per day degree varied from 0.13 to 0.35. This level of variation indicates that factors other than temperature must influence the searching activities of wasps.

CHAPTER 7

GENERAL CONCLUSIONS

A number of conclusions can be drawn from my research:

1. Susceptibility to parasitism varies at different wasp densities and host instars. First instars are least susceptible to parasitism by *C. plutellae* and *D. semiclausum*. Increasing numbers of wasps increases their killing capacity, but decreases searching efficiency in the laboratory. For augmentation in the field, it should be useful to release parasitoids at the time when susceptible host instars are available. Also, parasitism of larvae will not prevent damage, so augmentation will only be a viable method if it is used to suppress cabbage moth accross generations.

2. Development of *C. plutellae* and *D. semiclausumis* is temperature dependent. Therefore, results of experiments using different constant temperatures can be used to predict the development and aging of parasitoids. This could be useful in augmentation when selecting the interval between releases.

3. Glasshouse experiments confirmed that increasing the number of wasps leads to increasing rates of parasitism, especially when they are released in the evening, but with diminishing returns. It appears that the timing of releases could be important in augmentation.

4. Field experiments reinforced the conclusion that increasing wasp densities in a release will lead to higher levels of parasitism, but the searching efficiency of wasps will be lower.

In future research, it will be necessary to investigate the role of parasitoids in the control of cabbage moth in relation to the number of wasps to release, the mix of natural-enemy species and the frequency of releases. Research on the best time of day to release parasitoids and the influence of weather is also important. It is crucial to study the success of augmentation in different seasons. It is possible that augmentation can only be relied an early in the growth of a crop and it could be followed by *B. thuringiensis* near harvest, or perhaps it can be effective all season. Attention should be given to the benefits and costs of augmentation, starting from rearing parasitoids in the laboratory to the implementation of releases in the field. Augmentation of natural enemies has proved to be a viable means of pest management of lepidopteran pests of crucifers in the United States of America (Biever *et al.*, 1994). It is likely that this means of pest management can also be effectively implemented in Australia and other countries.

APPENDIX 1.

REARING CABBAGE MOTH AND ITS PARASITOIDS

INTRODUCTION

Many techniques for rearing this insect pest have been described. Several researchers have used artificial diets (Biever and Bold, 1971; Agui *et al.*, 1975), but these are not readily adopted particularly in developing countries (Lim and Chan, 1986). Larval cabbage moth is easily infected by entomopathogenic bacteria (Liu and Sun, 1984) when they are reared on seedlings as a food source as in the method developed by Koshihara and Yamada (1976). The method of Liu and Sun (1984) involves a large cage to get better ventilation in order to prevent the infection by bacteria (Lim and Chan, 1986). The parasitoid *C. plutellae* was reared under similar condition to that of the cabbage moth in a simple rearing unit. Seedlings of *Brassica juncea* were supplied as food source. This method could produce an average of 78% parasitoid survival from each unit (Lim and Chan, 1986).

A technique for rearing *P. xylostella* on cabbage plants was implemented in my experiments. It has given a continuous supply of the cabbage moth. In addition, this method also served the rearing of its major parasitoids.

REARING PROCEDURES FOR CABBAGE MOTH

The initial colony of *P. xylostella* was taken from field-collected larvae. It was then reared at a constant temperature of 24 - 25 ^{o}C. This technique can produce a large number of larvae in various instars used for continuous culture, experiments and parasitoid rearing.

Common cabbage (*B. oleracea* var. *capitata*, cv. Green Coronet) plants were grown in pots (12.5 x 12 x 8 cm) in the glasshouse and were used as host plants. Different cages (51 x 31 x 30 cm) were provided for oviposition, pupae and adult emergence. Each cage contained four sides confined by fine mesh nylon and the bottom was a metal plate. One vertical side that can be closed and opened was a door where materials were put in or taken out.

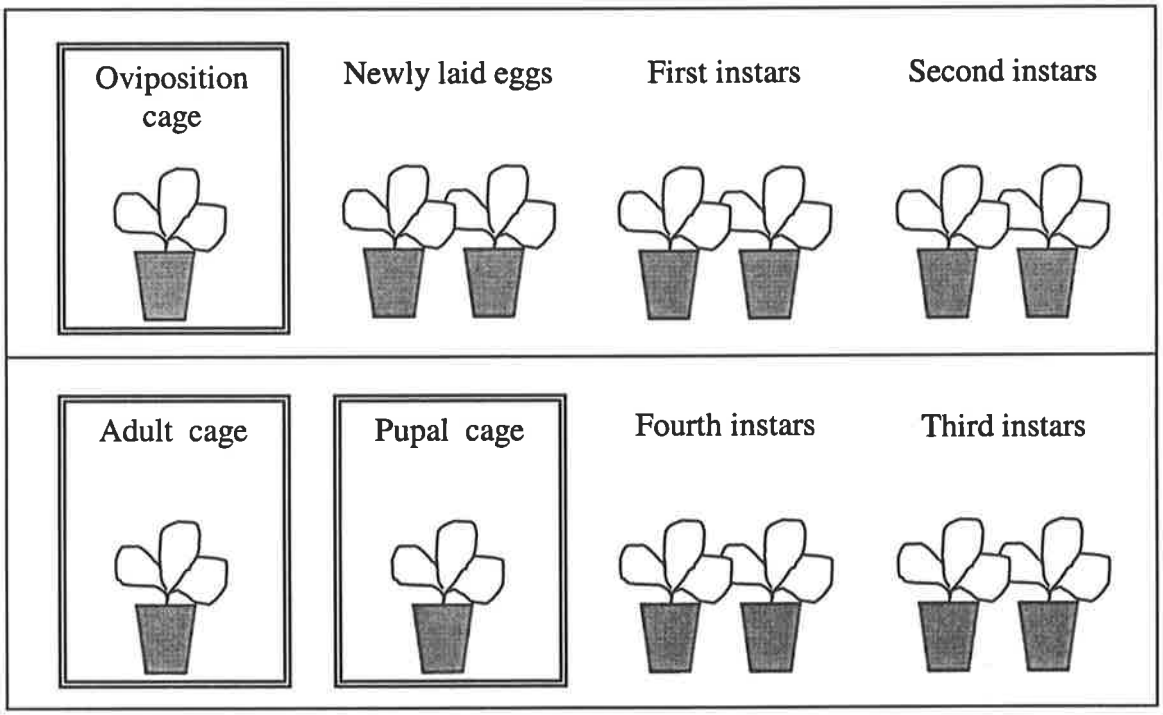

Figure A.1. Components for rearing the cabbage moth *P. xylostella*.

A potted-young plant, pure honey and water in a container with wick on it were placed into the oviposition cage containing hundreds of adult cabbage moth . After one or two days, the plant with newly deposited eggs was taken from the oviposition cage and put on the shelf with a label. When the eggs hatched the first instar larvae were put in the next position (Figure A.1.).

When the leaves have been almost consumed by the caterpillars fresh plants were supplied for them in close contact making sure that plenty of food-plants were available. They moved onto these new plants and the following day the remnants of the old plants were discarded. Dead moths were removed from the bottom of the cage with a vacuum. The wick and water were changed regularly. A plant containing third and fourth instar larvae was selected and put it into a cage for pupal formation. After several days, the cage with cabbage moth pupae was moved along the shelf to the place of the adult emergence cage. Newly emerged adults from the emergence cage were transferred into the oviposition cage. The old cage was removed to be cleaned and the old plants inside it were eliminated. Dirty cages were kept clean by washing them with detergents; some bleach (sodium hypochlorite) was added as a disinfectant.

REARING PARASITOIDS

Continuous rearing of the parasitoid *C. plutellae* has been achieved in the insectary at 24 - 25 ^{o}C. It required four cages (23.5 x 23.5 x 32 cm) for oviposition and development, and one small cage (16 x 16.5 x 21 cm) as a holding cage that only contained adult wasps and their food. The construction of cages was similar to those used for rearing the cabbage moth, but these had different doors where each simply uses a rubber band to tie a nylon mesh sleeve. All cages were placed on a shelf in a sequence according to wasp stages and ages. When numerous host larvae were offered, this rearing

method could produce a large number of parasitoids as needed for laboratory, glasshouse and field experiments.

Six cages were used to rear *C. plutellae*. A new rearing cage was set up each week as an oviposition cage. A potted-cabbage young plant infested with about 200 larvae of second and third instar cabbage moth was placed into a cage. Another fresh plant was added to the cage to give plenty of food for the hosts. After placing water in a container with a wick and some drops of honey were smeared on the top of the cage, 15 mated female parasitoids taken from a holding cage were released into the cage and left to oviposit as long as they lived.

Since the set up of new oviposition cage was implemented every week, so the oviposition cage was moved to the next oviposition after one week. When necessary, a new plant from the glasshouse was placed into a cage making sure that the old plant leaves were in contact with the new plant so that the larvae could easily moved to the new food sources. The water and the wick were changed and honey was added if necessary. Checking the plants, the water and honey were necessary at least every three days making sure the food for the wasps and hosts were sufficient. Any moths that had emerged were removed from the cage by using a vacuum, however, no wasps were not taken from cages until the first emergence occurred, 3 - 4 weeks after a cage was set up. Wasps that had emerged were removed and were placed into the holding cage. After four weeks, the plant material was removed and the empty cage cleaned.

Dead wasps found were removed from the holding cage by using an aspirator. The water and the wick are replaced regularly. Some paper towel was wetted with warm water to clean honey off the top of cage. Then after drying it with clean paper towel, four or five rows of honey drops were placed in the cage.

Figure A.2 exhibits the rearing unit of *C. plutellae*. Another parasitoid, *D. semiclausum* was reared in a same way with reduced cages.

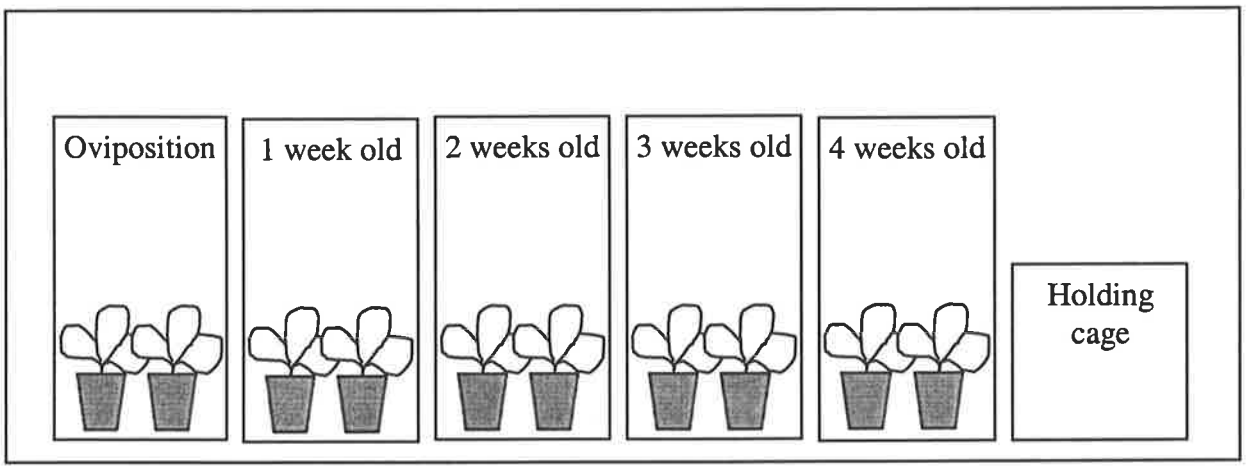

Figure A.2. Rearing unit of the parasitoid *Cotesia plutellae*.

DISCUSSION

In rearing the cabbage moth on rape seedlings, Liu and Sun (1984) applied a modification method made by Koshihara and Yamada (1976). Liu and Sun did not use a cover for the container in which the seedlings were grown, and these were placed inside a larger cage. This sort of cage provides better ventilation which seemingly assists to prevent bacterial infection. However, such a modified technique requires more space (Lim and Chan, 1986). The method developed by Koshihara and Yamada predisposed the larval cabbage moth to infection by bacteria (Liu and Sun, 1984). Lim and Chan (1986) developed a method of rearing to overcome problems of bacterial infection. In this method, they added an interconnecting ring to connect the lower feeding chamber and the upper feeding chamber.

In the rearing technique described here, young potted-cabbages were planted in a glasshouse equipped with an irrigation control system. Full fertilised UC soil was used as a medium for sowing cabbage seeds in pots. Fertilizers (N, P and K) were regularly given to the young plants. No insecticide was sprayed on these plants. Younger plants were used for oviposition and older ones for larvae. Healthy host plants, bigger cages and good conditions during the rearing allow sufficient air circulation to prevent stress and bacterial infection. Therefore, many healthy cabbage moth larvae in different instars can be produced by this technique.

Several labelled cages used for rearing parasitoids of cabbage moth allow the recognition of parasitoid stages. The availability of numerous cabbage moth larvae makes the rearing of parasitoids possible for efforts on biological control of the pest. Lim and Chan (1986) allowed the parsitoid to lay eggs for just 24 hours. In my rearing, parasitoids were left to oviposit as long as they lived, and therefore more parasitised host larvae could be obtained in each generation.

APPENDIX 2.

MEASURING INSTARS OF CABBAGE MOTH

INTRODUCTION

The larval stage of cabbage moth consists of four instars (Waterhouse and Norris, 1987). A reliable technique for distinguishing instars is measurement of the head width (Robertson, 1939), as the head is constant in size throughout any instar (Vos, 1953). However, familiarity with the instars makes it possible to differentiate them by examination under low magnification, without actual measurement.

HEAD WIDTH MEASUREMENTS

In the case of *P. xylostella*, an effort has been made to measure the head width by applying Dyar's Law. According to this law the head width of larvae increases in regular geometrical progression in sequential instars. Larvae of each instar were placed in a freezer that acts to paralyse them for measurement. By means of a binocular microscope fitted with a micrometer eye-piece, the head width of each larva was measured immediately before any distortion of cuticle happened (Robertson, 1939) and before it recovered from freezing.

Data were analysed by calculating the average of the head width of different instars, then a comparison among instars was made to test whether they followed Dyar's Law.

RESULTS AND DISCUSSION

The mean head width of each instar cabbage moth was as follows:

First instar (n = 15) : 0.163 mm (0.12 - 0.20 mm)

Second instar (n = 15): 0.274 mm (0.21 - 0.38 mm)

Third instar (n = 24) : 0.407 mm (0.37 - 0.50 mm)

Fourth instar (n = 18) : 0.586 mm (0.52 - 0.64 mm).

These results agree with those achieved by Vos (1953) for instars of *P. xylostella* in Indonesia (n = 10 for each instar).

The correctness of Dyar's Law should be proven by the identical ratios amongst:

Second instar : first instar

Third instar : second instar

Fourth instar : third instar (Robertson, 1939).

The ratios of the average head width in the cabbage moth larvae were:

Second instar : first instar = 1.7: 1

Third instar : second instar = 1.5 : 1

Fourth instar : third instar = 1.4 : 1.

These ratios slightly differ from those found by Robertson (1939) where the second instar : first instar and fourth instar : third instar were similar (i.e. 1.619 :1). Nevertheless, the ratios of different instars from these measurements are close enough although not identical. This points out that the increase in larval head width of various instars, at least, approximately follows the Dyar's Law. It is understandable that the ratios vary from one instar to another as samples taken for measurement were unequal. Figure A.3 and Table A.1 show head width ranges in first, second, third and fourth instars of cabbage moth larvae.

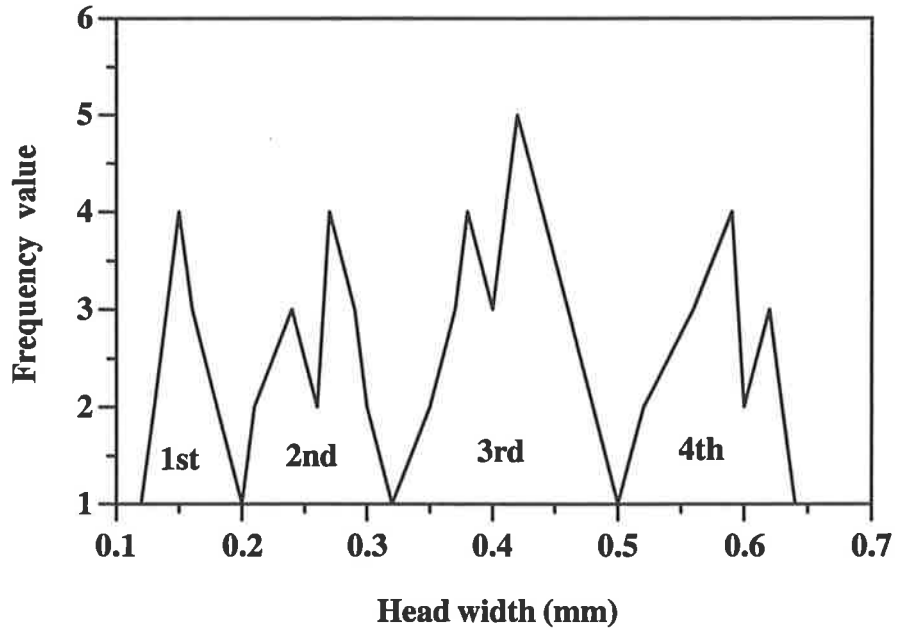

Figure A.2. Distribution of head capsule width in instars of cabbage moth.

Table A.1. Measurements of the head capsule width in the instars of cabbage moth (*P. xylostella*).

Cabbage moth instars*	Head width (mm)	Frequency values
First instar	0.12	1
	0.13	2
	0.15	4
	0.16	3
	0.18	2
	0.20	1
Second instar	0.21	2
	0.24	3
	0.26	2
	0.27	4
	0.29	3
	0.30	2
	0.32	1
	0.35	2
	0.37	3
	0.38	4
	0.40	3
	0.32	1
Third instar	0.35	2
	0.37	3
	0.38	4
	0.40	3
	0.42	5
	0.44	4
	0.46	3
	0.50	1
Fourth instar	0.52	2
	0.55	3
	0.56	5
	0.59	4
	0.60	2
	0.62	3
	0.63	2
	0.64	1

* Measurements for the first instar: 1-3 days after hatching, the second instar: 2-3 days after moulting, the third instar: 2-3 days after moulting and the fourth instar: 2-3 days old.

APPENDIX 3

ANALYSES OF VARIANCES AND MEANS FOR RATES OF PARASITISM, KILLING CAPACITY, SEARCHING EFFICIENCY AND NUMBER OF ENCOUNTERS

Table A.2a. Analysis of variance in RCBD with Genstat 5 for the rate of parasitism of *P. xylostella* by the parasitoid *C. plutellae* (Data were transformed into Arc Sine $\sqrt{x}$).

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	48.80	24.40		
Wasp (W)	3	3509.74	1169.91	27.86	< 0.001
Instar (I)	3	5369.09	1789.70	42.63	< 0.001
W x I	9	1282.43	142.49	3.39	0.006
Residual	30	1259.57	41.99		
Total	47	25631.72			

Table A.2b. Analysis of linear model with SAS for the rate of parasitism of larval cabbage moth by *C. plutellae* (Data were transformed into log (100 - % parasitism).

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Model	7	5.7719	0.8246	16.90	0.0001
Error	40	1.9520	0.0487		
Total	47	7.7239			
		Type I SS			
Instar (I)	3	2.5946	0.8649	17.72	0.0001
Wasp (W)	1	2.4467	2.4467	50.14	0.0001
W x I	3	0.7306	0.2435	4.99	0.0049
		Type III SS			
Instar (I)	3	0.3313	0.1104	2.26	0.0958
Wasp (W)	1	2.4467	2.4467	50.14	0.0001
I x W	3	0.7306	0.2435	4.99	0.0049

Table A.3. Means for the parasitism of *P. xylostella* by the parasitoid *C. plutellae* averaged over three replicates.

Instars (I)	% parasitism				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	4.60b	7.02c	8.89b	12.22b	8.18
2nd	11.11b	20.48bc	45.95a	64.61a	35.54
3rd	14.71ab	54.45a	53.33a	61.11a	45.90
4th	29.20a	30.00b	55.56a	60.00a	43.69
W-Mean	14.90	27.99	40.93	49.49	33.33

Means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

Table A.4a. Analysis of variance in RCBD with Genstat 5 for the rate of parasitism of *P. xylostella* by the parasitoid *D. semiclausum* (Data were transformed into Arc Sine $\sqrt{x}$).

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	8.78	4.39		
Wasp (W)	3	2306.14	768.71	30.16	< 0.001
Instar (I)	3	5971.33	1990.44	78.09	< 0.001
W x I	9	427.20	47.47	1.86	0.097
Residual	30	764.65	25.49		
Total	47				

Table A.4b. Analysis of linear model with SAS for tha rate of parasitism of larval cabbage moth by *D. semiclausum* (Data were transformed into log (100 - % parasitism).

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Model	7	7.0763	1.0109	32.34	0.0001
Error	40	1.2502	0.0312		
Total	47	8.3265			
		Type I SS			
Instar (I)	3	4.3780	1.4593	46.69	0.0001
Wasp (W)	1	2.1455	2.1455	68.65	0.0001
W x I	3	0.5528	0.1842	5.90	0.0020
		Type III SS			
Instar (I)	3	0.8674	0.2891	9.25	0.0001
Wasp (W)	1	2.1455	2.1455	68.65	0.0001
I x W	3	0.5528	0.1826	5.90	0.0020

Table A.5. Means for the parasitism of larval *P. xylostella* by the parasitoid *D. semiclausum* averaged over three replicates.

Instars (I)	% parasitism				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	4.43	8.90	21.10	27.80	15.56c
2nd	22.20	38.87	42.23	61.10	41.10b
3rd	43.33	58.87	48.90	62.20	53.33a
4th	41.10	51.13	68.90	77.80	59.73a
W-Mean	27.77	39.44	45.28	57.23	42.43

Means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

Table A.6. Analysis of variance in RCBD with Genstat 5 for the killing capacity of *C. plutellae* on larval *P. xylostella.*

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	0.02692	0.01346		
Wasp (W)	3	2.45559	0.81853	21.04	< 0.001
Instar (I)	3	2.57370	0.85790	22.05	< 0.001
W x I	9	1.04805	0.11645	2.99	0.011
Residual	30	1.16724	0.03891		
Total	47	7.27150			

Table A.7. Means for killing capacity of *C. plutellae* averaged over three replicates.

Instars (I)	Killing capacity (K)				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	0.046a	0.070b	0.094b	0.132b	0.086
2nd	0.120a	0.225b	0.622a	0.967a	0.483
3rd	0.159a	0.794a	0.764a	0.967a	0.671
4th	0.342a	0.359b	0.811a	1.016a	0.632
W-Mean	0.166	0.362	0.573	0.771	0.468

In a column, means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

Table A.8. Analysis of variance in RCBD with Genstat 5 for the killing capacity of *D. semiclausum* on larval *P. xylostella.*

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	0.02605	0.01303		
Wasp (W)	3	2.23772	0.74591	25.73	< 0.001
Instar (I)	3	4.39615	1.46538	50.54	< 0.001
W x I	9	0.81613	0.09068	3.13	0.009
Residual	30	0.86981	0.02899		
Total	47	8.34587			

Table A.9. Means for killing capacity of *D. semiclausum* averaged over three replicates.

Instars (I)	Killing capacity (K)				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	0.046b	0.095c	0.240c	0.330c	0.178
2nd	0.255b	0.495b	0.554b	0.973b	0.569
3rd	0.573a	0.894a	0.680b	0.990b	0.784
4th	0.543a	0.719ab	1.208a	1.506a	0.994
W-Mean	0.354	0.551	0.670	0.950	0.631

Means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

Table A.10. Analysis of variance in RCBD with Genstat 5 for the searching efficiency of *C. plutellae* on *P. xylostella* larvae.

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	0.010675	0.005338		
Wasp (W)	3	0.051063	0.017021	8.47	< 0.001
Instar (I)	3	0.283548	0.094516	47.02	< 0.001
W x I	9	0.163001	0.018111	9.01	< 0.001
Residual	30	0.060308	0.002010		
Total	47	0.568596			

Table A.11. Means for searching efficiency of *C. plutellae* averaged over three replicates.

Instars (I)	Searching efficiency (A)				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	0.046c	0.035c	0.023c	0.017b	0.030
2nd	0.120bc	0.113b	0.119b	0.121a	0.118
3rd	0.159b	0.397a	0.191ab	0.121a	0.217
4th	0.342a	0.179b	0.203a	0.127a	0.213
W-Mean	0.166	0.181	0.134	0.096	0.144

Means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

Table A.12. Analysis of variance in RCBD with Genstat 5 for the searching efficiency of *D. semiclausum* on larval *P. xylostella.*

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	0.005112	0.002556		
Wasp (W)	3	0.400123	0.133374	22.72	< 0.001
Instar (I)	3	0.693706	0.231235	39.40	< 0.001
W x I	9	0.263652	0.029295	4.99	< 0.001
Residual	30	0.176087	0.005870		
Total	47	1.538681			

Table A.13. Means for searching efficiency of *D. semiclausum* averaged over three replicates.

Instars (I)	Searching efficiency (A)				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	0.046c	0.047c	0.060b	0.041b	0.049
2nd	0.255b	0.247b	0.138b	0.122ab	0.191
3rd	0.573a	0.447a	0.170b	0.123ab	0.328
4th	0.543a	0.360ab	0.302a	0.188a	0.348
W-Mean	0.354	0.275	0.168	0.119	0.229

Means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

Table A.14. Analysis of variance in RCBD with Genstat 5 for encounters of *C. plutellae* with larval *P. xylostella.*

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	24.47	12.23		
Wasp (W)	3	2206.57	735.52	21.22	< 0.001
Instar (I)	3	2313.41	771.14	22.25	< 0.001
W x I	9	940.52	104.50	3.02	0.011
Residual	30	1039.67	34.66		
Total	47	6524.64			

Table A.15. Means for the number of encounters of *C. plutellae* with its hosts averaged over three replicates.

Instars (I)	Encounters				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	1.37a	2.12b	2.80b	4.00b	2.57
2nd	3.59a	6.78b	18.64a	28.96a	14.49
3rd	4.76a	23.80a	22.92a	28.96a	20.11
4th	10.25a	10.76b	24.36a	30.48a	18.96
W-Mean	4.99	10.87	17.18	23.10	14.03

Means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

Table A.16. Analysis of variance in RCBD with Genstat 5 for encounters of *D. semiclausum* with larval *P. xylostella.*

S.V.	D.F	S.S.	M.S.	V.R.	*P*
Block	2	23.66	11.83		
Wasp (W)	3	2012.83	670.94	25.61	< 0.001
Instar (I)	3	3440.18	1313.39	50.13	< 0.001
W x I	9	731.33	81.26	3.10	0.009
Residual	30	786.01	26.20		
Total	47	7494.00			

Table A.17. Means for the number of encounters of *D. semiclausum* with its hosts averaged over three replicates.

Instars (I)	Encounters				
	1 wasp	2 wasps	4 wasps	8 wasps	I-Mean
1st	1.37b	2.85c	7.19c	9.90c	5.33
2nd	7.65b	14.84b	16.63b	29.20b	17.08
3rd	17.18a	26.82a	20.40b	29.69b	23.52
4th	16.29a	21.58ab	36.24a	45.20a	29.83
W-Mean	10.62	16.52	20.11	28.50	18.94

Means followed by a common letter are not significantly different at $P = 0.05$ by Duncan's Multiple Range Test (DMRT).

APPENDIX 4

ANALYSES OF VARIANCES AND MEANS FOR RATES OF PARASITISM AND SUPERPARASITISM BY PARASITOIDS, THEIR DEVELOPMENT AND LIFE SPAN, AND THEIR SIZE AND FECUNDITY IN ADULT STAGE KEPT AT VARIOUS CONSTANT TEMPERATURES

Table A.18. Analysis of variance in RCBD with Genstat 5 for the rate of parasitism of the cabbage moth larvae by *C. plutellae* at different constant temperatures*.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	241.27	80.42		
Temperature	7	12432.21	1776.03	21.97	< 0.001
Residual	21	1697.51	80.83		
Total	31	14370.99			

* Data were transformed into Arc Sine $\sqrt{x}$.

Table A.19. Analysis of variance in RCBD with Genstat 5 for the rate of parasitism of the cabbage moth larvae by *D. semiclausum* at different constant temperatures *.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	211.18	70.39		
Temperature	7	9930.45	1418.64	58.93	< 0.001
Residual	21	505.52	24.07		
Total	31	10647.15			

* Data were transformed into Arc Sine $\sqrt{x}$.

Table A.20. Means for rates of parasitism of the cabbage moth larvae by *C. plutellae* and *D. semiclausum.*

Temperature (°C)	% parasitism	
	C. plutellae	*D. semiclausum*
	Mean ± S.E.M.	Mean ± S.E.M.
4	1.2 ± 1.25	6.2 ± 2.39
8	2.5 ± 1.44	13.8 ± 2.39
12	1.2 ± 1.25	30.0 ± 4.56
15	18.7 ± 7.74	62.5 ± 3.23
20	51.2 ± 10.87	77.5 ± 3.23
25	47.5 ± 3.23	76.2 ± 1.25
30	56.2 ± 10.87	45.0 ± 4.08
35	53.7 ± 3.75	16.3 ± 4.27

Table A.21. Analysis of variance in factorial RCBD with Genstat 5 for the self-superparasitism by *C. plutellae* on its hosts.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	101.74	33.91		
Temperature (T)	4	5766.57	1441.64	31.33	< 0.001
Instar (I)	3	4906.34	1635.45	35.54	< 0.001
T x I	12	5165.22	430.44	9.35	< 0.001
Residual	57	2623.01	46.02		
Total	79	18562.89			

Table A.22. Interaction between temperature and host instar on the self-superparasitism of cabbage moth caterpillars by *C. plutellae* and *D. semiclausum* averaged over 4 replicates.

Temperature	Host	Number of eggs laid per host	
(°C)	instars	*C. plutellae*	*D.semiclausum*
15	First	0.50	1.00
15	Second	0.75	2.00
15	Third	1.75	2.50
15	Fourth	1.75	4.25
20	First	0.50	2.25
20	Second	6.25	5.75
20	Third	14.50	12.75
20	Fourth	12.25	13.75
25	First	1.25	2.75
25	Second	16.00	10.25
25	Third	45.50	11.25
25	Fourth	10.75	14.75
30	First	1.75	2.75
30	Second	18.00	4.00
30	Third	37.50	10.25
30	Fourth	46.00	10.50
35	First	2.50	2.00
35	Second	11.00	5.75
35	Third	10.25	16.75
35	Fourth	18.00	3.75

Table A.23. Analysis of variance in factorial RCBD with Genstat 5 for the self-superparasitism by *D. semiclausum* on its hosts.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	11.200	3.733		
Temperature (T)	4	496.425	124.106	30.37	< 0.001
Instar (I)	3	901.300	300.433	49.31	< 0.001
T x I	12	523.575	43.631	7.16	< 0.001
Residual	57	347.300	6.093		
Total	79	2279.800			

Table A.24. Means for the developmental time of *C. plutellae* and *D. semiclausum* from egg to adult emergence maintained at different constant temperatures.

Temperature (°C)	Developmental time (days)			
	C. plutellae		*D. semiclausum*	
	Mean	95% C. I.	Mean	95% C. I.
15	47.5	3.73	36.8	3.67
20	24.6	1.97	20.2	1.10
25	16.5	2.38	13.9	0.41
30	10.2	1.61	11.8	0.88
35	9.8	1.71	*	-

* No successful development occured at 35 °C. C.I. = Confident Interval.

Table A. 25. Means for developmental time of *C. plutellae* at various constant temperatures averaged over 4 replicates.

Temperature (°C)	Developmental time (Days)			
	Egg-pupation		Pupae	
	Mean	95% C.I.	Mean	95% C.I.
15	30.0	2.94	17.5	1.51
20	14.6	1.68	9.9	1.74
25	11.0	2.04	5.4	0.78
30	6.6	1.66	3.6	0.76
35	5.8	1.56	3.9	1.04

C.I. = Confident Interval.

Table A. 26. Means for life span of *C. plutellae* at various constant temperatures averaged over 4 replicates.

Temperature (°C)	Life span (Days)			
	Females		Males	
	Mean	95% C.I.	Mean	95% C.I.
15	20.8	4.33	21.5	8.42
20	15.3	4.85	17.3	4.93
25	12.2	3.43	11.2	2.67
30	8.2	1.93	5.2	1.64
35	3.5	2.56	2.6	1.40

C.I. = Confident Interval.

Table A. 27. Means for developmental time of *D. semiclausum* at various constant temperatures averaged over 10 replicates.

Temperature (°C)	Developmental time (Days)			
	Egg-pupation		Pupae	
	Mean	95% C.I.	Mean	95% C.I.
15	20.3	3.16	16.5	1.76
20	10.6	0.69	9.6	0.69
25	6.8	0.30	7.1	0.23
30	6.1	0.71	5.7	0.48

C.I. = Confident Interval.

Table A. 28. Means for life span of *D. semiclausum* at various constant temperatures averaged over 10 replicates.

Temperature (°C)	Life span (Days			
	Females		Males	
	Mean	95% C.I.	Mean	95% C.I.
15	19.6	2.16	15.2	1.87
20	10.3	1.43	7.4	1.36
25	8.2	1.90	6.4	0.60
30	2.9	0.86	3.5	0.91

C.I. = Confident Interval.

Table A.29. Analysis of variance in RCBD with Genstat 5 for the head width of male *C. plutellae* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	0.0013	0.0004		
Temperature	4	0.0049	0.0012	3.77	0.033
Residual	12	0.0039	0.0003		
Total	19	0.0102			

Table A.30. Analysis of variance in RCBD with Genstat 5 for the head width of female *C. plutellae* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	0.0026	0.0009		
Temperature	4	0.0110	0.0028	6.41	0.005
Residual	12	0.0052	0.0004		
Total	19	0.0188			

Table A.31. Analysis of variance in RCBD with Genstat 5 for the hind tibia of male *C. plutellae* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	0.0063	0.0021		
Temperature	4	0.0405	0.0101	7.65	0.003
Residual	12	0.0159	0.0013		
Total	19	0.0626			

Table A.32. Analysis of variance in RCBD with Genstat 5 for the hind tibia of female *C. plutellae* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	0.0057	0.0019		
Temperature	4	0.0225	0.0056	5.20	0.012
Residual	12	0.0123	0.0011		
Total	19	0.0412			

Table A.33. Analysis of variance in RCBD with Genstat 5 for the egg load of female *C. plutellae* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	5301	1767		
Temperature	4	45734	11433	1.16	0.376
Residual	12	118380	9865		
Total	19	169415			

Table A.34. Analysis of variance in RCBD with Genstat 5 for the egg load of female *D. semiclausum* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	579.19	193.06		
Temperature	3	26688.69	8896.23	203.44	< 0.001
Residual	9	393.56	43.73		
Total	15	27661.44			

Table A.35. Analysis of variance in RCBD with Genstat 5 for the head width of male *D. semiclausum* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	9	0.0168	0.0019		
Temperature	3	0.0504	0.0168	9.91	< 0.001
Residual	27	0.0458	0.0017		
Total	39	0.1130			

Table A.36. Analysis of variance in RCBD with Genstat 5 for the head width of female *D. semiclausum* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	0.0109	0.0036		
Temperature	3	0.0276	0.0092	12.82	0.001
Residual	9	0.0065	0.0007		
Total	15	0.0449			

Table A.37. Analysis of variance in RCBD with Genstat 5 for the hind tibia of male *D. semiclausum* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	9	0.1075	0.0119		
Temperature	3	0.2602	0.0867	12.82	< 0.001
Residual	27	0.1827	0.0068		
Total	39	0.5505			

Table A.38. Analysis of variance in RCBD with Genstat 5 for the hind tibia of female *D. semiclausum* at various constant temperatures.

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	3	0.0092	0.0031		
Temperature	3	0.1328	0.0443	13.07	0.001
Residual	9	0.0305	0.0034		
Total	15	0.1725			

Table A.39. Medians of immature stages for developmental rates of *C. plutellae* at various constant temperatures.

Temperature	Medians of developmental rates (1/Days)		
(°C)	Egg - pupation	Pupae	Egg - adult emergence
15	0.03	0.06	0.02
20	0.07	0.10	0.04
25	0.09	0.20	0.06
30	0.14	0.25	0.10
35	0.17	0.25	0.10

Table A.40. Medians of aging rates for *C. plutellae* adults at various constant temperatures.

Temperature (°C)	Medians of aging rates (1/Days)	
	Females	Males
15	0.07	0.08
20	0.12	0.09
25	0.08	0.09
30	0.27	0.17
35	0.50	0.50

Table A.41. Medians of immature stages for developmental rates of *D. semiclausum* at various constant temperatures.

Temperature (°C)	Medians of developmental rates (1/Days)		
	Egg - pupation	Pupae	Egg - adult emergence
15	0.06	0.06	0.03
20	0.10	0.11	0.05
25	0.17	0.14	0.07
30	0.20	0.17	0.37

Table A.42. Medians of aging rates for *D. semiclausum* adults at various constant temperatures.

Temperature (°C)	Medians of aging rates (1/Days)	
	Females	Males
15	0.05	0.07
20	0.10	0.14
25	0.13	0.14
30	0.33	0.29

APPENDIX 5

ANALYSES OF VARIANCES AND MEANS FOR PARASITISATION BY PARASITOIDS IN THE GLASSHOUSE

Table A.43. Analysis of variance in factorial RCBD with Genstat 5 for the rate of parasitism of cabbage moth larvae by *C. plutellae* in the glasshouse

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	4	257.61	64.40		
Time (T)	1	78.45	78.45	4.47	0.056
Wasp (W)	1	115.44	115.44	6.57	0.025
T x W	1	4.19	4.19	0.24	0.634
Residual	12	210.72	17.56		
Total	19	666.41			

Table A.44. Analysis of variance in factorial RCBD with Genstat 5 for the rate of parasitism of cabbage moth larvae by *D. semiclausum* in the glasshouse

S.V.	D.F.	S.S.	M.S.	V.R.	*P*
Block	4	2433.7	608.4		
Time (T)	1	33.1	33.1	0.22	0.650
Wasp (W)	1	418.1	418.1	2.74	0.124
T x W	1	59.1	59.1	0.39	0.546
Residual	12	1833.9	152.8		
Total	19	4777.8			

Table A.45. Means for rates of parasitism by *C. plutellae* and *D. semiclausum* in the glasshouse experiment

Treatments		% parasitism ± S.E.M.	
Wasp density	Time	*C. plutellae*	*D. semiclausum*
1	Morning (7 am)	5.8 ± 1.40	17.2 ± 8.81
1	Evening (7 pm)	9.8 ± 1.25	16.4 ± 1.33
2	Morning (7 am)	10.65 ± 3.18	22.9 ± 9.85
2	Evening (7 pm)	15.52 ± 3.13	29.0 ± 6.07

APPENDIX 6

RESULTS OF FIELD EXPERIMENTS TO RELEASE *C. PLUTELLAE* FOR THE CONTROL OF CABBAGE MOTH

Table 6.1. Parasitisation of larval cabbage moth by the parasitoid *C. plutellae* at Lenswood

Dates	Wasp density	Location	Number of cabbage moth				Persentage	
			Infested	Captured	Parasitised*	Superparasitised	Parasitism	Superparasitism
31/3-2/4/95	10	Upper site	200	195	66	5	33.85	2.56
27-29/4/95	10	Upper site	200	140	48	0	34.29	0.00
16-18/5/95	10	Upper site	200	150	27	2	18.00	1.33
16-18/5/95	10	Lower site	200	152	21	0	13.82	0.00
1-3/6/95	10	Upper site	200	140	17	1	12.14	0.71
1-3/6/95	10	Lower site	200	147	42	1	28.57	0.68
8-10/4/95	20	Lower site	200	162	58	2	35.80	1.23
23-25/4/95	20	Upper site	200	125	73	6	58.40	4.80
23-25/4/95	20	Lower site	200	130	48	1	36.92	0.77

* Includes superparasitised larvae

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