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Ecology and behavior of Diadegma insulare (Cresson), a biological control agent of diamondback moth, Plutella xylostella (L.)

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Idris Bin Abd-Ghani

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Major professor

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ECOLOGY AND BEHAVIOR OF *DIADEGMA INSULARE* (CRESSON), A BIOLOGICAL CONTROL AGENT OF DIAMONDBACK MOTH, *PLUTELLA XYLOSTELLA* (L.)

By

Idris Bin Abd. Ghani

A DISSERTATION

Submitted to
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in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Entomology

1995

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ABSTRACT

ECOLOGY AND BEHAVIOR OF *DIADEGMA INSULARE* (CRESSON), A BIOLOGICAL CONTROL AGENT OF DIAMONDBACK MOTH, *PLUTELLA XYLOSTELLA* (L.)

By

Idris Bin Abd. Ghani

Diadegma insulare (Cresson) is an important parasitoid of diamondback moth, *Plutella xylostella* L., in North and Central America. In the United States and Canada, diamondback moth parasitism by *D. insulare* is nearly always > 75%. Field and laboratory studies were conducted to assess the ecology and behavior of *D. insulare*. *D. insulare* lived longer with high fecundity when fed on flowers of *Brassica kaber* (D.C) Wheeler, *Barbarea vulgaris* R. Br. and *Daucus carota* L. than on the other flowers. Flower's morphological characters, corolla length and openings, were positively correlate with longevity and fecundity of the parasitoid. *D. insulare* showed nine nectar-collecting behaviors that depended on the accessibility of the flower's nectar. Diurnal foraging activity of *D. insulare* females was influenced by temperature, light intensity and wind speed while male foraging activity was affected by temperature and light intensity. Activity generally began between 0800 and 1000 h, peaked between 1100 and 1300 h and stopped by 2100 h. Plant density did not affect *D. insulare* parasitism rate, sex ratio or foraging activity, but severely affected diamondback moth population. Parasitism of diamondback moth larvae occurred in all habitats except in the middle of the woodland. Percent parasitism was very high in most crop habitats and non-crop habitats (where *D. carota* is the major plant present). Diamondback moth laid more eggs on the *Brassica* crops varieties than on the wild Brassicaceae. Percent egg hatch was similar regardless of the host plant offered. Percent of diamondback moth larval survival was also higher on the cultivated than on wild Brassicaceae. There was no larval survival on *B. vulgaris*. Developmental time of unparasitized and parasitized diamondback moth larvae was similarly affected by

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the host plants. Percent parasitism was lowest on *Berteroa incana* L. D.C, *Lepidium campestre* R. Br. and *Erysimum cheiranthoides* L., but generally higher on cultivated varieties than on wild brassicas (except *B. kaber* and *Brassica nigra* L. Koch). In the field, the abundance of *D. insulare* and its parasitism rate were not significantly affected by the host plants (*Brassica* crops varieties). Although the lepidopterous insects collected in Michigan did not appear to be alternate hosts of *D. insulare*, I found that *D. insulare* parasitized two gelechiids that do not occur in Michigan. In nature, *D. insulare* could have many alternate hosts other than the plutellids, its major insect hosts, but this could be influenced by their length of exposure for parasitism. Information from my study will help to design *Brassica* crop agroecosystems that would favor *D. insulare*, reduce pesticide dependence and improve diamondback moth management.

DEDICATION

This dissertation is dedicated to my wife, Norhayati Abd.Mukti, without whose courage, understanding, patience and support none of it would have been possible

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ACKNOWLEDGMENTS

I wish to express my sincere thanks to Dr. Edward J. Grafius for his support, patience and encouragement throughout this process. I also wish to thank the members of my guidance committee: Dr. James Miller, Dr. Douglas Landis, Dr. James Kells, Dr. George Ayers and Dr. Suzanne Thiem. Special thanks go to Dr. S. Stephenson (Department of Botany and Plant Pathology, Michigan State University) for weed identification, Dr. Anthony Shelton (New York Agriculture Experiment Station, Cornell University) for twice donating cultures of diamondback moth, Dr. D. K. Weaver (South Atlantic Area, Stored-Product Insects Research and Development Laboratory, Savannah, Georgia) for supplying *S. cerealella*, Beth Bishop and Dr. Walter Pet for help in laboratory and field experiments, Dr. Larry Dyer and Dr. Paul Marino for cage design and ideas about wild flowers as nectar sources. The Michigan Vegetable Council, Michigan State University Agriculture Experiment Station and the Michigan State University Graduate School Dissertation Completion Fellowship Program are gratefully acknowledged for their financial support. Finally, to the faculty and staff of the Department of Entomology, my home for the last few years, I wish to acknowledge my gratitude.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1.

Figure 1

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.

LIST OF FIGURES

Chapter 1. Wildflowers as nectar sources for *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth, *Plutella xylostella* (L.)(Lepidoptera: Plutellidae).

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Appendix 2

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GENERAL INTRODUCTION

The diamondback moth, *Plutella xylostella* (L.), is an oligophagous insect and feeds on plants that contain mustard glucosides (Thorsteinson 1953). Important economic crops with mustard glucosides are members of the family Brassicaceae·grown both in temperate and tropical regions. Diamondback moth was first recorded as a pest in 1746 (Harcourt 1962). Since then there have been many accounts of its importance. In some countries such as Argentina, Australia, New Zealand and South Africa, diamondback moth caused serious economic losses to *Brassica* crops well before 1930 (Muggeridae 1930). In the middle of 1930's the moth was recorded as a pest of brassicas in many parts of the world (Robertson 1939).

Levels of diamondback moth infestation vary with locality, conducive environment, length of growing season, number of acres of brassicaceous crops grown and frequency of insecticide application (Lim 1986, Yamada & Koshihara 1978, Sun et al. 1978). Although there are evidences of pre-imaginal overwintering (Honda 1992, Dosdall 1994, Appendix 2) and adult hibernation (Talekar & Shelton 1993), it is generally accepted that DBM apparently does not survive in the severe winter weather (Harcourt 1986, Smith & Sears 1982, Yoshio 1987, Theobald 1926). In the northern United States, Harcourt (1986) suggested that annual infestations arise from adults that disperse from winter breeding sites in the southern United States and are carried northward in the spring, usually in the last half of May, by favorable winds and are favored by high temperature and low rainfall. Similarly in Japan, this insect migrates from southwestern islands, some of which are warm subtropical, to the cooler temperate climate of Honshu and Hokaido (Honda 1992). Similar migrations probably occur in other parts of the world such as New Zealand, Australia,

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South Africa, and southern parts of Chile and Argentina. Chu (1986) estimated that diamondback moth can fly continuously for several days as far as 3,000 km. Mass migration of diamondback moth is also reported from Finland to England and other part of Europe with distances over 3,680 km (French 1967, Lokki et al. 1978). These studies also indicate that diamondback moth adults can remain in continuous flight for several days and cover distances of 1000 km per day, but how the moths survive at such low temperatures and high altitude is not known.

Control of diamondback moth by conventional chemical pesticides has so far been the most popular method practiced by the majority of farmers throughout the world. Chemical insecticides, including pyrethroids (cypermethrin, deltamethrin, permethrin and esfenvalerate), insect growth regulators (chlorofluazuron), carbamates (carbaryl and methomyl), and organophosphates (metamidophos, dictrophos, triazophos and methyl parathion) are commonly used (Liu et al. 1982a & b, Ho et al. 1983, Perng et al. 1988, Maggaro & Edelson 1990, Cheng et al. 1992, Leibee & Savage 1992, Shelton & Wyman 1992, Fahmi & Miyata 1992, Fauziah et al. 1992). This unilateral approach and over reliance on chemicals has resulted in the development of insecticide resistance by diamondback moth (Ooi 1986). For example, in spite of spraying at higher than the recommended rates and changing insecticides to replace the ineffective ones, 70% of Malaysia's vegetable growers were still unsuccessful in controlling diamondback moth effectively (Lim 1974). It is not surprising that 30% of the production cost is used to buy insecticides (Lim 1974).

Resistance of diamondback moth to DDT and BHC was reported during the late 1950s (Henderson 1957). Organophosphates (OP) and carbarmates were used as alternative insecticides and again resistance problems arose (Ho 1965). Pyrethroids were used extensively to replace or alternate with the above-mentioned insecticides. Diamondback moth also developed resistance to pyrethroids, (Sun et al. 1978, Georghiou 1981, Miyata et al. 1982, Chen & Sun 1986, Tabashnik et al. 1987).

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Tactical reliance on new products to combat resistance, far from resolving the problem, has rendered the genetics and biochemical basis of the trait increasingly complex (Elliot et al. 1987). Liu et al. (1982a & b) found that diamondback moth resistance to diazinon (OP) showed significant cross-resistance to the pyrethroids such as permethrin, cypermethrin, deltamethrin and esfenvalerate. Fahmy & Miyata (1992) reported that diamondback moth resistance to insect growth regulators (IGR) gives broad spectrum cross-resistance to various types of insecticides. The occurrence of multiple resistance to many kinds of insecticides has also been reported by Liu et al. (1982b) and Cheng (1988). They found that this phenomenon was probably due to the presence of non-metabolic mechanisms of resistance in addition to the microsomal functional oxidase (mfo) enzymes. Diamondback moth also has been reported to be capable of developing resistance faster to most toxic insecticides like synthetic pyrethroids than less toxic insecticides like carbamate (Cheng 1988). This resistance resulted primarily from reduction in cuticular penetration, increase in detoxification and insensitivity of the site of action.

Different approaches have been tried to overcome the resistance developed by diamondback moth to chemical insecticides. For instance, microsomal oxidase inhibitors such as piperonyl butoxide and DDT-dehydrochlorinase inhibitors have been added as synergist but results were unsatisfactory (Liu et al. 1982a & b). Next, a microbial insecticide, *Bacillus thuringiensis* Berliner var. *kurstaki*, was used as an alternative method. However, resistance to *B. thuringiensis* developed, even to the genetically improved strains, within two to three years after its introduction in the field (Tabashnik et al. 1990, Jansson 1992). Tabashnik et al. (1991) reported that resistance to *B. thuringiensis* is more persistent than resistance to chemical pesticides like esfenvalerate. Schwartz et al. (1991) found that the resistance is physiologically based because resistant and susceptible larvae did not avoid feeding on *B. thuringiensis* treated leaves. The inability of mixtures or rotations of *B. thuringiensis* toxins to retard evolution of resistance and speed-up restoration of susceptibility in the absence of treatments was also pointed out by Tabashnik et al. (1992).

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The only long term advantage of *B. thuringiensis* over chemical pesticides is that it has fewer adverse effects on the predators and parasitoids of diamondback moth. This is because *B. thuringiensis* must be ingested to be effective and specific gut conditions are required for toxicity (Fast & Donaghue 1971).

Because it is safe to the environment and beneficial insects, has no cross-resistant to insects that are resistant to conventional insecticides (Soares & Quick 1992), and is compatible with other control methods (Iman et al. 1986, Kao & Tzeng 1992) studies to find ways to increase *B. thuringiensis* effectiveness have been intensified. For example, Soares and Quick (1992) reported that a new *B. thuringiensis* product (MVP), a δ-endotoxin toxin of *B. thuringiensis* bioencapsulated within a killed cell preparation of a genetically engineered of another bacterium (Pseudomonas)(Feitelson et al. 1990, Kronstad et al. 1983), performs five to six times better than the older *B. thuringiensis* formulations such as Dipel or Javelin. However, recent studies indicated that *B. thuringiensis* kills the parasitoid larvae within its host larvae (Idris & Grafius 1993c). Very recently, *B. thuringiensis*-transgenic *Brassica* crops have been developed and are reported to kill only homozygous and heterozygous susceptible larvae (Shelton & Tang 1994), indicating resistant problems will not be resolved except with intelligent use of this new method. For example, if *B. thuringiensis*-transgenic cabbage is used then it should be interplanted with non-transgenic plant as suggested by Ferro (1993) in planting *B. thuringiensis*-transgenic potatoes. The transgenic *B. thuringiensis* lines of cotton were reported not to express the δ-endotoxin at levels sufficient to have a relatively large influence on *Helicoverpa virescens* (F.)(Lepidoptera: Noctuidae) behavior, growth, survival or plant damage (Benedict et al. 1992).

In spite of the wide adaptability of diamondback moth towards different environments and insecticides, it appears to be held in check in some regions. For instance, in Canada, diamondback moth outbreaks do occur when populations fail to be held by biotic factors (Harcourt 1960). Marsh (1917), reported that diamondback moth is normally

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repressed by parasitoids and may become a serious pest only where the natural enemies are absent or ineffective (Lim et al. 1986).

Over 90 species of parasitoids of diamondback moth have been recorded in various parts of the world (Goodwin 1979). However, only about 60 of them appear to be important. Among these; 6, 38, and 13 species attack diamondback moth eggs, larvae and pupae, respectively (Lim 1986). Despite this range of parasitoid species, larval parasitoids of the genera *Diadegma* and *Microplitis, Cotesia* (= *Apantales*)(Braconidae) tend to dominate wherever they occur and are very important mortality factors for diamondback moth. The egg parasitoids belonging to the genera *Trichogramma* and *Trichogrammatoidae* contribute little to natural control even though research to find strains that prefer diamondback moth's eggs in the field have been increased quite recently (Keinmeesuka et al. 1992, Wührer & Hassan 1993, Klemm et al. 1992, Vasquez 1994). A few *Diadromus* spp., most of which are pupal parasitoids, also exert significant control (Talekar & Shelton 1993).

In Romania alone, over 15 species of Ichneumonidae and Braconidae act as primary and secondary parasitoids of diamondback moth (Mustata 1992). In North America, *Diadegma* spp. and *M. plutellae* (Muesback) are dominant (Marsh 1917, Pimental 1961 & 1968, Harcourt 1963a & b, Oatman & Platner 1969, Putnam 1968 & 1973, Lasota & Kok 1986). *Diadegma* and *Diadromus* species dominate in Europe (Hardy 1938), Africa (Ullyett 1947, Abbas 1988) and New Zealand (Hardy 1938, Todd 1959). In Russia, *Diadegma*, *Cotesia* and *Diadromus* spp. appear dominant (Kopvillem 1960a & b). *Cotesia* is an important genus in Asia and other tropical regions because *Diadegma* are less adapted to hot conditions (Chang 1974, Wang et al. 1972, Ooi 1986, Sastrosiswojo & Sastrodiharjo 1986, Talekar & Yang 1989, Yang et al. 1993).

Diadegma spp. are more competitive than the other diamondback moth parasitoids because they have excellent searching capacity, high fecundity, synchronize with the development of their host and are capable of avoiding superparasitism or multiple parasitism

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(Harcourt 1986, Bolter & Laing 1983, Waage 1983). *Diadegma* presence and abundance in *Brassica* crop agroecosystems were reported by Harcourt (1986) and Mustata (1992). Of the genera *Diadegma*, *D. semiclausum* (= *eucerophaga*)(Hellen)(Santoso 1979, Abbas 1988, Talekar & Chang 1989) and *D. insulare* (Cresson) (Harcourt 1969, Putnam 1973, Bolter & Laing 1983, Lasota & Kok 1986, Idris 1991) are the most important mortality factors for diamondback moth larval populations. For instance, parasitism of diamondback moth by *D. insulare* was between 74 an 90 % in Washington and Oregon, United States (Biever et al. 1992). In southern Ontario, Canada, *D. insulare* parasitizes as high as 75% of diamondback moth larvae (Harcourt 1969). In Indonesia, *D. semiclausum*, an introduced diamondback moth parasitoid from New Zealand, effectively suppressed diamondback moth population with > 80% parasitism in some areas (Sastrosiswojo & Sastrodiharjo 1986). In 1990, diamondback moth was effectively controlled by *D. semiclausum* and this parasitoid became the most important biocontrol agent of diamondback moth in Indonesia (Sastrosiswojo & Setiawati 1992). In the Cameron Highlands, Malaysia, *D. semiclausum* along with *Cotesia plutellae* (Kurdjumov) and *Diadromus collaris* (Gravenhost) were incorporated into the integrated diamondback moth management program package resulting in a significant reduction in diamondback moth infestation (Ooi 1992). Studies conducted in Taiwan indicated that *D. semiclausum* parasitizes > 70% within one season, and towards the end of that season diamondback moths could not be found in the field (Talekar & Yang 1989). *D. semiclausum* now occurs throughout the highland areas of Central Taiwan and provides substantial savings in diamondback moth control (Talekar 1992).

Parasitism rate of diamondback moth by *Diadegma* spp. varies with time, locations or regions, the dynamic and/or relation between each species, and its host population density (Mustata 1992, Biever et al. 1992, Waage 1983, Goodwin 1979). For instance, parasitism of diamondback moth by *D. insulare* is always high (>75%) in North America (Harcourt 1986, Idris & Grafius 1993b, Biever et al. 1992), but it varies greatly (1.5 to 70%) in South America and Caribbean Islands (Alam 1992). Generally, *Diadegma* spp. are

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effective in areas with temperature range between 15 and 25°C (Talekar & Yang 1991). At temperature approaching 30°C, parasitism drops sharply and more male progeny are produced (Yang et al. 1993). Therefore, in the tropical region *Diadegma* spp. are effective in Highland areas and inferior to *Cotesia* spp. in the lowland areas (Talekar 1992). In England, Waage (1983) found that although *D. semiclausum* aggregate in the field, its parasitism rate is independent of the host density. In Indonesia, Sastrosiswojo & Sastrodiharjo (1986) reported that the percentage parasitism of *D. semiclausum* is affected by the present of surrounding vegetation.

There is evidence that diamondback moth's parasitoids can develop resistant to pesticides applied in the field. In Michigan, diamondback moth parasitism by *D. insulare* in insecticide treated plots was not significantly different from parasitism in the untreated plots (Idris & Grafius 1993b). In Indonesia, Iman et al. (1986), Sastrosiswojo & Sastrodiharjo (1986), Santoso (1979), and Ooi (1986) also reported that *D. semiclausum* and *C. plutellae* seem to adapt to an environment of frequent pesticide application and their rate of parasitism of diamondback moth is not adversely affected. The female to male sex ratio of *C. plutellae* is also not altered if the pesticides are used judiciously (Ooi 1986).

In Taiwan, parasitism of diamondback moth by *D. semiclausum* and *C. plutellae* was no different whether the cabbages were grown in monoculture where no pesticides were used or in a mixed culture with non-brassicaceous crops, all of which were sprayed frequently with pesticide (Talekar & Yang 1989 & 1993). They also observed that *D. semiclausum* hovered over the insecticide treated *Brassica* crops but did not land. In Hawaii, parasitism o diamondback moth larvae was higher in *Brassica*-tomato plots than plots planted with brassicas crops alone which indirectly indicates that tomato plants had no long-range effect on parasitism activity of *C. plutellae* (Bach & Tabashnik 1990).

In the laboratory, *C. plutellae* and *D. semiclausum* were susceptible to malathion and methyl parathion, but they were as tolerant as diamondback moth larvae to fenvalerate (Chiang & Sun 1991). Fenvalerate is extremely toxic to *D. insulare* adults in the United

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States (Idris & Grafius 1993a). In another study, LC_{95} value increased 2-fold after *C. plutellae* was exposed to fenitrothion for 8 months (Ke et al. 1991). However, the pupae of *D. semiclausum* and *C. plutellae* (Talekar & Yang 1991, Kao & Tzeng 1992) and *D. insulare* (Idris & Grafius 1993c) were more tolerant to chemical insecticides than the adults. Although *D. insulare* pupae and adults are not killed by *B. thuringiensis* (Idris & Grafius 1993a), the parasitoid larvae within the *B. thuringiensis* intoxicated host larvae are indirectly killed (Idris & Grafius 1993c). Idris (1991) also found that parasitized diamondback moth larvae are less sensitive to most insecticides commonly used in brassicas crops fields than the non-parasitized diamondback moth larvae. Although acylurea (teflubenzuron) had no apparent activity against adult males of *D. semiclausum* and *C. plutellae*, females were severely affected by this IGR as the percent parasitism was significantly lower the treated than for the untreated individuals (Furlong & Wright 1993).

High rates of mortality achieved by *D. insulare* and other diamondback moth larval parasitoids, their increasing adaptability in fields that are frequently treated with pesticides, the less sensitive of their immature stages toward pesticides, and are not affected by plants interplanted with *Brassica* crop indicate there is a potential for using them in insecticide resistance management within an integrated diamondback moth management program. However, for the future, insecticides will remain a powerful and essential tool in integrated diamondback moth management. This is because high price short term crops, such as brassicas, need a very effective control method. However, their use must be minimized either through careful use or if other tactics fail to accomplish pest control effort (Binns & Nyrop 1992). Shelton et al., (1982) and Lumaban & Ross (1975) recommended that insecticides should be applied only during critical periods of crop growth or based on economic threshold level (ETL) of pest and crop damage.

A prime strategy for controlling diamondback moth is to build a broader ecological base that would make possible integration of various management techniques with more emphasis on the conservation and maximum use of naturally occurring beneficial insects

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(Tabashnik et al. 1991). Natural enemies could decrease the rate of herbivore adaptation toward any kind of selection pressure like pesticides exerted on them (Gould et al. 1991). However, the techniques and philosophies of using natural enemies like *D. insulare* are very important if we want to avoid pest evolving to develop resistance as it occurs on pesticides (Haynes et al. 1980). A rapid resistance developed by house fly, *Musca domestica* L., to its introduced parasite, *Nosonia vitripennis* (Pimental and Stone 1968) and the Australia rabbit response to the released of viral disease, *Myxomatosis* (Ratcliffe 1959), are two examples of pest evolving resistant to the biocontrol agents.

Using diamondback moth parasitoids as a control method has been emphasized to reduce the insecticide resistance problem in certain countries. In certain parts of Indonesia, *D. semiclausum* has been successfully used as biological agent for diamondback moth. An IPM package, based on ETL which takes into account the percentage parasitism of diamondback moth by *D. semiclausum* was superior over prophylactic control practiced by brassica crops farmers in Malaysia (Loke et al. 1992, Ooi 1992). However, the potential impact of *Diadegma* spp. like *D. insulare* on diamondback moth population dynamics will be severely limited by pesticides, especially in areas of high pest density as occurred on parasitoids of the cereal leaf beetle (Haynes & Gage 1981). The frequencies of pesticide spraying could be reduced to spot treatments with successful integration of biological and chemical control technologies (Grossman 1990, Gould et al. 1991). Manipulating plant-pest-parasitoid interactions in crop ecosystem is another better alternative (Gould 1991). The parasitoid management technique of growing beneficials in the field (refuges) is the best way to protect biocontrol agents in heavily sprayed cropping system (Grossman 1990). For instance, the potential of using wild *Brassica* such as yellow rocket, *Barbarea vulgaris* R. Br., as a food source and refuge for *D. insulare* was suggested to be included in an integrated DBM management (Idris & Grafius 1994).

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To combat pests via parasitoids one must know precisely the activity of the parasitoid and predators which limit pest populations. It is important that our interventions in natural ecosystems be done on the basis of thorough biocenotic data. Our intervention must be made in a way that it does not affect the beneficial fauna. In my study I examined some of the ecological factors and behavior or activity of *D. insulare* that may affect its population abundance and role as a biological control agent of diamondback moth. Information from this study could help us to have an idea of how to design *Brassica* crop agroecosystems that would favor *D. insulare*, reduce pesticide use and improve diamondback moth management.

HYPOTHESES

H-1: Wildflowers, nectar-collecting behavior of *D. insulare* and host plants are determinant factors in population abundance and role of *D. insulare* as a biological control agent of diamondback moth.

H-2: *D. insulare* parasitism rate is habitat-dependent.

H-3: Diurnal host foraging behavior of *D. insulare* varies with weather factors.

H-4: *D. insulare* has other hosts for overwintering that affect its population abundance in the field

OBJECTIVES

1. To find wildflowers that serve as nectar sources for *D. insulare*.
2. To study the nectar-collecting behavior of *D. insulare*
3. To study the *D. insulare* foraging activity as affected by weather factors.
4. To study the effect of plant density on the populations of diamondback moth and *D. insulare*

5. To investigate the influence of habitats on the parasitism of diamondback moth by *D. insulare*
6. To study the effects of host plants on oviposition, survival and development of diamondback moth and *D. insulare*
7. To search for alternate hosts of *D. insulare*

GENERAL MATERIALS AND METHODS

GENERAL MATERIALS AND METHODS

Sources of insects

Diamondback moth eggs (Geneva strain) were donated by Anthony Shelton, Cornell University. The eggs were put on fresh cauliflower leaves (grown in the greenhouse) in plastic pans (sterilized with clorox), with 3 x 6 cm screen lids, and kept in the growth chamber at 25 $\pm$ 2^{o}C, R. H $\pm$ 60 and a photo period of 16:8 (L:D). The hatched larvae were fed with new fresh broccoli leaves every day until pupation. Plastic pans were changed every other day to protect larvae from diseases. Pupae were collected and kept in Petri dishes at 5^{o}C or used for further rearing. In 1994, new diamondback moth colony of Geneva strain were donated by Anthony Shelton. This is because the previous colony had become infected by microsporidia disease.

D. insulare pupae were randomly collected from insecticide-free *Brassica napus* (canola) field at Michigan State University Research Farm in late May, each year. This is because, *B. napus* was planted as both early and late season crop while the other *Brassica* crops were planted late in the season. Pupae were brought back to laboratory for rearing.

Diamondback moth rearing

Oviposition cages were made of clear plastic tubes cut from 2 liter drink bottles (15 cm long x 12 cm diameter) and the cup. Screen lid (3 cm diameter) was constructed on each side of the plastic for ventilation. One end of the tubes was capped with a plastic plug, with three quarters of the plug cut out and the opening covered with an organdy cloth. The other end was attached to cup (with lid) by masking tape. Two holes (1.5 cm diam) on the lid were made and one half from the bottom of the cup was cut out prior to attachment of the plastic tube.

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A small glass vial filled with diluted honey (10%) with portion of tissue paper soaked in it, and paper towel were inserted through either hole of the cut cup lid. The cut cup of the cage was put in other three quater water filled cup. Water absorbed by a paper towel provided water and honey served as food source for the diamondback moth adults. The food and water were changed every day.

Approximately 100 diamondback moth pupae were placed in one oviposition cage. Oviposition cages were kept at room temperature (22 ± 3°C) and a photo period of 16:8 (L:D). A single aluminum foil strip, 2.5 cm x 7.5 cm, was provided as an oviposition substrate. The foil strip will be crumpled to create suitable ovipositional ridges and depressions, then smoothed to a flat surface. The fresh leaves of broccoli or cauliflower were crushed using hammer and then rubbed over the surface of the foil to increase the oviposition. Eggs were collected from the oviposition cages and used to start a new colony or kept at 5°C for future rearing.

***D. insulare* rearing**

A 500 ml plastic container nearly filled with water was used to hold the middle age cauliflower leaves. Holes were made in the cup cover and stems of four to six middles-aged cauliflower leaves were inserted into cup through the hole. The leaves were inoculated with diamondback moth third and early fourth instars. The cup and inoculated leaves were placed inside a 50 x 40 x 40 cm ovipositional cage (22 ± 3°C, 16L:8D photo period). *D. insulare* pupae (ca. 100 per cages) were placed inside the cage for adult emergence. *D. insulare* adults were fed with honey+water (10% honey) solution distributed on cotton dental wicks. The emerged males and females were kept in a cage without host larvae for 2 d to facilitate mating which is less frequent in the laboratory than in the field. Parasitized diamondback moth were collected about 24 h later and transferred to a plastic pan for experimental use or reared as above until pupation, for future rearing. To get high numbers of female I used only diamondback moth early fourth instars as hosts and kept both sexes of parasitoid together more than 4 d before used for parasitism.

CHAPTER

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CHAPTER 1

Wildflowers as Nectar Sources for *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae), a Parasitoid of Diamondback Moth, *Plutella xylostella* (L.)(Lepidoptera: Plutellidae)

ABSTRACT

The effects of wildflowers on the longevity and fecundity of *Diadegma insulare* (Cresson), one of the major parasitoid of diamondback moth in North America, *Plutella xylostella* L., were studied in the field. Wildflowers provided nectar sources for *D. insulare*. Longevity and fecundity of the parasitoid female varied with wildflower species and the morphological characteristics of the flower. Several flowers, including *Brassica kaber* (D.C.) Wheeler, *Barbarea vulgaris* R. Br., and *Daucus carota* L., supplied nectar and resulted in *D. insulare* longevity and fecundity equal to when honey+water was supplied as food. Others, including *Erysimum cheiranthoides* L. and *Thlaspi arvense* L., were not significantly better than no food at all. *Chenopodium album* L. and *Sonchus arvensis* L. did not provide available nectar, however, adult parasitoids fed on honeydew excreted by *Aphis fabae* (Scopli) feeding on the plants. Fecundity of *D. insulare* generally peaked 6 to 15 d after adult emergence. An increase in longevity and fecundity was correlated with flower corolla opening diameter but not with corolla length. Except on *B. vulgaris*, longevity and fecundity of *D. insulare* fed on flowers brought into the greenhouse versus in the field were not significantly different. Shading also increased longevity and fecundity of *D. insulare*. The oviposition behavior within the first minute of exposure to diamondback moth larvae was highly correlated with longevity and total fecundity of *D. insulare*, which we considered indices of food quality. Seasonal manipulation of the diversity and distribution of wildflowers in the cabbage field and adjacent habitats, as well as providing shade for *D. insulare*, could increase *D. insulare* effectiveness in management of diamondback moth.

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INTRODUCTION

Diadegma spp. (Hymenoptera: Ichneumonidae) are major mortality factors of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae)(Ooi 1992, Harcourt 1986). Success in using *Diadegma semiclausum* (Hellen) in integrated diamondback moth management has been reported in Malaysia and Indonesia (Ooi 1992, Sastrosiswojo & Sastrodiharjo 1986). In Michigan, the presence of wildflowers surrounding the field was thought to influence the DBM parasitism rate by *Diadegma insulare* (Cresson) in pesticide treated and untreated plots (Idris & Grafius 1993b). Zhao et al. (1992) found that *D. insulare* parasitism of diamondback moth was higher in the brassicas crops fields adjacent to nectar-producing plants than in the fields that were not surrounded by nectar-producing plants. In England, *Diadegma* sp.was observed feeding on the flowers of weeds (Filton & Walker 1992). The importance of wildflowers as food sources for adult parasitoids was reported by Van Emden (1963a & b, 1965a & b), Wolcott (1942), Leius (1967), Keven (1973) and Kopvillem (1960). Syme (1975) reported that the fecundity of *Hyssopus thymus* Girault (Hymenoptera: Eulophidae) females fed on various flowers was comparable to that of honey-fed females in most cases, and in some cases was significantly greater. The selective use of floral resources by the parasitoid, *Episyrphus balteatus* (Degeer)(Diptera: Syrphidae), on farmland in the United Kingdom was reported by Cowgill et al. (1993). An understanding of the relative importance of wildflowers to *D. insulare* may be important if we want to enhance its role and effectiveness in diamondback moth management.

The objectives of this study were: (1) to assess the effects of wildflowers on the longevity and fecundity of *D. insulare*, (2) to compare the longevity and fecundity of *D. insulare* fed on greehouse versus outdoor wildflowers or fed of plants+aphids versus plants-aphids, (3) to determine oviposition behavior of *D. insulare* fed on different flowers or honey+water, (4) to assess the effects of shading versus full exposure to sunlight on the longevity and fecundity of *D. insulare*, and (5) to correlate flower structure with *D. insulare* longevity and fecundity

MATERIALS AND METHODS

Food sources. Flowers of eight Brassicaceous weeds, five non-Brassicaceae (2, Asteraceae; one for Polygonaceae, Chenopodiaceae and Umbelliferae, respectively), and one cultivated *Brassica* crop (canola, *Brassica napus* L.) were used as the nectar sources for the parasitoid (Table 1). Brassicaceous weeds were emphasized because they are common in and near *Brassica* crops fields. They are also potential hosts for diamondback moth larvae and are tolerant to many herbicides used in brassicas crops.

Sources of insects. I used F_{18-20} of diamondback moth (Geneva strain) donated by Anthony Shelton, Cornell University in January, 1990. Diamondback moth were reared in the laboratory by feeding the larvae with live plants (broccoli leaves grown in the greenhouse)(see also general materials and methods). I used F_{2-3} field collected *D. insulare* which were reared in the laboratory out of the above diamondback moth strain.

Site of study. This study was conducted at the Michigan State University Research Farm during May, June, July, August and September 1993, using wildflower species available during each period.

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Longevity and fecundity. I enclosed the flowers and *D. insulare*, in a cylindrical screen cage (20 cm high & 10 cm diam) with circular styrofoam board covering the top and bottom of the cage, and one small slit at the side of the screen for introducing insects. I cut a 5 cm slit from the edge to the center of the bottom foam for the flowers stem. Each cage

Table 1. Species, common names, and families of wildflowers used for the study

Species	Common name	Family
Barbarea vulgaris R. Br.	yellow rocket	Brassicaceae
Berteroa incana (L.) DC.	hoary alyssum	"
Brassica kaber (D.C) Wheeler	wild mustard	"
Brassica napus L.	canola	"
Capsella bursa-pastoris (L.) Medic	shepherd's purse	"
Erysimum cheiranthoides L.	wormseed mustard	"
Lepidium campestre (L.) R. Br.	field pepperweed	"
Thlaspi arvense L.	field pennycress	"
Chrysanthemum leucanthemum L.	oxeye daisy	Asteraceae
Sonchus arvensis L.	perennial sowthistle	"
Rumex crispus L.	curly dock	Polygonaceae
Chenopodium album L.	common lambsquarters	Chenopodiaceae
Daucus carota L.	wild carrot	Umbelliferae

was tied on to a wooden stake erected close to individual flowering weeds (four spikes or two umbles per cages). I moved the cage to a new flower when the flower began to wilt (usually every 3 to 5 d) and the honey+water treatment was changed every 4 days. Each treatment (= flower species) was replicated eight times.

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One male-female pair of *D. insulare* (1 d old and not yet fed) was released into the cage using an aspirator inserted through a slit on the side of the screen. The opening was plugged with a cotton wick. To make sure a female was mated the male was kept in the cage for 3 d.

For control treatments, we put glass vials (21 x 70 mm) filled with honey+water (10% honey, v/v) in place of the flower, water alone or no food or water. I rolled a piece of tissue paper which was dipped into the vial of honey+water or water. The top of the vial was covered by the paper to avoid excessive evaporation. The vial was inserted through a hole in the bottom foam.

Four wild Brassicaceae (*B. vulgaris*, *T. arvense* and *E. cheiranthoides*) and one Umbelliferae (*Daucus carota* L.) were brought into the greenhouse and transplanted them in pots for comparisons study with other food sources in the field in May and August. The test on these nectar-producing plants were conducted using the cage and insects and at the same time as before.

In September, many of *Chenopodium album* L. and *Sonchus arvensis* L. were naturally infested by aphids, *Aphis fabae* (Scopli). For this study I inserted two branches of the plants+aphids or plants-aphids in place of the flower into the cage as before. Other treatments used for comparisons were water, no food or water and honey+water.

Daucus carota, which grows near the edge of forest (sides that protect the flowers from intense sun light in the afternoon were selected) was used in this study. Flower and insect were put in cage as before. Like in the greenhouse study, I used data of *D. carota* that exposed fully to sun light (unshaded) and other food sources in the above study for a comparison in July and August (the hottest moths in the summer).

I had only four replicates for *B. kaber*, *B. incana* and *D. carota* in June and September studies. These weeds were less abundant in early and end of the season but they were the only weeds that present throughout summer. This allows me to study the seasonal effect of food sources to the *D. insulare* longevity and fecundity. The

experimental set up was similar as before and honey+water was used as the control treatment.

Survival of the *D. insulare* females was recorded daily to measure the longevity. To measure fecundity I took the adult female parasitoid from the cage every 3 d and released it into a 400 ml transparent plastic container with a screen lid with 30 third instar diamondback moth larvae for 3 h before putting it back into the cage. My previous field experience indicated that no more than 25-27 third diamondback moth would be attacked and superparasitism would not occur (unpublished data). The presumably parasitized diamondback moth larvae were reared in the laboratory at 25 ± 2°C, 50-70% relative humidity and a photoperiod of 16: 8 (L:D) h until pupation, when the number of *D. insulare* and diamondback moth pupae were recorded. I did not dissect the parasitized host larvae for *D. insulare* eggs for fecundity measurement because there were no eggs encapsulated (Bolter & Laing 1983). In addition, dissecting host larvae for parasitoid egg was a laborious work and time consuming. Fecundity was calculated as the sum of all *D. insulare* pupae produced by a female *D. insulare* during her life (30 host larvae offered every 3 d).

Oviposition behavior. On day 9, in the August study, I also randomly selected four of the eight replicates for *D. carota*, *B. kaber*, *B. incana* and honey+water treatment from the above study (= 4 replicate per food sources) and recorded oviposition behavior (any attack on host made by the parasitoid that ended with inserting its ovipositor into host body) of *D. insulare* females, fed on these food sources, within 1 min, 5 min and 20 min of exposure to diamondback moth larvae. The observation was made from 1100 to 1450 h during when the females are active (unpublished data). Because of day-time constraint to monitor observation behavior I conducted separate observation (also in August) for *D. insulare* fed on *B. napus*, *C. bursa-pastoris*, *T arvense* and honey+water. *B. napus*, *C. bursa-pastoris*, and *T arvense* were not used in the above study (longevity and fecundity) because of difficulty in getting eight replicates for the whole period of study in August.

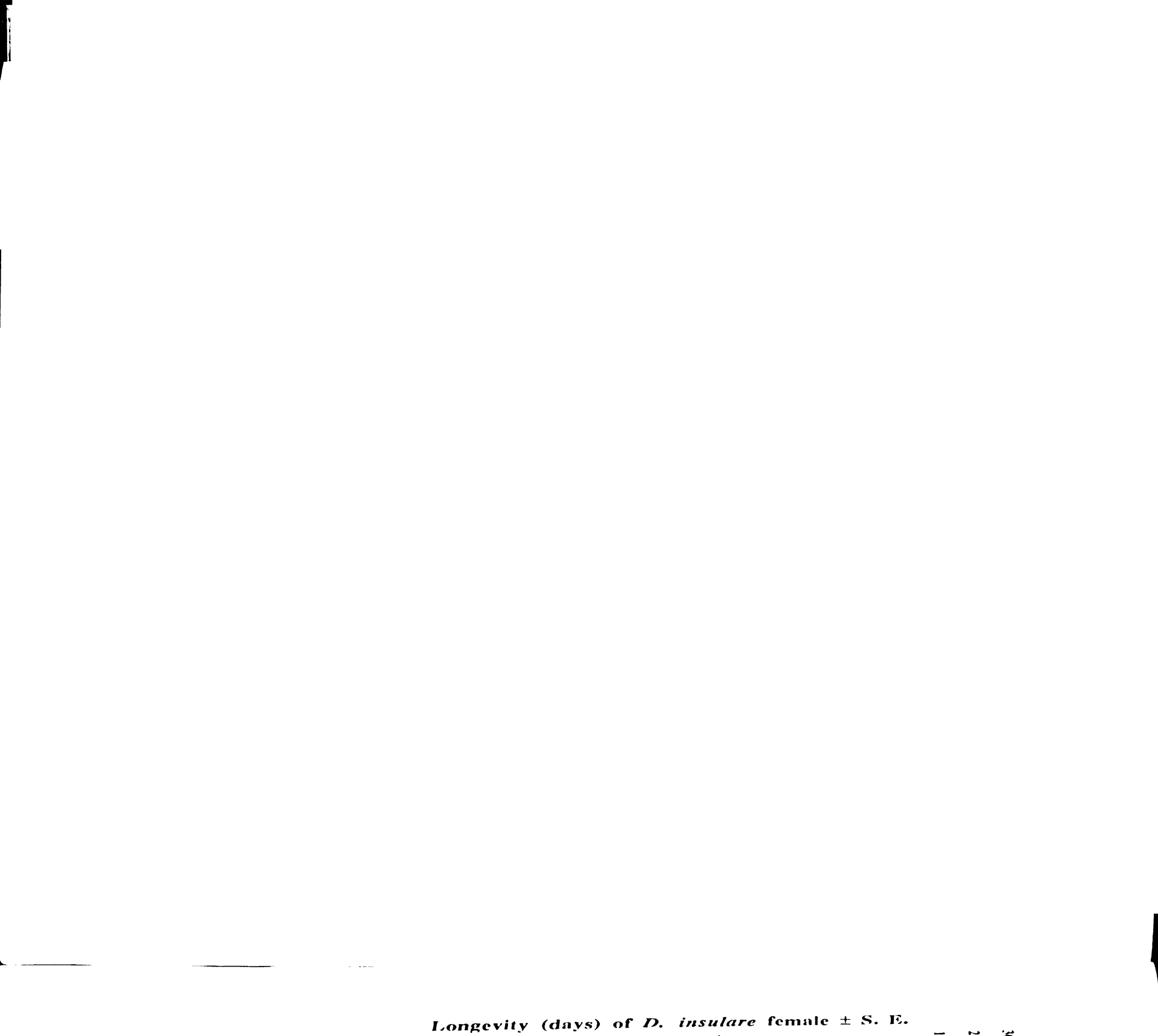
Result from honey+water treatment (control) was used to determine if the treatments of the two observations are comparable and analyzed together.

Relationship between flower structure with *D. insulare* longevity and fecundity. The corolla length and diameter of the opening for a sample of 10 flowers for each species per replicate were measured. Measurements were made from 1100 to 1300 h when flower corolla were fully open. I used the longevity and fecundity data from the above study to relate it with the corolla length and diameter of the opening.

Longevity and fecundity of *D. insulare*, ovipositional behavior of *D. insulare* fed on different food sources, and the corolla length and opening diameter of flowers were analyzed using 1-way ANOVA, while means were separated using Fisher's Protected LSD test (Abacus Concepts, SuperAnova 1991). The oviposition behavior of *D. insulare* females fed honey+water in two observation was analyzed by paired student *t* - test (MSTAT, Eisensmith & Russell 1989). Longevity and fecundity of *D. insulare* fed on flowers species tested in the greenhouse versus in the field, shaded versus unshaded and plants+aphids or plants-aphids treatments were analyzed together with the other treatments (= food sources). Relationships between longevity and fecundity and the length and opening diameter of flower corolla, the opening and length of the corolla, and ovipositional behavior of *D. insulare* within 1 min of exposure to host larvae were analyzed using regression analysis (Abacus Concepts, SuperAnova 1991).

RESULTS AND DISCUSSION

Longevity. In May, longevity of *D. insulare* females was significantly affected by food source or flower species ($F = 93.6$; df = 11,77; $P < 0.05$). For instance, *D. insulare* longevity was significantly higher when fed on *B. vulgaris* than on the other wildflowers, or water or without food (Fisher's Protected LSD, $P < 0.05$)(Fig. 1 A). In June, parasitoid longevity was also significantly higher when fed with *B. vulgaris* than with the


Longevity (days) of D. insulare female ± S. E.

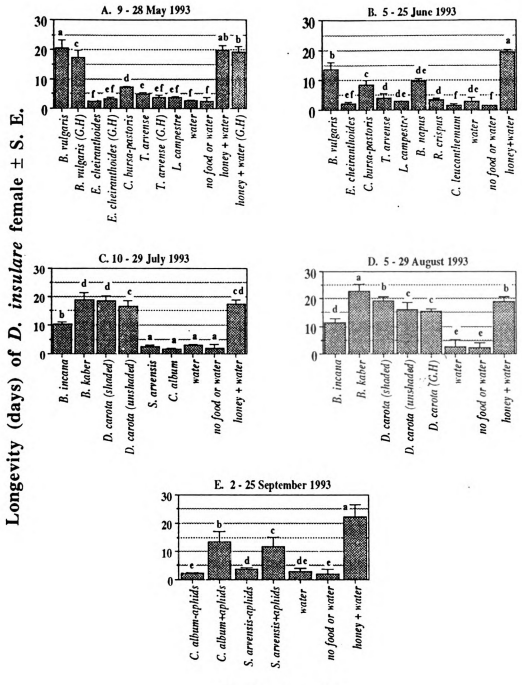


Figure 1. Longevity of *D. insulare* females fed on various wildflowers as nectar sources. (G.H) indicates the results from experiment conducted on plants brought into the greenhouse for study. Columns with different letters are significantly different (Fisher's PLSD, $P < 0.05$).

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other wildflowers, including *Rumex crispus* L. and *Chrysanthemum leucanthemum* L. (Fisher's PLSD, $P < 0.05$)(Fig. 1 B). However, longevity of *D. insulare* on *B. vulgaris* in June was significantly shorter than on honey+water. In July *D. carota* and *B. kaber* had similar impacts on the longevity of *D. insulare*, comparable to honey+water (Fisher's PLSD, $P > 0.05$)(Fig. 1 C). Although *D. insulare* longevity on *B. incana* was shorter than on *B. kaber* it supported *D. insulare* better than *C. album* and *S. arvensis* In August, longevity of *D. insulare* was higher when fed on *B. kaber* than on the other flowers or on the honey+water (Fisher's PLSD, $P < 0.05$)(Fig. 1 D).

In September, *C. album* and *S. arvensis*, offered additional food sources for *D. insulare* because they were harboring bean aphids, *Aphis fabae* (Scopli), which apparently provided honeydew for *D. insulare* (aphids were not present on these plants in June, July or August). This was clearly indicated by my September results where *D. insulare* lived longer on *C. album* and *S. arvensis*+aphids than on these plants-aphids (Fisher's PLSD, $P < 0.05$)(Fig. 1 E). Longevity of *Pholetesor ornigis* (Weed) (Hymenoptera: Braconidae) adults also increased when they were provided with aphid honeydew (Hagley & Barber 1992). However, longevity of *D. insulare* fed on these two weeds+aphids was significantly less than with honey+water. Honeydew from *A. fabea,* the apparent food source, may not have certain sugars or essential amino acids or they may be present in insufficient quantity compared to floral nectar (Baker & Baker 1983, Baker et al. 1978, Saleh & Salama 1971, Lamb 1959).

There was an increase in longevity of *D. insulare* from early to mid season when *B. kaber* and *B. incana* were used as food sources but not with *D. carota* or honey+water (Fig. 2). From August to September *D. insulare* longevity was reduced when fed on *B. incana* or *D. carota* flower nectar but not on *B. kaber*. This could be due to a change in food quantity or quality (sugar and amino acid content) of the flowers' nectar. However, values can not be compared statistically because they were different experiments, including possible differences in temperature, humidity and solar radiation. Lingren & Lukefahr

(1977) reported that for *Campoletis sonorensis* (Cameron)(Hymenoptera: Ichneumonidae), a parasitoid of tobacco budworm, *Heliothis virescens* (F.), longevity is affected by the quantity of extrafloral nectar produced by the cotton plant, which declines in the late season. These weeds emerge early in the season; flowering start in June, peak in July and August, decline in September but continues until frost (Buchholtz et al. 1981). There is no study on the temporal population trends of *D. insulare* in the field but its parasitism rate is also peak in July and August (Harcourt 1986).

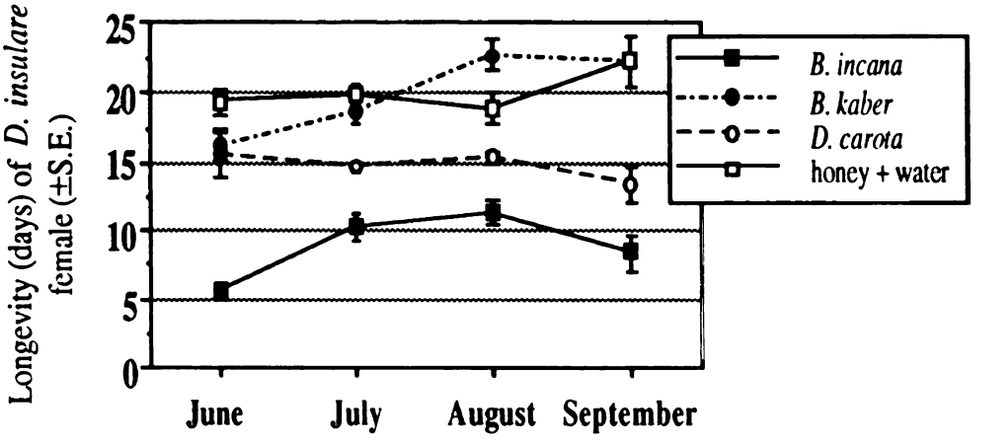

Figure 2. Longevity of *D. insulare* females fed on various wildflowers during June through September 1993

Fecundity. Total fecundity of *D. insulare* in May and June was significantly higher when *B. vulgaris* flowers or honey+water was used as food, compared with other foods offered (Fisher's PLSD, $P < 0.05$)(Fig. 3 A). In May and June, total fecundity of *D. insulare* fed on *B. vulgaris* was significantly lower than when it fed on honey+water (Fisher's PLSD, $P < 0.05$)(Fig. 3 A & B).

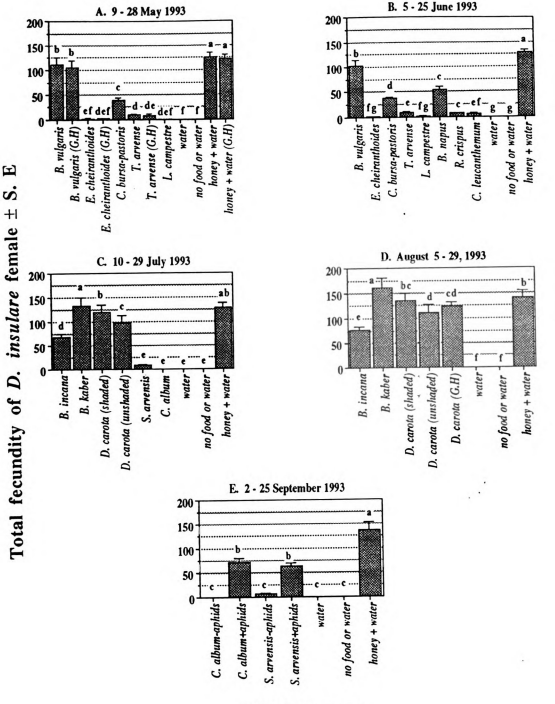

Figure 3. Total fecundity per lifetime of *D. insulare* females fed on various wildflowers as nectar sources. (G.H) indicates the results from experiment conducted on plants brought into the greenhouse for study. Columns with different letters are significantly different (Fisher's PLSD, $P < 0.05$).

In July, parasitoid feeding on *B. kaber*, *D. carota* or honey+water resulted in higher fecundity than on other food sources (Fisher's PLSD, $P < 0.05$)(Fig. 3 C). Although *B. incana* was not as beneficial for *D. insulare* fecundity as *B. kaber*, it still offered better food than the non-brassicas wildflowers, *S. arvensis* and *C. album*.

In August, total fecundity of *D. insulare* was significantly higher when fed on *B. kaber* than on the other flowers or honey+water (Fisher's PLSD, $P < 0.05$)(Fig. 3 D). Interestingly, longevity and total fecundity of *D. insulare* fed on *B. kaber* were significantly higher than when fed with honey+water in August (Fig. 2 & 3 D). This suggests that *B. kaber* is a better food for *D. insulare* than honey+water.

Fecundity of *D. insulare* fed on *C. album* or *S. arvensis*+aphids was significantly higher than these weeds-aphids (Fisher's PLSD, $P < 0.05$)(Fig. 3 E). However, this fecundity was very much lower than with honey+water.

In each month, total fecundity was zero when only water or no food was given to *D. insulare* (Fig. 3 A - E). However, in laboratory observations after 6 to 10 h of exposure to host larvae, unfed 1 d old *D. insulare* females did parasitize diamondback moth larvae (unpublished data). *D. insulare* without food or water, exposed to host larvae for 2 to 3 d before they died, parasitized at least 9 to 18 diamondback moth larvae, respectively (unpublished data). This suggests that *D. insulare* is a pro-ovigenic insect; food is not necessary for *D. insulare* egg maturation (as in mosquitoes) or for successful parasitism (Jervis 1993). Food, however, is necessary for *D. insulare* to live longer which indirectly increases fecundity. In addition, energy acquired from food helped the *D. insulare*, within a given time, to parasitizes more host larvae than if it was not given food at all or just water.

D. insulare fecundity tended to gradually increase from early to mid season when *B. kaber* or *D. carota* was used as food sources but not with *B incana* (Fig. 4). However, given the size of standard errors, increase may not be significant.

Fecundity patterns over the life of individual *D. insulare* were generally similar if food was sufficient to prevent early death. *B. vulgaris* in June; *B. kaber*, *D. carota* or honey+water in August; or *C. album* + aphids in September are shown as examples (Fig. 5). Fecundity was low on day 3 and peaked from day 6 to 15. On *C. album*+aphids (a moderately good food source), fecundity peaked on day 6 and declined thereafter. Inexperience or physiological development of *D. insulare* females may account for lower fecundity on day 3.

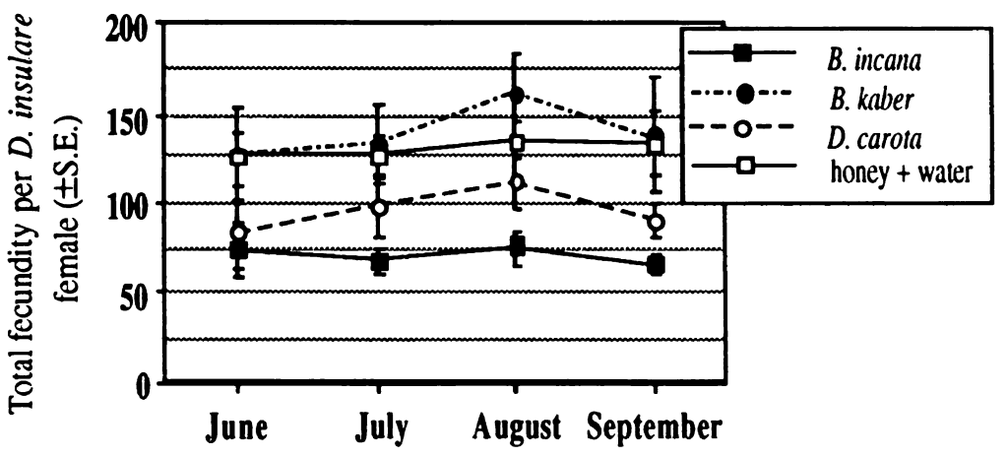

Figure 4. Total fecundity of *D. insulare* females fed with various wildflowers during June through September 1993

Longevity of *D. insulare* females was significantly shorter when fed on the *B. vulgaris* and *D. carota* flowers in the greenhouse than in the field (Fisher's PLSD, $P < 0.05$)(Fig. 1 A & D). However, this was not true when *E. cheiranthoides*, *T. arvense* and honey+water were used as food sources for the parasitoid (Fig. 1 A). Unlike longevity, fecundity of *D. insulare* fed on *B. vulgaris* and *D. carota* flowers in the greenhouse was not

significantly different from fecundity of parasitoid fed on these flowers in the field (Fisher's PLSD, $P > 0.05$)(Fig. 3 A & D).

Shading significantly increased longevity of *D. insulare* fed on *D. carota* in July (Fig. 1 C) and in August (Fig. 1 D). Like longevity, total fecundity of *D. insulare* in July and August were significantly higher when fed on the shaded than on the unshaded *D. carota* and several other food sources (Fisher's PLSD, $P < 0.05$)(Fig. 3 C & D).

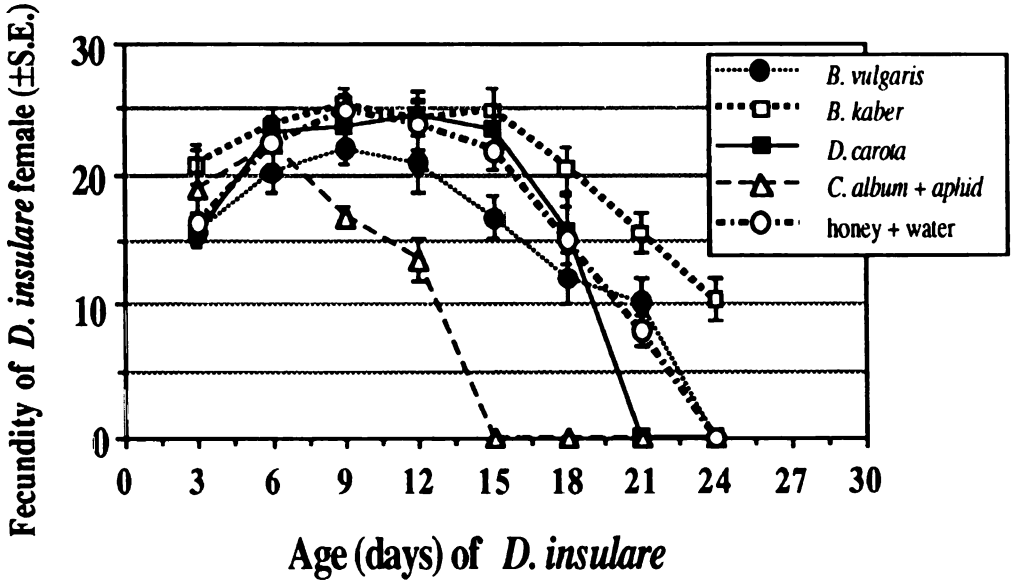

Figure 5. Fecundity pattern (beginning on day 3 after emergence from pupae) of *D. insulare* females fed on various wildflowers as nectar sources.

Oviposition behavior. The frequency of oviposition made by *D. insulare* fed honey+water in two separate observations was not significantly different (paired *t* - test, df = 3, $P > 0.05$). Therefore, the treatments from the two observations were comparable. The frequency of ovipositional behavior made by *D. insulare*, within 1 min of exposure to

the larvae, was higher when they were fed on *D. carota*, *B. kaber* or honey+water than when fed on other food sources (Fig. 6). Longevity and fecundity of *D. insulare*, which we consider as indices of food quality, were strongly correlated with the frequency of individual parasitoids initiating oviposition behavior within the first minute of exposure to the host (r = 0.91 and 0.87, Fig. 7 A & B).

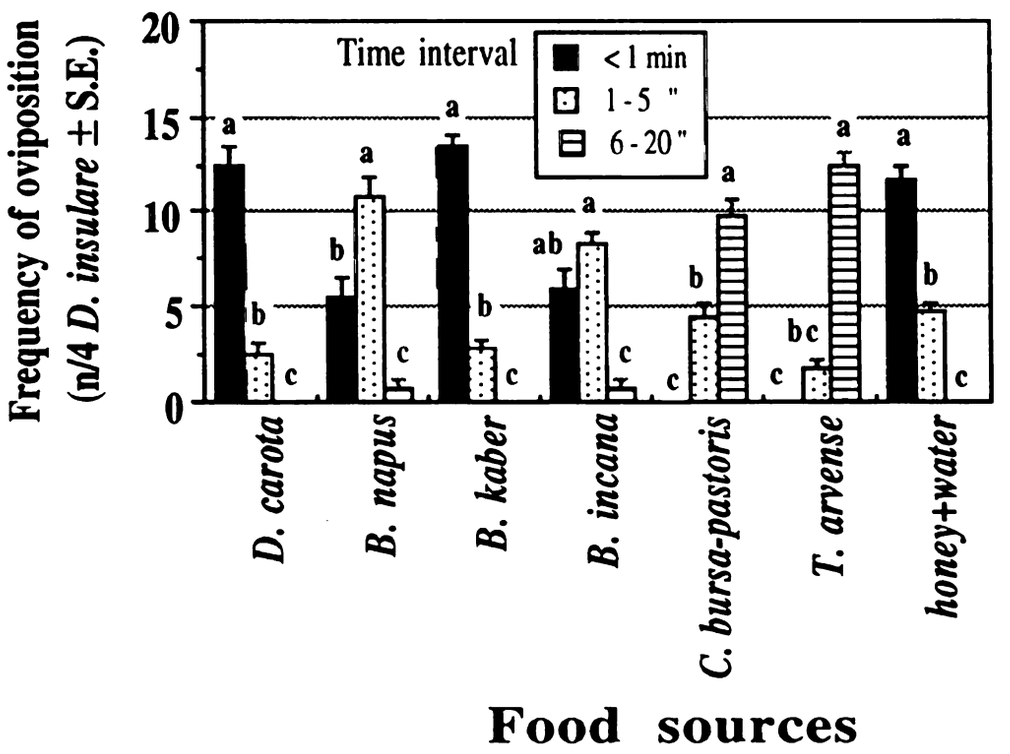

Figure 6. Frequency of oviposition behavior made by *D. insulare* females, fed on various wildflowers or honey+water, during the first 20 min of exposure to diamondback larvae. Columns with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

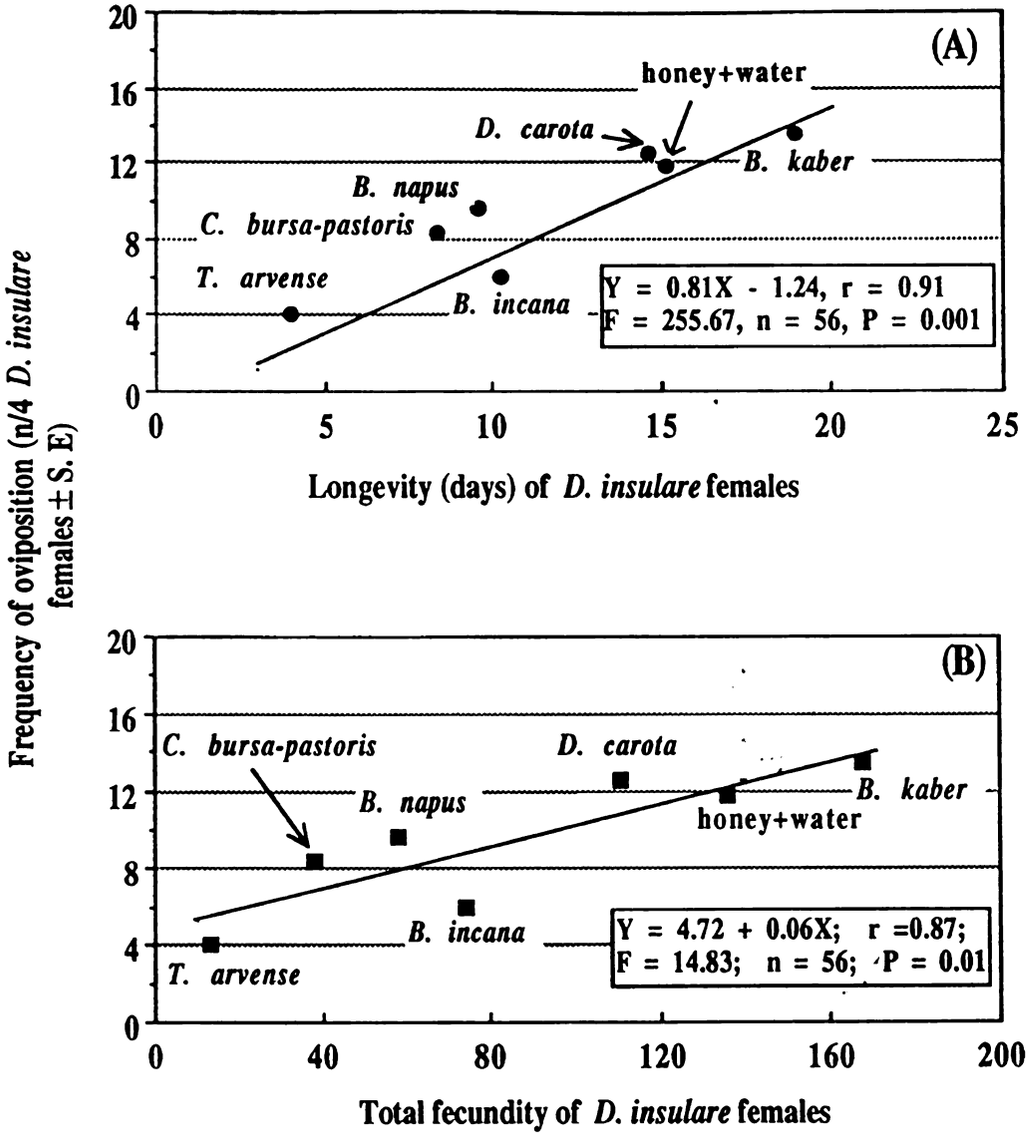

Figure 7. The relationship between longevity (A) or fecundity (B) and the frequency of ovipositional behavior made by *D. insulare* females within the first minute of exposure to host larvae.

Relationship of flower characters to *D. insulare* longevity and fecundity. Corolla lengths and opening diameters were significantly different among flower species ($F = 38.2$; df = 8, 56; $P = 0.0001$ and $F = 46.2$; df = 8, 56; $P = 0.0001$ for the corolla lengths and opening diameters, respectively). The corolla lengths of *B. vulgaris*, *B. napus* and *B. kaber* were significantly longer than corolla lengths of the other flowers, especially *D. carota* (Fisher's PLSD, $P < 0.05$) (Table 2). In contrast, the corolla opening of *D. carota*

Table 2. Corolla length and opening diameter of wildflowers

Species	Corolla length (mm ± S.E)	Corolla opening width (mm ± S.E)
Daucus carota L.	0.53 ± 0.02a	6.02 ± 0.31h
Brassica kaber (D.C) Wheeler	4.31 ± 0.13d	5.50 ± 0.20g
Brassica napus L.	4.81 ± 0.09d	3.83 ± 0.03f
Barbarea vulgaris R. Br.	4.44 ± 0.11d	2.80 ± 0.03e
Berteroa incana (L.) DC.	2.48 ± 0.50c	2.06 ± 0.03d
Capsella bursa-pastoris (L.) Medic	2.46 ± 0.03bc	1.67 ± 0.03c
Thlaspi arvense L.	1.71 ± 0.08b	1.20 ± 0.02b
Erysimum cheiranthoides L.	2.62 ± 0.03c	1.00 ± 0.20b
Lepidium campestre (L.) R. Br.	1.55 ± 0.04b	0.52 ± 0.02a

In column means with the same letter are not significantly different (Fisher's Protected LSD, $P > 0.05$).

was significantly wider than those of the other flowers; *L. campestre* had the narrowest corolla opening (Fisher's PLSD, $P < 0.05$)(Table 2). Regression analysis indicated that 14.4% ($F = 11.75$, $P = 0.001$) and 59.5% ($F = 102.82$, $P = 0.001$) of variation in the longevity of *D. insulare* could be explained by the corolla length and opening diameter, respectively (Fig. 8 A & B). There was a significant positive correlation between *D. insulare* longevity and corolla length even though a negative correlation was expected, if a

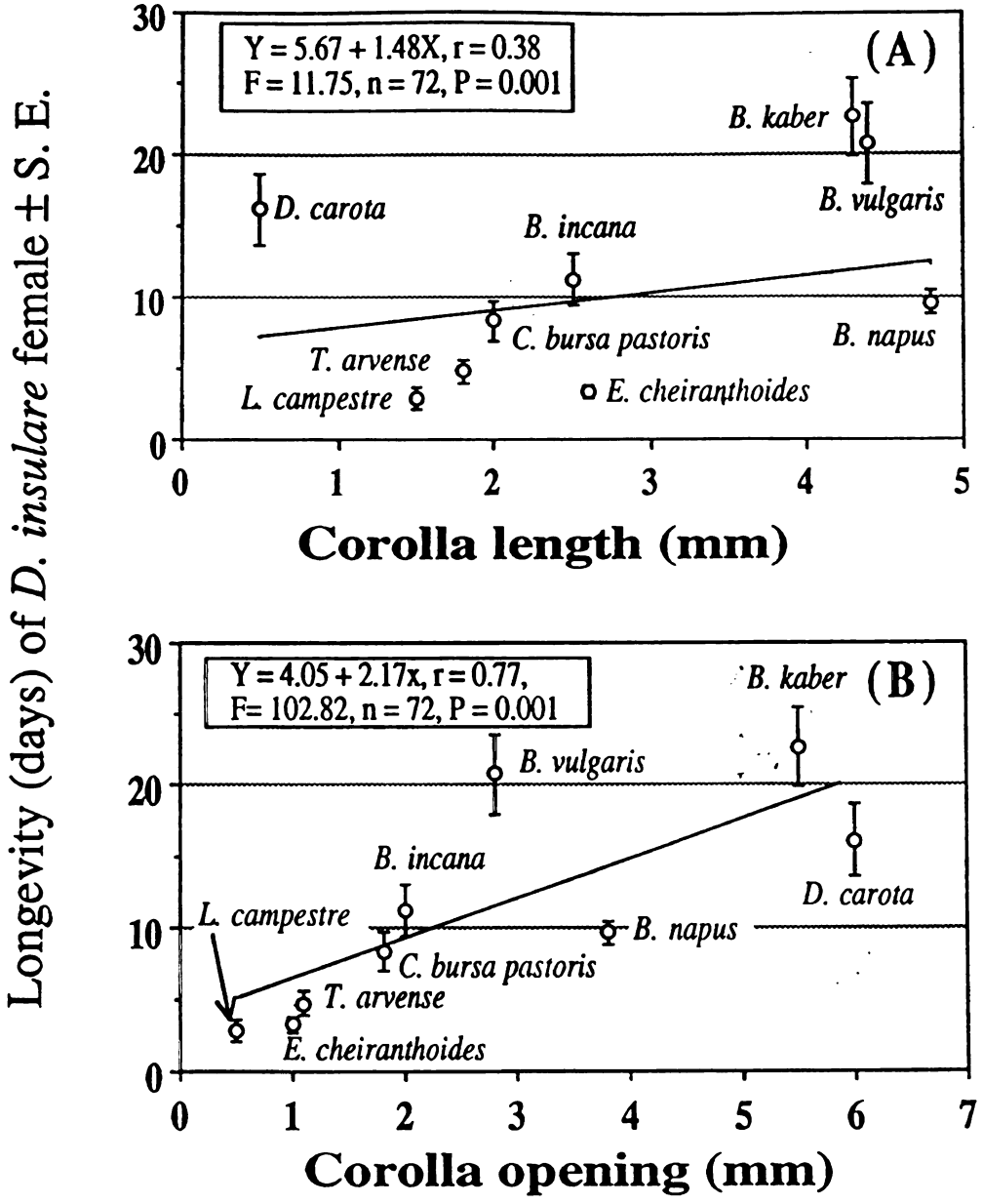

Figure 8. Longevity of *D. insulare* females in relation to corolla length (A) and opening (B) of wildflowers.

narrow corolla limited access to nectar by *D. insulare* (Fig. 8 A & B). This positive correlation is probably due to the high correlation between length and opening except for *D. carota* ($r = 0.79$; $F = 108.98$; $df = 1, 62$; $n = 72$; $P = 0.001$) rather than any factor resulting in increased longevity with longer corollas. For *D. carota* the corolla opening is large enough that length did not influence longevity. *B. kaber* petals are separated down to the base of the corolla providing easy access of the parasitoid to the nectaries, in spite of its length.

There was no significant relationship between the corolla length and the fecundity of *D. insulare* ($r = 0.37$, $F = 1.09$, $P = 0.33$)(Fig. 9 A). However, corolla opening explained 75% of the variation in *D. insulare* fecundity ($r = 0.87$, $F = 21.01$, $P = 0.003$, Fig. 9 B).

Subsequent to these studies I looked at the effect of *Scrophularia nodosa* L. (Scrophulariaceae) on the longevity and fecundity of *D. insulare* following similar procedure as above. It has a very wide corolla and is known to produce high amounts of nectar (Ayers et al. 1987). *D. insulare* fed on *S. nodosa* lived 25.3 ± 2.5 d ($n = 10$) and parasitized 170.3 ± 18.5 diamondback moth larvae (unpublished data). These were somewhat similar when the parasitoid were fed on *B. kaber*, the better food sources for *D. insulare* in my study.

There are also other factors affecting access to nectar besides corolla length and opening. The separation of the sepals and petals in *B. kaber* flowers exposes the basal part of the flower where nectar is located even for newly opened flowers. Thickness of the petals and sepals at the base of the corolla and sepals attached at the base, covering the bottom half of the corolla may also be important. I observed *D. insulare* apparently chewing or sucking at the base of *B. vulgaris* and *B. napus* flowers to get nectar. In some cases, a hole in the base of a petal was visible after *D. insulare* chewing.

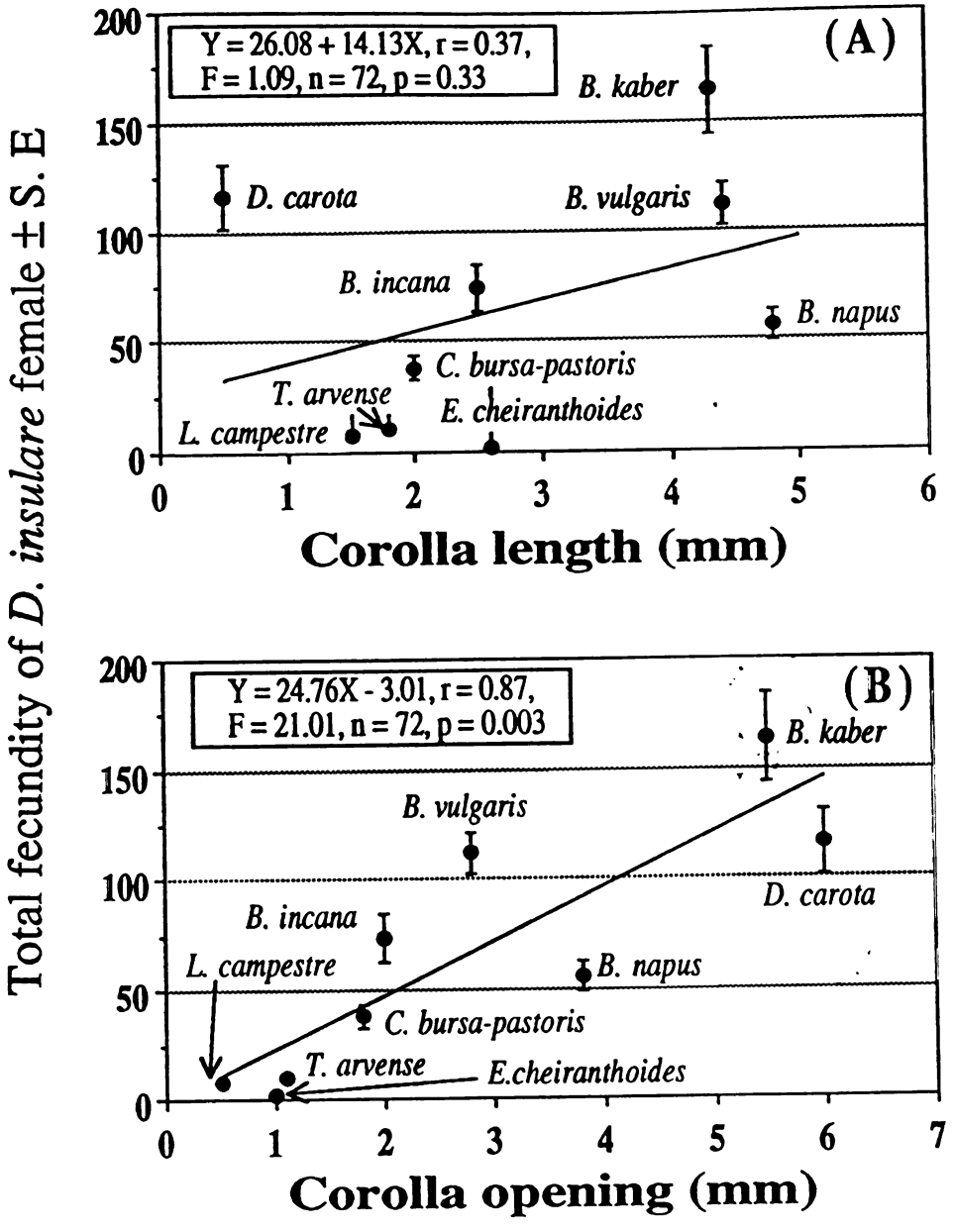

Figure 9. The relationship of fecundity of *D. insulare* females to the corolla length (A) and opening (B) of wildflowers.

In the field and the laboratory, I also observed squeezing or kicking behavior of *D. insulare* on the petals or sepals of *C. bursa*-pastoris and *T. arvense* flowers (narrow and short corollas with soft thin petals and sepals). *D. insulare* appeared to be trying to reach the nectar at the base of the corolla. I did not observe this behavior on *D. carota* flowers perhaps because they are wider and have shorter corollas.

CONCLUSIONS

Overall, results of my study indicate that *D. insulare* longevity and fecundity are dependent on the availability and accessibility of food (nectar) sources in and around the field. The accessibility of the nectar correlates with flower characters. Although the width of the corolla opening has a strong effect on both longevity and fecundity, it did not explain all the observed variation between wildflower species as food sources. Nectar quality and extrafloral nectar are probably important (Baker & Baker 1983) but I did not measure it. *C. album* and *S. arvensis* which did not have accessible nectar could indirectly provide food sources by harboring aphids which produce honeydew for the parasitoid.

Although *D. insulare* also used flowers of non-brassicas weeds, *D. insulare* may have coevolved with the diamondback moth to associate with the Brassicaceae weeds. However, Herrera (1993) found that evolution for adapting to other ecological factors are far more important determinants of fitness (longevity and fecundity) of the hawk moth, *Macroglossum stellatarum* L. (Lepidoptera: Sphingidae), than selection of floral morphology or phenotype. It is also possible that certain *Brassica* species like *B. kaber* may have evolved to have floral structures that attract *D. insulare* or other parasitoids. Flowers with accessible nectar might help increase parasitism of diamondback moth. In Michigan, *B. kaber*, which supported the highest longevity and fecundity of *D. insulare*, is most commonly infested by diamondback moth, 80-90% of which are parasitized

(unpublished data). Further study needs to be done on the parasitism rate of diamondback moth by *D. insulare* when these plants are used as food sources.

B. vulgaris, and *B. kaber* and *D. carota*, which are abundant in weedy areas and idle field in Michigan during early and middle to late season, respectively, could influence effectiveness of *D. insulare* as a biocontrol agent of diamondback moth. The distribution of these weeds could be manipulated in brassicas cropping systems to favor *D. insulare*. In addition, providing refuge (shading) for *D. insulare* is important for enhancing the effectiveness and role of this parasitoid in integrated diamondback moth management. Other nectar-producing plants may be even more suitable, providing more or better quality nectar or nectar over a longer period of time (e.g., *Pycnanthemem pilosum* Nutt. and *Scrophularia nodosa* L., Ayers et al. 1987). Design of crop management systems including management of natural enemy food sources will become more important as we try to integrate biological control with production of high value vegetable crops.

CHAPTER 2

Nectar-collecting Behavior of *Diadegma insulare* (Cresson)(Hymennoptera: Ichneumonidae), a Parasitoid of Diamondback Moth, *Plutella xylostella* (L.)(Lepidoptera: Plutellidae)

ABSTRACT

I observed nine nectar-collecting behaviors of *Diadegma insulare* (Cresson), a major parasitoid of diamondback moth, *Plutella xylostella* (L.). The most striking behavior, on *Barbarea vulgaris* R. Br. and *Brassica napus* L. flowers, involved chewing at the base of the corolla and creating holes that probably released the floral nectar. *D. insulare* apparently is not a pollen feeder as the anthers of flowers were never approached. *D. insulare* visited more frequently and spent longer times on flower species supporting longer life and fecundity (*B. vulgaris*, *Brassica kaber* (D.C) Wheeler, *B. napus* and *Daucus carota* L. Times spent per visit number to each flower specis were significantly affected by flower species and were significantly influenced by visit numbers by flower species interaction. The times spent by *D. insulare* on the more rewarding species, *B. kaber* and *B. vulgaris* increased with numbers of visits but declined between the fifth and sixth visits. This pattern was not true for poor nectar sources, *Berteroa incana* L. (D.C) and *Erysimumcheiranthoides* L. This suggests that *D. insulare*, after experience, was able to positively correlate nectar rewards with the flower characters. Flower color was not a factor influencing parasitoid choice to visit flowers. *D. insulare* spent significantly longer time at the upper one third of *D. carota* corolla and at the lower one third of *B. kaber* and *B. vulgaris* corollas than other flowers. Behavioral flexibility of *D. insulare* to flower characters and its nectar-collecting behaviors should be manipulated for increased impact of this parasitoid in diamondback moth control program.

INTRODUCTION

Diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), is the major pest of Brassicaceae crops worldwide. Pesticide resistance problems have forced growers to increase the frequency and rate of sprays. This leads to excessive use of pesticides that destroys the pest's natural biocontrol agents in *Brassica* crop agroecosystems (Lim et al. 1986).

The abundance of *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae) in the field and its role as major diamondback moth parasitoid was reported by Harcourt (1986). Pesticides continue to be the major means for controlling pests, but these are detrimental to *D. insulare* (Lingren et al. 1972, Idris & Grafius 1993a & b). However, judicious use of pesticides with good *Brassica* crop agroecosystem management could increase role of *Diadegma* in the field (Ooi 1992, Srinivasan & Krishna Moorthy 1991).

D. insulare live longer and are more fecund when fed on *Brassica kaber* (DC.) Wheeler, *Barbarea vulgaris* R. Br. or *Daucus carota* L., wildflowers commonly found in and around crop fields in North America (Buchholtz et al. 1981). Earlier studies indicated that the presence of wildflowers in the field increases the effectiveness of other parasitoids (van Emden 1963 a & b, Leius 1967, Kopvillem 1960, Keven 1973, Syme 1975, Zhao et al. 1992). *D. insulare* effectiveness could be increased by providing suitable wildflower nectar sources in or around the fields.

Floral structures, the corolla length and opening diameter of wildflowers affect longevity and fecundity of *D. insulare*. (Chapter 1). They may also influence the behavior of *D. insulare* in collecting nectar (Chapter 1). Different behavior of bumble bees, *Bombus* spp., on various flowers was observed more than 100 years ago by Charles Darwin

(Guiterman 1959). Darwin reported that individual bees made holes near to the nectaries of long tubular flowers by biting through the corolla with their mandibles or piercing them with their tongues. The specialist bumble bee, *B. consobrinus* Dhalb, is more efficient than generalist species in acquiring flower-handling skills on their specialty plants by probing in the vicinity of the nectary and quickly locating the nectar even without previous experiences (Laverty & Plowright 1988).

The objectives of my study were to (1) characterize nectar-collecting behaviors of *D. insulare* on various flowers that are used as food sources, (2) quantify the number of visits or visitors and times spend on flowers offered to *D. insulare*, (3) evaluate flower color choice, and (4) look at the possible learning ability of *D. insulare* to select more rewarding flowers in maximizing their nectar-collecting effort.

MATERIALS AND METHODS

Flowers used in my studies were common weed species and one *Brassica* crop plant (Table 1). I selected these weeds because they support a wide range in longevity and fecundity of *D. insulare* adults (Chapter 1)(Table 1).

Choice tests. Stalks of three flowers of each species were inserted through holes in the lid of a 300 ml plastic container almost filled with sucrose solution (0.5 g/ml). The flower species were randomly arranged in a circle about 4.0 cm from the center of the cover. A second 300 ml container, with 1.5 cm diam screened holes in the side, was put upside down on the first container and fastened with tape, creating a testing arena. The arena was put under white inflorescence light (Philips; FT2T12/CW/VHG, 160Watt, 44 cm above arenas), at 25 ± 2°C and 50-70% relative humidity. I randomly arranged the arenas parallel to the light.

An unfed female *D. insulare* (1 d old) was put in a freezer for 3 min for easy handling and released in the center of the testing arena through a hole in the upper

Table 1. Species, common names, and families of flowers used for this study, and mean longevity and fecundity of *D. insulare* when fed on these flowers

Species	Common name	Family	*D. insulare*[c]	
			Longevity(days)	Fecundity[d]
Barbarea vulgaris R. Br. [a]	Yellow rocket	Brassicaceae	21.5 ± 3.1	108.5 ± 10.4
Erysimum cheiranthoides L. [a]	Wormseed mustard	"	2.8 ± 0.4	3.6 ± 2.3
Thlaspi arvense L. [b]	Field pennycress	"	5.0 ± 0.6	7.8 ± 0.8
Brassica napus L. [a]	Canola	"	9.8 ± 1.0	52.3 ± 3.9
Brassica kaber (D.C) Wheeler [a]	Wild mustard	"	22.2 ± 2.5	160.7 ± 24.6
Capsella bursa-pastoris (L.) Medic [b]	Shepherd's purse	"	7.5 ± 0.8	35.5 ± 2.6
Berteroa incana (L.) DC. [b]	Hoary alyssum	"	11.0 ± 1.1	73.8 ± 7.5
Daucus carota L. [b]	Wild carrot	Umbelliferae	18.5 ± 1.4	115.4 ± 12.5

[a] Yellow flower

[b] White flower

[c] From Chapter 1

[d] Numbers of diamondback moth larvae parasitized per lifetime of *D. insulare* female

container. I used cotton to plug the hole. Females were allowed to acclimate for about 2 h in the arena before observation.

The nectar-collecting behaviors of *D. insulare*; the numbers of visits and time spent per visit per flower type, the numbers of visits and time spent at the base of corollas were recorded using an audio tape recorder for 30 min per observation session. These observations were repeated five times with new plants and insects each time.

To evaluate possible learning ability of *D. insulare* I used *B. vulgaris*, *B. kaber*, *B. incana* and *E. cheiranthoides* flowers, testing arenas were set up as before (five arenas = replications, one *D. insulare* and four flower species per replicate). Females were allowed to acclimate to the testing arena as before. Times spent per visit for six visits for each *D. insulare* female and flower species were recorded using an audio tape recorder.

No-Choice tests. Freshly emerged adult *D. insulare* females were released into cages (30 per 30 x 30 x 20 cm screen cage, one *D. insulare* per cage, six cages = replications) 1 d before the experiment to acclimate them to the cage environment. The cages were put under white inflorescent light as before, but the distance of the top of the cages to the light bulb was 20 cm. No food was given to the parasitoids before the experiment because I desired quick responses to the introduced flowers (previous observations indicated that *D. insulare* can survive up to 2 d without food). Environmental conditions were same as in the choice tests.

I inserted stalks of flowers of each species into glass vials (21 x 70 mm, 3 flowers per vial) filled with sucrose solution (0.5 g/ml). To prevent *D. insulare* from reaching the sucrose I used cotton to cover the vial mouth. *D. insulare* were observed feeding at this location. Six vials with flowers of a single species were put in the middle of each cage.

Fifteen minutes after introduction of the flowers I recorded the numbers of individual *D. insulare* visiting the flowers using audio tape recorder in 30 sec. I then took out the flowers with vials.

I introduced new flower species (randomly selected, excluding the species that just tested) with vials in the another cage for the next observation. After the sixth cage I returned to the first cage and repeated this process five times (= five replicates per species). The numbers of visiting *D. insulare* per flower species per observation were recorded.

In choice and no-choice tests (above) *D. insulare* females visited and fed at the bases of the flower corollas of some species. To quantify the visit times of *D. insulare* at the upper and lower parts of corollas I used a set up similar to the choice test experiment. However, I used one flower species per test arena. I subdivided the corolla into upper, middle and lower one thirds. Treatments were replicated five times (five *D. insulare* females per flower species) with new flowers each replication.

The number of visits and time spent per visit on flowers and on upper or lower one third of flowers per flower species, and comparisons of total visitors per 30 sec for each flower species were analyzed using 1-way ANOVA; and means were compared using Fisher's Protected LSD test. The time spent per visit number per flower species was analyzed using 2-way ANOVA (Abacus Concept, Super ANOVA 1991). I used correlation analysis to test the strength of relationships between time spent per visit with visit numbers (Abacus Concept, Super ANOVA 1991)

RESULTS AND DISCUSSION

Choice tests. Characterization of nectar-collecting behaviors. I observed at least nine distinct nectar-collecting behaviors of *D. insulare* (Table 2, Fig. 1 & 2). This indicates that there is behavioral flexibility of *D. insulare* in collecting floral nectar. Most of these behaviors have been reported for bumble bees (Guiterman 1959) but most have not been reported for parasitoids, especially the ichneumonids (Jervis et al. 1993). Therefore, this is the first report that an ichneumonid can behave like the bumble bee in trying to reach the

Table 2. Nectar-collecting behaviors of *D. insulare* females observed in choice test with various flowers

Behavior	Flowers							
	B. vulgaris	*B. napus*	*B. kaber*	*E. cheranthoides*	*T. arvense*	*C. bursa-pastoris*	*D. carota*	*B. incana*
Tried to get in corolla tube	+	+	+	+	+	+	+	+
Entered corolla tube	-	-	-	-	+	+	+	+
Kicked sepal or petal	-	-	-	+	+	+	-	+
Sucked or chewed at corolla base	+	+	+	-	-	-	-	-
Circled at corolla base	+	+	+	+	+	+	-	+

Number of visit and time spent per visit to flower (see Figure 1) or at the corolla base per flower species (Figure 2)

+, yes; -, no

floral nectar sources. However, unlike the bumblebees, *D. insulare* females were never seen feeding on anthers.

D. insulare tried to get in the corolla through the corolla opening on all flower species. However, they only entered the corolla of *Berteroa incana* (L.) DC., *Thlaspi arvence* L, *Capsella bursa-pastoris* (L.) Medic and *Daucus carota* L. flowers (Table 1). Kicking (using both front and hind legs) the soft, separated sepal or petal, was observed on *B. incana*, *Erysimum cheiranthoides* L., *T. arvense* or *C. bursa-pastoris*. *D. insulare* did not try to enter the corolla tubes of *Brassica kaber* (D.C) Wheeler flowers because the corolla base has a wide separation between the sepals or petals, and between the sepals and petals; to reach the nectar at base of the corolla, *D. insulare* could easily enter from the side. After examining the upper and lower corolla of *E. cheiranthoides* flower several times *D. insulare* finally tried to enter corolla tube from the upper section. However, sepals and petals of *E. cheiranthoides* are attached to form a corolla tube, and given the narrow corolla opening *D. insulare* could not enter the tube or reach the nectar.

D. insulare easily entered the wide, shallow corolla of *D. carota*. *D. insulare* circled the corolla bases of all other flower species offered, indicating a high affinity to get close to the actual food source. *D. insulare* appeared to suck or chew at the corolla base of *Brassica vulgaris* R. Br. and *Brassica napus* L. flowers and these were subsequently found to have holes that probably released the floral nectar. Apparently, *D. insulare* used its mandibles to make the holes to reach the nectar, as does the bumble bee (Guiterman 1959). Bentley & Elias (1983) and Keven & Baker (1984) reported that insects with mandibulate mouthpart often feed on discal or bowl-shaped flowers. *D. insulare* used these holes to suck nectar each time they visited the corolla base although sometimes they also tried to make new holes. This behavior appears similar regardless of *D. insulare* flower foraging experience. Laverty & Plowright (1988) also reported that with no previous foraging experience, workers of the specialist bumblebee, *B. consobrinus*, began probing in the vicinity of the nectary and quickly located the nectar.

Quantifying the numbers of visit and time spent per flower. The numbers of visits and time spent per flower per visit were significantly different among flower species (F = 36.6, 54.2; df = 7, 28; P = 0.001; n = 40)(Fig. 1 A & B). *D. insulare* made significantly more visits to *B. vulgaris* and *B. kaber* than to the other flower species (Fisher's Protected LSD, $P < 0.05$). They spent longer times per visit on *B. napus, B. vulgaris, B. kaber and D. carota* than on the other flower species (FPLSD, Fig. 1 B). This suggests that visiting these flowers is more rewarding or beneficial (Fig. 1 A & B); *D. insulare* generally preferred flowers that support long life and high fecundity (Table 1).

The number of visits made by *D. insulare* to *B. vulgaris*, *B. napus*, *B. kaber*, *E. cheiranthoides* and *D. carota* were significantly higher than to *T. arvense*, *C. bursa-pastoris* or *B. incana* (FPLSD, $P < 0.05$)(Fig. 1 A). The times spent per visit were also significantly longer on the *B. vulgaris*, *B. napus*, *B. kaber* and *D. carota* than on the *E. cheiranthoides*, *T. arvense*, *C. bursa-pastoris* and *B. incana* (FPLSD, $P < 0.05$)(Fig. 1 B). There was only *E. cheiranthoides* flower attracted many insects but short visits.

The numbers of visits to the corolla bases were significantly higher on *B. vulgaris*, *B. napus* and *B. kaber* than on the other flower species (FPLSD, $P < 0.05$)(Fig. 2A). Although *D. insulare* visited the base of *T. arvense*, *C. bursa-pastoris* and *B. incana* flowers, the numbers of visits to the bases of these flower species were not significantly different from zero (FPLSD, $P > 0.05$). *D. insulare* did not visit the base of *D. carota* corolla because its corolla tube is extremely short and widely open. The times spent per visit at the base of corollas were significantly different among the flower species (F = 31.8; df = 7, 28; P = 0.007; n = 40)(Fig. 2 B). Again, *E. cheiranthoides* attracted a moderate numbers of visits, but visits were very short

D. insulare spent significantly shorter times per visit at the flowers and at the corolla bases of *B. kaber* than at flowers of *B. vulgaris* or *B. napus* (FPLSD, $P <$ 0.05)(Fig. 1 & 2 B). Probably, *D. insulare* takes extra time to chew and make holes at the *B. vulgaris* and *B. napus* corolla base before sucking nectar. The intriguing question was

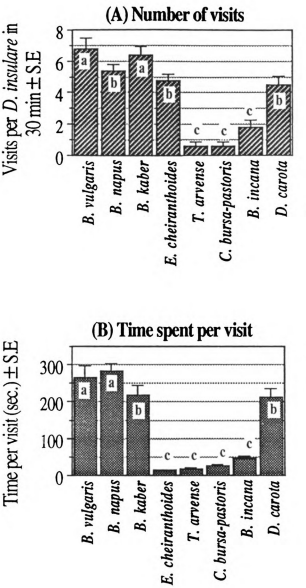

Figure 1. Number of visits (A) and time spent per visit (B) to flowers by *D. insulare* in 30 min in choice test experiment. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

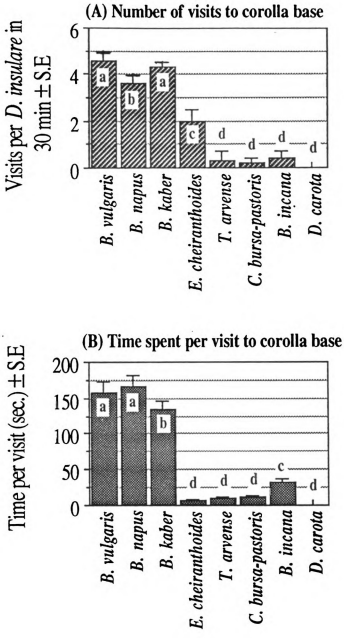

Figure 2. Number of visits (A) and time spent (B) to corolla base by *D. insulare* females in 30 min in choice test experiment. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

why *D. insulare* selected *B. vulgaris* in the presence of *B. kaber* where nectar is more easily accessable. I do not think that *D. insulare* was attracted to *B. vulgaris* more than to *B. kaber* because number of visits was similar. *D. insulare* used in my study were hungry, and this might prompt feeding attempts on whatever flower is first encountered in the testing arena. If true, longer time per visit would not necessarily mean the flower is good or preferred by the parasitoids. On the hand, *E. cheiranthoides* was apparently attractive (moderate number of visits) but not desirable (short time per visit); *E. cheiranthoides* is a poor nectar sources, based on longevity and fecundity (Table 1).

Flower color choice. No color preference was apparent. There was no significant difference in the number of visits to *E. cheiranthoides*, *B. napus* (yellow) or *D. carota* (white) flowers made by *D. insulare* (FPLSD, $P > 0.05$)(Fig. 1A)(Table 1). However, the number of visit to *E. cheiranthoides* and *D. carota* differed significantly from the numbers of visits to *T. arvense*, *C. bursa-pastoris* or *B. incana* (all are white). However, what appear to be white flowers to us may be reflecting some insect-attractive color at the center of the corolla which serves as an indicator for the presence of nectar and attracting the parasitoids (Matthew & Matthew 1978).

Possible learning ability to correlate food-foraging experiences with rewarding flowers. The times spent on *B. vulgaris* or *B. kaber* increased from first to fifth visits and decreased between fifth and sixth visits, possibly indicating satiation of the parasitoid. The times spent per visit by *D. insulare* to *B. vulgaris* and *B. kaber* were positively correlated with the number of times the *D. insulare* individual had visited that flower (visit numbers)($r = 0.42$ & 0.38; $F = 6.1$ & 4.8; df = 1, 28; $P < 0.05$; n = 10)(Fig. 3). In contrast, the times spent per visit by the *D. insulare* to *B. incana* and *E. cheiranthoides* decreased with the visit number. The times spent by *D. insulare* per visit to *B. incana* or *E. cheiranthoides* were negatively correlated with the visit numbers ($r = 0.64$ & 0.77; $F = 20.3$ & 39.8; df = 1, 28; $P < 0.05$; n = 10). The time spent per visit was also significantly influenced by the

interaction between flower species and visit number (2-way ANOVA, $F = 5.1$; df = 15, 96; $P < 0.01$; n = 20).

No-choice tests. Quantifying the numbers of visitors and time spent on the flowers. The numbers of visitors (= *D. insulare* females) per observation were significantly different among flower species ($F = 80.9$; df = 5, 15; $P = 0.001$; n = 30; FPLSD)(Fig. 4). Like the choice test (Fig. 1A), there were significantly more visitors (*D. insulare* females) to *B. kaber*, *B. vulgaris* and *D. carota* than to the other flowers (FPLSD, $P < 0.05$)(Fig. 4); there were fewer visitors to *E. cheiranthoides* flowers than to any other species. In the choice tests, *E. cheiranthoides* was visited often although *D. insulare* spent very little time on this flower. Apparently *D. insulare* could not distinguish between *E. cheiranthoides* and other attractive flowers, before landing. In contrast, in the no choice test, few visits were made to *E. cheiranthoides*, reflecting the poor quality or quantity of its nectar (Table 1). Numbers of visitors to *C. bursa pastoris* and *B. incana* were higher in this no choice test than in the choice tests. Results will also be different in nature as the diversity and abundance of wildflowers vary with habitat or landscape. In the field, like my no choice tests, some flower types are visited more frequently or have more visitors than would be expected, based on their respective abundance (Jervis et al. 1993).

The visit times in the upper one third of the flower's corolla were significantly different among flower species ($F = 44.3$; df = 3, 12; $P = 0.001$; n = 20)(Fig. 5A). *D. insulare* made longer visits to the upper one third of *D. carota* corollas than to the upper one third of *B. vulgaris*, *B. kaber* or *E. cheiranthoides* (FPLSD, $P < 0.05$). This is because *D. carota* has a very short wide corolla tube. Longer visits were made to the lower one third of *B. vulgaris* and *B. kaber* corollas than to the lower one third of *E. cheiranthoides* or *D. carota* corolla (FPLSD, $P < 0.05$)(Fig. 5B). Although the corolla tube of *B. kaber* is widely open as *D. carota* corolla (Chapter 1), *D. insulare* visited longer to the lower one third than to the upper one third of *B. kaber* corolla; the nectar source is readily accessible between the separated sepals and petals.

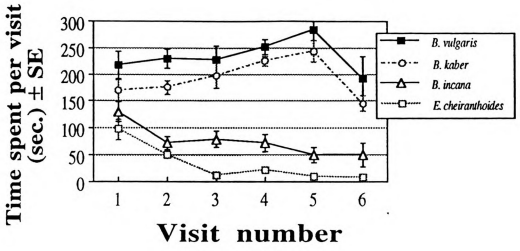

Figure 3. Time spent per visit to flowers by *D. insulare* females at different visit number in choice test experiment. [Visit number = first, second, third, fourth, fifth and sixth; visit to that flower species].

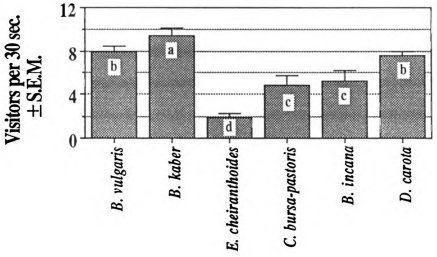

Figure 4. Number of visitors (*D. insulare* females) per flower species per 30 sec in no-choice test experiment. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

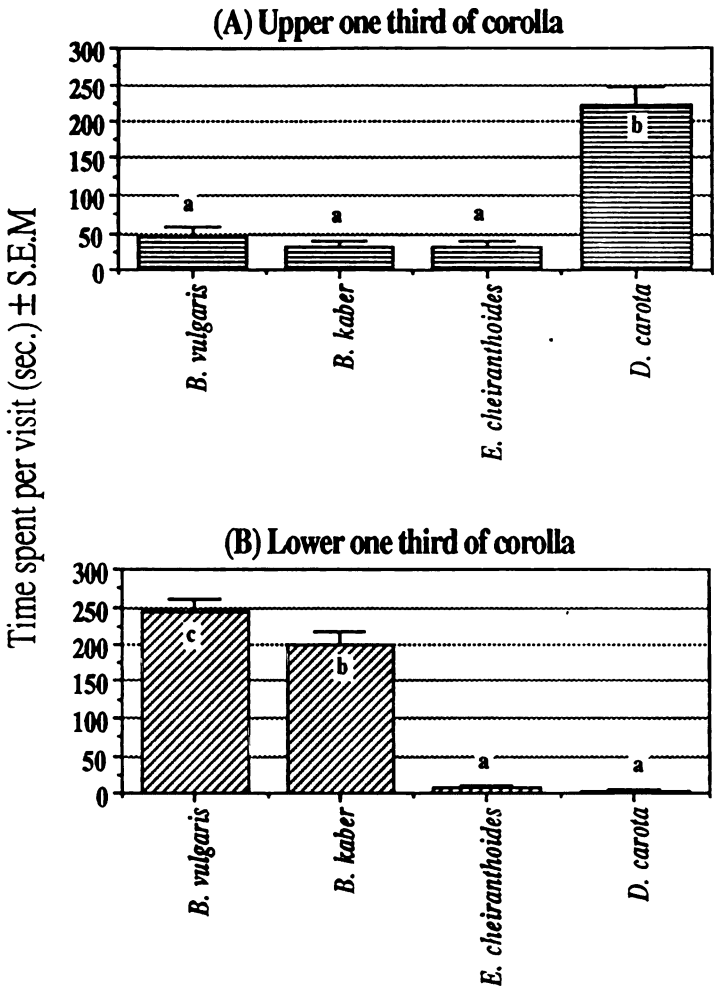

Figure 5. Time spent per visit at the upper (A) and lower (B) one third of corolla made by *D. insulare* in no-choice test experiment. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

I did not measure the number of visits and time spent on the middle one third of the corolla of all flower species. However, I observed *D. insulare* used this portion only to move from upper one third to the lower one third of all flower species.

Flower color choice. Results of no-choice tests showed a trend similar to the choice tests (Fig. 1 & 4). The number of visit to *D. carota* was as high as to *B. vulgaris*, and *D. carota* attracted significantly more visits than *B. incana* (Fig. 4). Thus, color again appeared not to be a factor affecting *D. insulare* behavior in flower choice (*B. vulgaris* and *E. cheiranthoides* is yellow but *D. carota, T. arvense, C. bursa-pastoris* and *B. incana* are white)(Table 1).

Jervis et al. (1993) believed that ichneumonids, being relatively large insects compared to braconids, and mostly lacking elongated mouth parts are largely excluded from using the nectar of (a) plants whose flowers or florets have narrow, tubular corollas, e.g. Asteraceae and Leguminosae; and (b) plants that have relatively wide corollas, but have their nectars well concealed, e.g. Convolaceae. They also suspected that wasps were feeding either partly or entirely at the extra floral nectaries of the plants. However, they failed to discuss why certain flowers like *B. vulgaris* or *B. kaber* attracted parasitoids in the field. *B. vulgaris*, for example, has sepals that stick together at the corolla base, but the sepals are thin enough to allow *D. insulare* to chew, making hole and sucking the nectar.

Behavioral flexibility of *D. insulare* in relation to flower characters and nectar-collecting behaviors should be manipulated for better utilization of this parasitoid in an integrated diamondback moth management program. My results suggest that *B. vulgaris*, *B. kaber* or *D. carota* can be integrated in *Brassica* cropping systems. They can be planted around the field or in patches or within the field. Russian researchers found that if rapid-flowering mustards are sown with brassica crops, parasitism of cabbage white butterfly larvae (*Pieris* spp.) by a braconid, *Cotesia (= Apantales) glomeratus* L. increased from 10% to 60% (National Academy of Science 1969). *C. glomeratus* is known to feed on

nectar from mustard flowers and, like *D. insulare*, females live longer and lay more eggs when these flowers are available.

CONCLUSIONS

Planting or leaving weeds around or within the vicinity of the field ecosystem may also harbor pests, but these can provide alternate hosts for the parasitoids. In place of weeds, we also can harvest only part of the *Brassica* crop, the remainder being allowed to flower, or intersow two *Brassica* crops. Wild brassicas such as *B. incana* or *C. bursa-pastoris* can be interplanted with brassicas crops. These *Brassica* spp. can also serve as food sources even though they are not as good as *B. kaber* or other wild flowers (Chapter 1).

Results of my study may be applicable to the temperate region since flowers that I tested are adapted to this climate. In the tropic or sub-tropical growing regions other flowers could better serve as nectar sources. Through a literature search and by examining Brassicaceae from all over the world planted at Michigan State University's Beal Botanical Garden I suggest that the Indian mustard, *Brassica juncea* L.(Czern), that is abundant in the tropics, could serve as an excellent food sources, equal to *B. kaber* for other diamondback moth parasitoids such as *Diadegma semiclausum* (Hellen)(Hymenoptera: Ichneumonidae) or *Cotesia plutellae* (Kurdjumov)(Hymenoptera: Braconidae). Flower characters of *B. kaber* and *B. juncea* are very similar, however, detailed studies need to be done on *B. juncea* and other flower species. *B. juncea* is now also being used as the most effective trap crop for diamondback moth in India (Srinivasan & Krishna Moorthy 1991 & 1992). Evaluating seasonality of flowering to provide floral resources throughout the season (Ayers et al. 1987) will also be important in using flowers to increase activity of *D. insulare* and other parasitoids.

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CHAPTER 3

Diurnal Foraging Activity of *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae), a Parasitoid of the Diamondback Moth (Lepidoptera: Plutellidae), in the Field

ABSTRACT

I studied the diurnal foraging activity of *Diadegma insulare* (Cresson) at the Collins Road Entomology Research Field Michigan State University during the summer of 1992 and 1993. Foraging activity was measured using sticky traps placed within the broccoli canopy and by direct or visual observation. Foraging activity of *D. insulare* males was positively correlated with light intensity, while female's activity was positively correlated with light intensity, temperature and wind speed. Relative humidity, percent cloud cover and time of day did not influence *D. insulare* catch. There was no significant difference between male and female catch. The patterns of males and females foraging activity at different times of day were significantly different from a uniform distribution except on 14 and 22 August 1993 for males and 14 August for females. Activity generally began between 0800 and 1000 h, peaked between 1100 to 1300 h and stopped by 2100 h. There was no significant correlation between the numbers of males and females caught on the same trap, suggesting that an increase in numbers of females does not attract more males. Males were caught more than females in September of both years, suggesting that males were more abundant or more active at the end of the season. The patterns of percent of the total day's catch of *D. insulare* male plus female catch at different times of the day in sticky traps were generally not different from visual observations. The numbers of *D. insulare* caught were positively correlated with the numbers of diamondback moth larvae per plant. This information could be useful for developing a model that can predict the peak diurnal activity of *D. insulare* in the field which would help with decisions on whether pesticides should be sprayed.

INTRODUCTION

Diadegma insulare (Cresson)(Hymenoptera: Ichneumonidae) is an important parasitoid of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), (Harcourt 1969 & 1986, Bolter & Laing 1983, Biever et al. 1992, Putnam 1968, Lasota & Kok 1986, Idris & Grafius 1993b). This parasitoid is native to central America (Carlson 1979, Waage & Cherry 1992). However, Carlson (1979) reported that *D. insulare* can be found as far as the Hawaiian Islands, and Argentina and Canada in South and North America respectively. It parasitizes *Hellula undalis* (F.)(Pyralidae) and *Plutella armoricae* (Busck)(Plutellidae)(Carlson 1979), but diamondback moth is its major host (Harcourt 1960 &1963). *D. insulare* is abundant in the field and parasitizes 50-80% of diamondback moth larvae in the field (Harcourt 1986).

Presently, insecticide treatment decisions for diamondback moth control in brassica crop fields are based on counts of larvae or damage to the leaves (Sastrosiswojo & Sastrodiharjo 1986, Palis 1983, Shelton et al. 1982, Stewart & Sear 1988). Even though the need for conserving beneficial arthropods is commonly recognized, explicit instructions cannot be given for sampling and using their numbers in decision making until their behavior, population dynamics, and parasitoid-pest-host relationships are understood to a greater degree.

Many laboratory studies of *D. insulare* have been conducted (Putnam 1968 & 1973, Bolter & Laing 1983, Harcourt 1963, Idris & Grafius 1993a & b), but information on this parasitoid's foraging behavior in the field is scant. Thus, my effort was made to learn some of this parasitoid's diurnal foraging activity and to determine if its foraging pattern is limited by weather factors or host numbers.

The objectives of this study were to: (1) determine diurnal foraging activity of *D. insulare*; (2) study the relationship between weather factors and *D. insulare*'s foraging activity; (3) determine attraction between sexes in the field; (4) compare the diurnal patterns of parasitoids caught by the sticky traps with direct or visual observation; and (5) compare the numbers of hosts per plant with the numbers of *D. insulare* caught on the sticky traps.

MATERIALS AND METHODS

This study was conducted in 1992 and 1993 at the Michigan State University Collins Road Entomology Field. In 1992, the experimental plot contained 20 rows of broccoli transplanted on 14-15 July, 0.6 m between plants, 1.5 m between rows, and 40 plants per row. I used 20:20:20 transplant fertilizer and kept the plot free of weeds manually.

On 28 and 30 August 1992, ten yellow sticky traps and 10 white sticky traps (Pherocon™ 1C trap - bottoms; Trece Inc., Salinas, California) were used to determined which color attracted more *D. insulare*. Because these traps have one-sided sticky coating material, each trap was folded in half to make a two-sided trap with sticky side out and placed upright on a 40 cm stake in the middle portion of the canopy. Broccoli leaves were trimmed as needed to make sure there were no broccoli leaves sticking to the traps. I found that there was no difference in numbers of parasitoids caught by the two colors and types of the traps. White sticky traps did not attract aphids or flies and its sticky coating material did not melt as readily during hot weather as on yellow sticky traps. Parasitoid identification and counting was also easier on white traps, therefore, I used white sticky traps in subsequent observations in 1992 and 1993.

***D. insulare* diurnal foraging activity, it's relationship to weather factors, and attraction between sexes.** On 11 and 13 September 1992, we placed 20 white sticky traps within the canopy of randomly selected broccoli plants at about 0630 h (Eastern Daylight Savings Time, EDT). *D. insulare* in the traps were sexed, counted and removed at 2 h intervals from 0800 to 2200 h.

In 1993, I planted 30 rows of broccoli and used 14 rows of each side of the plot for the study using sticky traps on one side and direct visual observation on the other, leaving two rows in the middle as buffer. On 14, 18 and 22 August, and 5 September, I conducted similar experiments and recorded the number of *D. insulare* caught at different times of the day (1 h interval), the temperature and relative humidity (Taylor Hygrometer, UCA, Thermometer corp., CA), sunlight intensity (Quantum Sense Meter; Li-COR, Inc., Lincoln, NE), wind speed (Turbo Meter; Davis Instruments, Hayward, CA) and cloud cover every 20 min from 0630 to 2200 h. Cloud cover was visually rated as sunny, partly sunny (< 50% cloud cover), partly cloudy (> 50% cloud cover), cloudy or fog.

The numbers of *D. insulare* males and females, and males plus females caught at different times of the day, and the patterns of males versus females catch were analyzed using χ^2 to determine if activity varied during the day (using the average of the day's catch as expected value, actual catch as the observed). I used multiple regression analysis to determine the relationship between *D. insulare* activity (trap catch) and weather factors (Abacus Concepts, SuperAnova 1991). Correlation analysis was used to test the hypothesis that more males were caught on traps with high counts of females (Abacus Concepts, SuperAnova 1991). A paired student's*t* -test was used to compare the total numbers of each sex caught per day (MSTAT, Eisensmith 1989).

Diurnal patterns of *D. insulare* caught by sticky traps versus direct or visual observation. Direct visual observations of *D. insulare* were made every hour, while walking along rows of broccoli and capturing with a sweep net all *D. insulare* seen on the same day as observations on the sticky traps (The number and turning angle of its zig-

zag flight pattern is less frequent and small, respectively, and this can be easily distinguished from flight pattern of other ichneumonids or braconids that normally observed in broccoli field) along 35 m of row. Observations of two adjacent rows were made simultaneously for an effective sampling unit of 70 m of row at each sampling. Captured parasitoids were identified, sexed, counted, and released. To compare the patterns of *D. insulare* caught on sticky traps with visually observations I transformed the *D. insulare* catch and observations hourly data to the percentage of the total day's catch or observation at each sample interval, then analyzed using χ^2 as above.

Relationship between the numbers of hosts per plant with numbers of *D. insulare* caught in the sticky traps. On 25 August 1993, I conducted an experiment to study the relationship between the numbers of diamondback moth larvae per plant with the number of *D. insulare* caught per trap. I randomly selected 3 broccoli rows (each row = block) and eight plants (each plant = replicate) per block in the experimental plot described above. Diamondback moth larvae from these plants were removed by hand. I placed laboratory-reared third instar diamondback moth on these plants (0, 3 or 6 per plant, randomly assigned within blocks) and let the larvae acclimate to the host plant for 24 h. On 26 August 1993, each plant was sampled to ensure it had the correct number of diamondback moth larvae as assigned and added new larvae where needed. At 1000 h I randomly placed sticky traps next to each treatment's plant. The numbers and sex of *D. insulare* caught per trap were recorded hourly from 1100 to 1700 h and *D. insulare* were removed as before. The numbers of *D. insulare* males and females caught per treatment were compared with diamondback moth density using regression analysis (Abacus Concepts, SuperAnova 1991).

RESULTS AND DISCUSSION

***D. insulare* diurnal foraging activity.** Females began foraging between 1000 and 1200 h on 11 September and between 0800 and 1000 h on 13 September 1992 that is 1-2 h later than the males (Fig. 1 A & B). Male foraging peaked at a similar time regardless of the temperature, but female foraging peaked earlier on warmer days (1000-1200 h) than on cooler days (1400-1600 h). Female and male activity ceased at the same time on both days.

The patterns of males and females caught on the sticky traps at different times of the day were significantly different from uniform distributions (χ^2= 28.5, 20.3 for males and females respectively; df = 7; $P < 0.05$) (Fig. 1A & B). The numbers of *D. insulare* (males plus females) caught at different times of the day were also significantly different from a uniform distribution on 11 September (χ^2= 25.8, df = 7, $P < 0.05$), but not on 13 September (χ^2= 9.6; df = 6; $P > 0.05$). The diurnal patterns of male catch were significantly different from the patterns of female catch at different time on both days (χ^2= 35.5, 17.3; df = 7; $P < 0.05$).

In 1993, females foraging began between 0900 h and 1100 h, 1-2 h later than the males, peaked between 1000 and 1300 h and ceased between 1900 and 2100 h (Fig. 2 and 3 A & C). Female *Microplitis croceipes* Cresson (Hymenoptera: Braconidae), a parasitoid of *Helicorverpa* spp., also begin foraging 1 h later than the males (Powel & King 1984). Except on 18 August, female foraging ceased at the same time as males. The activity of males plus females peaked at the same time as for females alone.

The diurnal patterns of males catch differed significantly from a uniform distribution on 18 August and 5 September 1993 (χ^2= 51.2 & 47.2; df = 15; $P < 0.05$). However, diurnal patterns of female catch differed significantly from a uniform distribution on all dates (χ^2= 26.1, 24.3, 27.0 & 33.3; df = 15; $P < 0.05$). Male plus female diurnal catch pattern was also significantly different from a uniform distribution (χ^2= 27.43, 57.6, 33.9 & 68.5; df = 15; $P < 0.05$). Male plus female diurnal catch pattern was also significantly different

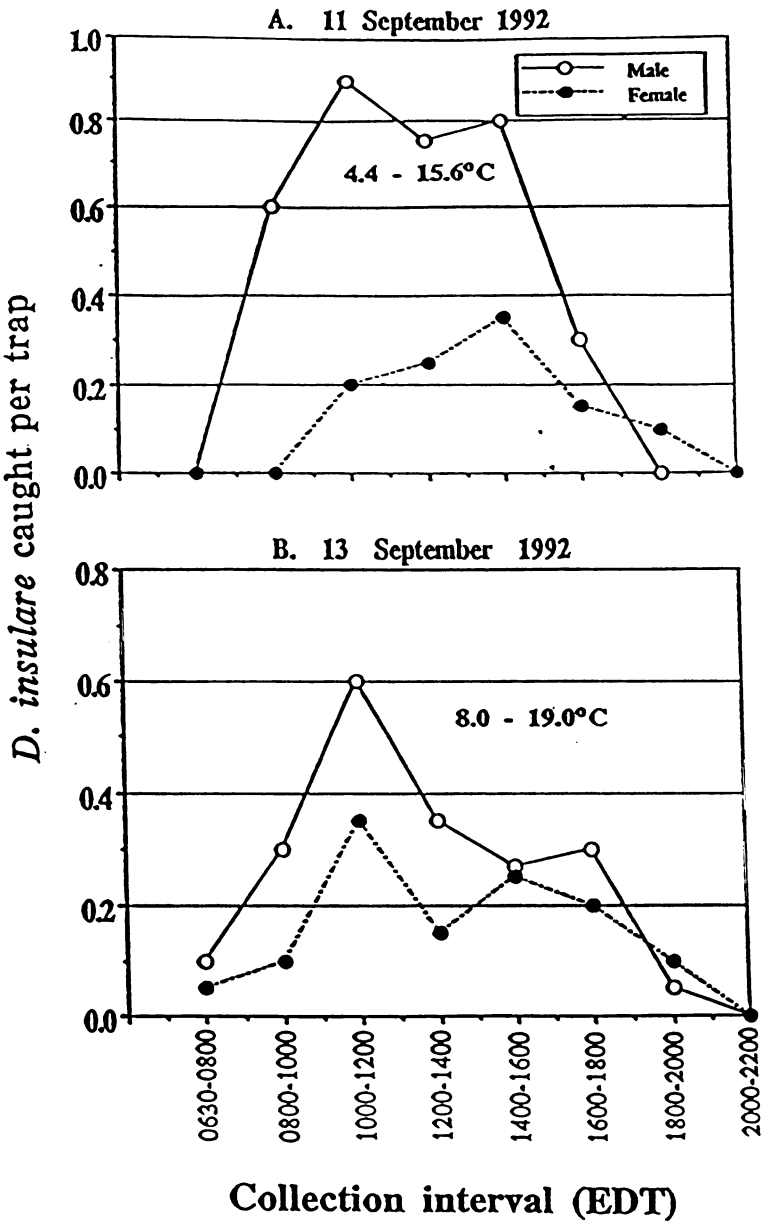

Figure 1. Diurnal patterns of *D. insulare* caught in the sticky traps on 11(A) and 13 (B) September 1993.

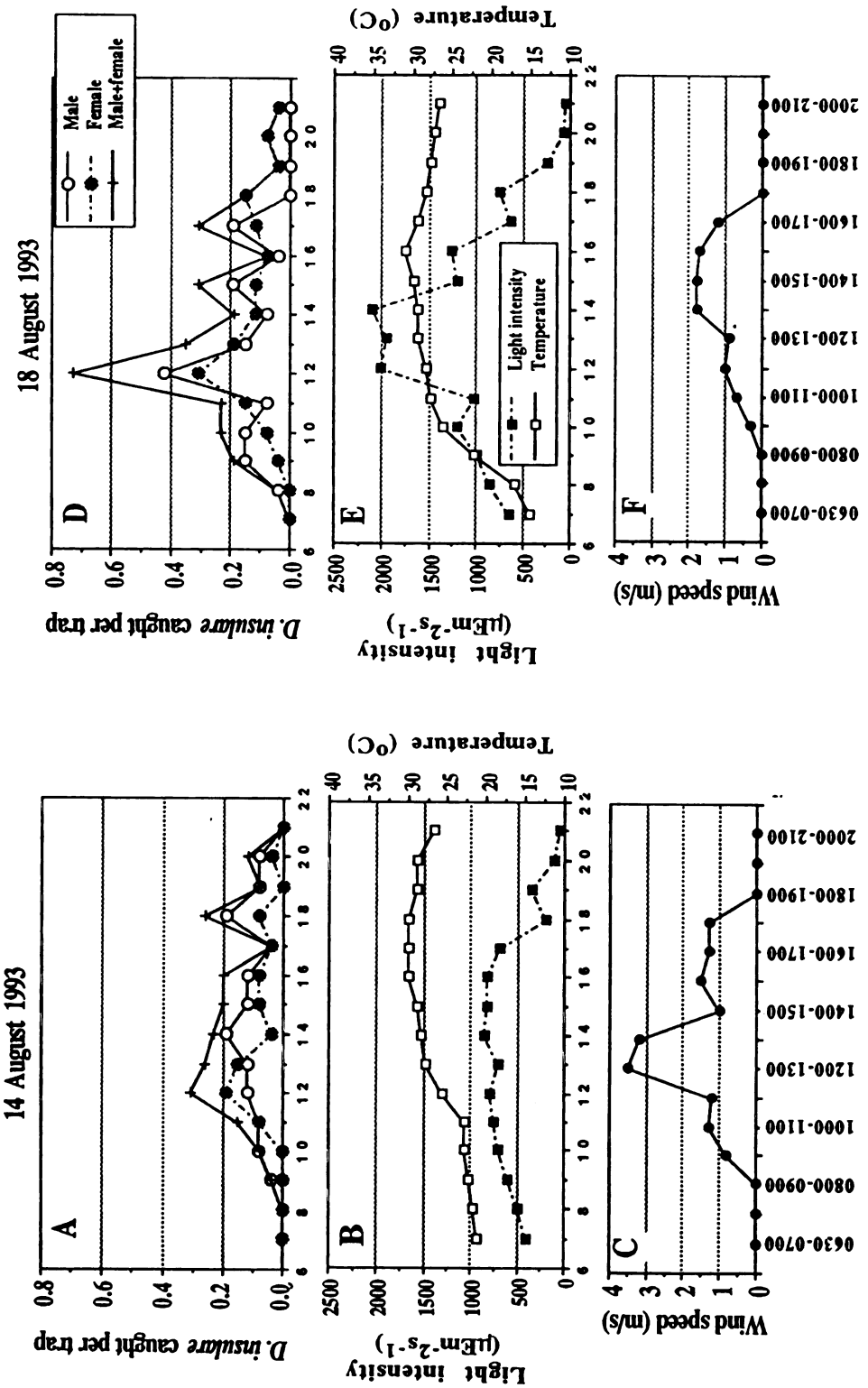

Figure 2. Diurnal patterns of *D. insulare* in the sticky traps (top), light intensity and temperature (middle), and wind speed (bottom) on 14 August (A to C) and 18 August (D to F) 1993.

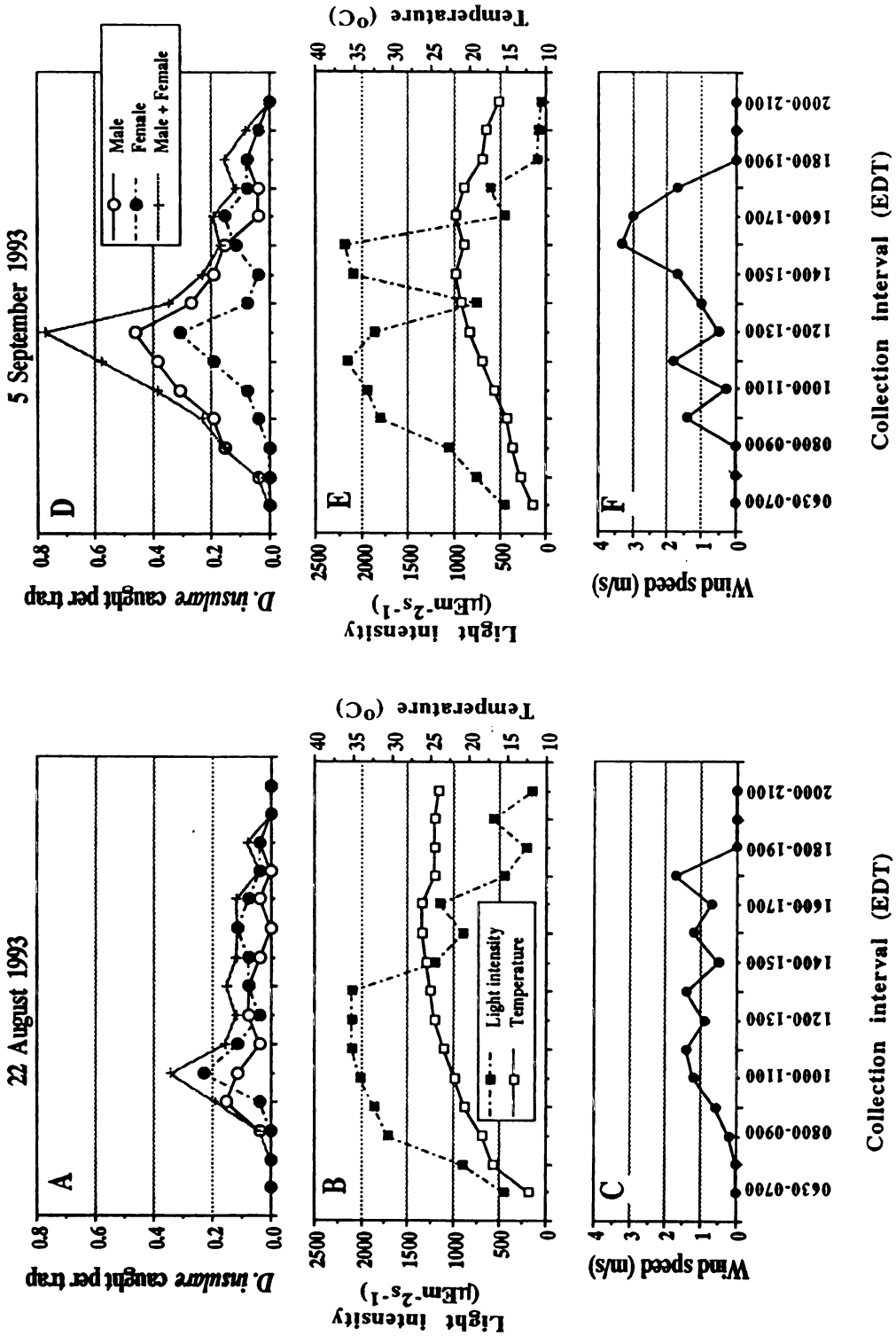

Figure 3. Diurnal patterns of *D. insulare* in the sticky traps (top), light intensity and temperature (middle), and wind speed (bottom) on 22 August (A to C) and 5 September (D to F) 1993.

from a uniform distribution (χ^2= 27.43, 57.6, 33.9 & 68.5; df = 15; $P < 0.05$). In contrast to 1992, there was no significant difference between male and female catch patterns (χ^2= 15.7, 9.8, 6.6, 18.5; df = 15, $P > 0.05$) (Fig. 2, 3 A & C). The total male catch per day did not differ from female catch in August of both years (paired *t*-test; df = 15; $P < 0.05$) but was significantly higher than the females catch in September in both years (paired *t*-test, df = 15, $P > 0.05$)(Fig. 2 & 3). This suggests that more male offspring were produced at the end of the cropping season. Low host larvae quality as a result of reduced food plant quality at the end of the season may shift the parasitoid sex ratio toward more males (Fox et al. 1990, Harcourt 1986).

Relationship between diurnal foraging activity with weather factors. Light intensity was significantly correlated with male, female and male plus female diurnal foraging patterns (Table 1). Temperature and wind speed were significantly correlated with only female foraging pattern, after stepwise elimination regression. Weather factors

Table 1. Multiple Correlation Statistics for *Diadegma insulare* foraging activity

Factors	d.f	Males[a]		Females[b]		(Males + Females)[c]	
		F	*P*	*F*	*P*	*F*	*P*
Light intensity	1, 54	15.49	0.0002	23.01	0.001	17.98	0.001
Temperature[d]	"	0.22	0.64	12.33	0.001	1.01	0.32
Wind speed[d]	"	0.78	0.38	6.12	0.016	1.45	0.23

[a], r = 0.55; $F = 4.97$; df = 1, 54; $P = 0.0009$
[b], r = 0.63; $F = 7.39$; df = 1, 54; $P = 0.0001$

explained 31.3, 40.3 and 39.8% of the variation in the male, female and male plus female catch patterns. Relative humidity and cloud cover were not correlated with male, female or male plus female catch on the sticky traps.

Light intensity was relatively higher on 18 and 22 August and 5 September 1993, especially between 1000 and 1500 h, than on 14 August 1993 (< 1000 $\mu Em^{-2}s^{-1}$, micro Einsteins per m^2 per sec, throughout the day)(Fig. 2 B, E & 3 B, E). However, *D. insulare* catch patterns on 14 and 22 August were similar (Fig. 2 & 3A). This indicates that factors other than light intensity affected foraging activity patterns of *D. insulare*. The diurnal foraging patterns of *D. insulare* males and females are shown by the lower *D. insulare* catch in the morning and afternoon when light intensity is low, but peaked in the mid-day when light intensity is peaked. Partly cloudy weather may lowered light intensity between 1300 and 1500 h on 5 September (Fig. 3 E).

Temperature was > 20°C throughout the day of 14 August and < 20°C on 5 September 1993 (Fig. 2 B). On August 18 and 22, temperature was lower than 20°C before 0800 h, between 22 and 32°C in the mid-day and above 24°C in late afternoon hours (Fig. 2 E & 3 B). However, more *D. insulare* males and females were caught on 5 September than on 14 and 22 August. This suggests that temperatures > 25°C do not increase *D. insulare* foraging activity. In the laboratory, the optimum temperature for *D. insulare* and *Diadegma semiclausum* (Hellen)(Hymenoptera: Ichneumonidae), another major parasitoid of diamondback moth, parasitism activity is 25-28°C (Bolter & Laing 1983, Talekar & Yang 1991). Females seemed more sensitive to low temperature than the males because low temperature in the morning delayed the start of females foraging activity 1-2 h especially on 5 September compared to males. Low temperature may reduce the numbers of active females and ,peak foraging activity as indicated on 11 September 1992 (Fig. 1 A). Bolter & Laing (1983) reported that 15°C is the minimum temperature for females *D. insulare* to actively parasitizing the host.

Light intensity was always around 500 $\mu Em^{-2}s^{-1}$, and temperature varied from below 12°C to around 22°C between 0630 and 0700 h. On the sunny morning of 18 August, when temperature and light intensity were above 15°C and 500 $\mu Em^{-2}s^{-1}$, respectively, males and females begin foraging 1 h earlier than on 14 (foggy morning) and 22 August (sunny). There was inconsistency of peak foraging time for both sexes even though the temperature and light intensity were high (Fig. 2 & 3 A, B, D, E). There was a drastic decline in the patterns of *D. insulare* males and female's activity 1-2 h after reaching their peaks. However, the foraging activities increased again between 1500 to 1900 h regardless of increase or decrease in temperature and decrease in light intensity (Fig. 2 & 3 A, B, D, E). Regardless of the afternoon temperature, foraging activity ceased when light intensity lower than 500 $\mu Em^{-2}s^{-1}$. This suggests that foraging ceased because of poor visibility in the late afternoon hours. *D. semiclausum* female used its visual perception for finding suitable host for egg laying (Talekar & Yang 1991). Males of *Campoletis sonorensis* (Cameron)(Hymenoptera: Braconidae), a parasitoid of *Helicoverpa* spp., also need adequate visual cues to locate females (McAuslane et al. 1990b). There were no *D. insulare* males captured during this period or collection interval, suggesting that good visibility prompted males to start foraging.

Wind speed was always lower than 4.0 m/s (14.8 km/h), but was correlated with the diurnal patterns of *D. insulare* female foraging activity ($r = 0.63$; $F = 6.12$; df = 1, 54; $P = 0.01$)(Fig. 2, 3 C & F). On 18 August, wind speed was lower than the wind speed on 5 September 1993, but the total females caught were not different on both days. This indicates that *D. insulare* may a have low wind speed threshold for its diurnal foraging activity. However, low wind speed threshold may have a detrimental impact on *D. insulare* foraging activity and parasitism rate during gusty winds. For example, On 11 September 1992, gusting wind (> 15 m per s) may be the factor that significantly reduced the number of females caught. Keller (1990) reported that the oviposition rate of *Cotesia rubecula* (Marshall)(Hymenoptera: Braconidae) was reduced the increasing wind speed. Wind

gusting above 4.4 m per s also inhibits *S. mesollana* (Géhin) (Diptera: Cecidomyiidae) flying to the wheat head to lay eggs (Pivnick 1993). Wind is important to carry sex pheromone released by *D. insulare* females that invokes males to find mates. Chemical signals released by female wasp that carried a long distance by wind was studied in detail by Lewis et al. (1971) and Eller et al. (1984).

Attraction between sexes. The numbers of males were not significantly correlated with the numbers of females caught on the same traps on 14 and 18 August and 5 September ($r = 0.05, 0.23, 0.19$; $F = 0.09, 2.55, 1.69$; $P = 0.77, 0.12, 0.20$)(Fig. 4 A, B & D). On 22 August, however, the number of males caught was negatively correlated with the numbers of females caught on the same traps (Fig. 4 C). This suggests that more females did not attract more males. There may be several reasons for this. First, females may not release sex pheromones during host foraging and are therefore not attractive to males. Second, females may call males by releasing pheromones while resting on a substrate and waiting for the males to come to her; hence female catch would be low, male catch would be high. Third, there may be intraspecific interference or competition between the males.

Diurnal patterns of *D. insulare* caught in sticky traps versus direct or visual observation. The patterns for percent of total day's catch of *D. insulare* males plus females on the sticky traps and visually observed at different time of the day were significantly different from a uniform distribution ($\chi^2 = 28.8, 25.6$ & 30.1, on 14, 18 and 22 August, respectively; df = 14, $P < 0.05$)(Fig. 5 A to C). Both sticky traps and direct visual observation counts indicated a similar time of peak parasitoid foraging activity on each day. There was no significant difference between the percent of total *D. insulare* males plus females caught on the sticky traps and those of visually observed at different time of the day on 14, 18 and 22 August 1993 ($\chi^2 = 18.05, 19.4, 8.9$; df = 14, $P > 0.05$)(Fig. 5 A to C). This indicates that sticky traps are as good as visual observation for monitoring foraging activity of *D. insulare*. Parasitoids may be recounted during visual observation

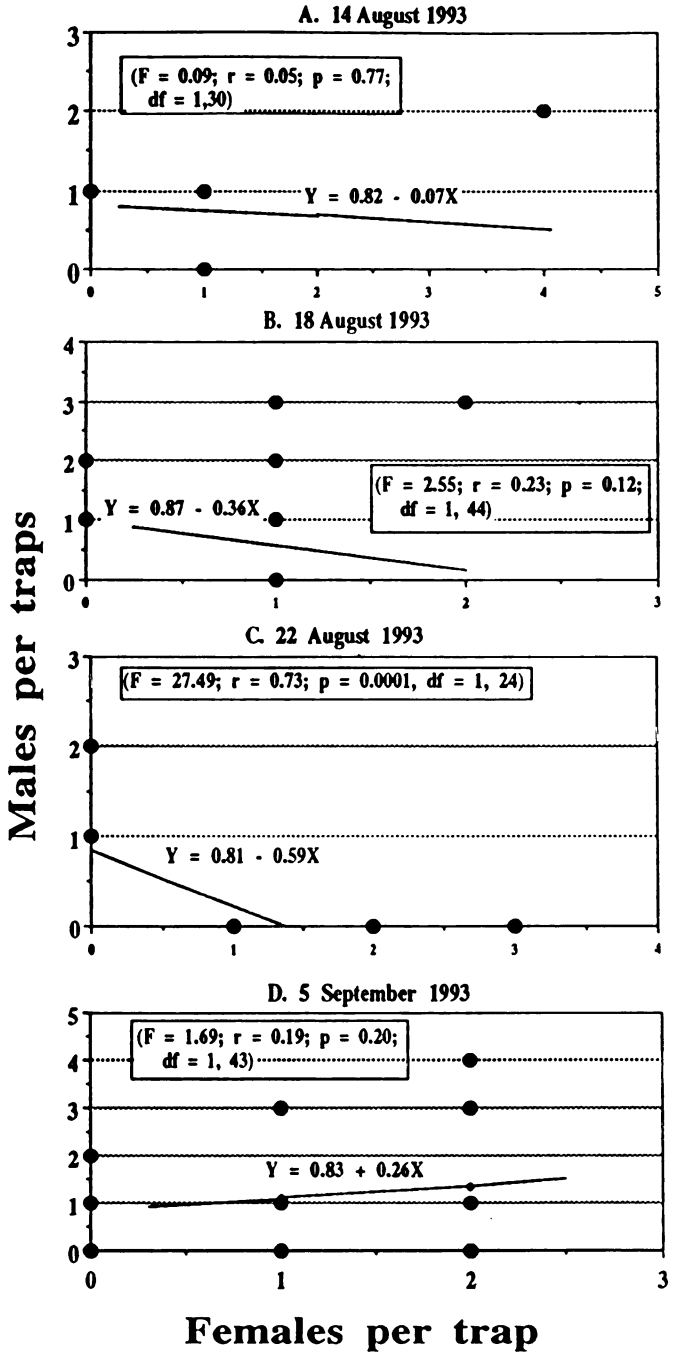

Figure 4. Relationship between the number of *D. insulare* males and females caught on the same traps.

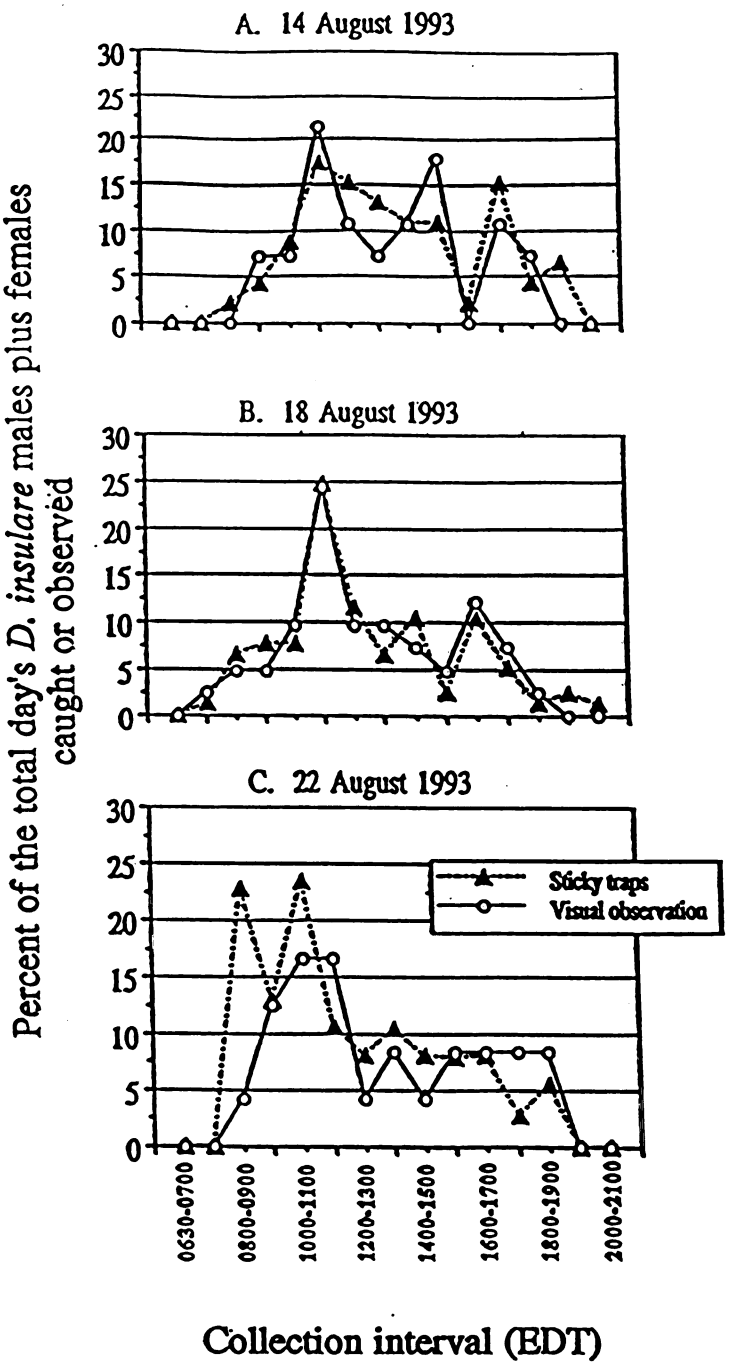

Figure 5. Comparison of the percent of the total day's *D. insulare* caught on the sticky traps versus direct or visual observations (males plus females).

because I released them from the sweep net after they were counted. However, using sticky traps means higher cost than visual observation and sticky traps do not give any direct information about *D. insulare* activity. Sticky traps may be more applicable to large brassica crop fields in developed countries where labor cost to hire people for field scouting is high. In contrast, the visual observation method may be better suited for small brassica crop growers especially in developing countries where the cost of labor is low and the price of sticky traps is high. Although I found that using sticky traps took less time than visual observation in counting *D. insulare* per unit time, sticky traps may only be suitable for brassicas crops that have a similar leaf canopy to broccoli. I also observed that the flight behavior of *D. insulare* is quite similar to another ichneumonid, *Diadromus substilicornis* (Gravenhorst), a pupal parasitoid of diamondback moth, in the cultivated brassica field. Otherwise we could monitor *D. insulare* visually without using a sweep net to verify identification.

Relationship between the numbers of hosts per plant and the numbers of *D. insulare* caught on the sticky traps. There was a significant correlation between the numbers of males and females, and males plus females caught per trap per 6 h and the numbers of host larvae per plant (Fig. 6 A to C). This suggests that *D. insulare* tend to aggregate, select and forage preferentially on plants with higher host's density. Similar results were also reported for *D. semiclausum* and *Diadegma fenestralis* (Holmgren) (Hymenoptera: Ichneumonidae)(Waage 1983). Aggregation of parasitoids may reduce the effectiveness of parasitism because of mutual interference among females (Harcourt 1986) and handling time on the host (Holling 1959).

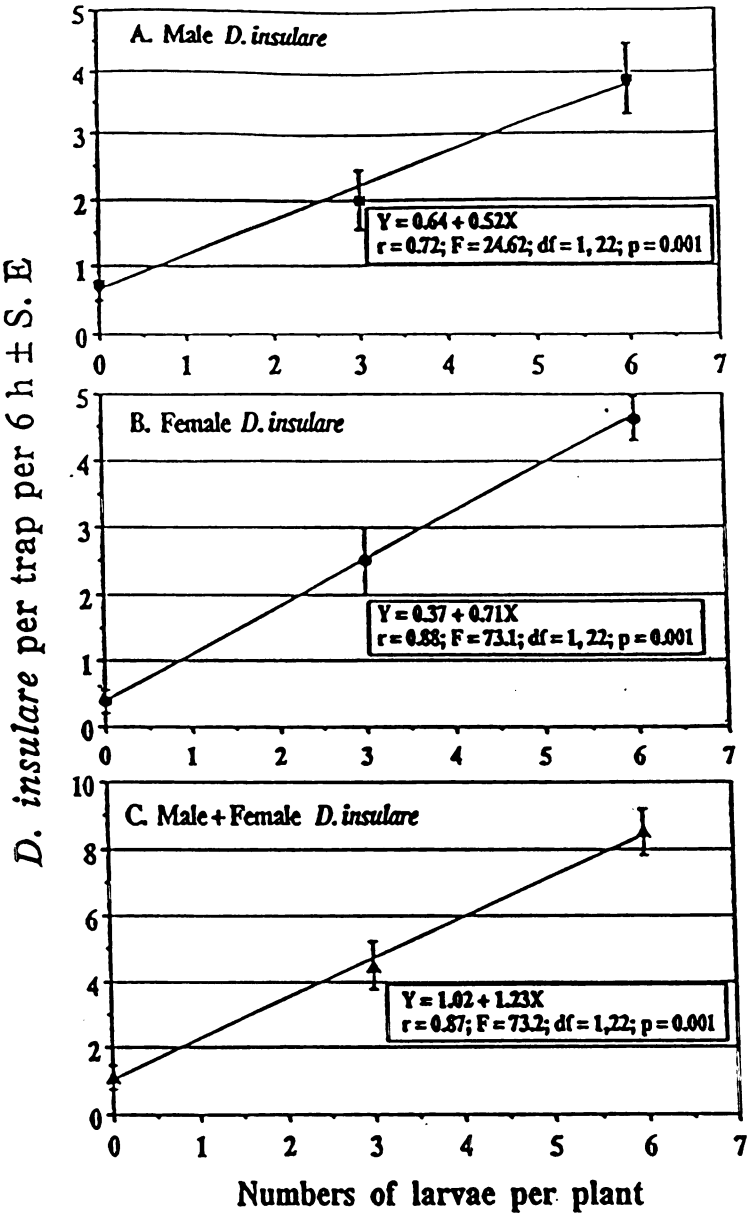

Figure 6. Relationship of *D. insulare* caught per sticky trap with different numbers of host per plant. Effect of host density (diamondback moth larvae) on *D. insulare* activity.

CONCLUSIONS

Pesticides continue to be an important tool for combating pests. However, *D. insulare* is highly sensitive to pesticide spraying (Idris & Grafius 1993a). Results of my study indicate that weather factors (light intensity, temperature and wind speeds) influenced the patterns of *D. insulare* diurnal foraging activity. This information could be useful in developing a model that can predict the peak diurnal activity of *D. insulare* in the field. In addition, a check list of numbers of *D. insulare* per unit catches or observation could be derived. This could help with decisions on whether pesticides should be sprayed. In addition, it could reduce the pesticides' effect on *D. insulare* and other natural enemies of diamondback moth and other *Brassica* crop pests in the field. In Malaysia, the numbers of *D. semiclausum* pupae have been used as important information before decision to spray pesticides is made in the integrated diamondback moth management program (Ooi 1992).

Both the sticky trap and visual observation are useful methods to monitor *D. insulare* activity in the field. However, their practicality will depend on the farm size, the cost of labor for scouting work and the price of the sticky trap. Further study is needed to improve diamondback moth integrated management programs especially for the numbers of host per plant that influence diurnal foraging activity of the parasitoid. Weather factors and diurnal foraging activity of parasitoid information are useful for insecticide treatment decisions to control crop pests and could improve pest management program.

CHAPTER 4

Effects of Plant Density on Diamondback Moth (Lepidoptera: Plutellidae) and Its Parasitoid, *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae)

ABSTRACT

Effects of plant density (broccoli, *Brassica oleracea* L. var. *italica*) on diamondback moth, *Plutella xylostella* L., and its parasitoid, *Diadegma insulare* (Cresson) were studied at the Collins Road Entomology Research Field, Michigan State University, in the summer of 1993. Mean numbers of diamondback moth small larvae (first and second instars) were not significantly different across the densities of broccoli planted (0.3 x 0.3 m, 0.6 x 0.6 m and 0.9 x 0.9 m between plants) and sampling dates. However, mean numbers of large diamondback moth larvae (third and fourth instars) and pupae and *D. insulare* pupae were significantly influenced by plant density and sampling date. Percent parasitism by *D. insulare* was not significantly affected by plant density, but was significantly affected by date (range = 35 to 95%, mean > 75%). Percent of *D. insulare* that were females (versus males) and numbers of *D. insulare* caught on sticky traps were not significantly influenced by plant density or date. Percent parasitism of diamondback moth larvae by *D. insulare* was significantly higher in the upper one third of the plant canopy than in the lower one third of the canopy. Temperature within the canopy was significantly influenced by plant density, canopy height and time of the day. Temperature and relative humidity (R.H.) were generally lower in the lower one third of the canopy than in the upper one third canopy. The interaction between plant density and canopy height also influenced the R H. within the broccoli canopy. Because plant density had no adverse affect on *D. insulare* parasitism and suppressed diamondback moth population (influenced the number of small larvae to reach 3rd or fourth instars), plant density for optimal yield and quality should be emphasized in an integrated management program of diamondback moth.

INTRODUCTION

The "resource concentration hypothesis" suggests that specialist insect herbivores should be more abundant where their food plants are concentrated (Root 1973). Many insect parasitoids must locate certain plants to find suitable insect hosts (Vinson 1985). By analogy with the resource concentration hypothesis for herbivores, specialist parasitoids may be more likely to find, or less likely to leave, concentrated patches of their prey's food plants (Sheehan 1986).

Concentration of host-plant resources involves at least five interdependent variables: patch size; plant density; distance between patches; plant diversity (i.e., presence of non-host plants); and plant quality (Karciva 1983). However, the response of insects colonizing different host plant concentrations or patches can vary (Macguire 1983, Sheehan & Shelton 1989). For example, larvae of diamondback moth, *Plutella xylostella* (L.)(Lepidoptera: Plutellidae), were more abundant on collards in large than in smaller patches while larvae of imported cabbageworm, *Pieris rapae* (L.)(Lepidoptera: Pieridae), were more abundant in smaller than in larger patches (Maguire 1983). In another study, Cromartie (1975) reported that the numbers of diamondback moth and imported cabbageworm per plant were not significantly different regardless of numbers of plants per patch.

The effects of plant density or spacing within a patch can be very useful in integrated pest management programs (Dent 1991). An increase in plant density may reduce pest numbers (A'Brook, 1964 & 1968; Farrell 1976; Tukahirwa & Coaker 1982) but not in all cases (Mayse 1978, Troxclair & Boethel 1984). Lower insect numbers in dense plantings may be caused by host plant condition and quality (Farrell 1976, Fox et al.

1990), excess vegetation acting as a deterrent (Delobel 1981), changes in the microenvironment unfavorable to the pest or favoring its natural enemies, and the crop's attractiveness (Coaker 1987). Parasitoids respond directly to plant properties (Shepard & Dahlman 1988, Martin et al. 1990, Turling et al. 1990), and reduced herbivore mortality from the action of natural enemies on poorer quality plants has been documented (Damman 1987). Plant quality, altered by treating collard plants with high or low N-fertilizer, did not affect diamondback moth ovipositional preferences (Fox & Eisenbach 1992), but indirectly affected parasitism rate and sex ratio of its major parasitoid, *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae)(Harcourt 1986, Fox et al. 1990). Fox & Eisenbach (1992) reported that *D. insulare* spent less time to begin host searching or searched more frequently on hosts that fed on high quality plant (high N-fertilized) than low quality plant (low N-fertilized).

Habitat types or preferences of parasitoids may also be different from those of their prey (Nordlund et al. 1988). The importance of spatial scale in the relation of parasitism to local host density was discussed in detail by Wadle & Murdoch (1988).

The objectives of this study were to investigate the effects of plant density on (1) diamondback moth numbers, (2) diamondback moth parasitism by *D. insulare*, (3) percent of *D. insulare* that are female, (4) foraging activity of *D. insulare*, (5) parasitism rate at different canopy heights and (6) plant canopy microclimate (temperature and relative humidity).

MATERIALS AND METHODS

Experiments were conducted at the Collins Road Entomology Field, Michigan State University, in the summer of 1993. I tested three different plant spacings; high (0.3 m between plants), medium (0.6 m between plants) and low (0.9 m between plants), as treatments in a 0.5 ha field. There were twelve 15 x 15 m plots with treatments (four

replications of each) arranged in a randomized complete block design. Broccoli (*Brassica oleracea* L. var. *italica*, 'Green Comet') was transplanted on 25-28 June. Transplant fertilizer 20:20:20 was applied immediately after planting. Plots were treated with glyphosate (1.12 kg active ingredient/ha, Monsanto, Kansas City, Missouri) 3 wk before transplanting and weeds were manually removed weekly after planting.

Diamondback moth population, percent parasitism and percent *D. insulare* females. Ten percent of the plants (120 in high, 60 in medium, 10 in low density) were randomly sampled weekly a long the transect, beginning July 21; numbers of small diamondback moth larvae (first - second instar), large larvae (third - fourth instar) and pupae; and *D. insulare* pupae were recorded. Second to fourth instars of diamondback moth and *D. insulare* pupae were collected from the plants every other week beginning 24 July and reared in the laboratory to measure the percent of *D. insulare* females versus males emerged. Plants where I collected *D. insulare* pupae and diamondback moth larvae were marked and not used for other data collection.

Foraging activity of *D. insulare*. *D. insulare* foraging activity was measured by randomly selecting four broccoli plants per replicate per treatment. White sticky traps (Pherocon™ 1C trap-bottoms, Trece Inc., Salinas, CA) were folded in half, sticky side out, and attached to wooden stakes with binder clips at 15 cm height within the broccoli canopy (six per plot). Traps were placed within the broccoli canopy at 0700 h on 7 and 22 August. *D. insulare* caught were recorded, sexed and removed every 3 h until 2000 h, when *D. insulare* activity ceases (Chapter 3).

Parasitism within canopy. Five plants were randomly selected from each plot on 18 and 23 August to compare the parasitism rate at top versus bottom canopy levels. The broccoli plant was divided into three equal sections; upper, middle, and lower. On 18 August, I collected diamondback moth second and third instars from upper and lower sections, and reared them in the laboratory until pupation as before. Numbers of diamondback moth and *D. insulare* pupae formed were recorded. On 23 August, all larvae

on these plants were removed by hand and replaced with 10 laboratory-reared diamondback moth larvae (second and third instars). Larvae were collected 24 h after release and reared as above to measure percent parasitism.

Canopy microclimate. I used wet bulb dry bulb hygrometers (Taylor Products, Fletcher, N.C.) to measure relative humidity (R.H.) and temperature within the canopy on 18 August. Four broccoli plants per replicate per treatments were randomly selected. Plant canopy was divided into three sections as before. Hygrometers were placed on the leaf stalk within upper or lower sections. Temperature and R. H were recorded every 20 min from 1000 until 1800 h.

Data for number of small and large larvae, diamondback moth pupae and *D. insulare* pupae were transformed using Log (1 + X); while percent parasitism data were transformed using arcsin $\sqrt{X}$ before analysis using 2-way ANOVA (density x date)(Abacus Concept, SuperAnova 1991). Percent *D. insulare* females and parasitism (arcsin $\sqrt{X}$ transformed) at upper and lower canopy among treatments were also analyzed by 2-way ANOVA. Three-way ANOVA were used to analyze the effects of plant density, time of day and plant canopy position on relative humidity and temperature within plant canopy. Numbers of *D. insulare* adults caught on sticky traps were analyzed using 1-way ANOVA. Where ANOVAs determined significant treatment effects, means were separated using Fisher's Protected LSD (Abacus Concept, SuperAnova 1991).

RESULTS AND DISCUSSION

Diamondback moth population, percent parasitism and percent *D. insulare* females. There were no significant differences in the mean numbers of small larvae per plant among plant densities ($F = 2.5$; df = 2 & 54; $P > 0.05$), across the dates ($F = 1.7$, df = 5 & 54, $P > 0.05$) and the interaction between these two factors was not significant ($F = 1.4$, df = 10 & 54, $P > 0.05$). Therefore, diamondback moths may have

laid eggs randomly in the plots which produced similar numbers of early instar. This suggests that the contrast between plant and soil background that occurred among the plant densities over the dates did not influence optomotor landing responses of adult diamondback moth females as reported for *Aphis craccivora* (Koch)(A'Brook 1968). Broccoli plants in the high density plots matured earlier, becoming less suitable for growth of small diamondback moth larva (Eigenbrode & Shelton 1990a), than the plants in the low density plots. Heavy rainfall may also affect small diamondback moth larvae, washing them from the leaves (Wakisaka et al. 1992), or increasing disease incidence (Wilding 1986). The upward leaf orientation in high density plots (0.3 m between plants) may also increase the impact of rainfall on small larvae compared with its impact in low density plots (0.9 m between plants).

Plant density (F = 19.9, df = 2 & 54, $P < 0.05$) and date (F = 14.4, df = 5 & 54, $P < 0.05$) significantly affected numbers of large larvae per plant. The mean numbers of large larvae per plant were generally lower in the low plant density than in the other two plant densities throughout the sampling period (Fig. 1 A). This agrees with the resource concentration hypothesis (Root 1973). However, Pimental (1985) reported that herbivores per plant surface were five time more abundant in sparse and dispersed plantings than in the dense planting. On most dates, numbers of large larvae are similar in the high and medium plant densities plots. Numbers of large larvae were lower in the early season (July) than in later of the season especially for the medium and high plant density (Fig. 1 A). Regardless of plant density, numbers of large larvae were highest on 6 August than on the other dates. There was a significant density and date interaction for numbers of large larvae collected per plant (F = 2.7, df = 10 & 54, $P < 0.05$).

Plant leaf quality is one of the factors that determines the abundance of diamondback moth populations in the late season because of its direct effects on early larval survivorship (Harcourt 1986). However, my August data showed that large larvae were

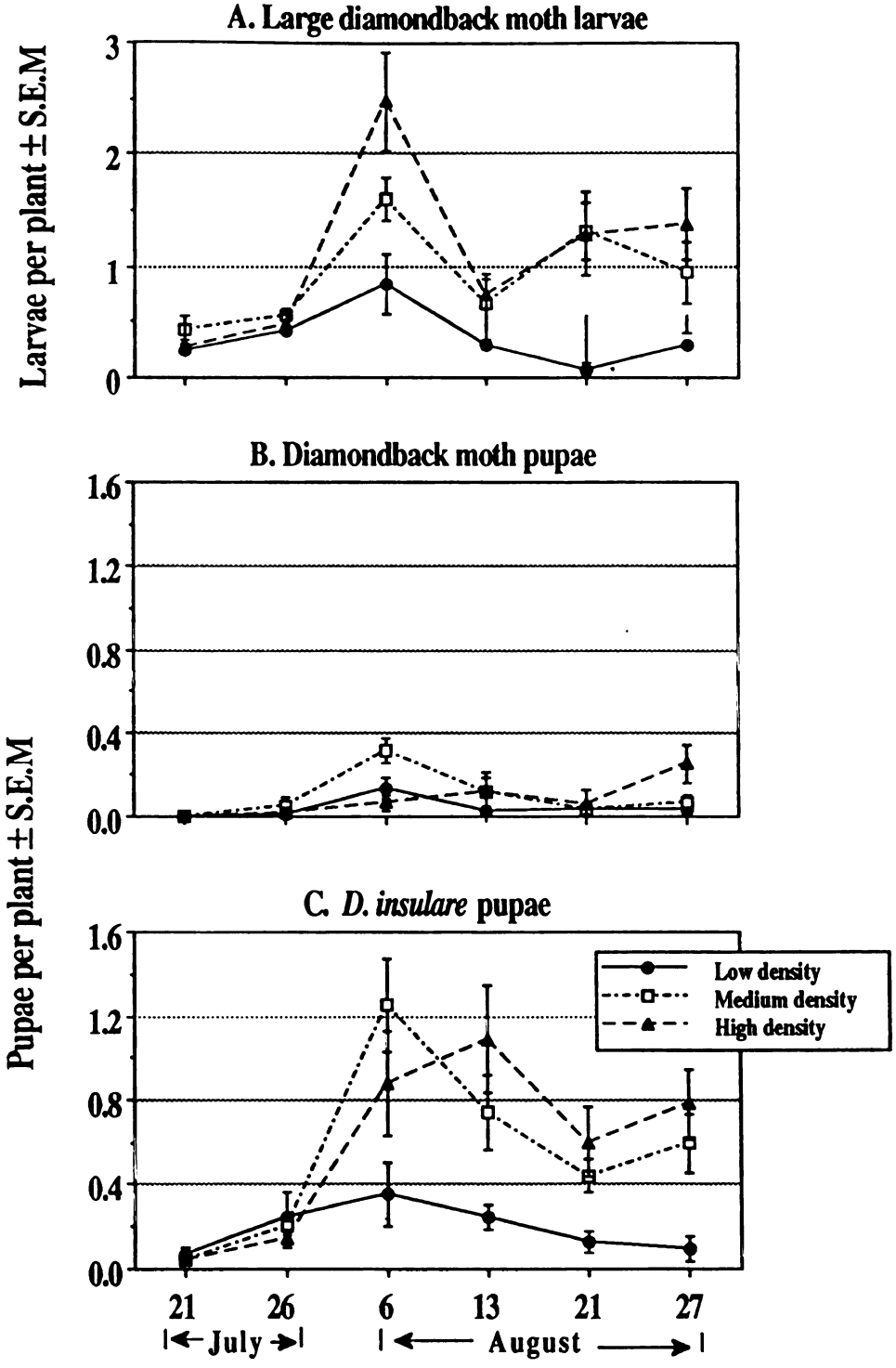

Figure 1. Number of diamondback moth large larvae (A) and pupae (B), and *D. insulare* pupae (C) in three different broccoli densities (0.3, 0.6 and 0.9 m between plants).

more abundant in the high and medium plant densities than in the low plant density (expected to have better quality leaf due to less competition between plants).

Plant density did not significantly influence the mean numbers of diamondback moth pupae per plant ($F = 2.5$, df = 2 & 54, $P > 0.05$). However, mean numbers of diamondback moth pupae were significantly different among dates ($F = 5.4$, df = 5 & 54, $P < 0.05$). Mean numbers of diamondback moth pupae per plant were significantly influenced by the plant density and date interaction ($F = 2.6$, df = 10 & 54, $P < 0.05$)(Fig. 1 B). Numbers of pupae collected across the dates showed a similar trend to large larvae (Fig. 1 A & B). I expected higher numbers of pupae in the low densities than in the high plant density plots. This is because of better plant quality in low density than in the high density (higher competition for growth between plants in the high than in low density) may allow more larvae to reach the pupal stage in the low density planting. However, heavy rainfall may have increased disease incidence (Wilding 1986) and loss to predators and parasitoids perhaps allowed fewer larvae to successfully reach the pupal stage (Wakisaka et al. 1992, Harcourt 1986) in the low densities plots.

Plant density ($F = 15.7$, df = 2 & 54, $P < 0.05$) and date ($F = 13.9$, df = 5 & 54, $P < 0.05$) significantly affected the mean numbers of *D. insulare* pupae per plant. Mean numbers of *D. insulare* pupae per plant were also significantly affected by the date by plant density interaction ($F = 3.1$, df = 10 & 54, $P < 0.05$)(Fig. 1 C). Except on 6 August, numbers of *D. insulare* pupae were higher in the medium or high densities than in the low plant density (Fig. 1 C); this trend was similar to both numbers of diamondback moth large larvae and pupae per plant (Fig. 1 A to C).

Regardless of sampling date or plant density, there were more *D. insulare* pupae than diamondback moth pupae (up to a 4 fold difference). This indicates that *D. insulare* is one of the most important natural enemies of diamondback moth agreeing with previous reports (Harcourt 1986, Idris & Grafius 1993, Biever et al. 1992). Mean percent parasitism ranged between 35 and 95%, averaging > 75% in all plots. However, percent

parasitism was not significantly affected by plant density (F = 1.3; df = 2 & 54; $P > 0.05$) or sampling date (F = 1.6, df = 5 & 54, $P > 0.05$). In contrast, Fox et al. (1990) reported that parasitism rate declined as the season progressed because plants became older (provided low quality food to the host larvae) which may have more adverse effects on *D. insulare* larvae than on its host larvae. Talekar & Yang (1993) reported that *Diadegma semiclausum* (Hellen)(= *eucerophaga*)(Hymenoptera: Ichneumonidae) parasitism rate increased as the brassicas crops grew older or was not affected by plant age.

Percent of *D. insulare* females (versus males) from field collected larvae and pupae ranged from 15 to 55% ($\bar{X}$ = 30.6% ± 12.4)(range for plant density x dates) but was not significantly different among plant densities (F = 1.0, df = 2 & 36, $P > 0.05$) or among sampling dates (F = 1.9, df = 3 & 36, $P > 0.05$). Fox et al. (1990) and Harcourt (1986) showed that plant quality resulting from low N-fertilized plants or increased plant age contributed to a male bias sex ratio of *D. insulare*. In my study both plant density and date affect plant growth and maturity, but did not consistently affect proportion of female *D. insulare*.

Foraging activity of *D. insulare*. The mean numbers of male or female *D. insulare* caught per trap per day were not significantly different among plant densities (male: F = 2.3, df = 2 & 18, $P > 0.05$; female:F = 1.9, df = 2 & 18, $P > 0.05$) or sampling dates (males: F = 0.18, df = 2 & 18; $P > 0.05$; females: F = 1.0, df = 2 & 18, $P > 0.05$). This suggests that *D. insulare* are abundant and visited the host's habitat regardless of the numbers of hosts per plant (there were fewer diamondback moth larvae in lower than in the higher plant density plots, Fig. 1 A). *Brassica* plants with zero hosts are still visited by *D. insulare* (Chapter 3) and *D. semiclausum* (Waage 1983).

The mean total males plus females caught were significantly different among plant densities (Fig. 2)(F = 3.7, df = 2 & 18, $P < 0.05$) but not between dates (F = 0.02, df = 1 & 18, $P > 0.05$). Mean total catch was significantly higher in medium and high than in the low density planting (FPLSD, $P < 0.05$) where diamondback moth larvae were also less

abundant. Regardless of plant density, the patterns of *D. insulare* caught in 3 h intervals per day were not different ($\chi^2 = 2.4$, df = 8, $P > 0.05$); they were active from 1100 to 2000 h (Chapter 3).

Parasitism within canopy. Percent parasitism of diamondback moth larvae within the upper or lower one third of the canopy were not significantly different among plant densities ($F = 0.2$, df = 2 & 18, $P > 0.05$). However, percent parasitism diamondback was significantly higher in the upper one third than in the lower one third of the canopy for all plant densities ($F = 4.5$, df = 1 & 18, $P < 0.05$; FPLSD, $P > 0.05$)(Fig. 3 A). Although parasitism of the larvae in the upper was higher than in the lower canopy for each plant density, percent parasitism on the lower canopy was also very high (79.8-83.6%). *D. insulare* females appear to have excellent host searching capacity (Lasota & Kok 1986), and parasitism is not severely affected by plant density. Percent parasitism of laboratory-reared diamondback moth larvae was not significantly different across plant densities ($F = 1.7$; df = 2 &18; $P > 0.05$) or height within canopy ($F = 0.9$, df = 1 &18; $P > 0.05$)(Fig. 3 B). There was no significant interaction between plant density and canopy height to influence percent parasitism of the field ($F = 0.4$, df = 2 &18, $P > 0.05$) or laboratory-reared diamondback moth larvae ($F = 0.3$, df = 2 &18, $P > 0.05$).

Canopy microclimate. The temperature within the canopy was significantly influenced by plant density, time of day and canopy height and the interaction among these factors (Table 1). Regardless of plant density and canopy levels, temperature was above 20-25°C for most of the day except between 1000 and 1100 h (Fig. 4 A & B). Temperature was higher in the upper one third canopy of low density plants than in the upper one third canopy of medium or high density plant between 1200 and 1500 h (Fig. 4 A). Conversely, temperature was lower in the lower one third of low density planting than in the lower one third canopy of the other two plant densities (Fig. 4 B). The daily temperature never exceeded 30°C; the upper threshold temperature for *D. insulare* is 35°C

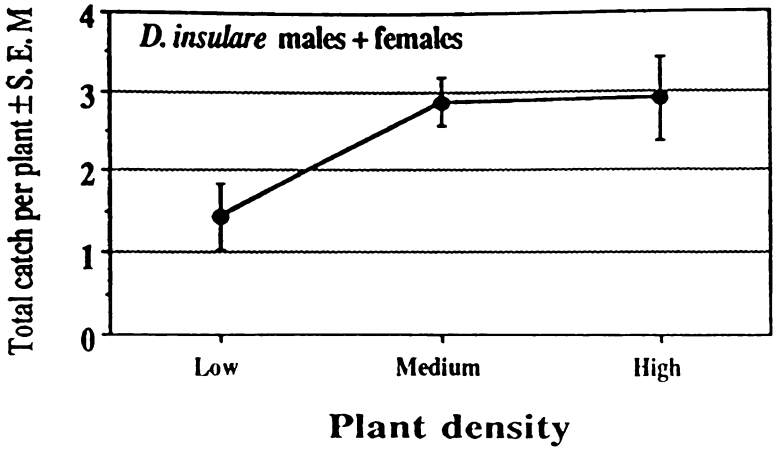

Figure 2. Total *D. insulare* males plus females caught per plant in three different broccoli planting densities (0.3, 0.6 and 0.9 m between plants).

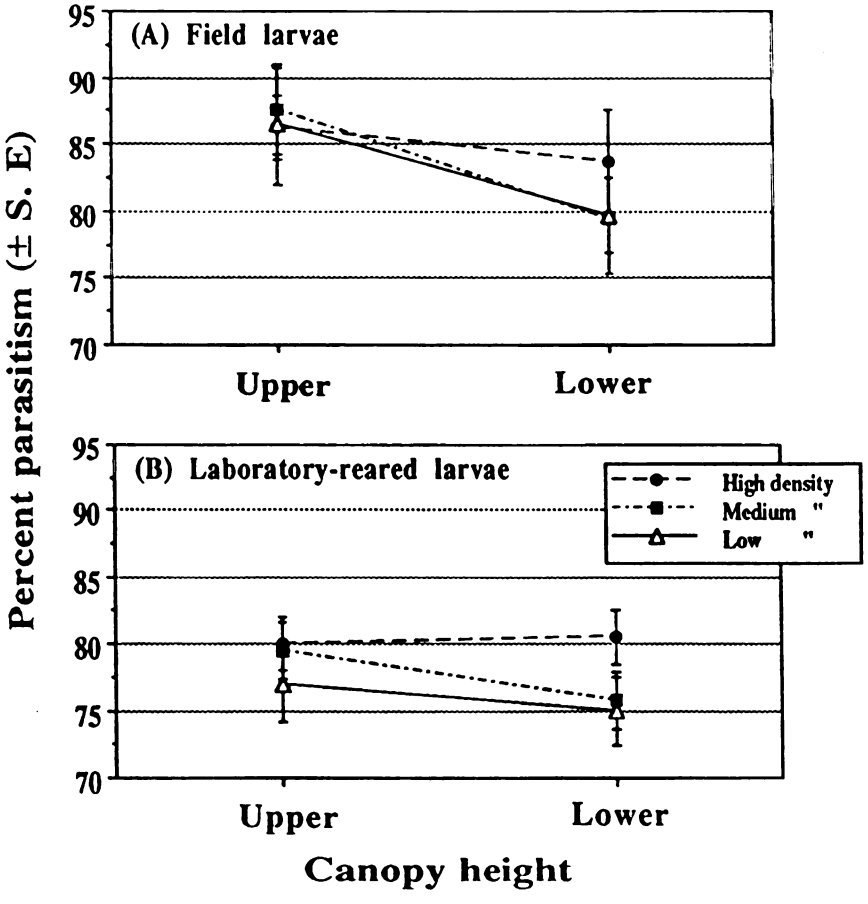

Figure 3. Percent parasitism of field (A) and laboratory-reared (B) diamondback moth larvae by *D. insulare* in the upper versus lower broccoli canopy in the three different broccoli planting densities (0.3, 0.6 and 0.9 m between plants).

(Bolter & Laing 1983). The moderate temperatures partly explains why the average percent parasitism was > 75% in all plant densities.

Table 1. ANOVA for effects of plant density, time of day and canopy height on the temperature (°C) within the broccoli canopy

Sources	df	*F* - value	*P* - value
Simple effects			
Plant density	2	8.8	0.001
Time of day	7	87.1	0.0001
Canopy height	1	26.1	0.0001
Interaction effects			
Density x time	14	3.6	0.0001
Density x canopy	2	20.0	0.0001
Time x canopy	7	21.8	0.0001
Density x time x canopy	14	2.2	0.0107
Error	144	-	-

Mean relative humidity (R. H.) within the canopy of broccoli was significantly influenced by plant density, time of the day, canopy height and by the interaction between plant density and canopy heights (Table 2). Mean R.H. in the uppet one third of canopy was lower than in the lower one third of the canopy for all plant densities, and it was higher in the lower one third canopy in low density than in the lower canopy of the medium or higher density broccoli (Fig. 5). Microclimate may be important, however *D. insulare*'s diurnal activity was not affected by R.H. in open field (Chapter 3).

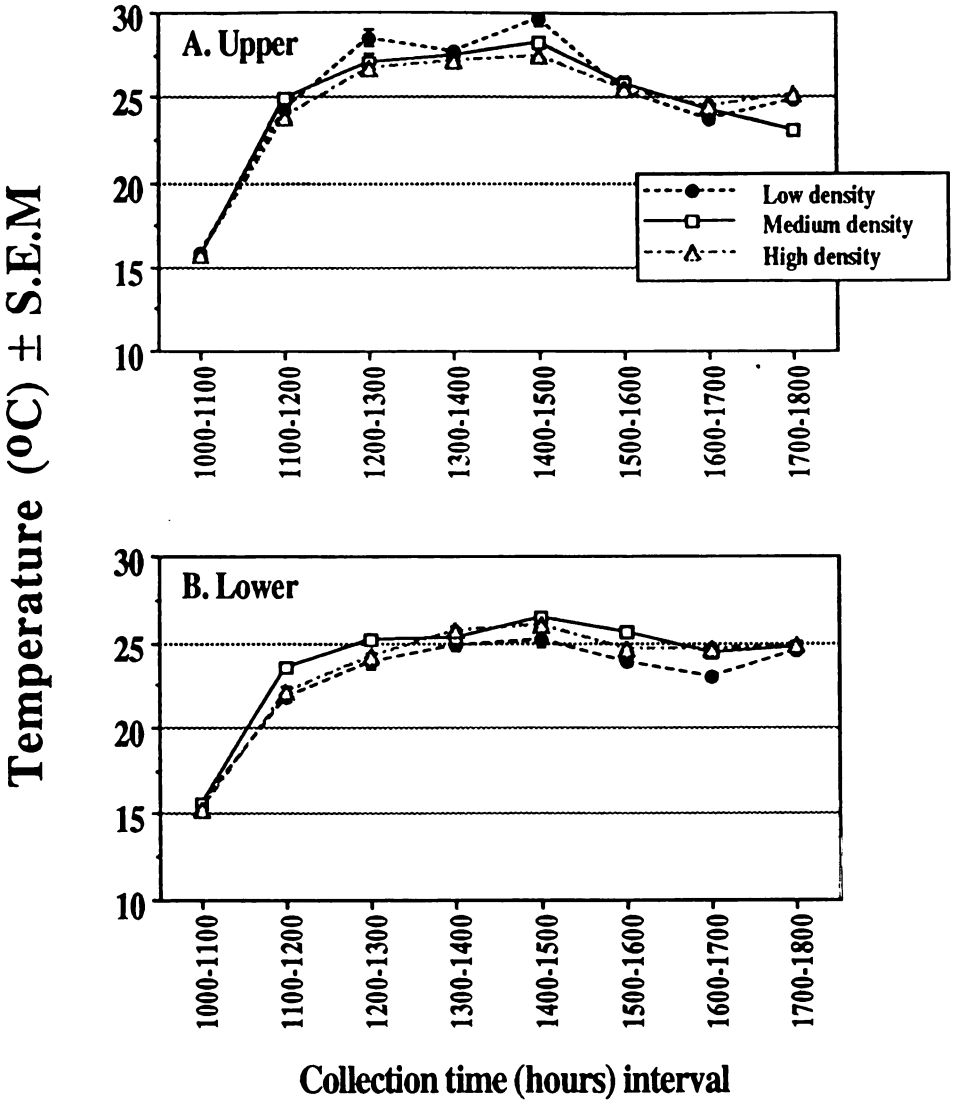

Figure 4. Temperature (°C) in the upper (A) versus lower (B) broccoli canopy planted in three different plant densities (0.3, 0.6, and 0.9 m between plants).

Table 2. ANOVA for effect of plant density, time of day and canopy height on the relative humidity (%) within the broccoli canopy

Sources	df	*F* - value	*P* - value
Simple effects			
Plant density	2	30.8	0.0001
Time of day	7	217.5	0.0001
Canopy height	1	394.9	0.0001
Interaction effects			
Density x time	14	1.5	0.1300
Density x canopy	2	40.7	0.0001
Time x canopy	7	0.8	0.5754
Density x time x canopy	14	0.7	0.7909
Error	144	-	-

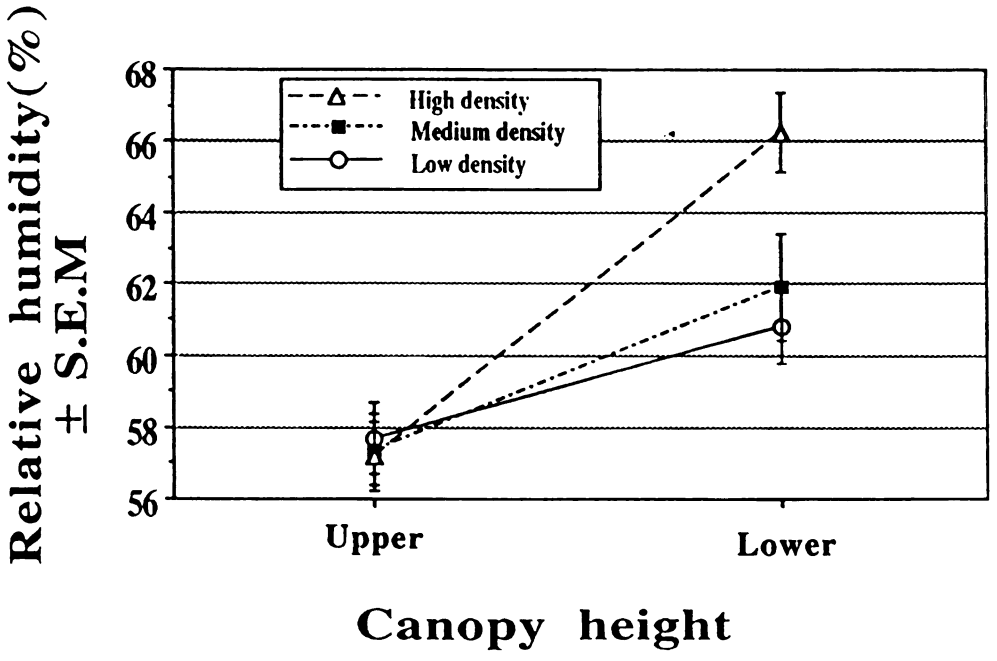

Figure 5. Relative humidity (%) in the upper versus lower broccoli canopy planted in three different plant densities (0.3, 0.6 and 0.9 m between plants)

The influence of interactions among plant density, time of the day and canopy height on temperature and R.H. may have direct or indirect effects on percent parasitism of diamondback moth by *D. insulare* and the survivorship of diamondback moth larvae (Fig. 3 A, 4 & 5) as well as the functional and numerical response of other diamondback moth natural enemies. For example, percent parasitism of diamondback moth larvae was higher in the lower one third than in the upper one third of broccoli canopy in all plant densities (Fig. 3 A). Low temperature and high R.H. in the lower canopy (Fig. 4 & 5) may favor the action of natural enemies, especially diseases (fungal, viruses and microsporidium), on both unparasitized and parasitized diamondback moth larvae. Other factors, such as low diamondback moth larval populations and leaf quality, are also involved.

CONCLUSIONS

Further study on the effects of plant density on diamondback moth populations and parasitism by *D. insulare* under different field locations and setting are necessary before recommendation of plant density can be made. However, because *D. insulare* parasitism rate, abundance of adults and sex ratio are not seriously affected by plant density, plant densities that suppress diamondback moth populations and produce optimal yield and quality should be emphasized.

CHAPTER 5

Influence of Habitats on the Parasitism of Diamondback Moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), by *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae)

ABSTRACT

Influence of habitats on the percent parasitism of diamondback moth larvae, *Plutella xylostella* L., by *Diadegma insulare* (Cresson) and its presence in habitats were studied at the Michigan State University Research Farm during the summer of 1992 through 1994. Percent parasitism was measured by placing broccoli plants infested with third instar diamondback moth in crop and non-crop habitats for 26 to 28 h. Numbers of *D. insulare* caught on the sticky traps placed in habitats were used to measure its presence in the respective habitats. Percent parasitism was significantly different among the habitats, although parasitism occurred in all habitats except in the center of the woodland. This suggests that *D. insulare* is very mobile and effective searcher. Percent parasitism was very high (> 40% to 60%) in most crop and non-crop habitats, however, it was significantly influenced by the interaction between habitats and dates (months and years) of observations conducted. The percent parasitism of diamondback moth larvae decreased as the distance of treatments in the corn field from the field edge increased, suggesting that the corn field is not a primary habitat for *D. insulare*. Numbers of *D. insulare* caught on the sticky traps was significantly lower in habitats without *D. carota*, *Brassica kaber* L., *B. nigra* L. or *Raphanus raphanistrum* L. than in habitats that have these weeds (nectar sources for *D. insulare*). This indicates that *D. insulare* preferred habitats that can provide food sources or suitable hosts or both. The present monoculture of brassica crops could be modified into intercropping or polyculture systems without negatively affecting the impact of *D. insulare* in diamondback moth management program.

INTRODUCTION

Gould & Stinner (1984) defined habitat as the physical area encompassing the resources that support the existence of an individual insect or insect population for a specific time. They define habitat heterogeneity as the environment being composed of significantly different parts within a particular landscape. Habitats can influence the population size and distribution size of the pest and its parasitoids (Cromartie 1975a & b, Hawkin & Sheehan 1994). Vinson (1985) outlined that habitat preference and the potential of host community location within the habitat are two of the nine steps necessary for successful parasitism. He also suggested that the interactions between the host's habitat and the parasitoid are depend on the active behavioral and physiological aspects of the parasitoid. A study conducted by Landis & Haas (1992) indicates that the microclimate of habitats, particularly in warm years, influences the movement and behavior of *Eriborus terebrans* (Gravenhost)(Hymenoptera: Ichneumonidae), a parasitoid of European corn borer, *Ostrinia nubilalis* (Hübner)(Lepidoptera: Pyralidae). Dyer & Landis (1993) and Sato & Ohsaki (1987) reported that the effects of habitat on parasitoid activity varied as the season progressed. Types of vegetation within or between habitats also affected parasitism by *Cotesia* (= *Apantales*) *glomeratus* L. (Sato & Ohsaki 1987).

The effects of habitat heterogeneity on the predator-prey dynamics are subject to specific dispersal behavior of the predator and prey (Kareiva 1987). Landis & Haas (1992) reported that the effectiveness of *E. terebrans* is influenced by the local landscape mosaic, including proximity of particular crops or other non-crops with the host habitats. The structures of landscape also influence the spatial distribution of adult food resources for this wasp (Landis 1993). Non-host plants in the heterogeneous habitat of polyculture

agroecosystems can affect the movement of herbivores and their natural enemies (Sheehan 1986, Andow 1988, Lawrence & Bach 1989). The specialist parasitoids might be less abundant in the structurally complex polyculture than in structurally simple monocultures; chemical cues used in host finding will be disrupted and parasitoids will be less able to find hosts, therefore, they are more effective in less diverse agroecosystems (Sheehan 1986, Andow & Prokrym 1990).

Diadegma insulare (Cresson)(Hymenoptera: Ichneumonidae), the major parasitoid of diamondback moth, used nectar sources from certain wildflowers that grew in different habitats (Idris & Grafius 1995a). Differential temperature in habitats may affect *D. insulare*'s fecundity, longevity and day-time foraging activity which indirectly determines the parasitism rate (Chapter 1). In addition, suitable habitats near the insecticide-treated field could provide refuge for *D. insulare*.

The objectives of this study were to (1) assess the presence or absence of *D. insulare* in different habitats, and (2) find out the influence of habitats on the percent parasitism of diamondback moth by *D. insulare*.

MATERIALS AND METHODS

The study was conducted at the Michigan State University Research Farm, East Lansing, Michigan, during the summers of 1992 through 1994. The habitats used were; beans (*Phaseolus vulgaris* L., *Pisum sativum* L. and *Glysine max* (L.) Merill), tomato (*Lycorpersicon esculentus* Mill), corn (*Zea maize* L.)and alfalfa (*Madicago sativa* L.) fields, apple (*Malus domestica* Borkh) orchard, weedy areas, and at the center and edge of woodland (Fig. 1). I did not use all these habitats in every observation because they were not always available.

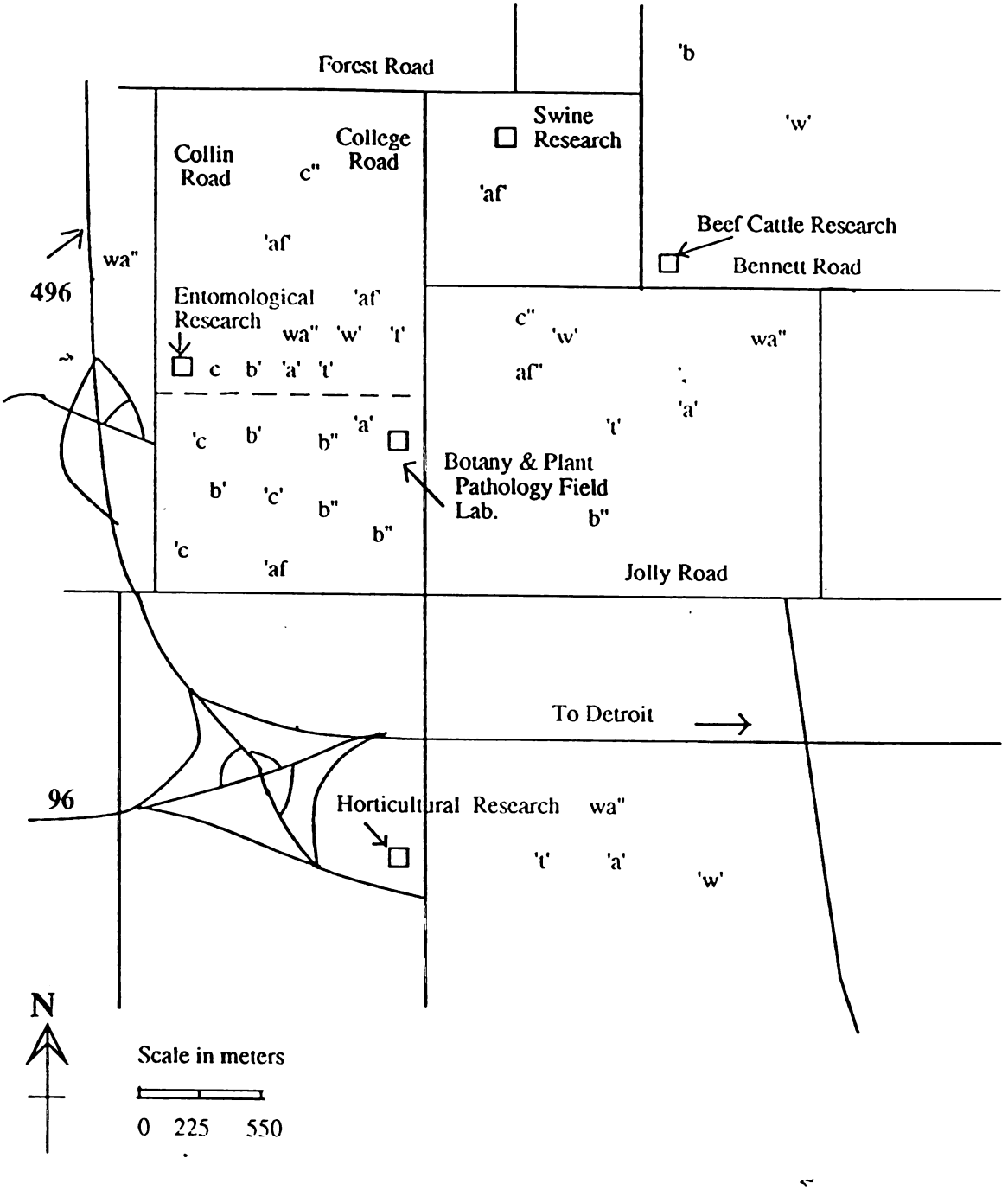

Figure 1. Location of habitats at Michigan State University Research Farm selected for the study (a, apple; af, alfalfa; b, beans; c, corn; t, tomato; w, woodland; wa, weedy areas). Letters with _", ' _', _' , and '_ indicate that the habitats were used only during 1992 and 1993, 1992 to 1994, 1993 and 1994, respectively.

Greenhouse grown broccoli plants, *Brassica oleracea* var. *italica* (L.) cav. 'Green Comet' raised in pot were used for the study. At two months old each broccoli plant was infested with ten second or third stadium diamondback moth larvae. Infested plants were kept in the greenhouse for 18 to 20 h before placing in various habitats. I added new diamondback moth larvae for plants that had less than 10 larvae per plant after setting out the plants.

Weedy areas used in 1992 had > 50% *Daucus carota* L. but only two replicates of weedy areas used in 1993 had a similar density of *D. carota* as in 1992. Weedy areas were not used as tested habitat in 1994 because there were only two small weedy areas available.

Influence of Habitat on Percent Parasitism. Among Habitats. I placed 20 infested broccoli plants in each habitat (five pots of broccoli plant per replicates = 50 larvae) between 1000 and 1200 h. Each treatment (habitat) was replicated four times. The next day between 1400 and 1600 h plants and larvae were collected. I randomly selected 20 larvae per replicate. Larvae were placed in a 14.5 cm diam Petri dish with 3 cm diam screen lid on the cover (20 larvae per dish per replicate) and brought to the laboratory. Larvae were fed broccoli leaves grown in the greenhouse and kept at 25 ± 2°C, photoperiod 16: 8 h L : D until pupation. The numbers of *D. insulare* and diamondback moth pupae formed were recorded. I did not dissect the diamondback moth larvae because *D. insulare* eggs are encapsulated and survival of *D. insulare* larvae is always high (Chapter 1, Bolter & Laing 1983).

Within the same habitat of non-host plant (corn). To determine within field influence on the parasitism of diamondback moth larvae I conducted a similar experiment on the same corn fields as before on 13-14 August 1994. However, I placed the treatments inside the corn field at 50, 100, 200 and 500 m from the field edge.

Percent parasitism of diamondback moth by *D. insulare* was calculated as the total number of *D. insulare* pupae divided by the total number of diamondback moth plus *D. insulare* pupae x 100 (Idris & Grafius 1993c). The percent parasitism (transformed using

arcsin $\sqrt{X}$) among habitats, at different distances from corn field edge, and at different habitats versus months or years were analyzed by 1-way and 2-way ANOVA, respectively. Fisher's Protected LSD (Abacus Concepts, SuperAnova 1991) was used to separate means when main effects were significant (no significant interaction between factors).

The presence of *D. insulare* in habitats. I used 40 white sticky traps (Pherocon™ 1C trap - bottom; Trece Inc., Salinas, CA) per habitat (10 traps per replicate, 10 m between traps) to assess the presence of *D. insulare* within the habitats. Each trap was folded in half to make a two-sided trap with sticky side out. Traps were placed upright on a 40 cm stake in; weedy areas, middle of alfalfa fields, and within the canopy of tomato, *Brassica kaber* L., *B.nigra* L. and *Raphanus raphanistrum* L.; along the edge and center of the woodland; or hung on apple tree branches, and corn leaves (50 m into the field). Trap height varied with habitat but ranged from 20 to 80 cm from the ground except for apple orchard (depending on the height of the apple tree). *D. insulare* trapped were recorded every day between 1800 and 1900 h for a week. I removed *D. insulare* from the traps every day. Numbers of *D. insulare* caught per trap per day in various habitats were analyzed using 1-way ANOVA and means were separated as above. Data were transformed using Log (1 + x) before analysis.

RESULTS AND DISCUSSION

Influence of habitats on the percent parasitism. Among Habitats. Percent parasitism was significantly different among habitats in all years (0-89%), and was high (> 40-60%) in most habitats regardless of the sampling dates and years (Fig. 2 to 4).

In 1992, percent parasitism ranged from 55% (bean) to 89% (tomato)(Fig. 2). Except at the woodland edge, parasitism was significantly higher in the tomato than in the other habitats (79%)(Fisher's PLSD, $P < 0.05$). In 1993, parasitism ranged from 3%

(woodland edge) to 87% (corn)(Fig. 3). Except in the alfalfa fields, parasitism in the other crop habitats was considerably higher (70-87%)(Fig. 3) and comparable to with 85-93% in a nearby broccoli field (unpublished data). The apple orchard, the only crop habitats used in the three sampling dates in 1993, had consistently high rates of parasitism (76-81%). Parasitism in the non-crop habitats (woodland edge and weedy areas) was low except on 15-16 August 1993 when parasitism at woodland edge was as high as in the crop habitats. On 12-13 August 1994, percent parasitism was significantly higher in the corn field (80%) than in the other habitats (0-40%)(Fisher's PLSD, $P < 0.05$)(Fig. 4). There was no parasitism recorded in the center of the woodland.

The percent parasitism of diamondback moth larvae was significantly affected by the interaction between habitats and dates (month: $F = 24.4$, df = 2 & 8, P = 0.001; year: 14.4, df = 4 & 27, $P = 0.001$)(Fig. 5 A & B). Parasitism at the woodland edge was significantly lower in September than in July and August 1993 (Fisher's PLSD, $P <$ 0.001)(Fig. 5 A). In 1994, parasitism was higher in the corn field than in the other habitats (Fig. 5 B).

Within the same habitat of non-host plant (corn). There was a significant correlation between percent parasitism of diamondback moth larvae and the distance from the field edge (r = 0.86, $F = 40.9$, df = 1 & 14, $P < 0.001$)(Fig. 6). Distance from the field edge explained 74.5% of the variation in the percent parasitism of diamondback moth larvae; decreased as the distances of the treatments from the edge into the corn field increased.

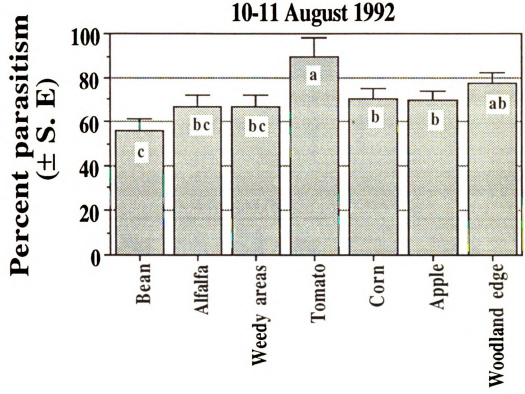

Figure 2. Percent parasitism of diamondback moth larvae by *D. insulare* in various habitats on 10-11 August 1992. In corn field treatment was placed ± 30 m from the field edge. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

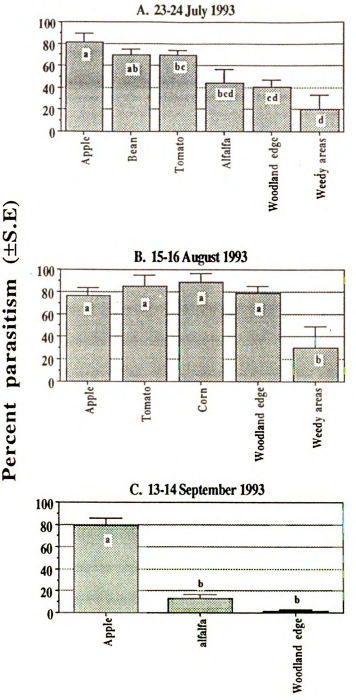

Figure 3. Percent parasitism of diamondback moth larvae by *D. insulare* in various habitats on 23-24 July (A), 15-16 August (B) and 13-14 September 1993 (C). In the corn field treatment was placed ± 30 m from the field edge. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

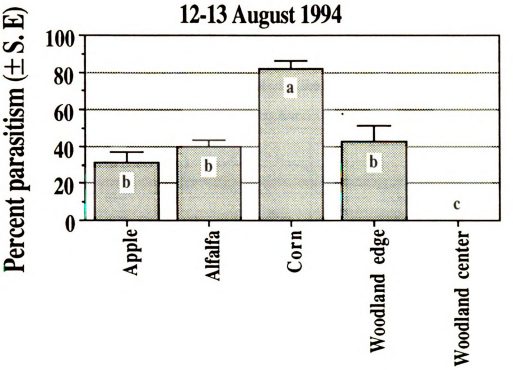

Figure 4. Percent parasitism of diamondback moth larvae by *D. insulare* in various habitats on 12-13 August 1994. In corn field treatment was placed ± 30 m from the field edge. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

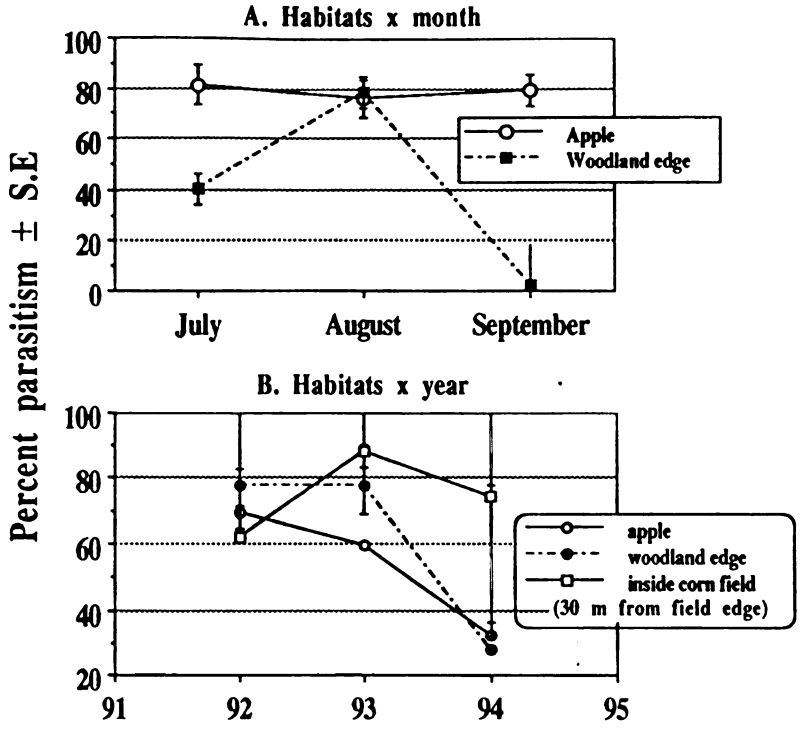

Figure 5. Percent parasitism of diamondback moth larvae as affected by the interaction between habitat and months in 1993 (A) and years (B).

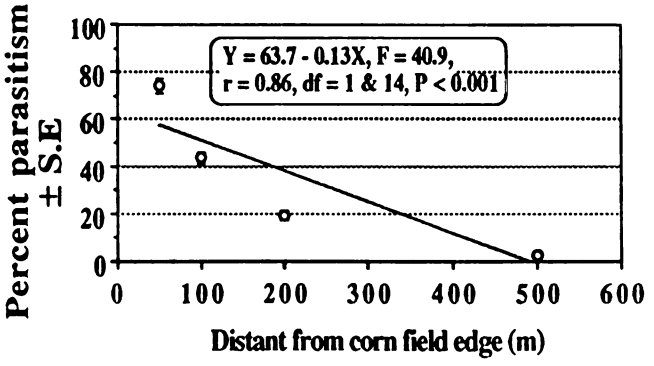

Figure 6. Relationship of percent parasitism of diamondback moth larvae by *D. insulare* and the distance from the field edge.

The presence of *D. insulare* in habitats. The numbers of *D. insulare* caught per trap per day on the sticky traps were significantly different among the habitats in both years (1993: $F = 4.1$, df = 9 & 27, $P < 0.05$; 1994: $F = 10.6$; df = 5 & 15, $P < 0.05$)(Table 1 & 2).

In 1993, numbers of *D. insulare* caught were significantly higher in traps placed at the woodland edge that had 50 to 70% *Daucus carota* L. than in traps placed with Asteraceae plus *Agropyron repens* (L.) Beauv, in the alfalfa, weedy areas or apple habitats (FPLSD, $P < 0.05$)(Table 1). There was a significantly difference between the numbers of *D. insulare* caught on traps placed in weedy areas and along the woodland edge where *D. carota* were the majority of plants present (FPLSD, $P < 0.05$). There were no *D. insulare* caught along the woodland edge where *A. repens* was > 90% of the plants present, and in the weedy areas where Compositae plus grasses or *A. repens* were the dominant weed present. In 1994, numbers of *D. insulare* caught were significantly lower in the tomato and corn fields than in habitats primarily with *B. kaber*, *B. nigra* and *R. raphanistrum* (Fisher's PLSD, $P > 0.05$). There were no *D. insulare* caught in the traps placed in the center of the woodland. This indicates that *D. insulare* is more abundant or prefers habitats that can provide them food sources or alternate hosts. In crop habitats, the numbers of *D. insulare* caught were somewhat higher in traps placed in the tomato and corn fields than in traps placed in the alfalfa field or apple orchard (Table 1 & 2).

As a kionobiont parasitoid (host larvae continue to develop after oviposition and are only killed in the late instar as oppose to idiobiont parasitoids which paralyze or kill the host larvae or pupae, respectively, after oviposition) *D. insulare* may have a restricted host range in a simple habitat within a particular landscape (Askew & Shaw 1986). Therefore, it has to be very mobile in heterogeneous habitats to find its alternate hosts. This explains why the parasitism of diamondback moth larvae occurred in all habitats except in the center of the woodland (Fig. 2 & 4).

Table 1. Number of *D. insulare* caught in various habitats from 12 to 18 August 1993

Habitats	Number of *D. insulare* caught per trap per day (± S.E)[a]
Woodland edge	
50 to 70 % *Daucus carota* L.	0.40 ± 0.16c
Asteraceae + *Agropyron repens (L.) Beauv*	0.05 ± 0.28ab
> 90% *A. repens*	0a
no weed but shrubs	0.15 ± 0.05b
Apple	0.08 ± 0.05ab
Weedy areas	
50 to 70 % *D. carota*	0.18 ± 0.05b
50 to 70 % Asteraceae weeds	0.03 ± 0.03ab
Asteraceae + grasses	0a
> 90% *A. repens*	0a
Alfalfa	0.05 ± 0.03ab

[a] In column means with same letter are not significantly different (Fisher's Protected LSD, $P > 0.05$)

Table 2. Number of *D. insulare* caught in various habitats from 14 to 20 August 1994

Habitats	Number of *D. insulare* caught per trap per day (± S.E)[a]
Woodland center	0a
Tomato	0.15 ± 0.05a
Corn	0.14 ± 0.08a
50 to 80% *Brassica nigra* (L.) (Black mustard)	1.60 ± 0.19b
50 to 70% *Raphanus raphanistrum* L. (wild radish)	1.50 ± 0.14b
50 to 70% *Brassica kaber* L. (wild mustard)	1.83 ± 0.17b

[a] In column means with same letter are not significantly different (Fisher's Protected LSD, $P > 0.05$)

In August 1992, parasitism was higher when larvae were placed in tomato than in alfalfa and corn, and apple habitats (Fig. 2). On 23-24 July 1993, however, percent parasitism in tomato was not different with alfalfa and apple habitats (Fig. 3 A). On 15-16 August, percent parasitism was similar across all habitats (70 to 90%) except in the weedy areas (30%)(Fig. 3B). This suggests that *D. insulare* were more abundant in habitats other than the weedy areas. On 12-13 August 1994, percent parasitism in the apple orchard and along the woodland edge is somewhat lower than the parasitism in these habitats in the same month of 1992 and 1993 (Figs. 2, 3 A & B, 4). This is probably due to lack of visual cues for *D. insulare* to locate its host or they were less active in the cloudy day (low light intensity) on the 12-13 August. The numbers *D. insulare* caught on the sticky traps were also positively correlated with the light intensity (Chapter 3). *Diadegma semiclausum* (Hellen)(Hymenoptera: Ichneumonidae), another important larval parasitoid of diamondback moth, uses its visual perception for finding a suitable host for egg laying (Talekar & Yang 1991). *Campoletis sonorensis* (Cameron)(Hymenoptera: Ichneumonidae), a parasitoid of *Heliothis virescens* (F.)(Lepidoptera: Noctuidae), also used visual cues to associate the host plant cotton, *Gossypium hirsutum* L., with the location of its host larvae, frass and damaged leaf (McAuslane et al. 1991).

The effect of very low light intensity in the center of the woodland on *D. insulare*'s response to the visual cues may partly explains why there was no parasitism when diamondback moth larvae were placed in the center of the woodland but 40 to 79% parasitism along the woodland edge (Fig. 4). Other factors including temperature, relative humidity, wind and odors may also involve. This result also indicates that woodland center was not a preferred habitat for *D. insulare*. In Indonesia, however, Hymenoptera parasitica were found more inside than along the woodland edge (Noyes 1989).

The percent parasitism in corn, tomato, bean, and apple habitats was consistently high (55 to 80%) for all sampling dates except in apple on 12-13 August 1994, compared with alfalfa (10 to 40%), woodland edge (3 to 80%) and weedy areas (20-69%) where

parasitism was highly variable (Fig. 2, 3 A to C & 4). This suggests that the former crop habitats are preferred by *D. insulare*. Probably, they are the better habitat for optimum parasitism and other *D. insulare* activity such as food finding. There may be alternate hosts for *D. insulare* in one or more of the other "preferred crop habitats". Other diamondback moth parasitoids, *D. semiclausum* and *Diadegma fenestrale* (Holmgren) (Hymenoptera: Ichneumonidae), use some tortricids of apples as their alternate host for overwintering (Hardy 1938). The parasitism of diamondback moth larvae in these crops may also depend on the *D. insulare* entering the habitat after the placement of the larvae.

Parasitism in the woodland edge was highly variable at least in part because of the variability in this habitat. In August 1992 and 1993 when parasitism was high, *D. carota*, one of the best wildflowers for nectar for *D. insulare* females (Chapter 1), was at peak flowering. In contrast, in July or September 1993, *D. carota* had just begun to flower or started to decline. In August 1994, however, *D. carota* was less abundant than in 1992 and 1993. The low number of *D. insulare* present, as indicated by the numbers of parasitoids caught on the sticky traps (Table 1), in woodland edge with few or no *D. carota* and dependency on the *D. insulare* entering this area after diamondback moth larvae was introduced may explain why the parasitism was low. A cloudy day on the sampling date may also have caused caused lower parasitism in August 1994 than in 1992 or 1993, partly sunny or sunny days. The presence of shrubs in the woodland edge, which likely has fewer *D. insulare* than in the woodland edge with *D. carota* (Table 1), will further reduce the light intensity, disrupt *D. insulare* visual cues and parasitism rate during the cloudy day.

Parasitism in weedy areas was also highly variable probably due to habitat variability. The weedy areas used for study in August 1992 (Fig. 2) had 50 to 70% *D. carota* . In July and August 1993, only one replicate had a density of *D. carota* similar to August 1992 (Fig. 2, 3 A & B). The other replicates had no *D. carota* but Asteraceae weeds+grasses, Asteraceae weeds+*A. repen* s or primarily *A. repens.* Percent parasitism was higher in August 1992 than on July and August 1993, indicating that diamondback

moth larvae placed in weedy areas with *D. carota* were parasitized more by *D. insulare* than in the weedy areas with less or no *D. carota*. (Fig. 2, 3 A & B). In July and August 1993, percent parasitism ranged from 10% in the replicate with *A. repens* to 75% in replicate with 50 to 70 % *D. carota*. This variability is shown by the high standard error of the mean for percent parasitism (Fig. 3 A & B). The numbers of *D. insulare* caught on the sticky traps placed among the weedy areas differed significantly (Table 1). This explains why the parasitism is highly variable and very low in areas with primarily Asteraceae+grasses or *A. repens*. Besides no food or less food available in the latter areas there also may be no alternate hosts of *D. insulare*.

Variability in environmental factors, especially light intensity and temperature, and habitats' compositions per unit time (months and years) determine the *D. insulare* activity and its parasitism rate (Fig. 5 A & B). Fluctuation in day temperature, light intensity and wind speed influenced the diurnal foraging activity of *D. insulare* (Chapter 3). The changes in value of particular habitats for *D. insulare* over time, habitat's composition, the presence of wildflowers and overshadows vegetation affected parasitism rate. *Apantales glomeratus* L. (Hymenoptera: Braconidae) responds similarly to *D. insulare*; *A. glomeratus* female host habitat location is disrupted by overshadowing vegetation on the host plant causing low parasitism of *Pieris rapae* L. (Sato & Ohsaki 1987). These results suggest that certain habitats are suitable for *D. insulare* parasitism activity. However, their suitability is subject to the interaction between those particular habitats and the environmental conditions.

The distance of treatments from the corn field edge into the field significantly influenced the parasitism rate (Fig. 6). Parasitism by *D. insulare* significantly decreased as the distance of treatments from the corn field edge increased. This indicates that corn field is not a preferred habitat for *D. insulare*. Probably, there was no alternate host for *D. insulare* in the corn field, but, its presence may be associated with food finding activity or temporary stay during the hotter time of the day. The need of shelter is also indicated by

the higher numbers of *D. insulare* caught along the woodland edge than in the weedy areas even though both habitats had high percent of *D. carota* present (Table 1). In another study, F_1 generation of *Eriborus terebrans* (Gravenhost)(Hymenoptera: Ichneumonidae), a parasitoid of the European corn borer, has no preference between the edge and in the middle of corn field (Dyer & Landis 1993).

D. insulare was present in many habitat types even though parasitism may not occur, and it is actively mobile in the heterogeneous habitats. In view of this fact, there will be a potential for manipulation of present *Brassica* crop field design or planting *Brassica* crops in polyculture system without affecting the role of *D. insulare* as a biocontrol agent of diamondback moth.

Results of these study showed that tomato plants had no adverse effect on *D. insulare* parasitism rate. The parasitism rate of diamondback moth by *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae), another important larval parasitoid of diamondback moth, was also not affected by the presence of tomato plants in *Brassica* crops field in Hawaii (Bach & Tabashnik 1990). However, tomato plants are reported to adversely affect the long range host finding by adult diamondback moth, probably due to the volatile compounds emitted by the tomato plants (Buranday & Raros 1975). This indirectly reduces the numbers of larvae and pupae per plant especially during the first 60 d after *Brassica* crops are transplanted to the field (Talekar et al. 1986). Therefore, tomato plants can be interplanted with *Brassica* crops.

Polyculture systems restrict natural enemies movement and they could become less effective biocontrol agents (Sheehan 1986, Andow & Prokrym 1990). However, Talekar & Yang (1991) reported that the parasitism rate of diamondback moth larvae by *D. semiclausum* in *Brassica* planted in polyculture (soybean, eggplant, corn, sweet potato, garden pea, tomato, garlic, okra and *Brassica* crops) was not different from parasitism in the monoculture *Brassica* crops. Result of my study also showed that corn, bean, and apple habitats have the potential to be interplanted with *Brassica* crops in polyculture

systems. The corn and apple habitats could also provide refuges for *D. insulare* during the hottest time in the day.

Horn (1987) reported that parasitism of diamondback moth larvae by *D. insulare* is lower in the non-tilled than in the tilled (weed-free) *Brassica* crop field. However, the presence of *D. carota* within any habitat can harbor *D. insulare* (Table 1), serves as nectar source (Chapter 1), and increases parasitism rate (Fig. 2 to 4). Results also indicate that the Brassicaceae weeds (*B. kaber*, *B. nigra* and *R. raphanistrum*) attract high numbers of *D. insulare* (Table 2). *B. kaber* and *D. carota* can be excellent nectar sources for *D. insulare* (Chapter 1). As such, these weeds could be interplanted within *Brassica* crop fields in a patch, between Brassica crop rows or around the field. Wild *Brassica*, *Brassica nigra* L. (Indian mustard), planted in one row per 15 rows of *Brassica* crops has been used as a trap crop in integrated diamondback moth management in India (Srinivasan & Krishna Moorthy 1991). The techniques of interplanting wild Brassicaceae or other non-Brassicaceae with *Brassica* crops may depend on the size of the field. I suggest that if the Brassica field is >10 ha then a patch or inte-row planting of wild Brassicaceae or other non-*Brassica* plants with the *Brassica* crop may favor parasitoid activity. *D. insulare* and probably other parasitoids of diamondback moth may be more abundant at the field edge that normally provide plenty of food to the parasitoid than in the interior field. However, the effect of field edge and size to the *D. insulare* population abundance, activity and parasitism rate need to be studied.

CONCLUSIONS

The integration of factors that could optimize the impact of *D. insulare* to control diamondback moth should be emphasized in the *Brassica* crops ecosystem management. However, it could only be achieved with intelligent modification of the current field

agroecosystem and/or field setting within any particular landscape. By doing so, the impact of other biocontrol agents on diamondback moth could also be increased.

CHAPTER 6

Effects of Wild and Cultivated Host Plants on Oviposition, Survival and Development of Diamondback Moth (Lepidoptera: Plutellidae) and Its Parasitoid, *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae)

ABSTRACT

I studied the effects of wild and cultivated host plants on diamondback moth, *Plutella xylostella* L., oviposition, egg hatch, larval survival, infestation level, parasitism rate by *Diadegma insulare* (Cresson), and the developmental time and sex ratio of *D. insulare*. Egg laying was highest on the cultivated varieties, especially broccoli, and lowest on wild spp., especially *Berteroa incana* L. DC. and *Erysimum cheiranthoides* L. Egg laying was generally higher on leaves of cultivated *Brassica* plants from the field than on leaves from the greenhouse. The reverse was true for leaves of wild species. Percent egg hatch was not significantly different among host plants. Percent diamondback moth larval survival was generally higher on the cultivated varieties than on wild species and there was no survival on *Barbarea vulgaris* R. Br. Developmental time of diamondback moth larvae was generally longer on the wild spp. than on the cultivated varieties. Percent parasitism by *D. insulare* was lowest on *B. incana*, *Lepidium campestre* R. Br. and *E. cheiranthoides*. Percent parasitism was higher when diamondback moth larvae fed on *B. kaber* than on the cultivated varieties. Parasitized diamondback moth larvae fed *E. cheiranthoides*, *T. arvense* and *B. incana* took significantly longer to develop to *D. insulare* pupae than when fed on the other *Brassica* varieties or species. Diamondback moth infestation and percent parasitism in the field were higher on broccoli than on the other crops. The distribution of *D. insulare* females was not significantly different among the crops. The presence of wild Brassicaceae, especially *B. vulgaris* and *B. kaber*, in the field could reduce diamondback moth populations, the impact of *D. insulare*, and increase the success of diamondback moth management programs.

INTRODUCTION

Diamondback moth, *Plutella xylostella* L.(Lepidoptera: Plutellidae), is an important pest of *Brassica* crops worldwide. Diamondback moth is also found on many wild Brassicaceae (Marsh 1917, Thorsteinson 1953, Harcourt 1986). It is a multivoltine insect with 4 to 17 generations per year in temperate and tropical regions, respectively (Harcourt 1986, Chelliah & Srinivasan 1986). The abundance of host plants and the action of its natural enemies are two keys biotic factors that regulate diamondback moth populations (Harcourt 1986, Fox et al. 1990, Ooi 1992).

The volatile compounds released by host and non-host plants attract or deter diamondback moth oviposition (Palaniswamy & Gillott 1986, Dover 1986, Reed et al. 1989, Raddiff & Chapman 1966). Extracts of a wild *Brassica* sp., *Erysimum cheiranthoides* L., also deterred oviposition by *Pieris rapae* L. (Lepidoptera: Peiridae) (Dimosk & Renwick 1991). Diamondback moth larval survival can be affected by toxic substances, lack of feeding stimulant in the host, and the morphological characteristics of the host plants' leaves (Eigenbrode & Shelton 1992, Hough-Goldstein & Hahn 1992, Gupta & Thorsteinson 1960a & b). Some of these compounds have been isolated and identified from several host and non-host plants (Cole 1976, Reed et al. 1989, Pivnick et al. 1994).

Tumlinson et al. (1993) reported that, besides recognizing odors from their host, parasitic wasps and flies also learn to identify compounds released by the plant on which the hosts feed. *Eucelatoria bryani* Sabrosky (Diptera: Tachinidae), a parasitoid of *Helicoverpa* spp., responds only to fresh plant tissues and not to the extracts tested (Martin et al. 1989). Volatile compounds released by plants affect host location and parasitism rate

by the braconid wasps *Microplitis croceipes* Cresson, *Cotesia marginiventris* Cresson, *Macrocentrus grandii* Goidarich and *Cotesia glomerata* L. (Steinberg et al. 1992, Udayagiri & Jones 1992, Turlings et al. 1990, McCall et al. 1993). Host plants also indirectly affect parasitoid development (McDougall et al. 1988, Ritter & Johnson 1991, McCucheon et al. 1991, Bentz & Barbosa 1990, Werren et al. 1992, Bloem & Duffey 1990, Riggin et al. 1992, Campos et al. 1990), flight behavior (McAuslane et al. 1990a) and movement (Keller 1987).

As a specialist parasitoid we expect *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae) to rely more on host related cues than do generalist parasitoids. If so, its parasitism may occur only when diamondback moth larvae are feeding on certain plants or plant materials. *Diaeretiella rapae* M'Intosh, a specialist parasitoid of aphids, is attracted to collard leaves and allylisothiocyanate (mustard oil) found in the collard leaves (Read et al. 1970). To the best of our knowledge there are no studies about the effects of host plant species on the interaction between diamondback moth and *D. insulare*. This tritropic interaction is important to be understood for more effective integrated diamondback moth management.

The objectives of this study were to find out the effects of several cultivated and wild Brassicaceae on (1) diamondback moth oviposition, percent egg hatch, larval survival, and developmental time; (2) parasitism rate, developmental time of parasitized larvae and the sex ratio of *D. insulare* and; (3) in the field, the level of diamondback moth infestation in the field, distribution of *D. insulare* and percent parasitism.

MATERIALS AND METHODS

Insects and Food Plant sources. The diamondback moths used were strain, G88 F97 (provided by Anthony Shelton, Cornell University, New York Agriculture Experiment Station, Geneva). It has been reared in the laboratory on broccoli, *Brassica oleracea* L. I

used a laboratory colony (F_{10}) of *D. insulare* collected from the Michigan State University Collins Road Entomology Research Field in 1993 for parasitism experiments.

Host plants used were five cultivated varieties and nine wild Brassicaceae (Table 1). The leaves of wild Brassicaceae were collected from the Michigan State University Research Farm and other places on the Michigan State University campus. To maintain the freshness of the detached leaves they were put in clear zip lock plastic bags and kept inside a cooler with ice, returned to the laboratory and kept in refrigerator. The host plants were also raised in the greenhouse for an experiment to compare the effect of field and greenhouse plants on diamondback moth oviposition.

Diamondback moth studies. Oviposition. *Choice and no-choice tests*. Choice tests were used to study oviposition by diamondback moth on field collected leaves from various hosts and compare oviposition on leaves from field and greenhouse plants. I used 14.5 cm diam Petri dishes with an 8.0 cm diam screen opening in the lid. To study oviposition on different field collected leaves, I cut 2 cm^2 of the leaf and randomly put them on moist filter paper around the edge inside the Petri dish (1.0 cm from the dish edge and 4.5 cm from the center, and 1.5 cm between the leaves). To compare oviposition on leaves collected from field and greenhouse plants, 2 cm^2 pieces of each were placed opposite to each other, 4.0 cm from the center of the Petri dish.

One 2 d old mated diamondback moth female was released at the center of dish. For easy handling the individual moth was put inside a glass vial (21 x 70 mm) plugged with cotton wick and put in the freezer for 3 min before release. The dishes were randomly placed 60 cm under white florescent light (Philip™, FT2T12/CW/VHG, 160 Watt) and kept at 25 ± 2°C. Treatments were replicates four times. Eggs laid were recorded after 4 h of oviposition.

I followed similar procedures of choice test for no-choice tests except three leaf pieces of a single host species were put around the edge of each Petri dish, 4.0 cm from the dish center.

Table 1. Species and common names of host plants used in the study

Species	Common names
Cultivated	
Brassica oleracea L. var. *italica* cv. Green Comet	Broccoli
B. oleracea L. var. *acephala* cv. Nagoya Mix	Flowering kale
B. oleracea L. var. *botrytis* cv. Early snowball "A"	Cauliflower
B. oleracea L. var. *capitata* cv. Early Great Dutch	Green cabbage
B. oleracea L. var. *capitata* cv. Ruby Ball	Red cabbage
B. napus L.	Canola
Wild	
B. kaber D. C. Wheeler	Wild mustard
B. nigra L. Koch	Black mustard
Berteroa incana L. DC.	Hoary alyssum
Erysimum cheiranthoides L.	Wormseed mustard
Capsella bursa-pastoris (L.) Medic	Shepard's purse
Barbarea vulgaris R. Br.	Yellow rocket
Lepidium campestre (L.) R. Br.	Field pepperweed
Raphanus raphanistrum L.	Wild radish
Thlaspi arvense L.	Field pennycress

Percent egg hatch. I took 50 eggs per replicate per plant species or variety from choice and no-choice test to measure the percent egg hatch. The eggs laid on a particular plant species or variety were placed on a new fresh leaf of the same plant in a similar Petri dish as before. More than one leaf was used if necessary to have at least 5 cm^2 per dish. Leaves were replaced with fresh ones after 12 to 15 h. Leaves and eggs were kept in the growth chamber (23 ± 2°C, 50 - 75% relative humidity (R.H) and a photo period 16 : 8 h (L: D) h for 4 d and the numbers of eggs hatched were recorded.

Percent larva survival and developmental time to pupation. Diamondback moth eggs were collected from each host plant (100 eggs per variety or species) and reared following the no-choice test above except I put three to five diamondback moth females per dish to get more eggs and larvae. I randomly selected 40 newly hatched first instars (ten per replicate) to study larval survival from hatch through second and third through fourth instars. The surviving second instars were used for accessing the survivorship from third through fourth instars. Five newly hatched first instars were used to study the developmental time from hatch through pupation (= five replicates, one larvae per replicate per host plant). Larvae for each experiment were placed in a similar type of Petri dish as above and kept as above. Larvae were fed with leaf of the respective host plants and leaves were replaced with fresh ones as above. Treatments (host plant + larvae) were kept as before. Numbers of surviving larvae at the end of second and fourth instars, and the time (day) of pupae formed were recorded.

***Diadegma insulare* studies.** Percent parasitism. A clear plastic container (12.0 cm and 8.0 cm diam top and bottom, respectively, and 10.0 cm high with 5.0 cm diam screen opening lid on top and two 1.5 cm screened openings on the sides of the container) was used. One cross cut was made on one side of the container for easy release and taking out the parasitoid. A 2 cm^2 piece of damaged leaf and 30-33 diamondback moth early third instars were put together in one plastic container. A mated and experienced 3 d old *D. insulare* female was released into the container using an aspirator and placed under white

inflorescent light (as in Chapter 2) at 25 ± 3°C for parasitism by *D. insulare* for 3 h after which the parasitoid was removed. Parasitized larvae were fed with leaves of the respective host plant until pupation. The number of *D. insulare* pupae and diamondback moth pupae formed were recorded.

Developmental time of parasitized larvae. To study the developmental time of parasitized larvae I used similar methods as for parasitism but only five early third instar from each host plant were exposed to *D. insulare* females (to make sure all larvae are parasitized). One larva, parasitized or unparasitized, was put inside the modified 14.5 cm diam Petri dish and fed as above until pupation. Time (day) of pupation of each parasitized and unparasitized larvae was recorded and treatments (= five larvae per treatment) were replicated four times.

The sex ratio of *D. insulare*. I randomly selected seven *D. insulare* pupae per replicate from the above experiment and put them in plastic container (= 35 pupae per host plant per container) and kept as before until adult emergence. *D. insulare* sexes were recorded on the day of emergence.

Numbers of eggs laid, percent egg hatch and larva survival from hatch to second and third to fourth instars, developmental times of unparasitized and parasitized larvae, and percent parasitism were analyzed using 1-way ANOVA and means were separated by Fisher's Protected LSD (Abacus Concept, SuperAnova 1991). The numbers of eggs laid on leaves collected from field and greenhouse were analyzed by 2-way ANOVA and whenever the main effects were significant means were separated as before (Abacus Concept, SuperAnova 1991). The sex ratio was analyzed using χ^2 and the lowest sex ratio as the expected value. The relationship between developmental time of parasitized and unparasitized larvae for each host plant was analyzed using regression analysis (Abacus Concept, SuperAnova 1991).

Field studies on diamondback moth infestation, parasitism rate and distribution of *D. insulare* adults. This experiment was conducted at the Michigan State University Collins Road Entomology Research Field in the summer of 1994. Plots were 7.0 x 7.0 m with 1.5 m between plots and 0.6 m between plants (100 plants per plots). Plots were arranged as a randomized block design with four replicates per treatment. The treatments were cultivated varieties of *Brassica*; kale, red cabbage, green cabbage, cauliflower and broccoli (Table 1). Transplant fertilizer 16:16:16 was broadcast before transplanting. Two month-old plants were hand-transplanted on 14 and 15 July 1994. To keep plots free from any pesticide treatment weeds were hand-pulled and hoed weekly.

Diamondback moth larvae and *D. insulare* pupae. The numbers of diamondback moth small larvae (first and second instars) and large larvae (third and fourth instars), and *D. insulare* pupae were sampled on randomly chosen plants (10 per replicate) on 15 and 25 August and 3 September.

Percent parasitism. I collected five second to fourth diamondback moth instars per replicate from non-sampled plants, to measure parasitism. Larvae were brought to laboratory, fed on the same host leaves collected from the same plots and kept as above until pupation.

Distribution of *D. insulare* adults. To assess the distribution of *D. insulare* adults in the experimental plots I walked along the rows of each replicate and caught the parasitoids using a sweep net, hourly (1100 to 1600 h, EDT) on 17 and 25 August. *D. insulare* adults caught were identified, sexed, recorded and released.

Percent parasitism was calculated as the number of *D. insulare* pupae divided by the total numbers of *D. insulare* + diamondback moth pupae x 100 (Idris & Grafius 1993b). Data were transformed using $\log(1 + x)$(for numbers of larvae) or $\arcsin\sqrt{x}$ (for percent parasitism) before analysis. Numbers of small and large larvae, and *D. insulare* adults caught, and percent parasitism were analyzed using 2-way ANOVA and, whenever mains

effects were significant and interaction between factors was not significant, means were separated by Fisher's Protected LSD (Abacus Concept, SuperAnova 1991).

RESULTS AND DISCUSSION

Diamondback moth studies. Oviposition. The numbers of eggs laid per host were significantly different among the host plants both in choice tests (F = 14. 23; df = 10, 30; $P < 0.05$) and no-choice tests ($F = 9.81$; df = 11, 33; $P < 0.05$)(Fig. 1A & B). In choice tests, diamondback moths laid significantly more eggs on broccoli than on the other host plants except canola (FPLSD, $P < 0.05$)(Fig. 1A). Numbers of eggs laid on canola (cultivated) were not significantly different from numbers on *B. kaber, L. campestre* or *T. arvense* (wild)(FPLSD, $P < 0.05$). In no-choice tests, there were no significantly differences in numbers of eggs laid on broccoli, canola, cauliflower, *B. kaber*, *B. nigra* or *T. arvense*. Diamondback moths laid significantly fewer eggs on *E. cheiranthoides* and *B. incana* than on the other wild species (FPLSD, $P < 0.05$)(Fig. 1B). The genus *Brassica* included both the most preferred and least preferred host plants for diamondback moth in the choice tests and plants with the lowest and highest egg laying, in the no-choice test.

Glucosinolates (mustard oils), commonly found in Brassicaceae plants, are the major oviposition stimulant for diamondback moth (Reed et al. 1989). Upon hydrolysis, glucosinolates give rise to different isothiocyanates depending on the Brassicaceae spp. or varieties. Different glucosinolates or similar glucosinolates with different concentrations have been identified in host (Brassicaceae) and nonhost plants (Cole 1976, Wallbank & Wheatley 1976). Recently, certain volatiles that are not a kind of glucosinolates from *B. juncea* and *B. napus* were found to be important in host-plant finding by diamondback moth (Pivnick et al. 1994). These secondary chemicals may explain the differences in preference and in the number of eggs laid by diamondback moth among the host plants in my study. For example, numbers of eggs laid were always highest on broccoli both in

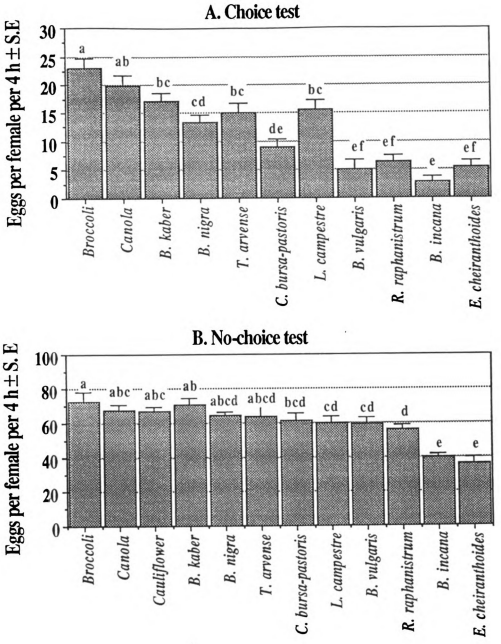

Figure 1. Numbers of eggs laid by diamondback moth females on *Brassica* plants in choice (A) and no-choice (B) test. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

choice or no-choice situations (Fig. 1 A & B), indicating it has chemicals that attracted diamondback moth to lay more eggs than on the other host plants.

Diamondback moth laid fewer eggs on *B. vulgaris* than on *B. nigra*, *T. arvense*, *L. campestre* or *C. bursa-pastoris* in choice tests, but, in no-choice tests the numbers of eggs laid on these species were not significantly different (Fig. 1 A & B). In no-choice tests, which simulate early spring situations where *B. vulgaris* is more abundant than other species, *B. vulgaris* is very acceptable for oviposition (Fig. 1 B)(Reed et al. 1989). Diamondback moth do not discriminate between different types of glucosinolates (Reed et al. 1989). *B. incana* or *E. cheiranthoides* may have lower concentration of glucosinolates and other water-soluble compounds (Renwick & Radke 1988) that attract fewer moths to lay eggs (Fig. 1 A & B). *B. incana* and *E. cheiranthoides* may also have oviposition deterrents which may outweigh the attractants. Similarly, deterrents (cardenolides) appear to outweigh the attractants (glucosinolates) for oviposition by *P. rapae* on *E. cheiranthoides* (Renwick & Radke 1987, Renwick et al. 1989).

The numbers of diamondback moth eggs laid were significantly different among host plants ($F = 24.5$, df = 10 & 66, $P < 0.05$), but not between host plant leaf collection (field versus greenhouse)($F = 0.13$, df = 1 & 66, $P > 0.05$). Numbers of diamondback moth eggs were significantly affected by the interactions between the host plants and their leaf collection ($F = 6.7$, df = 10 & 66, $P < 0.05$)(Fig. 2 A & B). Diamondback moth laid more eggs on the field leaves than on the greenhouse leaves of the *Brassica* crop varieties, except for canola (FPLSD, $P < 0.05$)(Fig. 2 A). In contrast, eggs were laid more on the greenhouse leaves of wild species except for *B. kaber*. This may due to chemicals or physical structures of a particular host plant (Gupta & Thorsteinson 1960b).

Percent egg hatch. Percent egg hatch was not significantly different among host plants ($F = 1.73$; df = 14, 42; $P > 0.05$). However, in a previous study percent egg hatch was significantly lower on *B. vulgaris* than on *T. arvense*, *C. bursa-pastoris* or broccoli (Idris & Grafius 1994). This contrasting result may due to the difference in diamondback

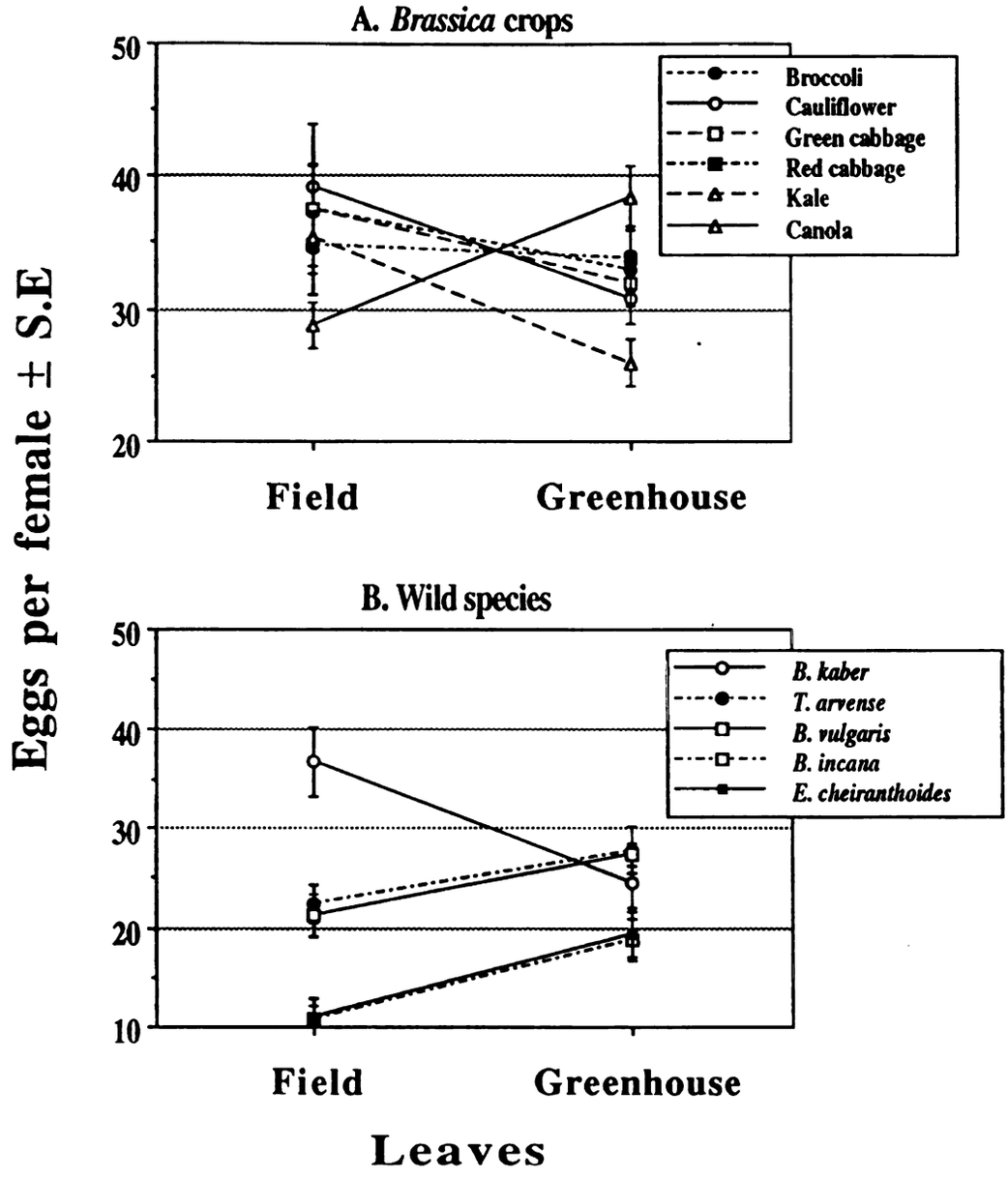

Figure 2. Numbers of eggs laid by diamondback moth on field and greenhouse leaves of *Brassica* crops cultivars (A) and wild species (B).

moth strain and method used. In this study, leaves were provided better aeration through a screened opening on the top of the Petri dish as compared with no screen in the study conducted by Idris & Grafius (1994). In the field, however, percent egg hatch may be affected by the density of the plants per unit area. In dense plant populations there may be higher concentration of plant volatiles within the canopy that could be lethal to the developing eggs as indicated by the detached leaf experiment in Petri dishes (Idris & Grafius 1994).

Percent larva survival and developmental time to pupation. Percent of diamondback moth larva surviving from hatch through second instar ($F = 31.96$; df = 14, 42; $P < 0.001$) and third through fourth instars ($F = 23.71$; df = 14, 42; $P < 0.001$), and larval developmental time from hatch to pupation ($F = 14.82$; df = 13, 39; $P < 0.001$) were significantly different among the host plants (Fig. 3 A, B & C). Percent survival from hatch through second instar was highest when larvae were fed on the cauliflower, but not significantly different from survival on broccoli or kale (FPLSD, $P > 0.05$)(Fig. 3 A). Survival rate was lower on red cabbage than on the other *Brassica* crop varieties (Fig. 3 A & B). Generally, larval survival rate was higher when fed on the *Brassica* crop varieties than on the wild species. Of the nine wild species tested, larval survival was lowest when fed on *B. vulgaris* and *B. incana* (Fig. 3 A & B).

An autolysis of 79 Brassicaceae and two related species indicated that 4-methylthiobutyl thiocyanate and 2-Hydroxy-2-phenylpropionitrile are found only in *B. incana* and *B. vulgaris*, respectively (Cole 1976). These two compounds may be toxic or feeding inhibitors to diamondback moth larvae. Thorsteinson (1953) reported that diamondback moth larvae do not feed on leaves containing allyl isothiocyanate. I observed that small larvae refused to feed and larger larvae initiated fewer feeding sites on *B. vulgaris* before they died. In contrast, 52% of diamondback moth larvae (reared from field collected populations) survived from hatch through second and 13% survived from third through fourth instars when fed on *B. vulgaris* (Idris & Grafius 1994). This suggests

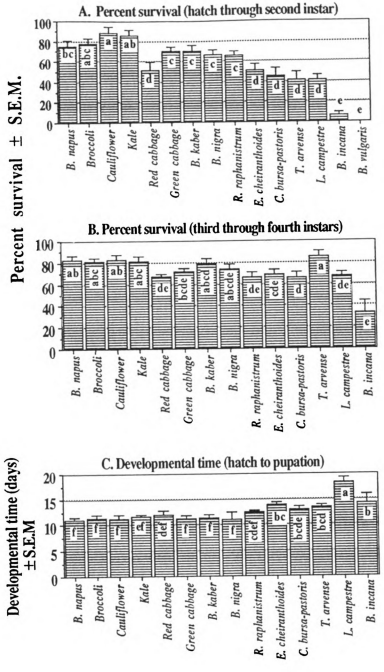

Figure 3. Percent of larval survival from hatching through second (A) and third through fourth (B) instars, and developmental time of diamondback moth larvae from hatch to pupation (C) when larvae were fed on various plants in no-choice test. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

some field diamondback moth populations may be resistant to toxic compounds found in *B. vulgaris*. In the current study I used diamondback moth (New York strain) that are susceptible to most pesticides used to control diamondback moth. Whether resistance to *B. vulgaris* is caused by the same mechanism as resistance to pesticides is not known.

There was no significantly difference in developmental time for diamondback moth larvae fed on all *Brassica* crop varieties and three wild species (*B. kaber*, *B. nigra* and *R. raphanistrum*)(FPLSD, $P > 0.05$)(Fig. 3 C). Similar results were reported when diamondback moth larvae fed on other Brassicaceae crops (broccoli, cauliflower and common cabbage)(AVRDC, 1987). Developmental time was significantly longer for larvae fed on *L. campestre* than on the *Brassica* crop varieties and other wild species (FPLSD, $P < 0.05$)(Fig. 3 A & B). However, Idris & Grafius (1994) found that developmental times of field collected diamondback moth larvae fed on wild species (*T. arvense* and *C. bursa-pastoris*) were not different from those fed on the broccoli. *L. campestre* may have an antifeedent that affected both the larva survival rate and developmental time. An antifeedent prolonged developmental time of *P. rapae* larvae to pupation (Hough-Goldstein & Hann 1992). In contrast, *B. incana*, which severely reduced larval survival rate showed similar effects as the other wild species on larval developmental time (Fig. 3 C).

***D. insulare* studies.** Percent parasitism. Parasitism of diamondback moth by *D. insulare* ranged from 0 to 91.5% and was significantly different among host plants ($F = 13.9$, df = 12 & 36; $P < 0.001$)(Table 2). Parasitism of diamondback moth larvae fed on *B. kaber* and *B. nigra* was as high as when diamondback moth larvae were fed on the Brassica crop varieties; it was lowest when *B. incana*, *L. campestre* or *E. cheiranthoides* were used as food for the larvae. These differences might be even larger in the field because diamondback moth larvae are exposed longer to parasitism in the field due to longer developmental time, especially when fed on *L. campestre* (Fig. 3C).

No parasitism occurred when *C. bursa-pastoris* was used as food for the diamondback moth larvae. I observed that *D. insulare* females did not initiate searching

Table 2. Effect of host foods on percent parasitism, developmental time of parasitized diamondback moth third instar, and sex ratio of *D. insulare*

Brassica species	Percent parasitism (± S.E.)	Developmental time (days ± S.E.)	Female to Male sex ratio (female:male)[1]
Brassica kaber	91.5 ± 3.8g	13.0 ± 0.3a	1 : 2.5
Broccoli	90.8 ± 2.2fg	13.0 ± 0.4a	1 : 2.3
Cauliflower	89.5 ± 6.5fg	12.8 ± 0.5a	1 : 3.3
Canola	87.3 ± 5.6efg	12.9 ± 0.5a	1 : 3.3
Kale	83.3 ± 2.2defg	13.8 ± 0.3a	1 : 3.1
B. nigra	81.3 ± 4.9defg	13.1 ± 0.5a	1 : 2.7
Red cabbage	79.5 ± 3.4def	13.5 ± 0.5a	1 : 3.6
Green cabbage	76.5 ± 5.6cde	13.5 ± 0.3a	1 : 3.4
R. raphanistrum	72.8 ± 4.9cd	13.9 ± 0.5a	1 : 3.8
E. cheiranthoides	65.5 ± 5.2bc	15.8 ± 0.3b	1 : 5.0
T. arvense	65.0 ± 6.5bc	16.3 ± 0.3b	1 : 4.8
B. incana	55.0 ± 6.5b	16.0 ± 0.6b	1 : 7.5
L. campestre	39.3 ± 3.9a	20.3 ± 2.2c	1 : 4.7
C. bursa-pastoris[2]	0.0	-	-
B. vulgaris[3]	-	-	-

[1] The variation in *D. insulare* sex ratio was significantly different ($\chi^2 = 23.6$, df = 12, $P < 0.05$)

[2] Parasitism did not occur in 3 h exposure of the diamondback moth larvae to *D. insulare*

[3] No diamondback moth larvae survived on *B. vulgaris*

behavior for diamondback moth larvae when *C. bursa-pastoris* was used to feed the larvae. I also noticed that there was a delay in showing searching and oviposition behavior by *D. insulare* when diamondback moth larvae were fed on *L. campestre*. Udayagiri & Jones (1992) reported that *Marocentrus grandii* Goidarich, a parasitoid of European corn borer, showed host searching behavior only to European corn borer fed on certain plants. In nature, *D. insulare* may also expected to respond differently with parasitoids' age, previous experience and host plant morphology as reported for other parasitoids (Steinberg et al. 1992, McCall et al. 1993, Keller 1987). Although I was not able to record parasitism when diamondback moth larvae fed on *B. vulgaris*, I suspect parasitism could occur in the field because some field-collected diamondback moth larvae survived on *B. vulgaris* in another study (Idris & Grafius 1994).

Developmental time. Time to develop to *D. insulare* pupa by the parasitized third instar of diamondback moth was significantly longer on *E. cheiranthoides*, *T. arvense* and *B. incana* than on the *Brassica* crop varieties and three other wild species (*B. kaber*, *B. nigra* and *R. raphanistrum* ($F = 19.7$, df = 12 & 36, $P = 0.001$)(Table 2). There was a positive correlation between time taken by parasitized and unparasitized larvae to form *D. insulare* and diamondback moth pupae (Fig. 4). This indicates that the effects of food plants on developmental time to pupation are similar for parasitized and unparasitized diamondback moth larvae. McCutcheon et al. (1991) reported that pre-imaginal development of *Cotesia marginiventris* Cresson (Hymenoptera: Braconidae), a parasitoid of soybean looper, *Pseudolupsia includens* Walker (Lepidoptera: Noctuidae), was severely affected by the resistant line of soybeans (McCutcheon et al. 1991). However, effects of host plants may be subject to the host insect's stage at the time of parasitism because different host's stages may be affected differently. For *Helicoverpa zea* (Boddie) larvae, the variation in host sterol composition in larvae affects the growth and development of its parasitoid, *Microplitis demolitor* Wilkinson (Hymenoptera: Braconidae) (Ritter & Johnson 1991). Developmental time of *Eriborus terebrans* (Gravernhost) to pupation is affected by

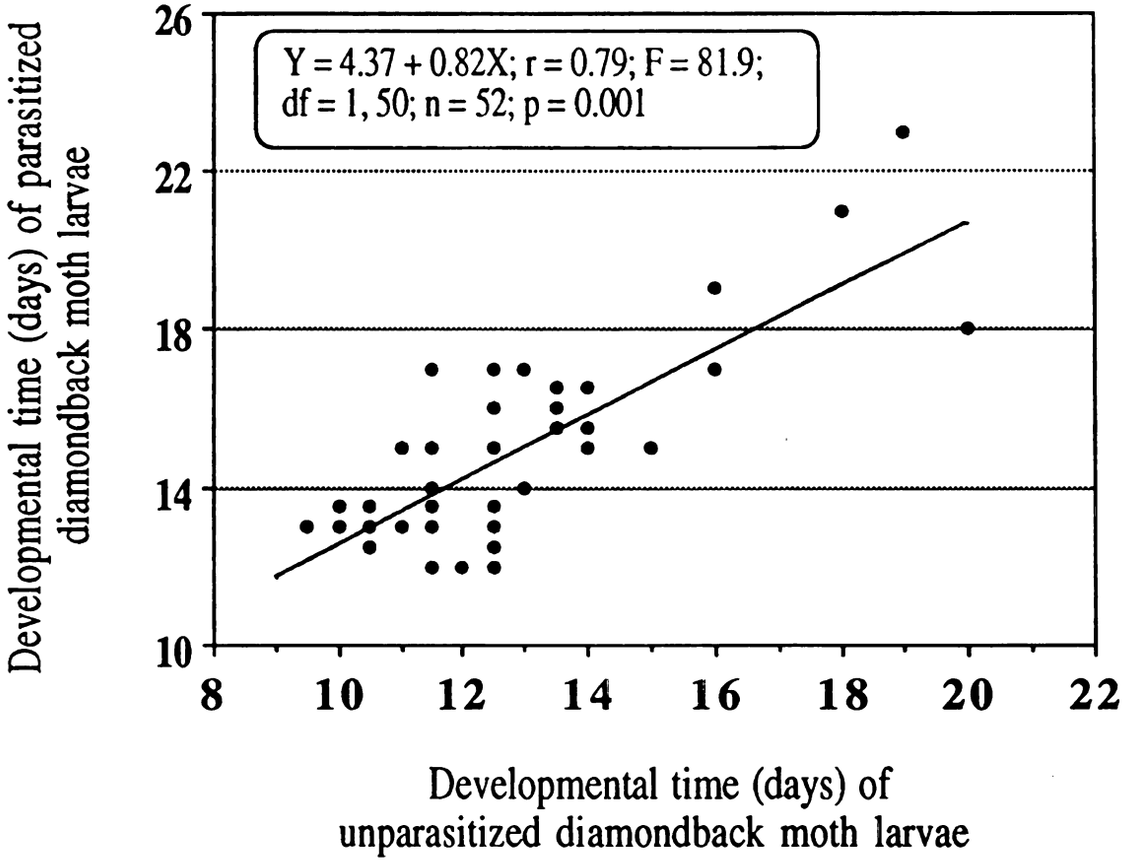

Figure 4. Relationship between developmental time of parasitized and unparasitizeed diamondback moth larvae fed on various host plants.

α- tertienyl, one of the secondary chemicals that affect European corn borer larval development (McDougall et al. 1988).

D. insulare sex ratio. Female to male sex ratio of *D. insulare* ranged from 1: 2.3 to 1: 7.5 and was significantly different among the host plants (Table 2). There were more females produced when diamondback moth larvae were fed on the cultivated varieties than on the wild species except for *B. kaber*, *B. nigra* and *R. raphanistrum*. Female to male sex ratio of *D. insulare* fed on broccoli was between 1: 1.7 to 1: 2.5 (Idris & Grafius 1993b) agreeing with my present result (Table 2). In another study, higher proportions of female *D. insulare* emerged from diamondback moth larvae fed on leaves of high N-fertilized than on the low N-fertilized collards (Fox et al. 1990). Percent female *Comperriella bifaciatea* Howard (Hymenoptera: Encyctidae) produced was 45% and 84% when its host reared on valencia orange (*Citrus sinensis* Osbeck) and yucca (*Yucca filipendula* Baker) plants, respectively (Smith 1957).

Field studies. Level of diamondback moth infestation in the field, distribution of *D. insulare* and parasitism. The numbers of small larvae ($F = 3.9$, df = 4 & 45, $P < 0.05$), large larvae ($F = 9.3$, df = 4 & 45, $P < 0.05$) and total larval counts per plant ($F = 9.3$, df = 4 & 45, $P < 0.05$) were significantly different among crops (*Brassica* cultivars). Numbers of small larvae on broccoli and green cabbage were significantly higher than on cauliflower, kale or red cabbage (FPLSD, $P < 0.05$)(Fig. 5 A). There were significantly more large larvae and total larvae on broccoli than on the other crops (FPLSD, $P < 0.05$)(Fig. 5 A, B & C). My results disagree with the report of Lasota & Kok (1986) where numbers of larvae on kale were as high as on broccoli or cauliflower. This contrasting result may due to the difference of *Brassica* cultivars used as reported by Lin et al. (1983) and Eigenbrode et al. (1990). Although diamondback moth in the field study were not reared on broccoli (unlike the laboratory strain), broccoli was the most common *Brassica* crop at this site for the past ten years.

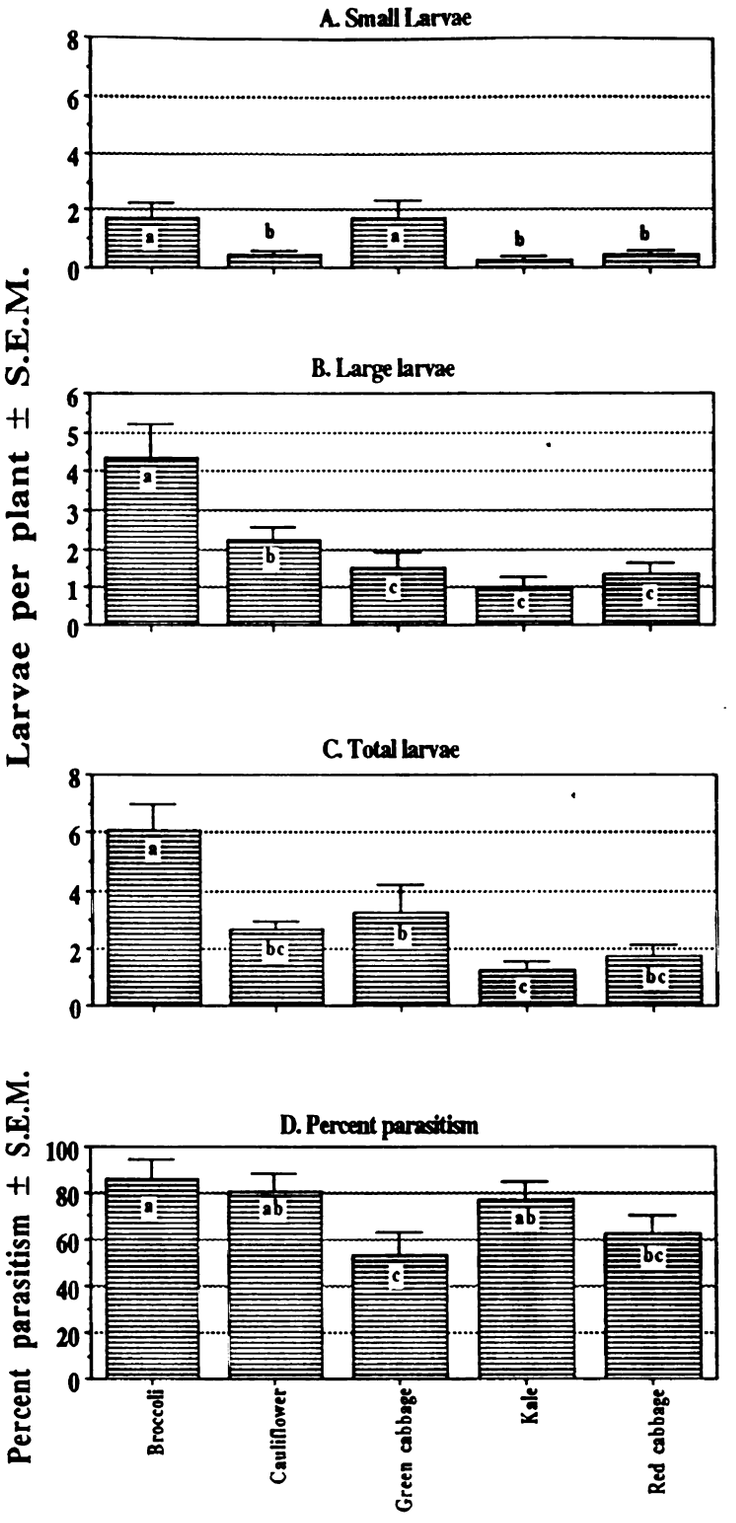

Figure 5. Distribution patterns of diamondback moth small (first-second instars)(A) and large larvae (third-fourth instars)(B), total larvae counts (C), and percent parasitism of the diamondback moth larvae by *D.insulare* (D) on different *Brassica* crops. Bars with different letters are significantly different (Fisher's Protected LSD, $P < 0.05$).

Numbers of small larvae per plant on three different dates were not significantly different (F = 0.3, df = 2 &45, P = 0.560). However, numbers of large larvae (F = 7.6, df = df = 2 & 45, P = 0.001) and total larvae (F = 4.0, df = 2 & 45, P = 0.001) were significantly different among the dates and were higher on 25 August and 3 September than on 7 July. A similar trend was also shown by the numbers of small larvae although differences were not significant.

The interaction between *Brassica* variety and sampling date did not influence the numbers of small larvae (F = 0.8, df = 8 & 45, P = 0.453), large larvae (F = 1.7, df = 8 & 45, P = 0.635) or total larvae (F = 0.3, df = 4 & 45, P = 0.731) per plant.

Percent parasitism of diamondback moth by *D. insulare* was significantly affected by crop (F = 2.7, df = 4 & 45, P = 0.021) and sampling dates (F = 4.2, df = 2 & 45, P = 0.006) but not by the interaction between these two factors (F = 0.2, df = 8 & 45, P = 0.673). Parasitism rate was significantly higher on broccoli (87%) than on green (53%) or red (63%) cabbage (FPLSD, $P < 0.05$)(Fig. 5 D). In contrast, parasitism of diamondback moth by *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumonidae) was highest on cabbage, followed by Chinese cabbage, cauliflower and broccoli (Talekar & Yang 1991). Percent parasitism of diamondback moth by *D. insulare* (= *insularis*) on Abbott and Cobb # five *Brassica* cultivars was significantly higher even though the diamondback moth infestation was higher on other cultivars (Lasota & Kok 1986). My results showed that this was not necessarily true because the total larval count on kale was lower than on the broccoli, but the parasitism rate on these two varieties was similar (Fig. 5 C & D). This suggests *D. insulare* is a good host searcher regardless of plant's leaf structure (kale leaves are much more curly than broccoli leaves). Percent parasitism over the dates showed similar trend as for the numbers of large diamondback moth larvae or total larvae.

Numbers of *D. insulare* males, females and total catch per trap were not significantly different among crops (F = 1.1, males; 1.4, female; 1.7, total; df = 4 & 30, P = 0.432) or sampling dates (F = 2.9, males; 0.9, female; 2.5, total; df = 1 & 30, P =

0.353). The interaction between crops and sampling dates did not significantly influence the numbers of *D. insulare* males, females or total (males plus females) caught per trap (F = 0.2,male; 0.1, female; 0.1, total; df = 4 & 30; P = 0.647). This indicates that the parasitoid was evenly distributed in field and apparently not affected by the volatiles released by the different crops. *Diadegma* may aggregate on plants with higher host numbers (Waage 1983, Chapter 3). However, in this study, numbers of *D. insulare* females caught per trap in broccoli were not significantly different from catch in the other crops even though the total larvae counts were significantly higher on the broccoli than on the other crops (Fig. 5 C). This may due to the low diamondback moth larval population density in the field during my study.

Results of my field study indicate that choosing the right *Brassica* cultivar could suppress diamondback moth infestation. Although percent parasitism was always higher on broccoli than some of the other crops, broccoli also supported high number of diamondback moth larvae (Fig. 5). Low numbers of diamondback moth larvae on red cabbage supported my laboratory results which indicate the low numbers of larvae surviving to pupation on red cabbage (Fig. 3 A & B; Fig. 5). Low percent parasitism appears to be a disadvantage of selecting red cabbage for planting.

Use of wild *Brassica* spp. in diamondback moth management. Results of my laboratory study and a previous report (Idris & Grafius 1994) suggest that an augmentation of *B. vulgaris* could reduce diamondback moth infestation early in the season. *B. vulgaris* seeds can be sown in the field or nearby before winter. They germinate in late April in the northern U.S. and the plants will be abundant in May and early June before planting of mid-to late-season *Brassica* crops. My no-choice test results, which may simulate an early spring situation, indicated that diamondback moth laid as many eggs on *B. vulgaris* as on the cultivated crops, cauliflower and canola but no larvae survived to second instar. Any larvae that might survive on *B. vulgaris* may be parasitized by *D. insulare* or sprayed with selective pesticide such as *Bacillus thuringiensis* var.

kurstaki Berliner without disrupting biological control of *D. insulare*. Alternatively, *B. vulgaris* could be killed by cultivation or herbicides before diamondback moth larvae mature. These tactics will reduce diamondback moth populations before the cropping season begins. Besides acting as a trap crop for diamondback moth, *B. vulgaris* also serves as excellent nectar source for *D. insulare* adults (Chapter 1). The presence of *B. vulgaris* may attract high numbers of *D. insulare* to stay longer around the field and increase parasitism rate. *B. vulgaris* could also act as refuge for diamondback moths susceptible to insecticides and aid in insecticide-resistance management of diamondback moth.

L. campestre and *B. incana* significantly prolonged larva development and caused high mortality to diamondback moth larvae. They could be intersown before winter or sown in May next to *B. vulgaris*. These weeds could be used as a trap crop after *B. vulgaris* is gone in June. Although *B. incana* and *L. campestre* are early season weeds like *B. vulgaris*, they grow and continue flowering throughout the summer. Their flowers can provide an additional food source for *D. insulare* adults (Chapter 1).

Diamondback moth oviposition is higher on *Brassica hirta* L. than on canola (Palaniswamy & Gillott 1986). In contrast, my results indicate that egg laying on *B. kaber*, closely related to *B. hirta*, and canola were not different. In addition, *B. kaber* was as good as the *Brassica* crop varieties for both diamondback moth development and *D. insulare* parasitism. In the United States, *B. kaber* is considered to be a troublesome weed (Buchholtz et al. 1981). *B. kaber*, however, is an excellent nectar source for *D. insulare* (Chapter 1). It grows throughout the summer season, and can easily be killed by herbicides normally used in Brassica fields (Buchholtz et al. 1981). In addition, the presence of *B. kaber* throughout planting season could be important near fields frequently treated with pesticide because it could provide refuge for the susceptible diamondback moth populations and hosts for *D. insulare*. This can slow down resistance build up, reduce pesticide use and maintain the presence of parasitoids in the field. Therefore, I have no

doubt that there will be more benefit than risk when *B. kaber* is used in diamondback moth management program. *B. kaber* can be grown outside the field or in patches within the field. *Brassica juncea* (L.) Czern., is currently used as a trap crop in a diamondback moth management program in India (Srinivasan & Krisna Moorthy 1991).

CONCLUSIONS

It is important for us to understand the tritrophic interaction between brassicaceous plants, diamondback moth and its parasitoids, especially *D. insulare*. This will enable us to effectively combine the effects of host plant, varieties or cultivar selection and planting of wild brassicaceous species, and use *D. insulare* to suppress diamondback moth populations and reduce pesticide dependence. Adoption of this type of integrated system will be more difficult than selecting a new cultivar or using a new pesticide. Demonstration and acceptance by leading growers will be required for larger scale adoption.

CHAPTER 7

Alternate Hosts of *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae), a Parasitoid of Diamondback Moth (Lepidoptera: Plutellidae): A Preliminary Search

ABSTRACT

Diamondback moth parasitism in the field in Michigan is high throughout the year and in a variety of habitats, in spite of low diamondback moth populations. This suggests that an alternate host may be involved. If so, it could perhaps be used to increase numbers and effectiveness of *D. insulare* in managing diamondback moth. I conducted a preliminary search for alternate hosts of *Diadegma insulare* (Cresson) at the Michigan State University Research Farm and three other locations near the campus area in the spring and summer of 1993 and 1994. Potential alternate host larvae and pupae were collected from; wild brassicas and brassicas crops, apple (*Malus domestica* L.) orchards, ornamental honeylocust tree (*Gleditsia triacanthos* L.), and corn (Zea mays L.) for further laboratory observation. I also used laboratory reared *Phthorimaea operculella* (Zeller) and *Sitotroga cerealella* (Oliver)(Lepidoptera: Gelechiidae) to see if *D. insulare* will parasitize these gelechiids. None of the Lepidoptera studied seemed to be important alternate hosts of *D. insulare*. However, the samples were small and few plants, except for Brassicaceae, were inspected for the alternate hosts. Surprisingly, *D. insulare* parasitized *Plutella porrectella* L., but neither host pupae nor parasitoid pupae were formed. *P. operculella* and *S. cerealella* were also parasitized by *D. insulare*. Percent parasitism of *P. operculella* ranged from 0-34.3% depending on the host instars parasitized. There were only two male *D. insulare* emerged from > 1000 *S. cerealella* larvae exposed for parasitism. This is the first report that *D. insulare* can parasitize *P. operculella* or *S. cerealella*. In contrast to the parasitized *P. xylostella* larvae, the development of these two gelechiids larvae was greatly shortened by parasitism. This suggests that *D. insulare* may have other hosts in nature because of the flexible ability to control its host development. Since microlepidopterans,

especially gelechiids and tortricids larvae are usually concealed within the webbed leaf or fruit, the temporal window (length of exposure for parasitism) of each host and the searching ability of *D. insulare* could partly determine the level of parasitism. Steps to speed up searching for the alternates host of *D. insulare* are discussed.

INTRODUCTION

Diadegma insulare (Cresson)(Hymenoptera: Ichneumonidae) is the new world species of the genus *Diadegma* and is recorded from southern Canada south to Venezuela and west to Hawaii (Carlson 1979). In Canada and United Statės, *D. insulare* is the major parasitoid of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) and often parasitizes > 80% of the host larvae (Harcourt 1986, Idris & Grafius 1993). *D. insulare* populations are abundant in *Brassica* crop fields (Harcourt 1986) and other crop fields (Chapter 5). For example, percent parasitism of diamondback moth larvae placed in crops such as tomatoes, corn or apples for 24-26 h was as high as parasitism in broccoli (Chapter 5).

Diamondback moth cannot survive the winter weather in Canada (Smith & Sears 1982), but may overwinter in Michigan (Idris & Grafius 1995b). Diamondback moth infestation in early season *Brassica* crops may be caused by populations migrating from the southern States of United State in the mid-May each year (Smith & Sears 1982, Harcourt 1962), by overwintering (Idris 1995) or brought with *Brassica* transplants from the southern United States. No one seems to have considered that some of its parasitoids might also be migratory. Putnam (1978) found that *D. insulare* does not survive the winter in Saskatchewan, Canada, but the other diamondback moth parasitoid, *Microplitis plutellae* (Muesback)(Hymenoptera: Braconidae) does. However, *D. insulare* is more abundant than *M. plutellae*. Recently, traps used to monitor the migration of potato leaf hopper from the southern United State accidentally caught diamondback moth but no *D. insulare* or other Hymenoptera (Rahardja, personal communication).

It is not known how *Diadegma* species associated with diamondback moth in the temperate zones overwinter. However, the most common method of overwintering in ichneumonids is diapause of the full-grown larva within its own cocoon (which may be within some host remains, such as a pupa)(Fitton & Walker 1992). In multivoltine Ichneumonidae, sometimes only a proportion of the late summer generation enters diapause, the remainder survive or perish, depending on weather. In many cropping situations *Diadegma* cocoons might be destroyed during winter plowing but wild Brassicaceae or crops left undisturbed could possibly harbor a large enough overwintering population to explain the sometimes high rate of parasitism of the spring generations of diamondback moth in the spring (Fitton & Walker 1992). In Michigan, we observed adults of *D. insulare* female searching or visiting the wild *Brassica*, *Erysimus cheiranthoides* L., as early as 17 May 1993 (Appendix 2).

Because diamondback moth can overwinter as an adult some workers have suggested that *Diadegma* must overwinter in association with another overwintering insect. Data in the literature suggests that many *Diadegma* species have wide host ranges. For example, Hardy (1938) reported that, in addition to diamondback moth, *D. semiclausum* (= *eucerophaga*)(Hellen) and *Diadegma fenestrale* (Holmgren) attack 8 and 24 species of Lepidoptera, respectively, none of them in the family Plutellidae. He also described *D. fenestrale* as very polyphagous because it also attacked one coleopteran.

Diadegma species that have more than one host often have some common factor linking the hosts. For example, *Diadegma chrysostictos* (Gmelin) parasitizes a small number of pyralid moths that live in a narrowly defined niche (Horstmann & Shaw 1984). *D. chrysostictos* is suspected to alternate between a micro and a macro-lepidopteran feeding on the same plant (Fitton & Shaw, 1992). However, reports of Horstmann & Shaw (1984) and Dijkerman (1990) indicate that *Diadegma* are relatively host-specific where the primary host is a microlepidoptera.

Other than diamondback moth, two macrolepidoptera, *Trichoplusia ni* (Hübner) and soybean looper, *Pseudoplusia includens* (Walker) (Lepidoptera: Noctuidae), are parasitized by *D. insularis* and *D. plutellae* (Harding (1976); both are synonymised to *D. insulare* (Azizad A. A. & M. Fitton, Natural History Museum, University of London, personal communication). These noctuids, however, were not listed as the alternate hosts of *D. insulare* (Carlson 1979). *D. insulare* is also reported to parasitize two microlepidoptera, *Hellula undalis* (F.)(Pyralidae) and *Plutella armoricacae* Busck (Plutellidae)(Carlson 1979). *Hellula* are tropical and subtropical species (Heppner 1987) and are not potential alternate hosts for *D. insulare* in Michigan. In contrast, *P. armoricacae* is recorded from Michigan (Department of Entomology Museum, Michigan State University), but its host plant, the horseradish (also Brassicaceae), is rare. Therefore, it also is probably not associated with the *D. insulare* abundance and high parasitism rate of diamondback moth in the early spring each year.

I have a strong belief that *D. insulare* must have alternate hosts in Michigan and other northern states of the United States. First its parasitism rate is high throughout the year and in a variety of habitats. Second, *D. insulare* is not a good migratory insect compared to its primary host, the diamondback moth (Putnam 1978, Smith & Sears 1982). Third, *D. insulare* was found in the field as early as the 17 May 1993 (Appendix 2).

The objectives of my study were to search for alternate hosts of *D. insulare* from the (1) insects associated with cultivated and wild Brassicaceae, (2) Lepidopteran found in *Brassica* crop fields, (3) remains in the spring of the previously year's broccoli crop, and (4) insects associated with nonhost plants of diamondback moth.

MATERIALS AND METHODS

Insects associated wild Brassicaceae. Wild Brassicaceae (50-100 plants per species per year) was collected from April through August of 1993 and 1994 from Michigan State University research farms, East Lansing, Michigan, and three locations adjacent to campus (Table 1). Each plant was pulled by hand and put on white paper placed on the ground. I shook each plant over the paper for about 3 min and collected all insect larvae and pupae. Thorough inspection was made of the flowers because larvae may feed and hide in between the florets (Marsh 1917). Larvae and pupae were brought to the laboratory for rearing.

Leaves of each plant were randomly selected and detached, brought to the laboratory and placed in 10 x 7 x 5 cm rearing pans (3 x 4 cm lid on top) at 25 ± 2°C and photoperiod of 16:8 (L:D) h. To keep the leaves fresh for few days I put wet paper towel inside the bottom of the pan before putting in the leaves. The numbers of newly hatched larvae were recorded for 10 d.

Field collected pupae were reared as above until adults emergence. Field collected and laboratory-reared larvae were divided into two groups to be used in separate observations. For group 1, larvae were put in the rearing pan as before and fed with leaves of the same plant species from which they were collected. Larvae of group 2 were exposed to parasitism by *D. insulare* as described in Chapter 1. Larvae from both groups were reared until pupation as before and I recorded the types and numbers of pupae formed. I also dissected the prepupae of *Plutella porrectella* L. and diamondback moth (n = 20 per insect species) from group 2 to determine the presence of *D. insulare* larvae. This was done because I wanted to know why there were no parasitoid or *Plutella porrectella* L. pupae formed from the parasitized *P. porrectella* larvae.

In the summer of 1993 and 1994, I also put white sticky traps (Pherocon™ 1C - bottoms, Trece, Inc., Salinas, CA) within patches of the Dame's rocket, *Hesperis matronalis* (L.), since it is reported as the main host plant for *P. porrectella* (L.)(Smith & Sears 1984). The traps were hung on the stems (10-20 cm below the highest level of the plants). *D. insulare* adults and other Lepidoptera caught on the traps were recorded and removed every day.

Lepidoptera larvae in the broccoli field. I collected all Lepidoptera larvae found in the broccoli field in the summer of 1993 and 1994 (Table 2). Larvae were subdivided into two groups and were subjected to separate observations as before.

Cultivated broccoli remains. On 28 April 1994, I set up six cages (180 x 165 x 165 cm high) in my 1993 broccoli experimental plots at the Michigan State University Collins Road Entomology Research Field . On 3 May, I pulled up the partially rotten broccoli remains and put 50-70 of them in each cage. To monitor adult *D. insulare* or other potential hosts I hung white sticky traps, 0.5 m from the ground on wooden stakes in the cages. On 7 May, six potted broccoli plants from the greenhouse, infested with diamondback moth second and third instars, were placed inside each cage. Larvae were collected weekly, brought to the laboratory and reared as before until pupation. The infested potted broccoli plants were replaced weekly and larval collection and rearing were continued until the end of June. Numbers of *D. insulare* adults or other Lepidoptera caught on the traps, numbers and types of pupae formed were recorded.

Insects associated with nonhost plants of the diamondback moth. Potato tuber moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae). I conducted these experiments in the laboratory. One month old greenhouse raised potted potato plants were put in 45 x 40 x 40 cm cages (two per cage).

In the first experiment, *P. operculella* eggs from laboratory culture were put on the potato leaves in the cages. After most eggs hatched we released several 6 d old-experienced *D. insulare* females into the cages for 3-4 d to parasitized the first instar of *P.*

operculella. I put a cotton wick wetted with honey+water (10% honey) in the cages as food for the parasitoids.

In the second experiment, I put *P. operculella* eggs in a 14.5 cm diam Petri dish until hatch. Second, third and fourth instar *P. operculella* were collected accordingly, and were released on the potted potato plants for parasitism as before.

After 4 d access by *D. insulare* the *P. operculella* larvae were collected from the leaves, stems and the tubers of the potted potato plants, put in 10 x 7 x 5 cm rearing pans half filled with potato tubers and kept at 25 ± 2°C and a photoperiod of 16:8 (L:D) h until pupation. The numbers of *P. operculella* and *D. insulare* pupae formed were recorded every day until all larvae pupated. I recorded the developmental time for each instar to form *P. operculella* or parasitoid pupae, and sexes of adults *D. insulare* emerged. Because each instar of *P. operculella* was exposed to parasitism separately I just recorded the day of the first five *P. operculella* or *D. insulare* pupae formed from the respective larval group (first, second, third or fourth instars) to measure the developmental time for parasitized versus unparasitized larvae.

In the third experiment, I cross-checked the occurrence of parasitism on diamondback moth by *D. insulare* produced from *P. operculella*. To do this, 30 third instar diamondback moth were exposed to one *D. insulare* female (reared from *P. operculella*) as described in Chapter 1 except the exposure time was increased from 3 h to 4 d. The presumably parasitized *P. xylostella* larvae were reared as before until pupation. Numbers of *D. insulare* and diamondback moth pupae formed were recorded.

All experiments were replicated four times. Percent parasitism was calculated as described in chapter 4 and analyzed by 1-way ANOVA (Abacus Concept, SuperAnova 1991). The differential in sex ratio of *D. insulare* produced from parasitized instars of *P. operculella* was calculated using χ^2 (1 : 3.2 *D. insulare* sex ratio from cross-checked experiment was used as the expected value)

European corn borer, *Ostrinia nubilalis* (Hübner)(Lepidoptera: Pyralidae). Fourty first instar *O. nubilalis* (donated by Dr. Douglas A. Landis, Department of Entomology, Michigan Sate University) were divided in two groups (five larvae per group per replicate). Group 1 was tested as a first instar. Group 2 larvae were fed on artificial diet (also donated by Dr. Landis) until they became second instar and then tested. Larvae of each group were exposed for parasitism by *D. insulare* as before. After *D. insulare* exposure, larvae were fed with fresh artificial diet every 3 d and reared to determine parasitism.

In August 1994, larvae of *O. nubilalis* were collected from a corn field at the Entomology Researh Field, brought to laboratory and reared as before to determine if *D. insulare* parasitism had occurred.

Tortricids in Apple Orchard. I conducted two separate studies. In the first study, I collected 1000-1100 apples from the Entomology Research Field and Trevor Nicchols Fruit Research Station, Fenville, Michigan, in July through September 1994. In the laboratory the fruit were carefully cut to look for tortricid larvae or pupae. All parasitoid pupae collected were kept as before and reared to parasitoid emergence. I also collected apple leaves and shoots, and put them in a rearing pan as before, to get fresh first or second instar tortricids for similar observations. The collected larvae were separated by species. Regardless of the larvae stages or if they were naturally parasitized in the field, I exposed them for parasitism by *D. insulare* as before. I supplied larvae with a thin slice of apple fruit on the second day of exposure. The presumably parasitized larvae were fed with a fresh apple slice every 4 d and reared. The types and numbers of pupae formed were recorded.

For the second study, larvae were collected from leaves, shoots, and 500 apple fruits from the field as before, but reared without exposing them to *D. insulare* for parasitism. Larvae were grouped by species, fed apple fruit, and reared as before until pupation. I recorded the types and numbers of pupae formed.

Angoumois grain moth, *Sitotroga cerealella* (Oliver)(Lepidoptera: Gelechiidae). *S. cerealella* (donated by Dr. D. K. Weaver, South Atlantic Area Stored-Product Insects Research and Development Laboratory, Georgia, USA) was used for the study. A folded black paper stapled at both ends (6 cm x 2 cm) was put in 400 ml plastic container (designed as described in chapter 1) for oviposition. Ten pairs of *S. cerealella* were released in the container for 2 d, after which they were taken out leaving the eggs on the black paper. After all the eggs hatched, I released five 6 d old and experienced *D. insulare* females into the container for 4 d to parasitize the first instar of *S. cerealella*. I provided only enough corn kernals during parasitism period to keep the larvae alive. I added more corn kernels 4 d later when *D. insulare* were removed. Presumably parasitized larvae were reared until adult emergence. The numbers of *S. cerealella* and *D. insulare* pupae formed, and the emerged adults of both insects (starting 10 d after eggs hatched) were recorded. Percent parasitism was calculated as before.

Mimosa webworm, *Homadaula anisocentra* Meyrick, a plutellid that associated with the ornamental honeylocust tree, *Gleditsia triacanthos* L. Larvae of *H. anisocentra* were collected from 250-300 *G. triacanthos* around the campus and the nursery field of Forestry Department, Michigan State University, Michigan in June and July 1994. Larvae were brought to laboratory, reared by feeding them with *G. triacanthos* leaves and flowers, and kept as before until pupation. The numbers of pupae formed were recorded.

RESULTS AND DISCUSSION

Insect associated with wild Brassicaceae. I found diamondback moth larvae on all wild Brassicaceae except *Neslia paniculata* L. (Table 1). Imported cabbageworm larvae, *Pieris rapae* L. (Lepidoptera: Pieridae), were collected from *Barbarea vulgaris* R. Br. , *Brassica kaber* (DC) Wheeler, *Raphanus raphanistrum* L. and *Sisymbrium officinale* (L.) Scop. Cabbage looper, *Trichoplusia ni* L. (Lepidoptera: Noctuidae), was found from

B. vulgaris, *R. raphanistrum* and *Hesperis matronalis* (L.). Other than Lepidoptera larvae, syrphid species (Diptera: Syrphidae) and lady beetle species (Coleoptera: Coccinellidae) were also collected. There were no *D. insulare* pupae formed from Lepidotera other than diamondback moth larvae collected in 1993 and 1994 in both larval groups tested. In the laboratory, I found mostly *P. xylostella* and five *O. nubilalis* larvae from field collected detached *Brassica* leaves. None of the *O. nubilalis* larvae were parasitized by *D. insulare.*

Most third and fourth instars of the *P. porrectella* collected in May 1993 (78.6%, n = 155) and June 1994 (93.7%, n = 180) successfully formed moth pupae. Regardless of larvae group tested, there were no *D. insulare* or other parasitoid pupae formed. In Ontario, Canada, Smith & Sears (1984) reported that *P. porrectella* was not parasitized by *D. insulare* but by *Itoplectis conquisitor* (Say)(Hymenoptera: Ichneumonidae). The external appearance of parasitized *P. porrectella* and *P. xylostella* larvae look similar at the prepupa stage. During pupal stage, parasitized *P. xylostella* formed a parasitoid pupa while parasitized *P. porrectella*'s body shrunk, failed to produced a cocoon and died, not forming either host or parasitoid pupa. Dissection of the larvae exposed to *D. insulare* indicated that there were no *D. insulare* larvae from the *P. porrectella* but ≈ 92% of parasitized *P. xylostella* contained *D. insulare* larvae. I also observed that *D. insulare* females were actively searching for *P. porrectella* larvae and ovipositing; behavior similar to what I usually see when the parasitoid is exposed to *P. xylostella* larvae. This indicates that the parasitoid eggs failed to survive in the host body. Physiological development of *P. porrectella* parasitized larvae was probably affected by a polydnavirus injected with the eggs during oviposition. The influence of ichneumonid parasitoids polynavirus on host physiology is common. For example, polynavirus of *Eriborus* (= *Diadegma*) *terebrans* (Gravenhost) is responsible for parasitism success of this parasitoid on European corn borer, *O. nubilalis* (Stoltz et al. 1981).

Table 1. Insect larvae collected from the wild Brassicaceae during the summer of 1993 and 1994

Weed Species	Common Name	Larvae[a]		
		Lepidoptera	Diptera	Coleoptera
Barbarea vulgaris R. Br.	Yellow rocket	ICW, DBM, CL	S	LB
Berteroa incana (L.) DC	Hoary alyssum	DBM	N	LB
Brassica nigra (L.) Koch	Black mustard	DBM	S	LB
Brassica kaber (DC) Wheeler	Wild mustard	DBM, ICW, UL*	S	LB
Capsella bursa-pastoris (L.) Medic	Shepher's purse	DBM	N	N
Erysimum cheiranthoides (L.)	Wormseed mustard	DBM	N	N
Lepidium campestre (L.) R. Br.	Field papperweed	DBM	S	LB
Lepidium densiflorum (Schard)	Greenflower pepperweed	DBM	S	LB
Lepidium virginicum L.	Virginia pepperweed	DBM	N	N
Neslia paniculata (L.) Desv.	Ball mustard	N	N	LB
Raphanus raphanistrum L.	Wild radish	DBM, ICW, CL	S	LB
Sisymbrium altissimum L.	Tumble mustard	DBM	N	LB
Sisymbrium officinale (L.) Scop.	Hedge mustard	DBM, ICW	S	N
Thlaspi arvense L.	Field pennycress	DBM	S	LB
Hesperis matronalis (L.)	Dame's rocket	PP, DBM*, UML, CL	S	N

[a] ICW, imported cabbage worm; DBM, diamondback moth (*Plutella xylostella* L.); UL, unidentified microlepidopteran; PP, *P. porrectela* L.; CL, Cabbage looper; UML, unidentified macrolepidopteran; S, syrphid larvae; N, none; LB, lady beetle; * , less than five collected.

Three *D. insulare*, ten *P. porrectella*, and three *P. rapae* adults were caught on the sticky traps placed within *H. matronalis* patches but there were no *P. xylostella* adults. The presence of *D. insulare* was not surprising because it attacked both *P. xylostella* and *P. porrectella* larvae in the laboratory.

Lepidoptera larvae found within the broccoli field. Except for diamondback moth larvae, none of the other field collected Lepidoptera larvae (from both larval groups tested) were parasitized by *D. insulare* (Table 2). In the laboratory, *D. insulare* females were not observed attacking Lepidoptera larvae other than diamondback moth and *P. porrectella* larvae. This suggests that, at least in Michigan, common insects that regularly or occasionally feed on *Brassica* plants are not alternate hosts of *D. insulare*.

Table 2. Lepidoptera larvae collected from the broccoli field in the summer of 1993 and 1994, and percent parasitism by *Diadegma insulare*

Insect species or family	Common name	Approximate numbers collected	Percent parasitism
Plutella xylostella L.	Diamondback moth	100	100
Pieris rapae L.	imported cabbageworm	70	0[a]
Trichoplusia ni L.	Cabbage looper	30	0[a]
Tortricidae	-	10	0[a]
Lymantridae (unknown sp.)	-	20	0[b]
Arctiidae (")	-	10	0[a, b]
Noctuidae (")	-	8	0[a, b]
Unidentified			
microlepidopteran[c]	-	-	-
macrolepidopteran	-	4	0[b]

[a] There was no parasitism even though all different larval stages were exposed for parasitism by *D. insulare*.

[b] Only late instars were exposed for parasitism and were fed broccoli leaves.

[c] Died because of food source problem

Cultivated broccoli remains. There were no diamondback moth or *D. insulare* adults caught on the sticky traps placed inside the cages until the end of June in 1993 or 1994, indicating *D. insulare* is not using diamondback moth as a host to overwinter. However, three *M. plutellae* adults (one female) were caught from one of the six cages. A total of 20 pupae of a *M. plutellae* were produced from diamondback moth larvae exposed for parasitism in the field cages and of these, ten *M. plutellae* adults emerged.

Insects associated with nonhost plants of the diamondback moth. Potato tuber moth, *P. operculella.* Parasitism was as high as 34% and was significantly lower on the later instars than on the earlier instars of *P. operculella* (FPLSD, $P < 0.05$)(Table 3). In contrast, percent parasitism of *P. xylostella* larvae by *D. insulare* is higher on the second and third instars than on the first or fourth instars (Bolter & Laing 1983, Harcourt 1960). Larger *P. operculella* larvae spend less time outside the plant (tuber, stem or leaf) than the smaller larvae (Metcalf & Metcalf 1951). Therefore, larger larvae have a shorter exposure time for parasitism to occur than the smaller larvae. Results of cross-checked parasitism showed that *D. insulare* produced from *P. operculella* parasitized 88.9% of diamondback moth larvae (Table 3). This is similar to parasitism rate by *D. insulare* originating from *P. xylostella* (Bolter & Laing 1983).

Regardless of the *P. operculella* instars parasitized, the male to female sex ratios of *D. insulare* from *P. operculella* were not significantly different from the sex ratios of *D. insulare* produced from cross-check parasitism; the sex ratio from cross-check parasitism is similar to the sex ratio of *D. insulare* originated from diamondback moth (Idris & Grafius 1993b, Chapter 6). Therefore, in a potato-*Brassica* intercropping, *D. insulare* originating from a potato field infested with *P. operculella* could parasitize as high a proportion of diamondback moth in the *Brassica* crop field as *D. insulare* from the *Brassica* crop field itself. The foreseeable limitation is that there would be less *D. insulare* produced from the potato field than from the *Brassica* crops field. However, the availability of *P. operculella* as an alternate host of *D. insulare* may allow us, if necessary, to use pesticides to

Table 3. Percent parasitism of *Phthorimaea operculella* (Zeller) by *Diadegma insulare* (Cresson), the male to female sex ratio of *D. insulare* and percent parasitism of *Plutella xylostella* (L.) by *D. insulare* produced from *P. operculella*

Observation	Instar of *P. operculella*				Cross-check parasitism
	First	Second	Third	Fourth	(third instar *P. xylostella*)
Percent parasitism	34.3c	25.3b	8.8a	0a	88.9[1]
The sex ratio[2]	5.4 : 1	4.5 : 1	3.5 : 1	-	3.2 : 1

Same letters in the row are not significantly different (Fisher's Protected LSD, $P > 0.05$)

[1] Mean of four replicates

[2] The male to female sex ratio was not significantly different (χ^2, $P > 0.05$)

control diamondback moth; *D. insulare* from the potato field could kill diamondback moth larvae in the *Brassica* field that escaped from pesticide treatment. This can indirectly slow down insecticide-resistance development.

Surprisingly, the time taken for parasitized *P. operculella* larvae to form *D. insulare* pupae was approximately 14 d, 4 to 6 d shorter than the time taken by unparasitized larvae to form *P. operculella* pupae. In contrast, time taken by unparasitized diamondback moth larvae to form diamondback moth pupae is 2 to 3 d shorter than time taken by the parasitized larvae to form *D. insulare* pupae (Idris & Grafius 1993c). This indicates that *D. insulare* larvae within the parasitized *P. operculella* larvae may be able to control the physiological development of the host to synchronize with its developmental time. Parasitized *P. operculella* larvae were also observed to pupate more openly or without full cover of frass on the outside of potato tubers compared with healthy pupae. These two intriguing behaviors; the *D. insulare* larvae within the parasitized *P. operculella* larvae and pupating behavior of the parasitized *P. operculella* larvae may have some biological

significance to control pests especially with the help of advanced biotechnology knowledge.

European corn borer, *O. nubilalis*. In the field, I did not find Lepidoptera larvae or pupae other than *O. nubilalis*. In the laboratory, no parasitism occurred on *O. nubilalis* larvae. *D. insulare* females did not approach the European corn borer larvae even with the frass around. This was not surprised me because the significant reduction in percent parasitism of the diamondback moth was reduced with distance from the edge of a corn field indicating that corn does not harbor alternate host of *D. insulare* (Chapter 4).

Although *D. insulare* parasitizes *H. undalis* (Carlson 1979), my results indicate that this parasitoid parasitizes only certain pyralid(s) that feeds on certain plants. Another species of pyralid, *H. rogatalis* (Hulst), that feeds on Portulacaceae and Amaranthaceae with Brassicaceae as its main food plant (Heppner 1987), may act an alternate host of *D. insulare*. However, *H. undalis* and *H. rogatalis* are not reported to occur in Michigan. There were no pyralids found from cultivated or wild Brassicaceae in my study. Searching for pyralids on Portulacaceae and Amaranthaceae plants should be initiated.

Tortricids of apple orchard. No *D. insulare* emerged from five different types of tortricid pupae collected in the field or exposed for parasitism in the laboratory. There were only one first and two second instars of *Grapholita molesta* (Busck), the oriental fruit moth, collected from apple fruit that I put in the rearing pan. A total of 60 of the six tortricid larvae, all in third or later instar, were collected from the apple leaves, shoots and fruits in the field (Table 4). None of these tortricids were parasitized by *D. insulare*.

My results and other studies (N. J. Mills, University of California Berkeley, personal communication) confirmed that codling moth, *Cydia pomonella* (L.), is not an alternate host of *D. insulare*. Three other *Diadegma* (= *Horogenous*) species are reported to parasitize *G. molesta* but they are not important parasitoids (Allen 1962). However, *P. xylostella* larvae placed in an apple orchard for 28 h were parasitized by *D. insulare* (Chapter 5). Therefore, there is a possibility that *D. insulare* use tortricids, like *G. molesta*

Table 4. Tortricids of apple orchard exposed for parasitism by *Diadegma insulare* (Cresson)

Scientific names	Common name
Cydia pomonella (L.)	Codling moth
Grapholita molesta (Busck)	Oriental fruit moth
Archips argyrospila (Walker)	Fruittree leafroller
Choristoneura rosaceana (Harris)	Oliquebanded leafroller
Platynota idaeusalis (Walker)	Tufted apple budmoth
Platynota flavedana (Walker)	Variegated leafroller

and *Platynota idaeusalis* (Walker), as alternate hosts to overwinter (Beddingger et al. 1994). However, I had only three small larvae (in nature, this is the only possible stages that are expose to parasitism by *Diadegma* spp.) of *G. molesta* and used laboratory-reared *D. insulare*. This study should be repeated by using more *G. molesta* small larvae which may need special laboratory rearing and expose them to field collected *D. insulare*.

Closely related species to *D. insulare*, *D. fenestrales* (also parasitizes *P. xylostella* larvae, Hardy 1938, Fitton & Walker 1992) and *Diadegma interruptum pterophorae* (Ahmead) parasitize tortricids of apple in Oregon and in Alaska, respectively (Carlson 1979). In Michigan, there are 47 species of microlepidoptera in apple orchards, and of these, 27 species are tortricids (Strickler & Whalon 1985). High numbers of tortricids in apple orchards increases the possibility that at least one of them could be an alternate host of *D. insulare*. However, further research is needed, including exposing as many small larvae of tortricids as possible to *D. insulare*, in the laboratory. In the field, collection of the tortricid larvae in the early spring and at the end of the summer may increase the possibility to get overwintered parasitized tortricid larvae.

Angoumois grain moth, *S. cerealella*. There were only two *D. insulare* males produced from >1000 first instar *S. cerealella* exposed for parasitism. The *D. insulare* adults emerged 6-9 d earlier than the *S. cerealella* adults. The developmental time for unparasitized larvae of *S. cerealella* is between 20 and 24 d (Metcalf & Metcalf 1951). This suggests that *D. insulare* larvae could alter host larval physiology to suit its life cycle or larval development.

In Egypt, *D. semiclausum* is reported to emerged from *S. cerealella* infesting stored grains (Ahmad Musa, personal communication). However, there was no *S. cereallella* collected from stored grain in a Michigan study (Russell 1980), indicating it is not common in Michigan. In the field, I did not get this moth form wheat or corn, but ichneumonid (probably *Diadegma* sp.) searching for hosts on the wheat head were observed.

Mimosa webworm, *H. aniscocentra*. I was able to get only three larvae (one third and two fourth instars) of *H. aniscocentra* from *G. triacanthos* trees sampled in May 1994. They were found from the flowers. I failed to find them from June onward. However, none of the three larvae were parasitized by *D. insulare*. I also found four pupae within webbed leaves. No *D. insulare* adults emerged from these pupae. However, *Diadegma* spp. are reported as the primary parasitoids of *H. aniscocentra* (Peacock , see Miller et al. 1987). This moth is probably not an important alternate host of *D. insulare*. A combination of increased parasitism from other parasitoids, heavy rains, and cold winter is perhaps reduce the local *H. aniscocentra* populations nearly to zero (E. R. Hart. , Entomology Department, Iowa State University, personal communication). This also explains why I was unable to collect enough larvae for my study.

Other pluttelids, feeding on non-brassicaceous plants that occur in Michigan are *Plutella armoraciae* Busck (Museum of Department Entomology, Michigan State University) and *Ypsolopha dentiferella* (F.)(Profant 1991). These are unlikely hosts for overwintering *D. insulare* adults in Michigan because their host plants are very rare. Plutellid close relatives, yponomeutids, have three species reported in Michigan (Profant

1991). *D. insulare* may also use them as alternate hosts, but further study is needed. In the Netherlands, Dijkerman (1990) reported that *Diadegma armillata* (Gravenhorst) parasitizes six species of Yponomeutidae.

Results of my preliminary search indicate that none of the Lepidoptera collected are the alternate hosts of *D. insulare*. Although *P. operculella* and *S. cerealella* cannot overwinter in Michigan and probably in other northern states of the United States and Canada, to my best knowledge, this is the first report that *D. insulare* parasitizes these two gelechiids. Therefore, I added two more species to the current list of Lepidoptera that can be the alternate hosts of *D. insulare* (Carlson 1979).

My results and from previous records (Carlson 1979) indicate that *D. insulare* is not a true specialist parasitoid. Besides diamondback moth as its major host (Harcourt 1986), *D. insulare* may have many alternate hosts other than plutellids. This would be facilitated by the ability of the *D. insulare* larvae to influence the physiological development of its host larva either by delaying or speeding up the parasitized host larvae entering prepupa stages when *D. insulare* comes out and pupates outside the host. Although delaying the host development is a common phenomenon for the endoparasites, forcing the host to pupate one to two weeks earlier is unusual. *D. insulare*'s influence on parasitized larvae to pupate more openly (*P. porrectella* and *P. operculella*) is also interesting. The second argument is that most plutellids may have evolved some kind of defensive mechanism, due to long association between the two insects, such as behavior to avoid an attack from *D. insulare* or an immune system to succumb the parasitoid eggs. *P. porrectella* has some type of defensive mechanism against *D. insulare* parasitism. Differential ability to encapsulate eggs of *Diadegma* spp. by *P. xylostella* are reported in Australia and England (Goodwin 1979, Fitton & Walker 1992, Hardy 1938). Another example is reported by Dijkerman (1990) where six species of Yponomeutidae, a close related family of Plutellidae, have differential ability to encapsulate the eggs of theirs parasitoid, *D. armillata*. He speculated that species showing high encapsulation rates are

those that have diverged early in the evolution of the genus, whereas the more recently evolved species showed an intermediate percentage or were not able to encapsulate eggs of their parasitoids. Therefore, *P. xylostella* and *D. insulare* may have become associated quite recently.

P. xylostella larvae are easily accessible for parasitism by *D. insulare*. In contrast, the potential of other insect's larva to become an alternate host is depend on their length of exposure for possible parasitism by *D. insulare*. This is because many Lepidoptera larvae are concealed or protected from the reach of a parasitoid like *D. insulare*. For example, the length of exposure for parasitism of *S. cerealella* and *P. operculella* is about 1 d after hatch. *P. opercullella* may also be exposed sometime during latter larval stages.

In Michigan and other northern states of the United States and Canada, the question of what insect species act as the alternate hosts of *D. insulare* is still widely open. However, I suggest that a search for *D. insulare*'s alternate hosts should be concentrated on the three microlepidopteran families; Pyralidae, Gelechiidae and Tortricidae. Thorough search of microlepidopterans associated with *Brassica* plants might also increase the chances to find the alternate hosts of *D. insulare*. Some ichneumonid parasitoids of apple tortricids parasitize unrelated Lepidoptera in the same orchard, if its primary hosts are less abundant (Brunner et al. 1981). The microlepidopterans, especially the pyralids, gelechiids and tortricids, on crops or plants other than Brassicaceae should be collected as many as possible or tested for parasitism in the laboratory. Laboratory rearing of the insects collected could really help the process of host searching but it may be laborious. Dissecting adult females late in the season to examine the condition of the ovarioles and fat body should also be conducted. If the abdomen of the females is full of active ovarioles, with mature eggs present, and the condition of fat body is normal then the parasitoid most probably overwinters as larvae within the host larvae (N. J. Mills, personal communication).

CONCLUSIONS

Result of this study could narrow down the areas, plants or habitats as well as the insect family to be searched for *D. insulare* alternate hosts in the future study. Identification of an alternate host will speed up the integration of factors responsible for *D. insulare* overwintering population into the total diamondback management program. For example, we could intercrop the host food plant of *D. insulare* 's alternate host within *Brassica* crop agroecosystem. This could increase the parasitism efficiency of *D. insulare* because it does not need to do much travel and spend longer time to find its alternate host.

I still believe that an alternate host or hosts are responsibles for *D. insulare* abundance and high parasitism of diamondback moth larvae in many different habitats, in spite of low diamondback moth populations. Identification of the alternate hosts would provide objectives for design of pest management system for increased level and stability of parasitism.

OVERALL CONCLUSIONS

OVERALL CONCLUSIONS

At least four developing countries; Malaysia, Indonesia, Taiwan and Guatemala, report success of controlling diamondback moth using parasitoids in their *Brassica* growing areas (Idris et al. 1995). The evolution and implementation of a biological control-integrated pest management (BC-IPM) system for *Brassica* crop, a 24 year case history, was discussed by Biever et al. (1994). In Guatemala, Biever et al. (1994) report the success of a biological control-integrated pest management program (BC-IPM) to manage lepidopteran insect pests using biological control agents (*Bacillus thuringiansis* var. *Kurstaki*), pest population monitoring, and early-season inoculative releases of beneficial agents; these have replaced the routine application of chemical insecticides to control diamondback moth and other brassicas crop pests. In this BC-IPM system *D. insulare* and *C. plutellae* are used as diamondback moth's parasitoids. They did not mention which of these two parasitoids gives more impact on the diamondback moth population. In Caribbean islands, parasitism of diamondback moth larvae by *D. insulare* is higher than by *C. plutellae* (Alam 1992) and the impact of *D. insulare* could be increased by knowing some of its ecological needs and behavior or activity in the field.

Results of my studies indicate that wildflowers; *B. kaber* and *B. vulgaris* (Brassicaceae) and *D. carota* (Umbelliferae), supply nectar that results in high *D. insulare* longevity and fecundity (Chapter 1). The increase in longevity and fecundity was strongly correlate with flower corolla opening diameters but not with corolla length. However, the width of corolla opening only explained 45% of the observed variation among wildflowers as food sources. The separation among the petals, and between sepals and petals increases the nectar accessibility for *D. insulare* on flowers that have narrow corolla openings.

Nectar quality is also probably important (Baker & Baker 1983, Kidd & Jervis 1989) but I did not measure it. High numbers of *D. insulare* caught in weedy areas and at woodland edge with > 50% *D. carota* (Chapter 5) indicate that *D. carota* has high quality nectar that attracts the parasitoid. *D. insulare*'s nectar collecting behaviors including chewing at the base of the corolla to access nectar (first recorded here)(Chapter 2) could be another cause of the variation in the relation between corolla width and *D. insulare* longevity.

Food source availability determines the impact of natural enemies or failure of insect biocontrol programs (Kidd & Jervis 1989). The role of wildflowers in the vicinity of crop field in reducing insect pests has been demonstrated (Leuis 1960, National Academy of Science 1969, Van Emdan 1963a & b). In southern Ontario, Canada, *B. vulgaris* and other wild Brassicaceae are abundant around the field in early spring (Harcourt 1986). *B. kaber* and *D. carota* also are abundant in Michigan and the northern states of United States (Buchholtz et al. 1981). As I have discussed above, *B. kaber*, *B. vulgaris* and *D. carota*, increased longevity and fecundity, and this may explain why *D. insulare* is abundant (Harcourt 1986, Chapter 4) and percent parasitism is always high in the field (Chapters 4 & 6). However, the current trend of farming systems, eliminating or causing these weeds to be sparsely distributed away from the field, disrupts the host foraging process of natural enemies, especially the specialist parasitoids (Wäckers et al. 1994), Although some parasitoids, such as *D. insulare* are very mobile in heterogeneous habitats (Chapter 5), their parasitism efficiency may be severely affected. When food or wildflowers are available in the vicinity of the host, this disruption would be minimized and parasitism efficiency increased (Wäckers & Swaans 1993, Wäckers et al. 1994). Therefore, field release of *D. insulare* may not be needed. This overcomes the problem of mass-rearing of *D. insulare* for use in field release programs (Adam 1994).

B. kaber can be planted in patches or rows within or near to cabbage fields. In India, the Indian mustard, *B. juncea* (L.) Czern., planted in one row per 15 rows of cabbage was found to be the most promising for successful management of diamondback

moth and the leafwebber, *Crocidolomia binotalis* Zeller (Lepidoptera: Pyralidae)(Srinivasan & Krishna Moorthy 1991). In U. S, however, *B. kaber* is considered as a troublesome weed (Buchholtz et al. 1981). In addition, reduction in crop related or unrelated weeds has been especially recommended as a pest control strategy earlier and has been adopted by many growers (van Emden & Williams 1973). These contradictory recommendations might confuse the farmers and make them wary in allowing weeds to be present around the field even though this may only involve maintaining weed populations in the headlands or hedgerows. Besides acting as food source for *D. insulare*, *B. kaber* also provides a refuge for insecticide-susceptible diamondback moth, has no adverse effect on the *D. insulare* sex ratio, could reduce the numbers of eggs laid and slow down insecticide-resistant build up by diamondback moth. Reports from other studies also partly support my argument. Thomas et al. (1992) reported that creating of "island" habitats, (e.g., planting *B. kaber* in patches within the *Brassica* field), in farmland can manipulate populations of beneficial arthropods, increasing predator densities and species composition which increases the stability and enhances biocontrol within the agro-ecosystem. The presence of weeds in a crop can also influence the contrast between the crop plant and its background (Smith 1969). If the pattern can be broken up with weeds then the contrast is reduced and the number of diamondback moth or other pests could also be reduced and at the same time the crop environment made more attractive to the natural enemies. All the above reasons obviously could outweigh the risk that may incur to the growers due to inclusion of *B. kaber* in cabbage ecosystem. However, the question is how to convince the growers? This is where an effective extension method(s) or workers are very important to ensure the success of this approach.

D. carota flower is the only non-brassicaceae weed tested that significantly prolong *D. insulare* life with high fecundity (Chapter 1). Another Umbelliferae, *Aegopodium podagraria* L., a ground-elder is also known to be frequently visited by various parasitoid species (Kevan 1973). A. *podagraria*'s exposed nectaries provide accessible nectar to

nectar feeders with short mouth parts (Leius 1960) like *D. insulare*, although *D. insulare* is also able to reach nectar by chewing at the flower base (Chapter 1). Although longevity and fecundity of *D. insulare* are significantly lower when fed on *D. carota* than on *B. kaber*, there are three advantages of choosing *D. carota* over *B. kaber*. First, it is not an alternate host plant for diamondback moth and grows in non-cultivated fields (Buchholtz et al. 1981). Second, *D. carota* is more easily controlled in a *Brassica* crops with herbicides or cultivation than the other Brassicaceae weeds. Third, it is an Umbelliferae, therefore, it will not pose any cross-fertilization risk with the *Brassica* crops as does *B. kaber* or other non-crop Brassicaceae. Cross-fertilization will hamper the seed production industry like canola seed. If the *Brassica* crops planted are a herbicide-resistant variety then the gene for resistant could be passed to the non-crop *Brassica* like *B. kaber*. The consequences of the wild beet populations for breeding, seed production and release of herbicide-resistant transgenic sugar beets was discussed by Boudry et al. (1993). Therefore, *D. carota* or other weeds that have similar characters should also be considered in designing *Brassica* crop ecosystem. Since *D. carota* is a biennial (first year, producing rosette of finely divided leaves and fleshy taproot weed and second year, bloom and dies) it needs to be planted one year ahead of *Brassica* crop planting. Subsequent planting may not be necessary because in the field it produces a lot of seeds.

Although I was not able to record parasitism of diamondback moth larvae by *D. insulare* when *B. vulgaris* was used as host food source (Chapter 6), results of my study and a report by Idris & Grafius (1994) indicate that *B. vulgaris* has potential to be used in insecticide resistant management. Methods of planting and manipulation of this weed were discussed in Chapter 6.

Honeydew of bean aphids, *A. fabea*, on *C. album* increased longevity and fecundity of *D. insulare* when compared with parasitoids that were not given any food or just water (Chapter 1). Although honeydew is rich in the amino acid, tryptophan (Hagen & Tassan 1972), it may not be as important food source for *D. insulare* as floral nectar

because it lacks food finding cues. Wäckers et al. (1994) reported that *Cotesia rebecula* L. (Hymenoptera: Ichneumonidae), a parasitoid of imported cabbageworm, *Pieris rapae* (Lepidoptera: Pieridae) neither responds to honeydew nor to volatiles of aphid infested leaves; they concluded that finding honeydew is a random process. However, leaving weeds or plants that can provide aphid honeydew outside the field could provide an extra food source for *D. insulare*. The spraying of L-tryptophan solution in olive orchards increases the numbers of the green lacewing *Chrysoperla carnea* L. in this tree canopy (McEwen et al. 1994).

Pesticides continue as important tools to combat pests. However, in integrated pest management it is generally accepted that only selective pesticides should be used and only if there are no other effective control methods available. Pesticide applications should also be based on economic threshold levels (ETL) that vary with pest, location and marketability of the cabbage (Shelton et al. 1982, Dornan et al. 1994, Stewart & Sear 1988). The impact of *D. insulare* on diamondback moth population would be severely reduced with the wrong timing of pesticide spraying. Idris & Grafius (1993a) found that all pesticides except *Bacillus thuringiensis* Berliner var. *Kursatki* were highly toxic to *D. insulare*. My results suggest that pesticides should not be applied between 1100 and 1300 h (Chapter 3) when *D. insulare* populations are most actively foraging. Effectiveness of pesticides may be reduced if sprayed early in the morning because leaves are wet with dew that dilutes the spray droplets. Therefore, the more appropriate time for spraying is in the late afternoon or evening. This practice could avoid killing of *D. insulare* as a result of direct impact of the pesticide sprayed, particularly if there are no refuges outside the field as discussed in Chapter 1. If *B. thuringeinsis* is used, its effectiveness could be optimized because the exposure time of the toxin to ultra violet (UV) light would be shortened. However, the time range when the parasitoid population is abundant in the field may vary with day and location (region) of the *B. thuringiensis* fields, and for different parasitoid species. This prediction needs further research because diurnal foraging activity of *D.*

insulare, especially the females, is also significantly influenced by weather factors (light, temperature and wind speed)(Chapter 3).

Percent parasitism of diamondback moth larvae is significantly affected by habitats (Chapter 5). Differential characteristics of the habitats (crops) used and the presence of food sources in the vicinity of the crop may be the most important factors influencing the parasitism rate. Host searching efficiency by specialist parasitoids, like *D. insulare* may be more reduced in certain habitats (Sheehan 1986), and in most cases efficiency is affected by the types of crop planted (Booij & Noorlander 1992). I did not directly measure the host searching efficiency of *D. insulare*. However, percent parasitism in the crop habitats studied is consistently high (55 to > 80%) indicating searching efficiency of *D. insulare* may not be severely affected. Similar results were observed at the woodland edge and in weedy areas with > 50% *D. carota* (Chapter 5). The high mobility of *D. insulare* in heterogeneous habitats indicates that *D. insulare* has a narrow host ranges per habitat or actively searching for food sources. Parasitism occurred on two gelechiids, *P. operculella* and *S. cerealella* in my research, although they cannot survive winter or are not common in Michigan, indicating that *D. insulare* is perhaps able to use insects other than plutellids as alternate hosts (Chapter 7). This may also explain why this parasitoid is actively mobile in such diverse habitat. Percent parasitism was also not severely affected by *Brassica* varieties or cultivars planted and plant density (= spacing)(Chapter 4). This suggests that plant density and improved cultivars that produce high yield and quality should be emphasized in planning for brassicas crops planting.

The above discussion indicates that *Brassica* crops could be planted in polyculture or intercropping systems without disrupting the impact of *D. insulare* in the field. It could be done as one or the combination of the following suggestions.

1. *Brassica* crop(s) could be interplanted with tomato because tomatoes have no adverse effect on parasitism rate of *D. insulare* (Chapter 5) or *C. plutellae*, (Bach

& Tabashnik 1990) . In addition, tomato plants repel diamondback moth adults and reduce oviposition (Bach & Tabashnik 1990, Burandy & Raros 1975).

2. *Brassica* fields should be designed so that they are surrounded or are very close to corn, bean or alfalfa fields, and apple orchard. Although these crops apparently do not have alternate hosts of *D. insulare*, they could provide refuges for the parasitoid when the *Brassica* crops field is sprayed with pesticide. Corn-soybean intercropping provides shade, reduced wind speed, alternate foods, and higher humidity and lower temperatures for soybean natural enemies (Tonhasca 1993).

3. Planting a few rows of small trees, that simulate a woodland edge, on the west side of the field could be beneficial. Besides providing shelter for *D. insulare* during hot days it also could protect the *B. thuringiensis* toxin, if applied, from the exposure to the intense UV light in the afternoon hours (Beegle et al. 1981). Trees, such as basswood species that provided a very significant food source of nectar for honey bees (Ayers & Batchtell 1995) and probably for *D. insulare*, can be used for the above purposes.

4. Wildflowers should be planted, as suggested above, before we plant *Brassica* crops. It could be a year ahead for *D. carota*, or in the fall for *B. vulgaris* and *B. kaber*. Therefore, parasitoids can be retained or stay longer in or around the field (Hagen et al. 1984), and the impact of *D. insulare* and other natural enemies on diamondback moth could be enhanced. The availability of food sources for the natural enemies in and around the field can overcome the need for mass releases of biocontrol agents (Wäckers & Swaan 1993). Certain wildflowers, such as *B. juncea*, can serve as a trap crop because diamondback moth prefers to oviposit on this weed rather than on the *Brassica* crops (Srinivasan & Krishna Moorthy 1991). Weeds also can act as a point of spore dissemination for insect pathogen because

insects infected with *Entomopthora* spp. usually will climb to top of weed canopy before die (Haynes et al., 1980).

5. Planting selected *Brassica* crops cultivars that reduce diamondback moth oviposition and larval survival (Chapter 6)(Stoner 1990, Eigenbrode & Shelton 1990 & 1992) but still allow parasitism by *D. insulare* (Chapter 6, Lasota & Kok 1986) is also important. In addition, planting of crops or weeds with more extended production of nectar sources close to *Brassica* crop field would increase the retention of *D. insulare* in the field (Wäcker & Swaah 1993). Some species of Scrophulariaceae (figwort family) might be especially useful for extended nectar production (Ayers et al. 1987 & 1991).

Intercropping is probably more easily accepted by farmers in the developing countries because it has been a common cultural practice for them where two or more crops and/or wild plants are grown simultaneously, sometime unintentionally, in the same field (Perrin & Phillips 1978). In more intensive farming, in the developed countries, intercropping seems to be inappropriate because of the difficulties with management and harvesting, particularly where specialized machinery is used. Herbicide use also complicates intercropping. In my opinion the second crop in an intercropping system could be treated as the less important crop and grown purely to attract pests away from the primary crop or to change the environment to promote the activity of natural enemies. In cotton/sesame intercropping using row strips of sesame constituting 5% of the total acreage, both these objectives were achieved (Pair et al. 1982). The sesame was highly attractive to *Heliothis* species from the seedling stage through the senescence and attracted an otherwise obscure parasitoid species, *Campoletis sonorensis*. This species, attracted only in the presence of sesame, parasitized large numbers of *Heliothis* species (Pair et al. 1982).

Although all the above suggestions would enhance the impact of *D. insulare* as an important biocontrol agent in integrated diamondback moth management, I personally think that its impact could be optimized if further study in the following areas are conducted.

1. It is important to identify of the stimuli and mechanism involved in food detection by *D. insulare*. The relative suitability of food sources is not determined only by its availability and quality but also by their detectability. Floral fragrances and visual stimuli determine detectability of floral nectar by *C. rubecula* (Wäckers 1994).

2. We should continue a thorough search for alternate hosts of *D. insulare* (Chapter 7). It is crucial to find alternate host because we can mix the plant(s) that found to act as host plant for *D. insulare*'s alternate hosts in *Brassica* polyculture or intercropping system.

3. Effects of the interaction between different patch sizes with plant density on both diamondback moth population dynamics and parasitism by *D. insulare* are important. Until my research, only the effect of different patch sizes on the diamondback population abundance has been studied (Pimental 1985). There is no study on the effect of either plant density or patch sizes on *D. insulare* population dynamics.

4. Since intercropping seems possible to use in managing diamondback moth population and *D. insulare*, study should also be conducted on the impact of this practice on other diamondback moth natural enemies, especially egg and pupal parasitoids. This is important because *D. insulare* can only kill diamondback moth's larvae. Effects on other pest and beneficial insects should be studied. Zhao et al. (1992) suggested that effects of intercropping with nectar producing plants will be different for different pest and beneficial species.

5. Developing a model, based on the weather information, *D. insulare*'s diurnal foraging activity and pesticide residue activity, to predict the best time for pesticide spraying could also help integrate pesticides and biological control.

Much research remains to be done before an optimal diamondback moth management system can be designed. However, these studies on parasitoid ecology and behavior and parasitoid-diamondback moth-host plant tritropic interactions will increase our ability to effectively use *D. insulare* in a system to manage diamondback moth. Similar studies on other parasitoid-pest-host plant systems could improve management of these pests as well. Only by accepting and studying pest management in a multicrop or regional perspective can we design systems optimal for long term sustainable management.

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APPENDIX

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1995-3

Title of thesis or dissertation (or other research projects):
Ecology and Behavior of Diadegma insulare (Cresson), a Biological Control Agent of Diamondback Moth, Plutella xylostella (L.)

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

None

Investigator's Name (s) (typed)
Idris Bin Abd. Ghani
Department of Entomology
Michigan State University

Date June 30, 1995

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies: Included as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

Voucher Specimen Data

Page 1 of 1 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Plutella xylostella (L.) Diamondback Moth	Plutella xylostella (L.) Host: Broccoli Lab. colony (Geneva strain) June 15, 1994 Idris A. Ghani					5	2		
Diadegma insulare (Cresson)	Diadegma insulare (Cresson) Host: Plutella xylostella (L.) Location: MSU Research Field Idris A. Ghani, July 15, 1994					6	4		

(Use additional sheets if necessary)

Investigator's Name(s) (typed)
Idris Bin Abd. Ghani

Department of Entomology

Michigan State University

Date June 30, 1995

Voucher No. 1995-3

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

5 July 1995

Date

APPENDIX 2

Evidence of Pre-imaginal Overwintering of Diamondback Moth, *Plutella xylostella* (L.)(Plutellidae) in Michigan

Evidence of Pre-imaginal Overwintering of Diamondback moth, *Plutella xylostella* (L.)(Lepidoptera: Plutellidae) in Michigan

ABSTRACT

I investigated the possibility of overwintering diamondback moth, *Plutella xylostella* L., at the Michigan State University Research Field. I inspected 550 to 600 (50-70 of each species every 5 d) early spring season weeds; *Barbarea vulgaris* R. Br., *Thalpsi arvense* L. and *Capsella bursa-pastoris* (L.) Medic, for diamondback moth eggs, larvae and pupae on 10, 15, 20 and 25 May 1993. One diamondback moth third and 24 fourth instars were found but no eggs. On 25 May, however, three first instars were found. In the laboratory, I recorded more first instar from detached weed leaves collected on 20 and 25 May than in direct field inspection. This suggests an oviposition occurred sometime in Mid-May, and egg hatch was delayed or that mortality of early instars was higher in the field than in the laboratory. Four pupae were also collected on 20 and 25 May, indicating they originated from the overwintering late instars of diamondback moth. Plant debris or sod may protect the overwintering larvae because the temperature in the debris is higher than the air temperature. I suggest further research on overwintering site of diamondback moth and *D. insulare* should be conducted although *Diadegma insulare* (Cresson) pupae and parasitized diamondback moth larvae were not found in our investigation.

INTRODUCTION

Diamondback moth, *Plutella xylostella* L., is a major *Brassica* crops pest worldwide. In Michigan, it commonly occurs at relatively low population densities, rarely reaching outbreak levels. This is probably due to the abundance of *Diadegma insulare* (Cresson)(Hymenoptera: Ichneumonidae), a larval parasitoid, that regulates diamondback moth populations. Parasitism rates of 70-100 percent were reported in the US (Biever et al. 1992, Idris & Grafius 1993) and Canada (Harcourt 1986).

Diamondback moth is believed not to overwinter in Canada. For example, in southern Ontario, Smith & Sears (1982) found that no diamondback moth life stages survived winter conditions in the field, or simulated winter conditions in the laboratory. Populations are thought to die out completely each year to be replaced in spring by migrants from the south (Philip and Mengersen 1989). Recent observations indicated that pre-imaginal stages of diamondback moth may successfully overwinter in Alberta, and that volunteer canola plants provided an early larval food source (Dosdall 1994).

In United States, diamondback moth adults apparently overwinter beneath crop debris in Colorado (Marsh 1917) and New York (Harcourt 1957). In upper midwestern States (Michigan, Wisconsin and Minnesota), diamondback moth populations are not thought to overwinter but early infestations often occur near *Brassica* crops debris, indicating that overwintering of adults in protected areas is possible (Mahr et al. 1993).

The objectives of my study were to determine whether diamondback moth overwinters in Michigan, and to identify possible overwintering life stages.

MATERIALS AND METHODS

In early spring 1993, three weed species, *Barbarea vulgaris* R. Br., *Thalspi arvense* L. and *Capsella bursa-pastoris* (L.) Medic were abundant in the previous season broccoli experimental field at the Michigan State University Collins Road Entomology Research Farm and other areas at the Michigan State University Farm. On 10, 15, 20 and 25 May, I selected the above weeds randomly from any patches they grew. The plants were pulled out of the ground and inspected for the presence of diamondback moth larvae or pupae by placing individual weeds on white paper placed on the ground. The number of larvae and pupae found on each weed species were recorded separately. I reared larvae in 25 x 15 x 10 cm covered rearing pans in the laboratory at 25 ± 2°C and photoperiod of 16:8 (L:D) h until pupation, to evaluate parasitism.

To determine the presence of diamondback moth eggs I randomly selected and detached leaves from each plant. Detached leaves (by species) were kept in the laboratory as described above and checked daily for 5 d for egg hatch.

Overwintering of adult diamondback moth was evaluated by setting up five cages (180 x 165 x 165 cm) in and near our experimental field previously planted with broccoliprevious broccoli field in early April 1993. I pulled up broccoli plant residue by hand and put the remains of 50-70 plants in each cage. To catch the emerged diamondback moth adults I hung white sticky trap (Pherocon™ 1C - bottom; Trece Inc., Salinas, CA) on a wood stake. Sticky traps were inspected for diamondback moth adult emergence every other day. I also put five potted broccoli plants in each cage for the emerged adults to lay eggs. The presence of diamondback moth's eggs or larvae on broccoli leaves was checked using a 10x magnifying glass once every 3 d. Traps and the presence of eggs or larvae were monitored until end of May 1993.

The Michigan State University Climatological Resources Center (Dr. Jeff Andresen) provided air and soil temperature data. Degree-days (dd) accumulation above

7.3°C, developmental threshold for diamondback moth (Butts & McEwen 1981), was calculated following Zalom et al. (1983).

RESULTS AND DISCUSSION

I found 24 fourth instar diamondback moths from the three early spring season weeds (Table 1). They were found on the first sample data, 10 May. One late third instar was also found on *B. vulgaris* on 10 May. Most larvae and eggs were found on *B. vulgaris*. There were no eggs collected before 20 May (based on the larvae from detached leaves collected on this date, Table 1). I did not find any diamondback moth first or second instars before 25 May. On 25 May, however, three first instars were recorded from *B. vulgaris*. On the same day we found three pupae from *B. vulgaris* and one from *C. bursa-pastoris*. There were 11 and 23 diamondback moth first instars recorded from the detached leaves collected on 20 and 25 May, respectivey. No *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) or other parasitoids pupae were recorded from weeds inspected in the field or reared from diamondback moth fourth instars. There were no diamondback moth adults caught by the sticky traps in the field cages. I did not find diamondback moth eggs or larvae on leaves of potted broccoli pots placed inside the cages.

The average daily maximum air temperature and soil temperature above sod or debris surface was relatively similar (Fig. 1 A & B). However, the minimum temperature above debris was warmer than the air temperature. In December 1992, and from January to March 1993, the air and soil temperature were much lower than 7.3°C, but the numbers of days below freezing were higher (28 > 20 d) than in the other months of both years (Fig. 1 A to C). In February 1993, when average temperature was the lowest, it snowed for 17 d (Fig. 1 C), causing accumulation of snow above the ground. The total degree-days (dd) above 7.3°C was 45.8 dd from December 1992 to January through March 1993,

Table 1. Diamondback moth larvae or pupae or first instar counted from weeds and detached weed leaves

Weed species	Dates	Diamondback Moth					
		Larvae[a]				Pupae[b]	First instar from detached leaves[c]
		1st	2nd	3rd	4th		
Barbarea vulgaris R. Br.	10 May	0	0	1	2	0	0
	15 May	0	0	0	3	0	0
	20 May	0	0	0	6	1	11
	25 May	3	0	0	4	2	23
Thalspi arvense L.	10 May	0	0	0	1	0	0
	15 May	0	0	0	0	0	0
	20 May	0	0	0	1	0	3
	25 May	0	0	0	2	0	6
Capsella bursa-pastoris (L.) Medic	10 May	0	0	0	0	0	0
	15 May	0	0	0	1	0	0
	20 May	0	0	0	0	0	2
	25 May	0	0	0	1	1	8
	Total	**3**	**0**	**0**	**24**	**4**	**53**

[a] No parasitoid pupae formed from field collected larvae that were reared in laboratory
[b] No parasitoid pupae were found

[c] First diamondback moth instar originated from eggs laid on weed leaves that were detached and brought to laboratory on the stated date

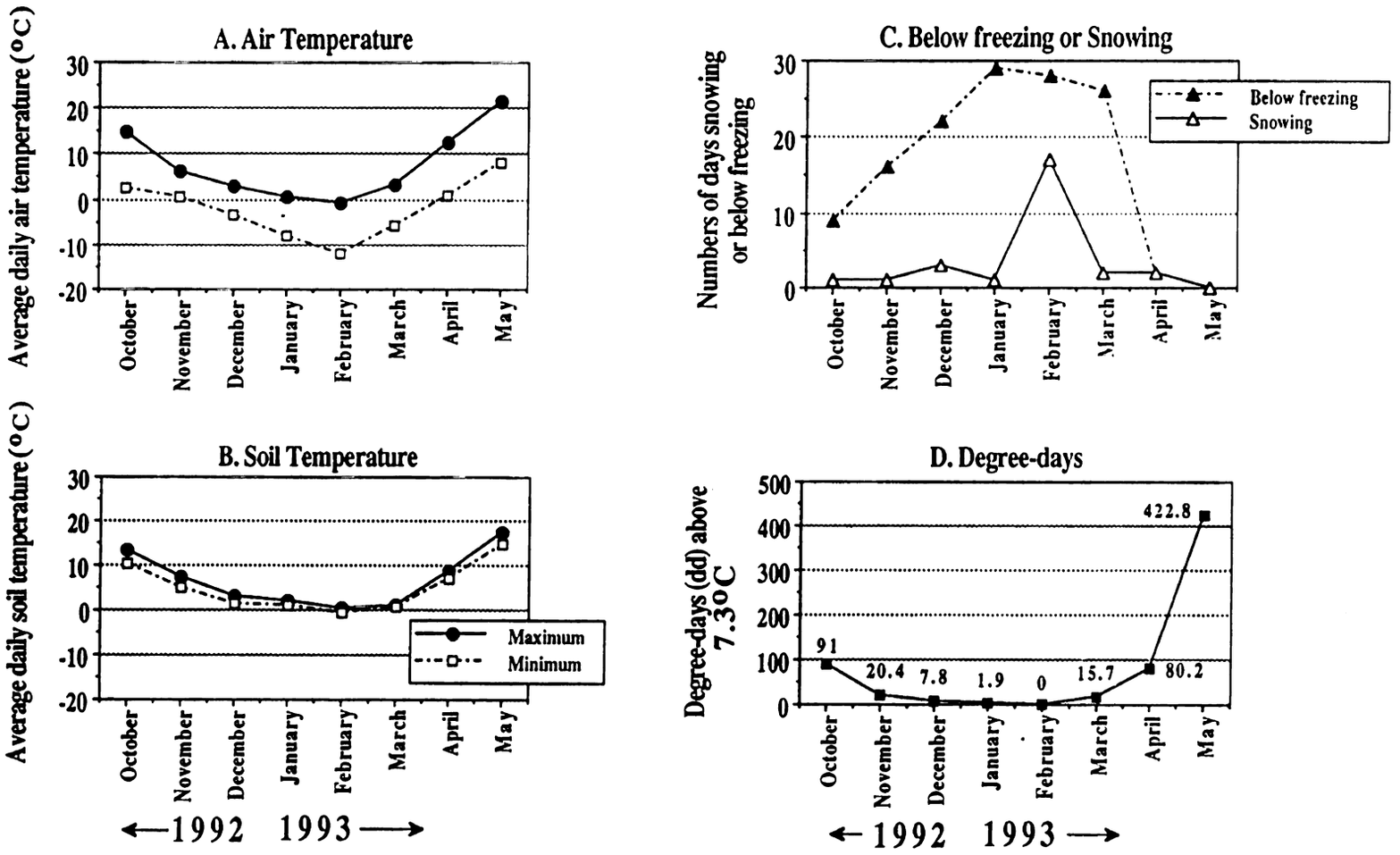

Figure 1. Average daily air (A) and soil (above debris or sod surface)(B) temperature, numbers of days snowing or below freezing (C) and the degree-days accumulation (D) for October to December, 1992 and January to May, 1993 (Michigan State University Horticulture Farm, 1.5 km southeast of Collins Road Entomology Farm).

but it was 217 dd from October through December 1992 to January through April 1993 (Fig. 1 D).

The above results clearly indicate overwintering of DBM larvae is occuring in Michigan. Overwintering is supported by the fact that first, there were no eggs or first and second (early) instars found until long after the third or fourth (late) instars (Table 1). The diamondback moth late instars are reported to have very low super cooling points (-14.3°C), suggesting that some of them can tolerate below sub-freezing temperature (Hayakawa et al. 1988). Higher temperature in or below the debris than above the debris surface and higher accumulation of snow in February than in the other months (Fig. 1C) were also likely protecting the diamondback moth larvae. Diamondback moth larvae may have begun to enter diapause in November 1992 when weeds were dead (no food available), and the minimum and maximum air temperature were less than 7.3°C (Fig. 1 A). The successful overwintering larvae may have continued development in late April 1993, when early season weeds flourished (food became abundance) and temperature was moderate (Fig. 1 A).

Secondly, the developmental period of diamondback moth larvae from hatch to the third or fourth instars found in this study required 110 or 170 dd above 7.3°C (Butts & McEwen 1981). Butts & McEwen (1981) reported that the second, third and fourth instars required 70, 60 or 40 dd to become third, fourth or pupae respectively. In England, Hardy (1938) reported that developmental period of the diamondback moth larvae (from hatch to pupation) was over two months at 10°C. At above 7.3°C, the degree-days accumulated in late April was 80.2 dd and in May was 422.8 dd (°C)(Fig. 1 D). Degree-day accumulation required by diamondback moth to complete one generation is 293 dd (°C)(Butts & McEwen 1981). According to these heat unit accumulation we would expect diamondback moth first and second instars to overwinter successfully. In the laboratory, however, I observed these two larval stages survived for only a week when placed in empty 15.0 cm diam Petri dishes and kept at 4°C, while the third and fourth instars survived over two

months (unpublished data). This suggests that the diamondback moth third and fourth instars were the one that successfully overwintering. At the time of sampling, overwintered third or fourth instars should have been in the fourth or pupated. However, I found only four pupae on 20 and 25 May, perhaps due to predation. The development of diamondback moth third and fourth instars may be prolonged because the weed leaves or flower buds are not the best food for this insect (personal observation). Otherwise these late instars should have been pupating at the time of sampling (based on the accumulated degree-days, Fig. 1 D and Butts & McEwen 1981).

Thirdly, diamondback moth pupae may overwinter within or under the debris. They can also tolerate super-cooling down to -19.2°C (Hayakawa et al. 1988). However, at above 7.3°C, the development from pupae to adult would require 100 dd (Butts & McEwen 1981). Mortality of an egg is 100% at below 10°C (Hardy 1938)(the maximum air temperature between mid-October 1992 to week three of April 1993 was lower than 10°C, Fig. 1 A) or if exposed to chilling temperature for 60 d (Honda 1992). This suggests that our field collected larvae did not originate from adults emerged from any overwintering diamondback moth's pupae.

Fourth, in my field cage study, there were no diamondback moth eggs observed or adults caught even though they were monitored until the end of May. This suggests that adult moths did not overwinter in Michigan. Similarly, in Alberta, Canada, diamondback moth adults were first caught by the emergence traps on 26 May, indicating adults may originate from the successful overwintering larvae (Dosdall 1994).

Fifth, in southern Ontario, Canada, where temperature is similar to Mid-Michigan area, diamondback moth adults arrive from the southern United States around mid-May (Harcourt 1986). This tends to agree with my result that showed there were considerable numbers of first instars recorded from the detached leaves collected on the 20 and 25 May, suggesting an oviposition began in Mid-May, 1993 (Table 1). If oviposition occurred, the developmental time from egg hatch to third or fourth instars would require 23 d at 20°C

(Salinas 1986). Therefore, it is impossible that larvae collected in this study were the offspring of these migrants.

Six, the average daily maximum air temperature was lower then 7°C in March 1993 (Fig. 1 A), and no oviposition observed at this temperature (Hardy 1938). Oviposition by the successful overwintered diamondback moth adults could occur in late April when the average daily maximum air temperature was at 12°C, but it would require 13 d for egg to hatch (Hardy 1938). If this happened then the diamondback moth first instars should have been in the field and collected on 10 May (my first sampling date). On this date, however, only third and fourth instars were found (Table 1). Therefore, if any diamondback moth adults successfully pass the winter they could not be the source for the larvae that I collected.

D. insulare females may not be that active in late fall especially in October or November. Therefore, less diamondback moth larvae were parasitized and of these only few or none survive the winter (none in my collection). I did observe *D. insulare* adults foraging for host on 25 May. They may have originated from overwintering cocoons since *D. insulare* is apparently not as good a migrant as diamondback moth adults (Putnam 1978).

CONCLUSIONS

This is the first evidence of pre-imaginal diamondback moth successfully overwintering in Michigan and other states in the northern U.S. However, the numbers of successful overwintering individuals may be significantly reduced in colder winters.

This result indicates the importance of proper treatment on the previous *Brassica* crops field for managing diamondback moth. Tilling of field before planting is a common practice that may indirectly destroy overwintering diamondback moth, *D. insulare* pupae or parasitized larvae although no *D. insulare* pupae or parasitized larvae were found in this

study. Further research on overwintering sites for diamondback moth and *D. insulare* should conducted. For example, by carrying out several tillages or other practices on the previous field that may reduce diamondback moth but increase *D. insulare* survival.

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