Contributions to the biology of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), and its larval parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae)

by

Sadia Munir

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Plant Science

Department of Agricultural, Food and Nutritional Science
University of Alberta

Abstract

The diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) is a destructive, and widely distributed species occurring universally wherever Brassicaceae are grown. *Plutella xylostella* was first reported in western Canada in 1885 and now causes extensive crop yield losses, depending on the year, throughout the Canadian prairies. Biological control through its major larval endoparasitoid, *Diadegma insulare* (Hymenoptera: Ichneumonidae), has been an important management strategy in North America. In western Canada, the parasitoid is responsible for a greater degree of parasitism than other native parasitoid species, providing an opportunity for integration of biological control with other management strategies of *Plutella xylostella*. My investigation focused on in-depth understanding of the parasitoid's ecology, bitrophic and tritrophic interactions among the host plant species, *P. xylostella* and *D. insulare*. My studies on oviposition preferences and developmental performance of *P. xylostella* and *D. insulare* on host plants with water deficit stress indicated that although *P. xylostella* females preferred to deposit eggs on vigorous plants, not those under water stress, their preimaginal development on non-stressed plants was similar to that on stressed plants. However, water stress had a strong effect on developmental parameters of *D. insulare.*

My studies on the development of *D. insulare* at various constant temperature regimes indicated that most of the fitness parameters and the rate of parasitism by *D. insulare* increased with a decrease in temperature. Investigations on selective floral plant species and their impact on the life-history traits of *P. xylostella* and *D. insulare* showed that none of the floral plant species were favored by the pest or parasitoid. However, floral species had a contrasting effect on various life-history traits of a pest-parasitoid system.

A four-year field survey of *P. xylostella* and its associated parasitoid fauna in southern Alberta, Canada, indicated the dominance of larval parasitoids, particularly *D. insulare,* in most years.

Preface

This thesis is submitted for the degree of Doctor of Philosophy at the University of Alberta. All of the work presented herein was conducted under the supervision of professor Dr. Lloyd Dosdall in the Department of Agricultural, Food and Nutritional Science, University of Alberta, between September 2010 and June 2014.

This research is to the best of my knowledge original and independent work, except where references and acknowledgments are made to previous work. A version of Chapters 1, 2, 3 and 5 have been published. Dr. Lloyd Dosdall was involved at the early stages of concept formation for all the projects. He assisted with the data collection for the project in Chapter 6 and contributed to manuscript edits of Chapter 2 and 3. Dr. John O'Donovan contributed to thesis manuscript revisions at an early stage and provided guidance in data analysis for the project describes in Chapter 3. Dr. Dean Spaner was involved in thesis manuscript composition and revisions at the early stages. Dr. Andrew Keddie contributed to final manuscript revisions and edits.

Acknowledgments

First and foremost, all the praises, appreciation and thanks to Almighty Allah, the most compassionate and the giver of bountiful blessings.

I would like to extend my sincere gratitude to my supervisor, late Dr. Lloyd Dosdall for providing me the opportunity to work in his laboratory under his esteemed guidance and supervision. I appreciate all his contributions of time, ideas, expert advice, constructive criticism, invaluable mentorship, encouragement, support and funding to make my Ph.D. experience productive and stimulating and for widening my horizons. The joy and enthusiasm he had for this research were contagious and motivational for me, even during tough times in the Ph.D. pursuit. I would like to thank Dr. John O'Donovan for his gentle and valuable supervision when I needed it the most. I will always admire his support, encouragement and invaluable guidance.

I would like to thank Dr. Andrew Keddie and Dr. Dean Spaner for being a part of my supervisory committee and for their helpful comments, expert advice and willingness to help. I warmly thank Dr. Stephen Strelkov, Dr. Vera Mazurak and Dr. Dean Spaner for their support that led me to successful completion of this program.

I am grateful to Dosdall's lab group Swaroop Kher, Ravindran Subarmanian and Sharavari Kulkarni, with whom I had the opportunity to work with. The group has been a source of friendships as well as good advice and collaboration. I am also thankful to all the summer students in the Dosdall lab for their help and assistance.

I gratefully acknowledge the funding sources, Canola Council of Canada, the Alberta Canola Producers Commission, Agriculture and Agri-Food Canada and the Natural Sciences and Engineering Research Council of Canada that made my Ph.D. work possible.

I would like to thank my family especially my parents for all their love, encouragement and prayers. I am grateful to my husband, Muhammad Jakir Hasan, for his understanding and support. Lastly, I would like to express my gratitude to everyone who contributed to the successful completion of my doctoral degree program.

I would like to dedicate this work to Dr. Lloyd Dosdall

Table of Contents

List of Tables

List of Figures

List of Abbreviations and symbols

d	day(s)
h	hour(s)
L:D	light to dark ratio
r.h	relative humidity
m	meter
cm	centimeter
mm	millimeter
mg	milligram
C°	degrees Celsius
ha	hectare

Chapter 1: General Introduction

A version of this chapter has been published:
Munir S, Dosdall LM, O'Donovan. 2015. Evolutionary Ecology of Diamondback Moth, *Plutella xylost*ella (L.) and *Diadegma insulare* (Cresson) in North America: A Review. Annual Research and Review in Biology 5(3): 189-206.

1.1 The pest - *Plutella xylostella*

The diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) is believed to be the most widely distributed species of Lepidoptera, occurring universally wherever Brassicaceae are grown (Talekar & Shelton 1993; Sarfraz et al. 2005a). The largest number of species (nine species) of the genus *Plutella* (Sch.) has been recorded in the USA. Seven species are known in South America while only two species have been recorded in Europe (Kfir 1998). Six species of the genus *Plutella* are economically important worldwide. Most have limited distribution including *Plutella porrectella* (L.) in Ontario, Canada, *P. annulatella* (Curt.) in Finland, *P. antiphona* (Mey.) in New Zealand, *P. balanopis* (Mey.) in Southern Africa, *P. armoraclae* (Bus.) in Colorado, USA (Kfir 1998). In contrast, *P. xylostella* is found throughout much of the world wherever host plants are cultivated.

The geographical origin of *P. xylostella* is uncertain. It is generally believed to have originated in the Mediterranean region (Harcourt 1954). However, Kfir (1998) speculated that *P. xylostella* might have originated in South Africa due to the richness and diversity of its parasitoids (14 species) and host plant species (a total of 175 species of which 32 are exotic). The coevolution of *P. xylostella* and its host plants most probably began in these regions 54 to 90 million years ago (Kfir 1998).

North American populations of *P. xylostella* are most probably of European origin and were likely introduced about 150 years ago (Hardy 1938). *Plutella xylostella* was first reported in

western Canada in 1885 (Harcourt 1962), and now occurs almost annually throughout the Canadian prairies wherever its host plants are cultivated (Anonymous 1996; Dosdall et al. 2004b, 2011). In both eastern and western Canada, *P. xylostella* originates primarily from an annual adult population migration from southerly regions. Alberta and Saskatchewan populations of *P. xylostella* are usually seasonal. The Saskatchewan population originates from Texas, whereas the origin of the Alberta population has not been identified. The moth is a weak flyer, usually fly within 2m of the ground. However, moths are carried by the wind and travel up to 1500 km, and densities vary considerably from year to year (Smith & Sears 1982; Dosdall et al. 2004b; Hopkinson & Soroka 2010). *Plutella xylostella* has been reported to survive under mild winter conditions in western Canada (Dosdall 1994), but successful overwintering is considered a rare phenomenon (Dosdall et al. 2008).

1.1.2 Host plants and their importance

Plutella xylostella is an oligophagous pest that feeds exclusively on brassicaceous crops (Talekar & Shelton 1993). Brassicaceae represents one of the oldest and most widely distributed plant groups; it comprises 338 genera and 3,709 species (Prakash 1980; Warwick et al. 2006) providing a great diversity of food products from its 39 species worldwide (Warwick et al. 2006; Dixon 2006). Archaeological evidence indicates that Brassicaceae was important to human societies as long ago as 5000 BCE (Yan 1990). For centuries Brassicaceae crops have been a major source of food (e.g., broccoli, cauliflower, brussel sprouts, cabbage, collard) and condiments (e.g., mustard) for humans and fodder (e.g., turnip) for domesticated animals. The *Brassica* oilseed crop (also known as rapeseed) has been cultivated in Europe as a source of lamp oil since the Middle Ages (Raymer 2002) and as a lubricant for steam engines till World War II (Downey 1990). In North America, early voyagers introduced brassicaceous crops in 1541

(Shelton 2001). In the early 1970s, Canadian plant breeders developed rapeseed with low erucic acid and low glucosinolates and coined the name "canola." Most canola currently planted in North America comprises hybrid cultivars (a new plant result from cross pollination of two distinct plant species) of *B. napus,* which reach maturity in 95 days. In the United States, canola is mainly grown in North Dakota, Minnesota, Montana, and the Pacific Northwest: in Canada, principal areas of canola production are Saskatchewan, Alberta, Manitoba, British Columbia, and Ontario (Weiss et al. 2009).

Canada is the world's largest exporter of canola/rapeseed, accounting for 74% of Canadian export trade (Soyatech 2017). The Canadian canola industry adds over $26.7 billion/year to the Canadian economy (Canola Council of Canada 2017). In western Canada (Manitoba, Saskatchewan, Alberta, and British Columbia), canola, *Brassica napus* L. and *Brassica rapa* L. and mustard, *Brassica juncea* (L) Czern. and *Sinapis alba* L., are the primary host crops of *P. xylostella* (Philip & Mengerson 1989). In eastern Canada (Ontario, Quebec, New Brunswick, Nova Scotia, Prince Edward Island, Newfoundland, and Labrador), *P. xylostella* can also be pestiferous in the areas of brassica crop production (Madore 2010). *Plutella xylostella* can also feed and develop on many Brassicaceae weeds that are common in agriculture cropland across the country (Sarfraz et al. 2011).

1.1.3 Pest status

Plutella xylostella is a major economic pest of Brassicaceae crops in more than 100 countries across the globe and can cause up to 90% crop loss (Alam 1992; Morallo-Rejesus & Sayaboc 1992; Talekar 1992; Talekar & Shelton 1993). Before the introduction of synthetic insecticides in the late 1940s, *P. xylostella* was not reported as a major pest of brassicaceous crops. However, the pest status of *P. xylostella* began to increase in the 1950s as important

natural enemies were eliminated with the extensive use of synthetic insecticides. In 1953, *P. xylostella* became the first agricultural pest to develop resistance to DDT (Ankersmit 1953; Johnson 1953; Talekar & Shelton 1993). Since that time, it has shown resistance to almost every known synthetic insecticide class including organophosphate, pyrethroid, and carbamate insecticides. Moreover, *P. xylostella* has also developed resistance to relatively new chemistries such as avermectins, macrocyclic lactones, neonicotinoids, oxadiazines, pyrazoles, insect growth regulators and nereistoxin analogue insecticides (Shelton & Wyman 1992; Yu & Nguyen 1992; Mohan & Gujar 2003; Ninsin 2004; Sayyed et al. 2004; Sarfraz et al. 2005a).

Plutella xylostella host plants are abundant and widely distributed. Year-round crucifer cultivation, combined with the overuse and misuse of insecticides, can result in control failures and increased crop damage. More than 500 instances of arthropods have been recorded to develop resistance against particular pesticides, and *P. xylostella* has been observed to develop insecticide resistance rapidly (Georghiou & Lagunes-Tejeda 1991).

One of the main causes of the severe *P. xylostella* pest status in many parts of the world is the absence of potential and effective parasitoids (Lim 1986). *Plutella xylostella* has the capability to migrate long distances via air currents. However, there is no record of migration of any of its parasitoids (Curtis 1860; Ormerod 1891; Gray 1915; Miles 1924; French 1967; Bretherton 1982; Chapman et al. 2002). Moreover, the destruction of natural enemies by the application of broad-spectrum insecticides has contributed to the major pest status of *P. xylostella*.

Brassicaceae is a very diverse plant family, grown in all Canadian agricultural regions and includes many indigenous species as well as invasive weeds (Warwick et al. 2003). The area devoted to Brassicaceae crops has increased dramatically in Canada in recent decades. For

instance, the total seeded area of canola in western Canada rose from 7.34 to 8.09 million ha during the period 2008-2016, and this provides a resource readily exploited by *P. xylostella* (Statcan 2016). Furthermore, pest populations can increase rapidly due to their high reproductive potential (Talekar & Shelton 1993).

In Canada, the pest status of *P. xylostella* in any given year is dependent primarily on its arrival time from southern regions of North America, the size of invading populations, the number of population influxes, and environmental and biological conditions in the area of its invasion (Dosdall et al. 2008, 2011; Miluch 2010).

1.1.4 Economic importance

Plutella xylostella causes significant yield losses wherever brassica crops are grown in the world. Its management alone results in a US$4-5 billion annual cost to the global economy (Furlong et al. 2013). The cost of controlling *P. xylostella* during outbreaks in western Canada is substantial. For instance, $86 million in 2001, $4 million in 2003 and $3.5 million in 2005 have spent on management efforts (Dosdall et al. 2008).

Damage caused by *P. xylostella* in Southeast Asia can be very severe; sometimes crop losses are more than 90% (Talekar & Shelton 1993; Verkerk & Wright 1996). In Australia, *P. xylostella* is the leading pest of both canola and brassicaceous vegetables. The estimated crop losses in canola/rapeseed are $3 million, and control costs are $6 million. *Plutella xylostella* also attacks the 136,000 hectares of major brassica vegetable crops and the crop losses in an average year are estimated to be $8 million, and control costs $12 million (Gu et al. 2007; Furlong et al. 2008a).

Plutella xylostella damages brassica vegetables and field crops regularly throughout Europe. There are no comprehensive data available on yield losses due to *P. xylostella* feeding,

but during hot and dry weather conditions severe infestations and high yield losses can occur, while in most years, the damage is below the economic injury level and the pest can easily be controlled by applying insecticides (Shelton 2001).

Mexico is a major producer of broccoli and related crucifers (30,000 ha) with a total farm gate value greater than the U.S. $63 million. *Plutella xylostella* significantly reduces the yield and quality of the crop and accounts for the majority of insecticide use in crucifer production (Diaz-Gomez et al. 2000).

Plutella xylostella is present throughout the United States and ranks as one of the major pests in the Southeast and Pacific Northwest regions (Harcourt 1957; Buntin 1990; Brown et al. 1999). In the southeastern USA, the moth constitutes 90% of damage inflicted to canola from seedling to crop maturity (Buntin 1990; Ramachandran et al. 2000). In California, which is the major fresh market broccoli producer of the USA with a farm gate value of $450 million, crop losses were estimated to be greater than $6 million due to a severe infestation in 1997 (Shelton & Roush 2000).

In most years, *P. xylostella* causes minor economic damage in Canada, but in some years, populations reach outbreak densities, and extensive crop losses occur (Dosdall et al. 2011). For instance, in 1995, the pest caused substantial crop damage in western Canada and Quebec, with the combined economic losses estimated at least $40 to $50 million (Braun et al. 2004). Outbreaks responsible for economic damage to canola and mustard in western Canada have occurred approximately every two to three years since 1995. However, the frequency of economically damaging densities is not correlated with increases in the area devoted to canola production (Dosdall et al. 2008).

1.1.5 Life history and biology

The biology of *P. xylostella* has been studied extensively under both laboratory and natural conditions in relation to ecological factors. Both biological and developmental parameters vary due to differences in host plant species, temperature, and population distribution (Alizadeh et al. 2011). *Plutella xylostella* has a short life cycle, and its population may increase up to 60-fold from one generation to the next (De Bortoli et al. 2011). The moth is multivoltine and can produce four to 20 generations per year in temperate and tropical regions, respectively (Harcourt 1986; Vickers et al. 2004). In Canada, an early arrival time of invading adults under favorable environmental conditions could enable completion of more generations of this multivoltine species than a later invasion (Dosdall et al. 2008). Usually, three generations per year occur in Alberta (Philip & Mengersen 1989), and four to five in Ontario (Harcourt 1960).

The life cycle of *P. xylostella* from egg to adult is on average 32 days and ranges from 21 to 51 days under field conditions (Harcourt 1957). Time to maturity is highly dependent upon climatic conditions. At constant temperature, development can occur from 8-32^{o}C and under fluctuating temperature from 4 to 38^{o}C (Liu et al. 2002). In a recent study, *P. xylostella* development has been observed at different constant (7, 22, 30^{o}C) and fluctuating (0-14, 15-29, and 23-37^{o}C) temperatures. The development was very slow at lowest constant (7^{o}C) and fluctuating temperatures (0-14^{o}C) while fast growth of *P. xylostella* was recorded at highest constant (30^{o}C) and fluctuating temperatures (23-37^{o}C) (Bahar et al. 2012).

The moth species have four life stages: egg, larva, pupa, and adult (Fig. 1-I). Oviposition mainly occurs at night in the first 24 to 48 hours after mating and then declines gradually. Egg laying reaches zero, 10 days after adult emergence (Alizadeh et al. 2011). Each female can lay 200-356 eggs either singly or in small clusters (Harcourt 1957; Talekar et al. 1994; Justus et al.

2000). Host plant species greatly influence oviposition. For instance, oviposition on the brassicaceous host plant (*Brassica napus* L.) is reported to be higher than non-brassicaceous hosts (*Cleome hassleriana* Chod. and *Tropaeolum majus* L.) (Sarfraz et al. 2010b).

Eggs are oval and pale to yellow (Fig. 1-I) (Alizadeh et al. 2011). Egg hatching occurs from 4 to 8 days post-oviposition (Harcourt 1957). Larvae are pale yellow with a dark head in early instars with the body becoming a light to dark green in later instars (Fig. 1-I). The larva has V-shaped anal legs. First-instar larvae are leaf miners, feeding in the spongy mesophyll tissue of leaves. Other larval instars feed on all tissues of leaves, buds, flowers, stems, and siliques (Anonymous 1996; Alizadeh et al. 2011). Under Canadian field conditions in eastern Ontario, the average times for development from first to the fourth instar are 4.0, 3.6, 3.4, and 4.2 days; and for pupation 7.8 to 9.8 days (Harcourt 1957). The adult moth is slender and grayish (Fig. 1-I) (Ooi & Keldeman 1979, De Bortoli et al. 2013). Adults are more active at dusk and feed on floral nectar near agricultural fields. The first generation of *P. xylostella* usually develops on brassicaceous weeds with following generations feeding on cultivated Brassicaceae (Harcourt 1957; Khan et al. 2005). The mean longevity of females is significantly shorter than males (Alizadeh et al. 2011), and also males have longer flight times than females (Goodwin & Satyanarayana 1984; Harcourt 1986). Development and survival vary widely depending on the quality of food, the quantity of adult feeding, the difference in host plant cultivar and sources of carbohydrate (Winkler et al. 2005; Alizadeh et al. 2011).

1.1.6 Host-pest relationships /bitrophic interactions between the host plant and *P. xylostella*

Plutella xylostella has a wide ecological host range. The genetic and phenotypic flexibility of *P. xylostella* enables it to survive throughout the year in areas where environmental conditions

are favorable and host plants are readily available (Campos et al. 2004; Campos et al. 2006). The moth feeds exclusively on plants of the family Brassicaceae, particularly the genus *Brassica*, which are widely distributed geographically (Table 1-I) (Warwick et al. 2006). However, evidence of its occasional occurrence on sugar snap peas (*Pisum sativum*, Fabaceae) in Kenya (Knolhoff & Heckel 2011), Taiwan and the Philippines (Lohr 2001; Shelton 2001), the chenopodiaceous vegetable *Salsola kali* L. (prickly saltwort, Russian thistle) in Russia (Talekar et al. 1985), and okra in Ghana (Anonymous 1971) has been recorded. Sarfraz et al. (2010) reported development of *P. xylostella* on non-Brassicaceae host plant species like spider flower, *Cleome hassleriana* Chod. (Capparaceae), and garden nasturtium, *Tropaeolum majus* L. (Tropaeolaceae). However, *P. xylostella* could be considered as much of a generalist feeder than as a specialist due to worldwide availability of wild and cultivated Brassicaceae host plant species (Pichon et al. 2006; Furlong et al. 2013).

A wide range of sulfur-containing secondary plant metabolites, the glucosinolates, characterizes Brassicaceous plants. More than 100 different glucosinolates have been identified (Rask et al. 2000) in 16 families of dicotyledonous angiosperms (Charron & Sams 2004). The family Brassicaceae contains a unique defensive system known as the glucosinolate-myrosinase system or "mustard oil bomb" or, more recently, as a toxic mine (Ahuja et al. 2011). Glucosinolates and myrosinase are triggered by abiotic and biotic stress or come together upon plant tissue damage and release toxic hydrolysis products such as isothiocyanates and nitriles (Hopkins et al. 2009; Ahuja et al. 2011). Glucosinolates are feeding and oviposition stimulants for brassica specialists while feeding deterrents and toxic to generalist herbivores (Li et al. 2000). Brassicaceae specialist herbivores have a mechanism to overcome this toxicity (Futuyma & Agrawal 2009; Hopkins et al. 2009). For instance, the larvae of *P. xylostella* have evolved a

defensive mechanism to detoxify the toxic hydrolysis products by an enzyme, glucosinolate sulfatase, present in the midgut. The enzyme actively prevents the formation of toxic hydrolysis products by converting glucosinolates to desulfoglucosinolates rather than more toxic nitrile and isothiocyanates. This mechanism enables *P. xylostella* herbivory on a broad range of brassica plants (Ratzka et al. 2002; Hopkins et al. 2009). Saponins are another group of significant defense chemical compound present on the leaf surface of some *Barbarea* spp. They act as feeding deterrents but are attractants for oviposition for *P. xylostella* (Badenes-Perez et al. 2011, 2014). For instance, wintercress (*Barbarea vulgaris*) attracts *P. xylostella* through glucosinolates, but occurrence of triterpenoid saponins in this plant species inhibits larval development (Shinoda et al. 2002). Recently, the whole genome of *P. xylostella* has been sequenced as a means to understand the genetic and molecular basis for adaptation to plant defense compounds and for the evolutionary success of this pest (You et al. 2013).

The performance of *P. xylostella* varies on cultivars of the same plant species with different glucosinolate contents and profiles. For example, maximum feeding by *P. xylostella* larvae has been noticed on various cultivars of *Brassica rapa* (L.) with intermediate glucosinolate content in a laboratory experiment (Siemens & Mitchell-Olds 1996) or with little myrosinase content (Li et al. 2000). In contrast, higher densities of *P. xylostella* larvae are reported to be associated with plant cultivars having higher glucosinolate contents (Bidart-Bouzat & Kliebenstein 2008). Similarly, glucosinolates like 3-butenyl and 2-phenylethyl are toxic to *P. xylostella* at high concentrations (Nayyer & Thorsteinson 1963). Allyl isothiocyanate stimulates egg production in *P. xylostella* adults (Hillyer & Thorsteinson 1969). However, at sufficient concentrations, isothiocyanates are reported to be toxic for larvae and adults and act as feeding deterrents to brassica specialists (Li et al. 2000; Mitchell-Olds et al. 1996). Types and

concentration level of toxic hydrolysis products depends upon the nature of the glucosinolates, the reaction conditions and myrosinase activity (Ahuja et al. 2011). Li et al. (2000) indicated that myrosinase activity and the rate of release of glucosinolate hydrolysis product during herbivory influencs feeding behavior of *P. xylostella* more than glucosinolate concentration.

For host plant location, recognition, oviposition, stimulation and feeding initiation, *P. xylostella* adults not only rely on different types and concentrations of glucosinolates but also on additional chemical and physical stimuli, plant volatiles, cardenolides, host plant nutritional quality, waxes, plant morphology or a combination of these factors (Badenes- Perez et al. 2004; Shelton & Nault 2004; Bukovinszky et al. 2005; Sarfraz et al. 2006; Renwick et al. 2006; Hopkins et al. 2009). The presence of unidentified olfactory stimuli that attract *P. xylostella* to brassicaceous plants has also been reported (Palaniswamy et al. 1986; Pivnick et al. 1990a).

Plutella xylostella adults can also respond differently to different host plant volatiles emitted following insect damage. Females rely on these volatile cues to recognize acceptable hosts for progeny survival and fitness and to reduce competition for food (Abuzid et al. 2011). Reddy & Guerrero (2000) reported three cabbage green leaf volatiles that are highly attractive to *P. xylostella* females. Enhancement of the insect pheromone action by green leaf volatiles could have important practical applications in pest management.

Host plant genotype and quality significantly affect the survival and development of *P. xylostella*. Among commercial crop species including *Brassica napus* L., *Brassica rapa* L., *Brassica juncea* (L.) Czem., *Sinapis alba* L., *Brassica oleracea* L., and *Brassica carinata* Braun, *P. xylostella* preferred to oviposit on *S. alba*, because of its preference for the rather glossy leaf surface of this host plant and its higher concentrations of aromatic glucosinolates. Larval and pupal development was usually fastest on *B. juncea* and *S. alba*, and slower on *B. oleracea* and *B.*

carinata than on several other Brassicaceae (Sarfraz et al. 2007). The preferences and performance of *P. xylostella* vary significantly among wild and cultivated brassicaceous species. *Sinapis alba* is the most preferred host followed by *B. rapa*, *B. juncea*, and *B. napus* among the cultivated species (Dosdall et al. 2011), while *Sinapis arvensis* L. followed by *Erysimum cheiranthoides* L. and *Capsella bursa-pastoris* (L.) are preferred wild brassicaceous hosts (Sarfraz et al. 2011). However, few studies confirm that *P. xylostella* prefers wild over cultivated species despite lower fitness consequences on wild species (Begum et al. 1996; Charleston & Kfir 2000). Moreover, most wild Brassicaceae plants contain higher levels of glucosinolates than cultivated species (Gols & Harvey 2009). Overall, canola and mustard proved to be the most suitable hosts for *P. xylostella* due to a shorter developmental time, and increased survival and egg deposition on these plants (Rabia et al. 2010). Furthermore, the strong preference of *P. xylostella* for some Brassicaceae species over others offers valuable dead-end trap cropping opportunities (Serizawa et al. 2001). The most commonly proposed potential dead-end trap crop for *P. xylostella* is yellow rocket, *Barbarae vulgaris* R. Br. var. *arcuata*. Which stimulate adult oviposition but donot support larval survival of *P. xylostella* (Badenes- Perez et al. 2014).

Variations in the host plant nutritional quality due to plant stress and plant vigor also influence the performance of insect herbivores directly. *Plutella xylostella* field distributions are significantly associated with some nutrients (nitrogen, sulfur, and potassium) in canola leaf tissues (Sarfraz et al. 2010a). *Plutella xylostella* was less attracted for egg laying on sulfur-deficient plants (Gupta & Thorsteinson 1960; Marazzi et al. 2004). Females select plants for oviposition on which pre-imaginal survival of their offspring is greatest, and larval development is fastest (Sarfraz et al. 2009a). Intermediate levels of fertility, rather than low or high levels, are optimum for survival and development of young individuals, pupal weight, and longevity of

adults (Sarfraz et al. 2009a). Plants growing under fertile soil conditions usually support higher densities of insect herbivores than plants growing under less fertile soil conditions (Fox et al. 1990; Price 1991; Meyer & Root 1996; Dosdall et al. 2004a). *Plutella xylostella* is highly migratory and travels long distances without feeding over several days from northern Mexico to western Canada; this behavior, selecting the most nutritious plants, is an advantage concerning migration and subsequent re-colonization (Chapman et al. 2002; Dosdall et al. 2004b; Sarfraz et al. 2005a).

Accumulating evidence indicates that host plant morphological characteristics like leaf color, size, and their position on the plant, epicuticular waxes, trichome density, chemosensory stimulation, and abiotic factors affect *P. xylostella* oviposition, development, and herbivory (Sarfraz et al. 2006; Renwick et al. 2006). For instance, *P. xylostella* females prefer glossy cultivars (i.e., low surface wax) over waxy cultivars (normal wax bloom) for oviposition; though larval survival is reduced on glossy cultivars (Badenes-Perez et al. 2004). Some studies report oviposition preference of *P. xylostella* on the lower leaf surfaces of host plants (Alizadeh et al. 2011; Charleston & Kfir 2000; Satpathy et al. 2010), while others report a higher oviposition preference on the upper surfaces of crucifer leaves (Harcourt 1957; Talekar & Shelton 1993). Similarly, egg numbers laid and trichome density are positively correlated (Agerbirk et al. 2003; Talekar et al. 1994). A recent study showed a positive correlation between *P. xylostella* oviposition choice and larval survival on undamaged host plants (Zhang et al. 2012).

Specific plant characteristics provide antibiosis and antixenosis resistance to *P. xylostella*. Plants responsible for antibiosis cause reduced insect size or weight or have an indirect effect by increasing the exposure of the insect to its natural enemies resulting from prolonged developmental time. The plants that show antixenotic resistance have reduced initial infestations

or a higher emigration rate of the pest than more susceptible plants (Sarfraz et al. 2006). Morallo-Rejesus (1986) reported that more than 88 plant species, belonging to the families Asteraceae, Fabaceae or Euphorbiaceae, possess repellent(s) for *P. xylostella* oviposition and herbivory.

1.1.7 Natural enemies of *P. xylostella*

Collectively, natural enemies are known to attack all stages of *P. xylostella*, often keeping populations under economic threshold levels (Table 1-II). Amongst all natural enemies, both generalists and specialists, parasitoids are the most important biological control agents in natural areas and agroecosystems. Over 135 parasitoid species have been documented worldwide that utilize different stages of *P. xylostella* (Delvare 2004). The most common reported in the literature include six species of egg parasitoids, 38 larval, and 13 pupal parasitoids (Lim 1986; Talekar & Shelton 1993).

The following species achieve most control of *P. xylostella* in many parts of the world: *Cotesia plutellae* (Kurdjumov), *Diadegma semiclausum* (Hellen), *Diadromus collaris* (Gravenhorst), *Oomyzus sokolowskii* (Kurdjumov), *Diadegma insulare* (Cresson) and *Microplitis plutellae* (Muesebeck) (Lim 1986; Talekar & Shelton 1993; Talekar 1997; Xu et al. 2001; Sarfraz et al. 2005a). However, in different geographical areas of the world, various parasitoid species dominate and are responsible for suppressing *P. xylostella* populations. For instance, *Diadegma* spp. and *Diadromus* spp. predominate in Europe (Hardy 1938), New Zealand (Todd 1959) and South Africa (Kfir 1997). *Diadegma semiclausum* (Hellen), *Diadegma rapi* (Cameron) and *Diadromus collaris* (Grav.) collectively are responsible for 93% parasitism in Victoria, Australia (Goodwin 1979). *Diadegma semiclausum* also has been reported to keep the *P. xylostella* population below economic threshold levels in some parts of Europe, Africa, Asia (Talekar & Shelton 1993), Malaysia, Taiwan, Philippines, Indonesia, Thailand, Zambia, New Zealand and

Australia (Lim 1992; Furlong & Zalucki 2007). The most abundant parasitoids in East Africa are *Diadegma mollipla* (Holmgren) and *Oomyzus sokolowskii* (Kurdjumov) (Lohr & Kfir 2004). In Ethiopia, *Diadegma* spp. and *Cotesia plutellae* (Kurdj.) are key parasitoid species (Ayalew et al. 2004). *Cotesia plutellae* and *O. sokolowskii* are considered the most promising biological control agents in China (Liu et al. 2000). In the relatively hotter lowlands of many Asia-Pacific regions, *C. plutellae* is the dominant and most efficient larval parasitoid of *P. xylostella* (Talekar & Shelton 1993). In the Eastern Cape (South Africa), four species viz., *D. mollipla*, *C. plutellae*, *D. collaris* and *O. sokolowskii*, are recorded as the principal parasitoids of *P. xylostella* (Smith & Villet 2004).

In general, egg parasitoids contribute little to the biological control of *P. xylostella* because they require frequent mass releases (Talekar & Shelton 1993). As they are not always host specific, they pose a threat to non-target species (Goulet & Huber 1993). Larval parasitoids are most useful by having greater control potential and belong mainly to three genera, *Diadegma, Apanteles,* and *Microplitis* (Lim 1986). Lim (1992) noted that the ability to function as biological control agents varies among species. It usually depends on the direct relationships of natural enemies with their hosts, environment and interspecific interactions.

In Canada, three hymenopterous parasitoid species, *D. insulare* (Cresson), *M. plutellae* (Muesebeck) and *D. subtilicornis* (Gravenhorst) are found to attack larval, pupal and pre-pupal stages of *P. xylostella* (Harcourt 1986; Anonymous 1996; Braun et al. 2004; Dosdall et al. 2004b). *Microplitis plutellae* (Muesebeck) (Hymenoptera: Braconidae) is a primary larval endoparasitoid of *P. xylostella,* especially in North America. It has been recorded from Iowa, Colorado, Idaho, California, Utah, South Carolina, New York, Alberta, Saskatchewan, and Ontario (Harcourt 1960; Braun et al. 2004), also occurring in Taiwan, Laos, and Cambodia (Kirk

et al. 2004). *Microplitis plutellae* undergoes obligatory diapause as a prepupa or pupa and so is consequently cold hardy, which enables it to overwinter in western Canada (Putnam 1978). The mature parasitic larva emerges from the final-instar host and spins its own brown, oval cocoon that adheres to any available surface such as a stem, leaf, or wall of a cage (Harcourt 1960; Putnam 1968; Gharuka et al. 2004). On average, adult *M. plutellae* lives for 20 days producing 316 eggs per female, but has a shorter lifetime, resulting in lower overall fecundity compared with *D. insulare.* However, number of eggs produced per day is similar for both parasitoids (Bolter & Laing 1983). *Microplitis plutellae* kills and emerges from fourth instars, while *D. insulare* kills and emerges from the prepupal stage and spins its cocoon inside the loosely woven cocoon of its host (Harcourt 1960; Putnam 1968). Xu et al. (2001) reported that *M. plutellae* heavily parasitized *P. xylostella* and provided higher parasitism rates than *D. insulare* in the late season, but *D. insulare* may be more suitable for field release to augment biocontrol of *P. xylostella*.

Diadromus species (Hymenoptera: Ichneumonidae) are prepupal and pupal solitary parasitoids of *P. xylostella* in various parts of the world including England (Hardy 1938), Holland (Lloyd 1940), Canada (Harcourt 1960; Anonymous 1996; Braun et al. 2004), Australia (Goodwin 1979), Moldavia (Mustata 1992), South Africa (Kfir 1997, 1998), China (Liu et al. 2000), India (Chauhan & Sharma 2004), France, Turkey, Bulgaria, Georgia and Greece (Kirk et al. 2004). Two species of *Diadromus* have been reported to parasitize *P. xylostella* to date (Sarfraz et al. 2005a).

Although most studies of natural enemies attacking *P. xylostella* focus on parasitoids, mortality caused by invertebrate predators historically has been very much ignored, likely underestimated and certainly poorly understood (Lim 1992; Talekar & Shelton 1993; Symondson

et al. 2002; Furlong et al. 2004; Ma et al. 2005a, b). The efficient use of predators needs to be considered and analyzed (Polis et al. 1989). The most common groups of insect predators reported in cabbage fields are the generalist coccinellids, chrysopids, syrphids and staphylinids (Alam 1992). Almost 175 genera of spiders in rice fields of Korea are associated with the suppression of *P. xylostella* when densities are high (Lee & Kim 2001). The combined effect and interaction of multiple predator species may be non-additive but sometimes this interaction is synergistic, and the impact of multiple species is greater than the sum of individual species (Simberloff & Holle 1999; Griswold & Lounibos 2006). Some recent publications have added valuable information about the role of predators in control of defoliators (Reddy et al. 2004; Furlong et al. 2008b; Furlong & Zalucki 2010). For example, the development of specific DNA markers of a range of prey species permits their identification from gut samples of predators. Given that predators are often described as generalists and difficult to observe in the field, this technique may help identify the most important predatory species. With this information, these predator species may be augmented in some manner to increase effectiveness (Symondson et al. 2002; Ma et al. 2005a).

1.2 The principal parasitoid of *P. xylostella* in Canada: *Diadegma insulare*

1.2.1 Origin and distribution

The genus *Diadegma* Froster (Hymenoptera: Ichneumonidae: Campopleginae) represents a large group of koinobiont endoparasitoids of Lepidoptera with 201 species known to occur worldwide (Yu & Horstmann 1997). Several *Diadegma* species, including *D. fenestrale* (Holmgren), *D. insulare* (Cresson), *D. leontiniae*, *D. mollipla*, *D. rapi*, and *D. semiclausum*, are reported to attack *P. xylostella* (Azadah et al. 2000; Wagener et al. 2004). There is a wide

geographical variation in the predominance of *Diadegma* species, with the majority (131 species) having a Palearctic and a few (33 species) having a Nearctic distribution (Talekar & Shelton 1993).

Diadegma insulare (Cresson) (Hymenoptera: Ichneumonidae) is one of the key parasitoids of *P. xylostella* in North America (Harcourt 1963; Lee et al. 2003). The parasitoid is distributed in North America: Canada, United States, Maxico; South America: Venezuela; Caribbean: Cuba, Jamaica, Puerto Rico, West Indies, Dominican Republic (Sourakov & Mitchell 2000, Furlong et al. 2013).

The origin of *D. insulare* in western Canada is unknown, but it likely migrates northward in spring along with its hosts rather than overwintering (Dosdall & Mason 2010).

1.2.2 Host range of *Diadegma* species

Diadegma species were initially assumed to have broad host ranges (Hardy 1938), although more recent research indicates that many *Diadegma* species are relatively host-specific (Fitton & Walker 1992). For instance, *D. armillata* is known to attack numerous species of the family Plutellidae (Dijkerman 1990), while the host range of *D. semiclausum* is restricted to *P. xylostella* (Abbas 1988; Wang & Keller 2002). However, *D. insulare* is a solitary, host-specific larval endoparasitoid of *P. xylostella*. (Fitton & Walker 1992; Mukenfuss et al. 1992; Idris & Grafius 2001).

1.2.3 Taxonomy of *D. insulare*

The taxonomic position of *D. insulare* is as follows:

Kingdom -- Animalia

Phylum -- Arthropoda

Class -- Hexapoda

Order -- Hymenoptera

Family -- Ichneumonidae

Subfamily-- Campopleginae

Genus --*Diadegma*

Species --*Diadegma insulare*

1.2.4 Developmental biology/ life history

Unlike its host, the developmental biology of *D. insulare* has not been studied extensively. *Diadegma insulare* has four distinct stages: egg, larva, pupa, and adult. The egg is rounded, clear and lacks projections. The larva of *D. insulare* is white, segmented and bears a short (1/4 of the total length of the larva) narrow abdominal "tail" (Fig.1-II). The larva is very active. The adult is a small wasp, approximately 6 mm long, slender and black, with brown and yellow striped legs and dark abdomen from the upper side but the underside is yellow (Sourakov & Mitchell 2000; Lee et al. 2003). The female has a distinct ovipositor used to penetrate the host larva cuticle for egg deposition (Fig.1-IV). After 10 to 15 days, a single parasitoid emerges as a mature larva from the host prepupa and spins its cocoon within that of the host where it can easily be distinguished (Fig.1-II & III) (Harcourt 1960; Putnum 1968; Sourakov & Mitchell 2000).

The number of generations per year corresponds to the number of generations of its host as one host larva supports only one parasitoid larva (Sourakov & Mitchell 2000). Although it can

parasitize all four larval instars, emergence always occurs from the prepupa of *P. xylostella* (Putnam 1968). However, the specific larval instars parasitized by *D. insulare* usually affect the sex ratio of emerging parasitoids. More males than females are produced from early instar hosts while with later instars the progeny consists of a greater proportion of females (Fox et al. 1990; Monnerat et al. 2002). Similarly, more female wasps are produced when *D. insulare* oviposits on hosts on highly fertilized plants, suggesting that sex allocation decisions of female parasitoids are directly influenced by not only host quality, but food plant quality as well (Fox et al. 1990; Fox et al. 1996). On average, at 23°C adult *D. insulare* live for 26 days and a female will lay 814 eggs during this period (Bolter & Laing 1983).

Temperature plays a significant role in the survival, development, reproduction, and parasitism of *D. insulare.* The developmental period, from egg to adult, is approximately 58, 13, and 11 days, at 7, 22, and 30^{o}C respectively, as reported by Bahar et al. (2012). Although larvae survived the highest temperature, high pupal mortality of *D. insulare* was observed. This may explain the greater effectiveness of this parasitoid in cooler regions than tropical areas (Bahar et al. 2012). Okine et al. (1996) studied the effect of low temperature on the survival of *D. insulare* pupae and the consequences of parasitism on the feeding rate of diamondback moth larvae and found that adult emergence decreased with long-term storage at 4^{o}C. No emergence of *D. insulare* was observed after 49 days in storage. The highest emergence of 82% was obtained from cocoons stored at 4^{o}C for 14 days compared to 92% of cocoons that were not subjected to cold storage. More males than females emerged from cocoons stored at 4^{0}C.

Adults require a continuous nectar source for survival and to increase longevity. As a result, they prefer habitats with abundant food resources (Idris & Grafius 2001) that enhance their fecundity and longevity (Lee & Hemipel 2008). A good nectar source can increase the longevity

of *D. insulare* females from 2 to 5 days to more than 20 days (Edward & Grafius 1997). Similarly, sites with flowering plants like alyssum, *Lobularia maritime* (L.) Desv. (Brassicaceae) (Johanowicz & Mitchell 2000), or with borders of flowering buckwheat, *Fagopyrum esculentum* Moench (Polygonaceae) in cabbage fields enhance *D. insulare* populations (Lee & Heimpel 2008). The number of *P. xylostella* larvae parasitized by a single *D. insulare* female may vary from zero to 150, depending upon the food source (Edward & Grafius 1997).

1.2.5 Importance of *D. insulare* as a biological control agent

Diadegma insulare is one of the most important biocontrol agents attacking diamondback moth larvae especially in North America (Harcourt 1960, 1963; Fitton & Walker 1992; Lee et al. 2003; Sarfraz et al. 2005a). Almost 10 species of *Diadegma* have been introduced worldwide, due to their effectiveness in parasitizing different larval instars of *P. xylostella* (Lim 1986; Talekar & Yang 1993). Compared with other parasitoids, its proficient host-searching skills, ability to avoid multiparasitism and superparasitism, and synchronization with its host's developmental stage, make it suitable for use as an auxiliary method for the integrated management of *P. xylostella* (Harcourt 1969; Bolter & Laing 1983; Harcourt 1986; Wang & Keller 2002; Xu et al. 2001).

Host-specialist parasitoids appear to have greater efficiencies than generalists in locating hosts. They have more specialized adaptations to overcome host defenses than generalist species that display relatively plastic foraging behavior (Wang & Keller 2002). *Diadegma insulare* is a host specific and efficient host searcher and shows very flexible behavior sitting motionless near the silken thread, waiting for *P. xylostella* larva to climb and then attacks it. Sometimes, it travels down to the larva suspended by its silken thread and attempts quickly to parasitize it (Sarfraz et al. 2005a).

Diadegma insulare not only can decrease the pest populations by parasitizing 70-90% of *P. xylostella* larvae, but it also reduces 30-80% food consumption by the parasitized larvae, consequently, decreasing the damage to the crop (Mukenfuss et al. 1992; Mitchell et al. 1997; Sourakov & Mitchell 2000; Monnerat et al. 2002). In North America, *D. insulare* has been recorded on average to parasitize over 80% of larvae. They are able to locate hosts within 8-10 seconds of landing on the damaged leaf surface (Xu et al. 2001; Hutchison et al. 2004). Under field conditions, this parasitoid has accounted for 98% parasitism in South Texas on cabbage (*Brassica oleracea* L.) (Legaspi et al. 2000). From 1994 to 2003, 62-82% parasitism of *P. xylostella* by *D. insulare* was reported on cabbage plants in Minnesota and more than 90% in South Carolina (Lee et al. 2003). In 1992, *D. insulare* accounted for 30% of *P. xylostella* parasitism in Saskatchewan and 45% in Alberta in canola crops (Braun et al. 2004).

Overall, *D. insulare* is reported to be a better and more efficient parasitoid by causing higher mortality of *P. xylostella* than other larval parasitoids in relatively cool regions of North America (Xu et al. 2001; Bahar et al. 2012).

1.2.6 Tritrophic interactions among host plant-pest and parasitoid

To date, only a few studies have focused on tritrophic interactions involving the host plant, *P. xylostella,* and *D. insulare*. Many biotic and abiotic factors affect the survival, longevity, effectiveness, performance, and distribution of insect pests directly and their natural enemies indirectly. Understanding these factors and their influence on bitrophic and tritrophic interactions involving host plant, pest and parasitoid are critical when designing a long-term and effective management strategy to control the pest.

Parasitoid life history traits are influenced by choices made by their herbivore hosts, mediated by host plant quality (Vet & Dicke 1992; Godfray 1994). The nutritional quality of

plants consumed by the herbivore host of *D. insulare* affects the sex ratio of the parasitoid; more female parasitoids emerged from *P. xylostella* larvae on well-fertilized plants (Fox at al. 1990). Similarly, the performance of *D. insulare* is improved when *P. xylostella* larvae are reared on highly fertilized plants (Sarfraz et al. 2009b; Dosdall et al. 2011). Increased soil fertility not only enhanced development and survival of *D. insulare* but also increased infestations of *P. xylostella*. Maintaining relatively high levels of soil fertility is appropriate for the integrated management of *P. xylostella* in canola, because healthy, strong and well-nourished plants can better compensate for insect attack than plants under nutrient stress (Dosdall et al. 2004a; Sarfraz et al. 2005b).

The host plant genotype on which the *P. xylostella* larvae were reared has major impacts on the survival and parasitism success of *D. insulare.* For instance, egg to the pre-pupal growth of the parasitoid was fastest on *B. juncea* (L.) and slowest on *B. oleracea* L., whereas pupal development was shortest on *B. napus* cv. Liberty. Parasitoids reared on *B. napus* cv. Q2 survived for a shorter period without food comparative to other host plant genotypes tested, suggesting that fewer nutrients are stored during host development on this plant variety. Overall *P. xylostella* larvae parasitized by *D. insulare* consumed less foliage than non-parasitized larvae (Sarfraz et al. 2008).

Habitat manipulation plays a major role in population size, distribution and specific dispersal behavior of pest and parasitoid (Kareiva 1987; Hawkins & Shaheen 1994). For instance, Idris & Grafius (2001) suggested intercropping tomato and corn with cabbage in a *P. xylostella* management program to enhance the population and activity of *D. insulare*. Similarly, planting *Anethum graveolens* L. in field margins significantly increased the number of adult *Diadegma semiclausum* Hellén in the crop (Winkler et al. 2010). Diversification of the agroecosystem by providing flowering plants is an important tool in conservation biological control to enhance the

survival and effectiveness of parasitoids (Winkler et al. 2009). However, flowering field edges may benefit herbivores and inadvertently increase pest density if not selected with caution (Van Emden 1964; Zhao et al. 1992; Baggen & Gurr 1998; Romeis et al. 2005). Various field and laboratory studies showed that adult parasitoids lived longer and were more fecund when fed on floral nectar, honey or other carbohydrate sources (Foster & Ruesink 1984; Idris & Grafius 1997). For instance, parasitism of *P. xylostella* was observed to be higher in broccoli (*B. oleracea* var. botrytis L.) adjacent to nectar-producing plants than in broccoli not bordered by nectar-producing plants (Zhao et al. 1992). Numerous wildflowers, including wild mustard (*Sinapis arvensis* L.), wild carrot (*Daucus carota* L.), and yellow rocket (*Barbarea vulgaris* R. Br.), can increase longevity and fecundity of *D. insulare* (Buchholtz et al. 1981; Idris & Grafius 1997). Johanowicz & Mitchell (2000) reported that the presence of alyssum, *Lobularia maritime* L*.,* near cultivated crucifers, extended the lifespan of *D. insulare*.

Resource variation and spatio-temporal distribution have a significant impact on the physiology of herbivore pests, which in turn mediates pest-parasitoid interactions, as well as the effectiveness, survival, development, size, longevity, and fecundity of parasitoids (Moon et al. 2000; Sumerford et al. 2000; Teder & Tammaru 2002). The density and distribution of a parasitoid's population are correlated with the density and distribution of its herbivore's host plant. For instance, field populations of *D. insulare* are often grouped, with distributions that correlate with their herbivore host populations where host plants have high sulfur content (Ulmer et al. 2005; Sarfraz et al. 2010b; Dosdall et al. 2011). Spatio-temporal studies conducted by Sarfraz et al. (2010a) in commercial fields of canola (*B. napus* L.) in southern Alberta, Canada revealed that *P. xylostella* populations accumulated at different levels when its host plants were in the early flowering stage, while *D. insulare* adults showed significantly aggregated, but more

uniform distribution as the parasitoid moved into the crop later in the season. However, the *M. plutellae* population distribution was aggregated in mid-flowering season. The close spatial associations between densities of *D. insulare* and *P. xylostella* indicated that host abundance was the main determinant of parasitoid distribution patterns. At a finer scale, spatial distributions of nutrients in leaf tissue and their correlations with the herbivores and parasitoids showed that sulfur has a positive effect on the distributions of *D. insulare* but not on *M. plutellae.* However, the relationships between nutrients and the distribution of *P. xylostella* and parasitoids were inconsistent and may be complicated by the effects of the spatial associations between parasitoids and their hosts.

1.3 Background of research

Considerable progress has been made in developing integrated management strategies for several insect pest species that can infest canola/oilseed rape crops. However, one important area of research that requires additional analysis involves identifying strategies to enhance the effectiveness of beneficial insects. Beneficial insects can reduce infestations of insect pests, and in some cases, they have been the primary agents responsible for ending outbreaks. Natural enemies hold major advantages as components in the integrated management of insect pests. Once established, they can become permanent fixtures of canola agroecosystems and can provide control that is very specific and cost-effective. Also, pest control with beneficial insects avoids or minimizes chemical insecticide applications and so enhances the environmental sustainability of canola production.

My research focuses on *P. xylostella* and the natural enemies that help keep its populations regulated. Diamondback moth can cause considerable reductions in yield of canola

depending on the year and location, and insecticide applications are currently the only control strategy available to producers (Philip & Mengersen 1989). The importance of *P. xylostella* as a pest of the crop is predicted to increase as the effects of climate change become more manifest (Dosdall et al. 2008). However, sometimes parasitoids are known to terminate outbreaks completely. For instance, *P. xylostella* outbreaks in Alberta in 2003 and 2005 were terminated primarily through the activity of the parasitoid, *D. insulare* (Dosdall, unpublished data). Unfortunately, many farmers needlessly sprayed their crops with insecticide in those outbreaks because they lacked appropriate forecasting information on the distribution and abundance of *D. insulare* populations. Two other parasitoid species, *M. plutellae* and *D. subtilicornis*, also attack *P. xylostella* in western Canada and sometimes inflict high levels of parasitism (Braun et al. 2004). However, despite the importance of *D. insulare*, *D. subtilicornis* and *M. plutellae* in managing *P. xylostella* outbreaks in canola, very little is known about their life histories and habitat requirements, and we lack forecasting strategies to assess their abundance levels and distributions.

1.4 Objectives of research

The primary objective of my study is to explore research areas pertaining to *P. xylostella* and its primary parasitoid *D. insulare* that have been overlooked or not studied in depth. The developmental biology of *P. xylostella* and bitrophic interactions involving the host plant and pest have been studied extensively, but research on many aspects of the biology and tritrophic interaction involving the host plant, *P. xylostella* and *D. insulare* is lacking. Knowledge and understanding of a parasitoid's bioecology and tritrophic interactions are crucial to the development of biological control programs. Moreover, to counter increasing levels of insecticide

resistance in *P. xylostella* and to reduce the reliance on chemical pesticides, emphasis should be given to incorporating biocontrol agents in pest management plan. An overall goal of my research is to contribute to the elaboration of an efficient management system integrated with biological control agents, and consequently, make canola/mustard production more sustainable. It is anticipated that, ultimately, this study will provide valuable information and a better understanding of the development, life history traits and responses of the parasitoid to ecological factors.

Overall, this thesis consists of five studies, each with two or more specific objectives. Each objective was tested under a specific hypothesis. In Chapters 2 and 3, experiments were designed to understand oviposition preferences of *P. xylostella*, bitrophic and tritrophic interactions involving the host plant, *P. xylostella* and *D. insulare,* particularly when the host plant was under water deficit stress. I tested the hypotheses that: (a) plant water status influences the ovipositional preferences of *P. xylostella;* (b) plant water status affects development and fitness parameters of the second and third trophic levels; (c) host plant water status influences pest and parasitoid and their interactions differently

In Chapter 4, development and fitness attributes of *D. insulare* were tested under different temperature regimes. I tested the hypotheses that: (a) when reared on *P. xylostella*, developmental parameters and percentage parasitism of *D. insulare* are affected by temperature; (b) and the parasitoid life history traits like longevity and survival decline at higher constant temperatures.

In Chapter 5, my experiment was designed to understand the selective effects of floral and non-floral food sources on the pest-parasitoid system. I tested the hypotheses that: (a) sugar feeding enhances the longevity of pest and parasitoid; (b) floral nectar acts selectively on both pest and parasitoid; (c) floral nectar has contrasting/different effects on life-history traits such as

longevity and body weight.

In Chapter 6, the diversity and abundance of the parasitoid fauna associated with *P. xylostella* among commercial canola/mustard fields in southern Alberta was investigated. I tested the hypotheses that: (a) the parasitoid fauna associated with *P. xylostella* is diverse; (b) and diversity and abundance vary with particular crop and time.

Chapter 7 provides a general discussion and summarizes the major findings from a series of laboratory experiments examining the various research objectives discussed above. Finally, future research needs in understanding the bioecology and relationships between pests and parasitoids under climatic factors are summarized.

Table 1-I. Host plants of *Plutella xylostella*

Cultivated Cruciferous			
Cultivar/Species	**Common name**	**Plant type**	**Reference**
Brassica carinata L.	Ethiopian mustard	Vegetable, Oilseed	Ayalew et al. 2004; Sarfraz et al. 2007, 2008
Brassica juncea L.	Indian mustard, brown mustard	Vegetable, Trap crop, Oilseed	Brown et al. 1999; Srinivasan & Krishna 1991; Sarfraz et al. 2007; Soufbaf 2010
Brassica napus L.	Canola, Canadian turnip, rutabaga	Vegetable, Oilseed	Idris & Grafius 1996; Brown et al. 1999; Sarfraz et al. 2007, 2008; Golozadeh 2009; Silva & Furlong 2012
Brassica nigra L.	Black mustard	Vegetable, Spice	Idris & Grafius 1996
Brassica oleracea L. var. acephala	Collard, flowering kale	Vegetable	Idris & Grafius 1996; Badenes-Perez et al. 2004; Gathu et al. 2008
Brassica oleracea L. var. alboglabra	Kale	Vegetable	Talekar & Shelton 1993
Brassica oleracea L. var. botrytis	Cauliflower	Vegetable	Idris & Grafius 1996; Reddy et al. 2004; Golozadeh et al. 2009
Brassica oleracea L. var. sabauda	Savoy cabbage	Vegetable	Abro et al. 1985
Brassica oleracea L. var. capitata	Cabbage	Vegetable	Abro et al. 1994; Idris & Grafius 1996; Golozadeh et al. 2009; Silva & Furlong 2012
Brassica oleracea L. var. gemmifera	Brussels sprouts	Vegetable	Talekar & Shelton 1993
Brassica oleracea L. var. gongylodes	Kohlrabi	Vegetable	Reddy et al. 2004; Golozadeh et al. 2009
Brassica oleracea L. var. italica	Broccoli	Vegetable	Idris & Grafius 1996; Reddy et al. 2004
Brassica rapa L. var. pakchoi	Pak choi	Vegetable	Talekar & Shelton 1993
Brassica rapa L. var. pekinensis	Chinese cabbage	Vegetable	Talekar et al. 1994; Liu & Jiang 2003; Silva & Furlong 2012
Brassica rapa L.	Canola	Oilseed	Sarfraz et al. 2007
Raphanus sativus L.	Radish, bier radish	Vegetable	Abro et al. 1994
Sinapis alba L. (= *Brassica hirta* Moench)	White mustard, yellow mustard	Vegetable, spice	Brown et al. 1999; Sarfraz et al. 2007, 2008

Table 1-I. Continued

Wild Cruciferous			
Cultivar/Species	**Common name**	**Plant type**	**Reference**
Arabidopsis thaliana (L.) Heynh	Thalecress, mouse-earcress		Ratzka et al. 2002
Barbarea vulgaris (L.) R. Br.	Yellow rocket, rocketcress		Idris & Grafius 1996; Shelton & Nault 2004; Badenes-Perez et al. 2004
Berteroa incana (L.) DC.	Hoary alyssum		Idris & Grafius 1996
Capsella bursa-pastoris (L.) Medik.	Shepherd's purse, mother's-heart		Idris & Grafius 1996; Sarfraz et al. 2012
Cardamine flexuosa With.	Flexuous bittercress		Muhamad et al. 1994
Descurainia sophia L.	Flixweed		Talekar & Shelton 1993
Erysimum cheiranthoides L.	Wormseed mustard, treacle mustard		Renwick & Radke 1990; Idris & Grafius 1996
Erysimum cheiranthoides L.	Treacle-mustard		Sarfraz et al. 2011, 2012
Erucastrum arabicum Fisch. & CA. Mey.	-		Ayalew et al. 2006
Lepidium campestre (L.) R. Br.	Field pepper-grass, pepperweed		Idris & Grafius 1996
Lepidium virginicum L.	Virginia pepperweed, peppergrass		Begum et al. 1996
Raphanus raphanistrum L.	Wild radish, wild rape, charlock		Idris & Grafius 1996; Gathu et al. 2008
Rorippa indica (L.) Hiern	Indian marshcress		Muhamad et al. 1994; Begum et al. 1996
Rorippa islandica (Oeder) Barbas	Marsh yellowcress		Muhamad et al. 1994
Rorippa micrantha (Roth.) Jonsell	-		Gathu et al. 2008
Rorippa nudiuscula (E. Mey. ex Sond.) Thell.	-		Gathu et al. 2008
Sinapis arvensis L. (= *Brassica kaber* (DC) Wheeler)	Wild mustard, crunchweed		Idris & Grafius 1996; Sarfraz et al. 2011, 2012
Sisymbrium altissimum L.	Tumbling mustard, tall hedge mustard		Talekar & Shelton 1993
Thlaspi arvense L.	Stinkweed, pennycress, Frenchweed		Idris & Grafius 1996

Table 1-I. Continued

Non-Cruciferous			
Cultivar/Species	**Common name**	**Plant type**	**Reference**
Tropaeolum majus L.	Nasturtium, Indian cress	Flowering ornamental plant	Renwick & Radke 1990
Cleome species	Spider plant	Flowering plant	Sarfraz et al. 2005c
Pisum sativum L.	Peas	Pulse	Gupta & Thorsteinson 1960; Lohr 2001; Lohr & Gathu 2002; Rossbach et al. 2006; Henniges-Janssen 2011ab
Hibiscus esculentis L.	Okra, Lady fingers	Vegetable	Gupta 1971

Table 1-II. Examples of some common natural enemies of *Plutella xylostella*

Natural Enemy	Host stage attacked	References
A- Parasitoid		
Trichogrammatoidea bactrae (Nagaraja) *Trichogramma pretiosum* Riley *Trichogrammatidae* spp.	Egg	Liu et al. 2004
Diadegma insulare (Cresson) *D. fenestrale* (Holmgren) *D. mollipla* (Holmgren) *D. varuna* Gupta *D. leontiniae* (Brèthes) *D. rapi* (Cameron)	Larva	Azidah et al. 2000
D. semiclausum (Hellen) *Apanteles ippeus* (Nixon)	Larva	Furlong & Zalucki 2007
Cotesia plutellae (Kurdjumov)	Larva	Verkerk & Wright 1996
Microplitis Plutellae Muesbeck	Larva	Braun et al. 2004
Diolcogaster claritibia	Larva	Fernandez-Triana et al. 2014
Oomyzus sokolowskii (Kurdjumov)	Larva-Pupa	Shi et al. 2004
Tatrastichus ayyari (Rohwen)	Pupa	Ooi & Lim 1989
Brachymeria phya (Walker)	Pupa	Furlong & Zalucki 2007
Diadromus collaris (Gravenhorst)	Pre-pupa, Pupa	
D. subtilicornis (Gravenhorst)	Pre-pupa, Pupa	Braun et al. 2004
Pteromalus spp.	Pupa	Chauhan & Sharma 2004
B- Pathogen		
Bacillus thuringiensis Berliner	Larva	Bauer 1995
Zoophthora radicans (Brefeld) Batko *Beauveria bassiana* (Balsamo) Vuillemin *Metarhizium anisopliae* (Metsch.) Sorokin *Paecilomyces farinosus* (Holm ex SF. Gray) *Nomuraea rileyi* (Farlow) Sampson *Fusarium* spp. *Pandora* spp. *Erynia* spp. *Conidiobolus* spp. *Scopulariopsis* spp.	Larva	Cherry et al. 2004a Vandenberg et al. 1998 Kirk et al. 2004
Granuloviruses (GVs) Nucleopolyhedrovirus NPVs Cypovirus CPVs	Larva	Woodward et al. 2004 Cherry et al. 2004b
Steinernema carpocapsae (Weiser) *Heterorhabditis* sp. *Nosema bombycis* (Negali) *Vairimorpha* sp.	Larva	Baur et al. 1998 Mason et al. 1999 Idris et al. 2004 Anuradha 1997
C- Predator		
Lycosids Linyphiids	Mostly Larva	Quan et al. 2011; Ortiz 2011
Syrphids Staphylinids Reduviids Nabids Carabids	Egg, Larva	Ortiz 2011
Coccinella spp.	Egg-Larva	Gabriela 2011

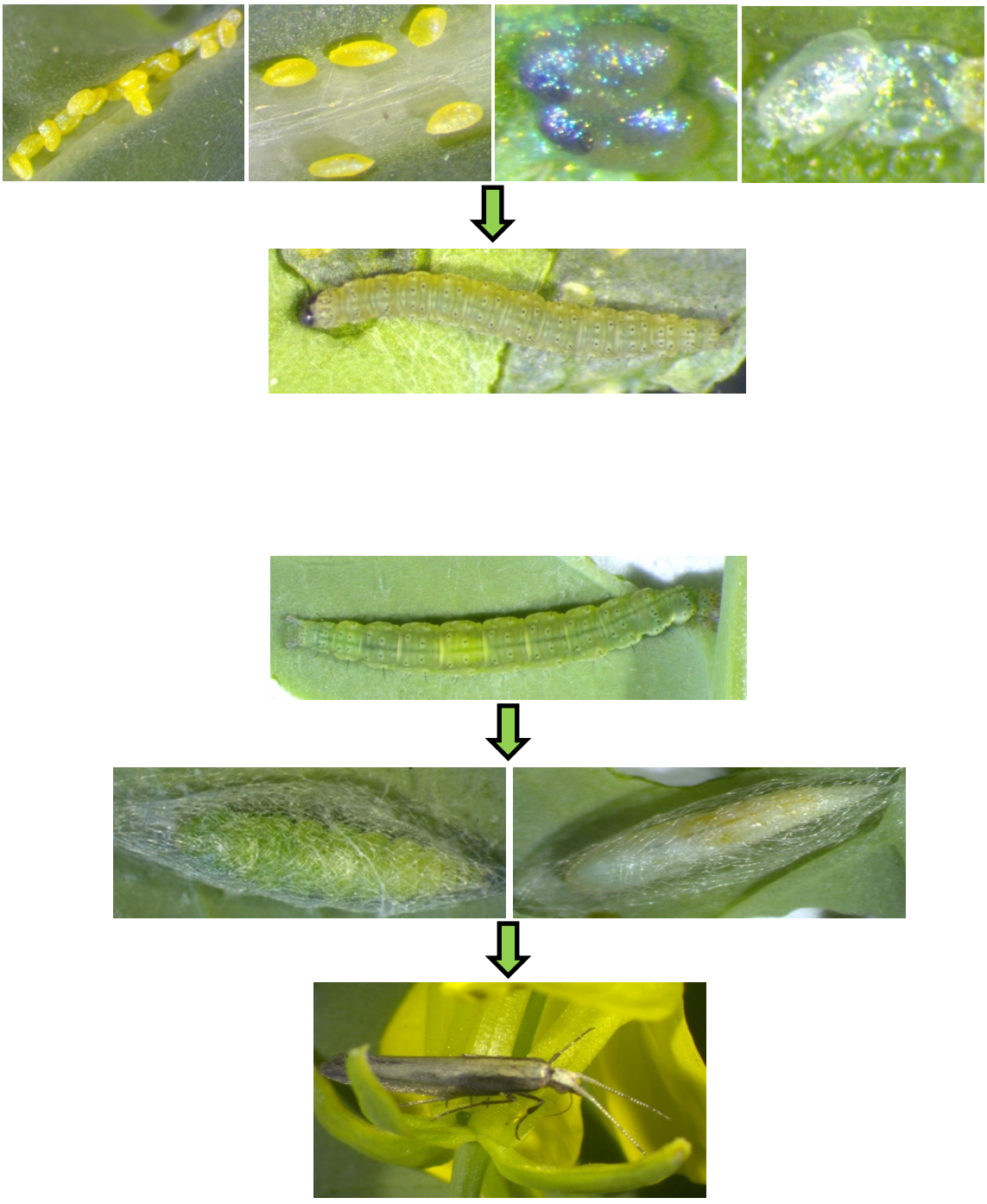


Figure 1-I. Biology of Diamondback moth; A- Newly laid eggs in cluster; B- Eggs laid singly; C- Mature eggs; D- Egg shells; E- 2nd instar larva; F- 3rd instar larva; G- 4th instar larva; H- Prepupa; I- Pupa; J- Adult

Photo credit: Sadia Munir

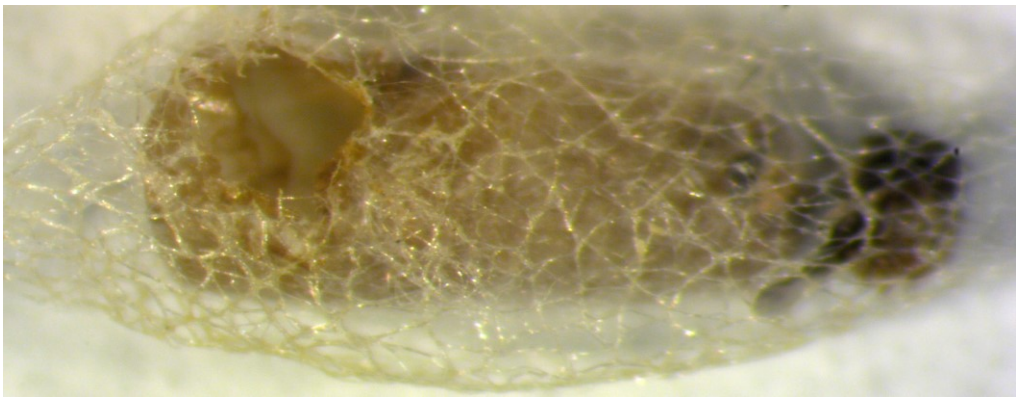


Figure 1-II. *Diadegma insulare* larva, spinning its cocoon inside the cocoon of *P. xylostella*

Photo credit: Andrei Sourakov (From Featured Creatures, 2000)

Figure 1-III. *Diadegma insulare* cocoon; mature & empty

Photo credit: Sadia Munir

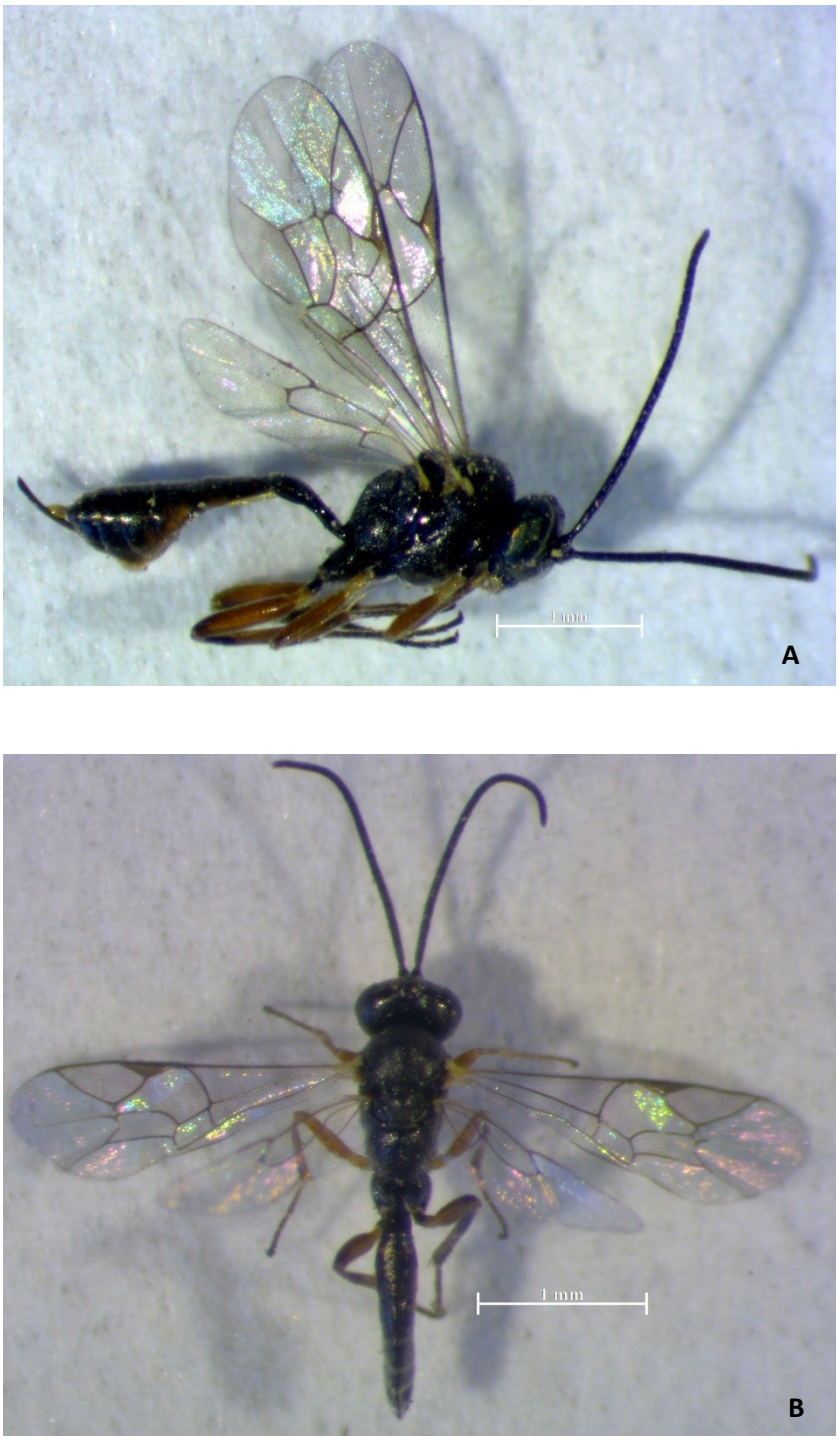


Figure 1-IV. *Diadegma insulare* A- Female B- Male

Photo credit: Sadia Munir

Chapter 2: Oviposition preferences of *Plutella xylostella* (L.) (Plutellidae: Lepidoptera) on water-stressed and non-stressed plants of *Brassica napus* L.

A version of this chapter has been published:

Munir S, Dosdall LM, O'Donovan. 2017. Oviposition preferences of *Plutella xylostella* (L.) (Plutellidae: Lepidoptera) on water-stressed and non-stressed plants of *Brassica napus* L. Journal of Entomology and Zoology Studies 5(4): 1143-1147.

2.1 Introduction

Plants experience several environmental biotic (e.g., imposed by other microorganisms & insects) and abiotic (e.g., drought, heat, cold & salinity) stresses that not only impact their growth and development (Saranga et al. 2001), but also their fitness and interaction with herbivores (Moran & Showler 2005; Sarfraz et al. 2009a). Water deficit stress is perhaps the most important abiotic stress to which plants are exposed (Sanghera et al. 2011; Pathak et al. 2014). The alteration in host plant quality often influences the response of insect herbivores, including their biological and life history traits (Mattson 1980; Koricheva et al. 1998; Daane & Williams 2003; Scheirs & De Bruyn 2005).

The effects of plant water stress on the insect attraction, oviposition and development can be very complex, uncertain and variable (Holtzer et al. 1988; Oswald & Brewer 1997; Showler & Moran 2003). The overall performance of insect herbivores can be altered on host plants experiencing water deficit relative to plants not under stress (White 1974). Oviposition of Lepidopteran pests can be enhanced (Wolfson 1980; Rubberson 1996; Showler & Moran 2003), reduced (Slosser 1980) or not affected (Badenes-Perez et al. 2005) in plants under water deficit stress. In addition to stress patterns, several other factors can determine female oviposition behavior, such as quality of the host plant (Craig et al. 1989; Singer 2003, 2004), preference as to where on an individual plant to lay eggs, leaf age (Price 1991; Badenes-Perez et al. 2005), leaf

size, internode length (Price et al. 1987), leaf and root-damaged plants (Silva & Furlong 2012), presence of previously laid eggs on the plant, leaf shape, and secondary plant compounds (Chew & Robbins 1984; Thompson & Pellmyr 1991; Freitas & Oliveira 1996; Textor & Gershenzon 2009). Survival of immature stages in Lepidoptera is greatly influenced by the oviposition choices of adult females (Renwick 1989).

The impact and importance of stressed host plants in mediating plant-herbivore interactions are unclear. Stress may induce contrasting patterns in oviposition, development and feeding preferences among herbivore species due to a change in plant suitability and attractiveness (Schoonhoven et al. 2005; Gutbrodt et al. 2011). The diamondback moth is a serious, worldwide pest of brassicaceous crops (Furlong et al. 2013), and its extensive geographic distribution encompasses regions and seasons where its host plants may develop under moisture deficit stress. So far, only one study has been conducted to determine the responses of *P. xylostella* to water stressed and non-stressed plants of cabbage (*Brassica oleracea* L.) (Badenes-Perez et al. 2005). However, the present study is focussed on canola (*Brassica napus* L.), a major economically important oilseed crop in Canada (Canola Council 2016).

The objective of this research was to investigate if diamondback moth, *Plutella xylostella* L., responds differently to water-stressed and non-stressed plants regarding ovipositional preferences.

2.2 Materials and methods

2.2.1 Experimental plants and insects

Four and six-week-old *Brassica napus* L. var. Q2 plants were used in the experiment. The plants were grown individually in plastic pots (15 cm diameter) using Metromix-220 (WR Grace

& Co, Ajax, ON, Canada) as a potting medium. Three seeds of *B. napus* were placed in a pot, and after emergence, seedlings were thinned to one per pot. Pots were thoroughly watered and placed in a growth chamber at a constant temperature of 21 ± 0.5°C, 40-50% r.h., and 16L: 8D photoperiod.

Plutella xylostella adults originated from a laboratory colony maintained on *B. napus* plants. *Plutella xylostella* were collected from different commercial fields of *B. napus*, *Brassica juncea* (L.) Czern. and *Sinapis alba* L. throughout Alberta, Canada and were periodically added to the laboratory colony to maintain the genetic diversity.

2.2.2 Imposition of water stress

All pots were watered daily to saturation until they reached the desired age of four or six-week old plants. Plants were randomly allocated to two alternative treatments: water-stressed or non-stressed (control). Plants of the control treatment were watered at 88 ml/day/plant throughout the experiment. For the water-stressed plants, irrigation was reduced to 30 mL/d/plant for four days and finally withheld for two to three days before the beginning of the experiment. All tests were initiated approximately 48 h after these conditions were imposed.

2.2.3 Assessment of leaf water potential

At the beginning of the water stress treatment, the leaf water potential (bar) of one randomly selected, fully expanded leaf from the center of each plant was measured using a Scholander pressure bomb (Model-610; PMS Instrument Co., Corvallis, OR). It is a reliable, practical and quick method of measuring water potential of plant tissues developed by Scholander (Scholander et al. 1965).

2.2.4 Oviposition choice test

Ovipositional preference of *P. xylostella* on water-stressed and non-stressed four- and six-week-old *B. napus* was determined under greenhouse conditions at 22 ± 0.5ºC, 50-70% r.h., and a photoperiod of 16 L: 8 D in the wooden screened cages. Each cage was assembled randomly with two plants of *B. napus,* one water-stressed and other non-stressed plant of the same age. The experiment was conducted as a choice test (water-stressed versus non-stressed), and it was replicated four times. Six pairs of newly eclosed *P. xylostella* adults were released in each cage and female moths were allowed to oviposit either on stressed or non-stressed plants of same age. Moths were also provided with 10% honey water on cotton wicks immersed in 20-mL plastic cups as a sugar source. After 48 h exposure to both treatments, adults were removed and plants were examined for eggs. Total numbers of eggs deposited on stressed and non-stressed plants were counted in the laboratory using a dissecting microscope.

2.2.5 Plant parameters

Plant stem height and stem diameter were measured at the end of the oviposition choice experiments. Stem diameter was measured using vernier calipers (Electronic Caliper, Mastercraft) at 10 cm above the root/shoot junction.

2.2.6 Statistical analysis

Variables were tested for normality and homoscedasticity, before subjecting them to the analysis. A two-way analysis of variance (ANOVA) (PROC MIXED) was performed to determine the effects of water treatments on oviposition preferences of four or six-week-old plants. If significant treatment effects were indicated, means were compared at the 5% level of significance using Fisher's Least Significant Difference (LSD) test (SAS Institute 2012). PROC TTEST for leaf water potential was performed. Correlations (PROC CORR) were determined

between plant height and egg deposition, and plant stem diameter and egg deposition (SAS Institute 2012).

2.3 Results

Leaf water potential of the water-stressed plants was significantly more negative (indicating a low leaf water potential) than the leaf water potential of non-stressed *B. napus* ($t = 9.64$; df = 6; $P < 0.0001$). Water stress affected the oviposition decisions of *P. xylostella* females. On average, 2.15 times more eggs were laid on non-stressed than the stressed plants ($F = 8.88$; df = 1, 12; $P = 0.0115$) (Fig. 2-I). Plant age also had a significant effect on ovipositional preference. The mean number of eggs laid on six-week-old *B. napus* plants was three times greater than on four-week-old non-stressed plants regardless of water treatment ($F = 19.43$; df = 1, 12; $P = 0.0009$) (Fig. 2-II). In general, 2.34 and 1.65 times more eggs were laid on six- and four-week-old unstressed *B. napus* plants than on the stressed plants, respectively (Fig. 2-III). There was no significant interaction between water treatment and plant age ($F = 4.26$; df = 1, 12; $P = 0.0613$). A significant positive correlation was found between oviposition and plant height ($r = 0.64$; $P = 0.0069$), but no correlation existed between oviposition and plant stem diameter ($r = -0.164$; $P = 0.54$).

2.4 Discussion

Greater ovipositional preference by insect herbivores for water-stressed host plants has been observed in many earlier studies (Wolfson 1980; Showler & Moran 2003; Reay-Jones et al. 2007; Seagraves et al. 2011). However, the effects of plant water stress on insect attraction can be inconstant, unpredictable and complex (Holtzer et al. 1988; Oswald & Brewer 1997). For

instance, no significant differences in *P. xylostella* ovipositional preferences were found between the water-stressed and non-stressed cabbage (*Brassica oleracea* L.) and yellow rocket (*Barbarea vulgaris* R. Br.) plants (Badenes-Perez et al. 2005).

In the present study, a clear ovipositional preference for non-stressed plants of *B. napus* was observed for *P. xylostella*. Significantly more eggs were laid on four- and six-week-old non-stressed *B. napus* plants than on water-stressed ones. These contradictory results relative to previous studies might reflect differences in host plant species used in different experiments. Female *P. xylostella* might evaluate host plant quality (regarding plant water status and nutritional value) and preferred suitable hosts for oviposition by morphological and physical characteristics or might prefer to oviposit on plant tissues that are high in water content (Seagraves et al. 2011). Furthermore, moths may choose an oviposition host that meets more than just the nutritional needs of their offspring. Hence, maximizing the chances of their progeny survival and growth (Bonebrake et al. 2010).

Ovipositional preference can be driven by plant age. A positive correlation between oviposition by *P. xylostella* and plant age has been observed in plant species like cabbage and yellow rocket (Badenes-Perez et al. 2005). In this study, a significant positive correlation between oviposition and increasing plant height was detected. Female moths may receive more stimulating visual and olfactory cues for oviposition as a result of the greater total leaf area in older plants. For example, three times more eggs were laid on six-week-old, as compared to four-week-old plants. Older plants may also offer more oviposition sites, the potential for shelter from natural enemies and more rich resources, for larval development (Badenes-Perez et al. 2005).

Water stress causes a reduction in shoot/stem growth. Reduced growth is one of the most evident and consistent responses of plants to water deficit (Mattson & Haack 1987; Waring &

Cobb 1992). The strong significant positive relationship between total number of eggs laid and plant stem height, indicated that females select healthier plants on which their offspring can develop. In general, the research findings support the preference-performance hypothesis, according to that oviposition preference should correspond with host suitability. Thus, female phytophagous insects select to oviposit on host plants that optimize the fitness of their progeny (Jaenike 1978). The study results confirmed that *P. xylostella* females preferred to deposit eggs on six-week-old vigorous plants, not under water stress to ensure the successful development and survival of their offspring.

Acknowledgments

Funding for this study from the Canola Council of Canada, Alberta Canola Producers Commission, Agriculture and Agri-Food Canada and the Natural Sciences and Engineering Research Council of Canada is gratefully acknowledged. For technical assistance, we are grateful to R. Subramaniam and K. Van Camp.

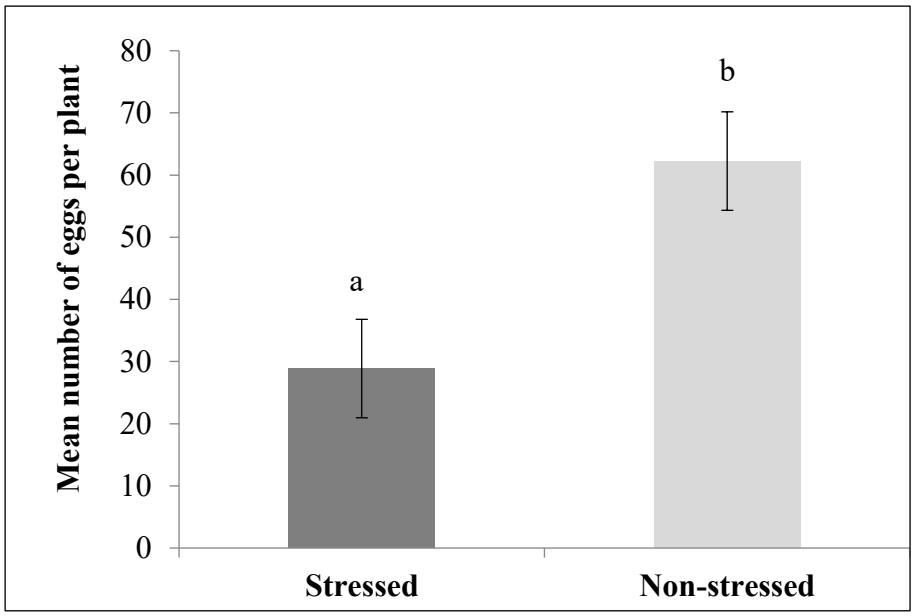


Figure 2-I. Mean (± SE) eggs of *Plutella xylostella* deposited on water stressed and non-stressed plants.

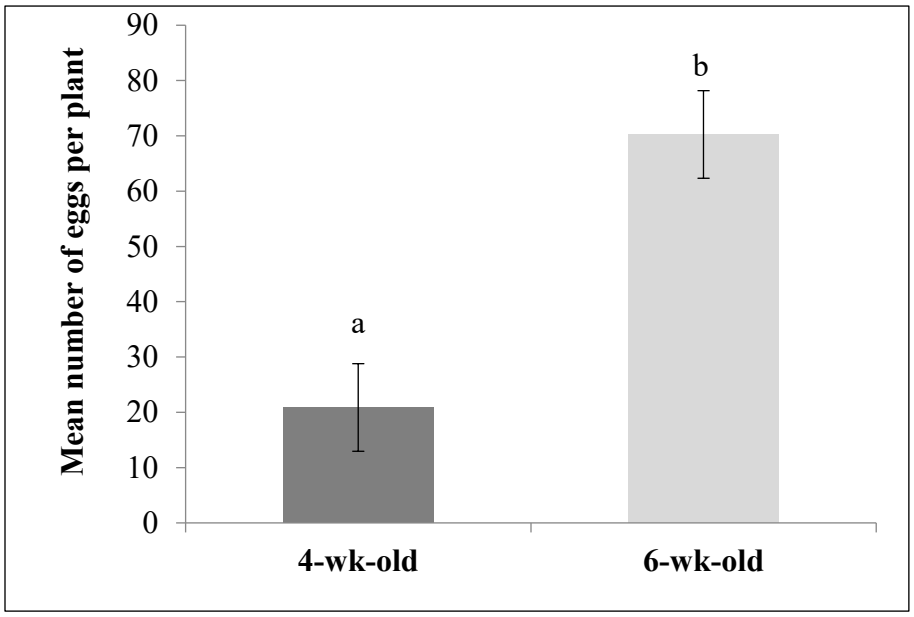


Figure 2-II. Mean (± SE) eggs of *Plutella xylostella* deposited on 4- and 6-week-old plants.

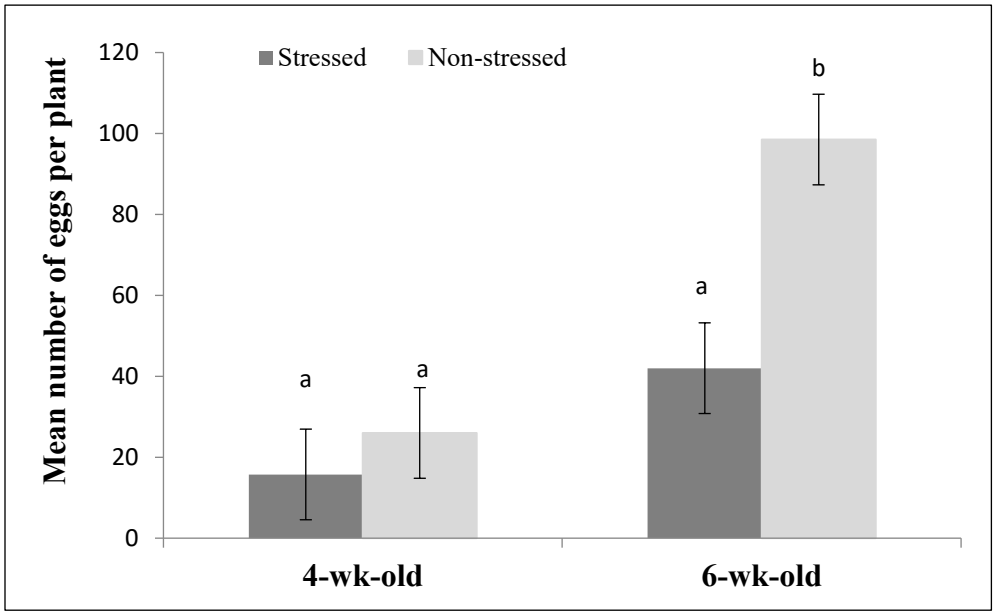


Figure 2-III. Mean (± SE) eggs of *Plutella xylostella* deposited on 4- and 6-week-old stressed and non-stressed *Brassica napus*. Means followed by the same letter are not significantly different at 5% level (Fisher's PLSD test following ANOVA).

Chapter 3: *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) development is altered by *Plutella xylostella* (L.) (Plutellidae: Lepidoptera) reared on water-stressed host plants

A version of this chapter has been published:
Munir S, Dosdall LM, O'Donovan JT, Keddie BA. 2016. *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) development is altered by *Plutella xylostella* (L.) (Plutellidae: Lepidoptera) reared on water-stressed host plants. Journal of Applied Entomology 140: 365-375.

3.1 Introduction

Climate change can have diverse effects on all living organisms that are linked through trophic relationships with plants, herbivores, and natural enemies. The equilibrium, functioning, and overall stability of an ecosystem depend on the relative responses of each trophic level and species. These reactions are highly diverse and variable when exposed to different climatic extremes (Tylianakis et al. 2008; De Sassi & Tylianakis 2012; Romo & Tylianakis 2013). Climate changes are likely to have major impacts on the presence, physiology, production, abundance and distribution of plants (Rustad et al. 2001; Anwar et al. 2007); population density, herbivory (Bale et al. 2002), distribution (Trnka et al. 2007), phenology (Parmesan 2007), emergence time (Dewar & Watt 1992; Whittaker & Tribe 1996, 1998) and voltinism (Zvereva & Kozlov 2006) of the insect herbivores; and their natural enemies distribution, abundance, activity and fitness (Romo & Tylianakis 2013). Many studies have indicated that the effects of climate change on plants such as elevated CO_2 (Thomson et al. 2010), higher temperature and drought (Bale et al. 2002; Aslam et al. 2013; Romo & Tylianakis 2013), altered precipitation patterns (Haile 2002) and ozone concentration (Valkama et al. 2007) can impact phytophagous insects.

Studies that examine the effect of water deficit stress on lepidopteran insects generally indicate inconsistent and variable responses in performance of herbivores. The performance of

herbivores under water deficit stress conditions can be neutral (Miles et al. 1982; Moran & Showler 2005; Rouault et al. 2006), decrease (Inbar et al. 2001; Badenes-Perez et al. 2005; Rouault et al. 2006), or increase (Mattson & Haack 1987; Rouault et al. 2006). For instance, Gutbrodt et al. (2011) reported a contrasting developmental response to water stress by two lepidopteran species of the same feeding guild. *Pieris brassicae* (L.) development was faster on drought-stressed than on well-irrigated plants, while *Spodoptera littoralis* (Boisduval) showed retarded development on stressed plants. Similarly, the infestation of cabbage aphid, *Brevicoryne brassicae* L., on water-stressed rape, *Brassica napus* L., was observed to be more severe than on non-stressed plants (Burgess et al. 1994; Popov et al. 2006). Water deficit stress can influence plant physiological processes by altering plant metabolism and biochemistry that consequently changes herbivore performance (Hsiao 1973; Beck et al. 2007; Showler 2012). Moreover, due to the inadequate availability of water, host plant suitability and quality for utilization by herbivores can decline (Mattson & Haack 1987; Showler 2012).

Herbivores and their natural enemies respond differently to temperature and water deficit stress and natural enemies are more sensitive to environmental change than their herbivore counterparts (Romo & Tylianakis 2013). For example, water stressed cassava host plants positively influenced the development of the cassava mealybug, *Phenacoccus herreni* Cox & Williams (Hemiptera: Pseudococcidae), but adversely affected its natural enemies depending on parasitoid development and the species concerned (Calatayed et al. 2002).

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a widely distributed and destructive oligophagous pest of brassicaceous crops (Talekar & Shelton 1993; Furlong et al. 2013). *Plutella xylostella* control and yield losses in brassicas are estimated to cost the world economy US$ 4–5 billion annually (Furlong et al. 2013). Climate change and an

increasing brassicaceous crop production area is predicted to enhance the pest status of *P. xylostella* (Dosdall et al. 2011). With every +2°C increase in average summer temperature and drought, 2-5 more generations of *P. xylostella* can develop (Olfert et al. 2011). More than 135 parasitoid species have been recognized to attack different life stages of *P. xylostella* (Delvare 2004). *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) is a solitary, koinobiont, host-specific endoparasitoid of *P. xylostella* larvae, and is considered one of the most important *P. xylostella* biological control agents in Nearctic and Neotropical regions (Azidah et al. 2000; Sarfraz et al. 2005a). As compared to other larval parasitoids, it is a most competitive and efficient host searcher (Xu et al. 2001; Wang & Keller 2002) and can parasitize up to 90% of *P. xylostella* larvae (Sourakov & Mitchell 2000). The population dynamics of *D. insulare* are highly synchronized with its host (Harcourt 1960) as the number of generations per year corresponds to the number of generations of its host (Putnam 1968; Sourakov & Mitchell 2000).

Despite being an important, principal, and effective biological control agent, extensive research on factors affecting *D. insulare* developmental biology is lacking. To date, only two studies have been evaluated the impact of water-stressed host plants on *P. xylostella* (Badenes-Pérez et al. 2005; Wachira et al. 2009), but how this water stress affects its natural enemies is not known. The objectives of this study were to address the tritrophic interactions between host plants, *P. xylostella,* and its specialist parasitoid wasp *D. insulare* and to evaluate the influence of water-deficit stressed first trophic level producers (host plant) on the developmental biology of third trophic level consumers (parasitoid).

3.2 Materials and methods

3.2.1 Experimental plants and insects

Two different species of Brassicaceae, *Brassica napus* L. var. Q2 and *Sinapis alba* L. var. AC Pennant were used in all experiments. The plants were grown individually in plastic pots (13 cm diameter) using Metromix-220 (WR Grace & Co. Ajax, ON, Canada) as a potting medium. Three seeds of each plant species were placed in a pot, and after emergence, seedlings were thinned to one per pot. Pots were watered thoroughly and placed in a growth chamber at a constant temperature of 21 ± 0.5°C temperature, 40-50% r.h., and 16 L: 8 D photoperiod. Four-week-old plants were used for all experiments.

Plutella xylostella and *D. insulare* adults originated from a laboratory colony maintained on *B. napus* plants. Moths and wasps were collected from different commercial fields of *B. napus*, *Brassica juncea* (L.) Czern. and *S. alba* throughout Alberta, Canada and were periodically added to the laboratory colony to maintain genetic diversity.

3.2.2 Imposition of water stress

All pots were watered daily to saturation until they reached the desired age. For both experiments (*P. xylostella* and *D. insulare* development), plants of each species were allocated randomly to two alternative treatments: water-stressed or non-stressed. Non-stressed plants were watered at 88 mL/d/plant throughout the experiment, while water-stressed plants were under the same irrigation regime until one week before the experiment. Irrigation for the water-stressed plants was reduced to 60 mL/d/plant for four days and finally to 30 mL/d/plant, three days before the beginning of the experiment, and this irrigation regime was followed throughout the experiment.

3.2.3 Assessment of leaf water potential and other host-plant parameters

At the beginning of the water stress treatment, the leaf water potential (bar) of one randomly selected, fully expanded leaf from the center of each plant was measured using a pressure bomb (Model-610, PMS Instrument Co., Corvallis, OR). The water status (leaf water potential) of both host plant species was affected under water-stressed conditions. Therefore, the commonly used and most affected physiological parameters of the host plants under water-deficit conditions were determined.

Plant stem height (cm) and stem diameter (mm) were measured at the end of each developmental study. Stem diameter was measured using vernier calipers (Electronic Caliper, Mastercraft) at 10 cm above the root/shoot junction. The total number of leaves per plant was also counted after imposing the water stress conditions. The total leaf surface area (cm^2) of one randomly selected, fully expanded leaf from the center of the plant was measured for both treatments using a leaf area meter (Model 3100, LI-COR, Lincoln, Nebraska, USA). Host plants were dried at room temperature for two weeks after the developmental study was completed and then oven dried at 60ºC for 48 h. Total dry weights of plants (mg) and dry weights of individual plant organs for both stressed and non-stressed *S. alba* and *B. napus* were measured on an electrical balance (Model XS204, Mettler-Toledo, Greifensee, Switzerland).

3.2.4 Effect of water-stressed plants on development of *P. xylostella*

The experiment was conducted as a no-choice test (water-stressed vs. non-stressed plants), separately for the two different plant species, *B. napus,* and *S. alba*. Pest development was assessed in wooden screened cages (40 × 40 × 80 cm) arranged on a greenhouse bench at 22 ± 0.5º C, 50-70% r.h., and 16 L: 8 D photoperiod. Each cage contained a pot with either a stressed or non-stressed plant, of either *B. napus* or *S. alba*. For each plant species tested under stressed or

non-stressed conditions, four such cages were maintained in a completely randomized design. Ten to 15 eggs of *P. xylostella* per plant were attached to leaves by first allowing the females to oviposit on tinfoil dipped in cabbage/ *B. napus* leaf extract. Times for each developmental stage (larva, pupa, and adult), adult longevities without food and mortalities were recorded for both stressed and non-stressed treatments of each plant species. Pupae were harvested, weighed and maintained in their respective cages until adult emergence.

3.2.5 Effect of water-stressed plants on development of *D. insulare*

The experimental setup, plant species, and water treatments were the same as indicated in the *P. xylostella* development study. Third instar *P. xylostella* larvae (160-170) were allowed to be parasitized by six to eight pairs of one to two-day old *D. insulare* in a cage with host plant material for 24 h, and then 10 larvae per plant were transferred to the experimental cages. Time to each developmental stage, adult longevities without food and mortalities of adults were recorded for both stressed and non-stressed treatments of each plant species. *Diadegma insulare* pupae were harvested, weighed within 24 h of pupation and maintained in their respective cages until adult emergence. After adult eclosion, the silk cocoons were also weighed on an electrical scale (Model XS204, Mettler-Toledo, Switzerland). Forewing, hindwing and hind tibia length of adult *D. insulare* were measured with AxioVision 4.8.2 (Carl Zeiss, Jena, Germany).

3.2.6 Statistical analysis

Variables were tested for normality and homoscedasticity before subjecting them to the analysis. Data were log transformed for the diamondback moth longevity test, but untransformed means are presented for clarity. Analysis of variance (PROC MIXED) for a completely randomized design was performed to determine the treatment effects on development, longevity, adult body weight, pupa, and silk weight of *P. xylostella* and *D. insulare*, and also on the

forewing, hindwing and hind tibia length of *D. insulare*. If significant treatment effects were indicated, means were compared at the 5% level of significance using Fisher's PLSD (Protected Least Significant Difference) test (SAS Institute 2012). Correlations (PROC CORR) were determined between pupal weight and silk weight, pupal weight and longevity, pupal weight and adult weight of *P. xylostella*; and between pupal weight and silk weight, pupal weight and adult weight, adult weight and wing length, adult weight and tibia length, and longevity and body size (forewing length, hindwing length and hind tibia length) of *D. insulare*. The total dry weight and mean dry weight of individual plant organs, plant height, plant diameter, the number of leaves and leaf surface area of stressed and non-stressed plants were compared using a two-tailed Students *t*-test with PROC TTEST (SAS Institute 2012). All data were analyzed by SAS version 9.3.

3.3 Results

3.3.1 Assessment of host-plant parameters under water-stress

The plant species and water regime used in both *P. xylostella* and *D. insulare* developmental studies were similar. Therefore, only the results of host plant parameters measured in the *D. insulare* development study are presented.

Water deficit influenced most of the plant parameters studied. Water-stressed plants had visual signs of water deficit such as leaf rolling, wilting, yellowing or discoloration of lower leaves. Leaf water potential of the water-stressed plants was significantly more negative (indicating a low leaf water potential) than leaf water potential of non-stressed *B. napus* and *S. alba* plants (*B. napus*: $t = 8.76$; df = 6; P = 0.0001), (*S. alba*: $t = 7.65$; df = 6; P = 0.0003) (Fig.

3-I). The absolute values for leaf water potential were 2.23 and 2.80 times higher in the water-stressed than on non-stressed *B. napus* and *S. alba* plants, respectively.

Non-stressed *B. napus* and *S. alba* had significantly increased stem height, greater total dry weight, dry weight of individual plant organs and greater leaf surface area than their water-stressed counterparts. However, no significant differences were detected between the total number of leaves of stressed and non-stressed *B. napus* or *S. alba* (Table 3-1).

3.3.2 Effect of water stressed host plant on *P. xylostella* development

Development of *P. xylostella* from larva to pupa and from pupa to adult was not significantly affected by water-stressed and non-stressed treatments (larva to pupa: $F = 1.41$; $df = 1, 12$; $P = 0.25$); (pupa to adult: $F = 0.97$; $df = 1, 12$; $P = 0.34$), or by host plant species (larva to pupa: $F = 0.10$; $df = 1, 12$; $P= 0.75$); (pupa to adult: $F = 3.63$; $df = 1, 12$; $P = 0.08$). Mean development time from larva to adult on stressed plants was recorded as 12.50 ± 0.26 (SE) days, and on non-stressed plants was 13.03 ± 0.26 (SE) days. Although there were no significant effects of water treatment and plant species on development of *P. xylostella*, a trend of slightly more rapid development (1.04 days early) was observed on stressed *S. alba* plants (Table 3-II). Similarly, longevity, pupal and silk weights were similar and not significantly affected by stress treatment or host plant species, indicating that these parameters were not influenced by water stress and host plant species (Table 3-II). Significant positive correlations were detected only between female weight and silk weight ($r = 0.65$, $P = 0.006$), but correlations between pupal weight and longevity ($r = -0.12$, $P = 0.63$), pupal weight and silk weight ($r = -0.001$, $P = 0.99$), pupal weight and male weight ($r = 0.13$, $P = 0.61$), and pupal weight and female weight ($r = 0.25$, $P = 0.33$) were not significant.

3.3.3 Effect of water-stressed plants on development of *D. insulare*

Developmental parameters for time of egg to pupa and egg to adult were significantly modified by water stress and plant species (egg to pupa: $F = 5.41$; $df = 1, 12$; $P = 0.0384$, $F = 13.91$; $df = 1, 12$; $P = 0.0029$) (Fig. 3-IIA), and (egg to adult: $F = 6.32$; $df = 1, 12$; $P = 0.0272$, $F = 12.22$; $df = 1, 12$; $P = 0.0044$) (Fig. 3-IIC). However, development from pupa to adult was not significantly affected by water treatment and plant species (pupa to adult: $F = 2.68$; $df = 1, 12$; $P = 0.1277$, $F = 3.09$; $df = 1, 12$; $P = 0.1042$) (Fig. 3-IIB). Mean development time from egg to pupa and egg to adult was shortest on non-stressed *B. napus* plants (8.35 ± 0.42 and 15.85 ± 0.66) and longest on stressed *S. alba* (10.93 ± 0.42 and 19.83 ± 0.66, respectively), while development took place almost at the same rate from pupa to adult. No significant interactions of water treatment and plant species were detected for any developmental stage (pupa to adult: $F = 0.09$; $df = 1, 12$; $P = 0.7707$, and egg to adult: $F = 0.03$; $df = 1, 12$; $P = 0.8637$, respectively), indicating that these parameters were influenced independently by water stress and host plant species.

Parasitoid longevity was affected significantly by both water treatment ($F = 5.44$; $df = 1, 12$; $P = 0.0380$) and plant species ($F = 50.41$; $df = 1, 12$; $P < 0.0001$) (Fig. 3-III). In general, longevity was 1.5 days longer on *B. napus* as compared with *S. alba* regardless of water treatment and development required, and 1.15 days more on stressed as compared with non-stressed plants regardless of species. The interaction of water treatment and plant species was also significant for adult longevity without food ($F = 9.08$; $df = 1, 12$; $P = 0.0108$). Thus, this parameter was influenced by water treatment, but varied between the plant species. For instance, the longevity of the parasitoids was 1.3 days greater on stressed as compared with non-stressed *B. napus*, while there was no significant difference between stressed and non-stressed *S. alba.*

Diadegma insulare pupa and silk weight were significantly influenced only by plant species ($F = 95.57$; $df = 1, 12$; $P < 0.0001$ and $F = 4.93$; $df = 1, 12$; $P = 0.0464$, respectively). In general, heavier pupae were produced on *B. napus* under non-stressed conditions (4.51 ± 0.12mg), while pupal silk was found to be heavier on *S. alba* under water-stressed conditions (1.05 ± 0.07mg).

Adult weight was significantly affected by water treatment ($F = 99.08$; $df = 1, 24$; $P < 0.0001$), plant species ($F = 21.75$; $df = 1, 24$; $P < 0.0001$) and sex of the parasitoid ($F = 19.64$; $df = 1, 24$; $P = 0.0002$) (Fig. 3-IV). In general, the adults were heavier, especially in non-stressed conditions on both *B. napus* (0.41± 0.02mg) and *S. alba* plants (0.62 ± 0.02mg) as compared with their stressed counterparts, regardless of parasitoid sex. Similarly, females were heavier than males on non-stressed plants regardless of plant genotype. A significant interaction of water treatment and plant species ($F = 25.11$; $df = 1, 24$; $P < 0.0001$), water treatment and parasitoid sex ($F = 27.48$; $df = 1, 24$; $P < 0.0001$), and water treatment, plant species and parasitoid sex ($F = 23.96$; $df = 1, 24$; $P < 0.0001$) were also detected for adult weight. Thus, this parameter was influenced by water stress, but differed based on host plant species and adult parasitoid sex. However, no significant interaction was detected between host plant species and sex of the adult parasitoid ($F = 1.15$; $df = 1, 24$; $P = 0.2945$).

Hindwing length was the only parameter among forewing and hind tibia length influenced by plant species ($F = 6.46$; $df = 1, 12$; $P = 0.0259$). Hindwing length was larger on *B. napus* host plants.

For most of the biological parameter studies, no significant correlations were detected. For *D. insulare* reared on *P. xylostella* larvae that consumed the host plant, significant negative correlations were found between some parameters like pupal and silk weight ($r = -0.55$, $P =$

0.0246), adult weight and forewing length (r = -0.59, P = 0.0153), adult weight and hind wing length (r = -0.66, P = 0.0049), and a positive significant relationship occurred between hind wing and hind tibia length (r = 0.79, P = 0.0002), regardless of water treatment. If the host plant was non-stressed, significant positive correlations were found between forewing and hind wing length (r = 0.95, P = 0.0003), forewing and hind tibia length (r = 0.79, P = 0.0195), and hind wing and hind tibia length (r = 0.78, P = 0.0202), but negative correlations existed between adult weight and forewing length (r = -0.82, P = 0.0114), and adult weight and hind wing length (r = -0.73, P = 0.0373). Similarly, if the host plant was under water-stressed conditions, significant positive correlations were found only between silk weight and forewing length (r = 0.73, P = 0.0363), and hindwing and hind tibia length (r = 0.86, P = 0.0053). No correlations were found between the longevity and body size of the parasitoid.

3.4 Discussion

Any change in plant quality induced by water stress could directly alter life history parameters of insect herbivores and indirectly influence parasitoids either in a positive or negative way (Godfray 1994; Inbar et al. 2001; Brodeur & Boivin 2004; Pritchard et al. 2007). Plant architecture in terms of branching pattern, the size of different plant parts, shape and position of leaves and flower organs, is greatly influenced by environmental factors such as light, temperature, humidity and nutrient status (Reinhardt & Kuhlemeier 2002). Reduced water availability results in limited cell division due to impaired mitosis and obstructed cell elongation due to loss of turgor that ultimately diminishes growth (Farooq et al. 2009). Water deficit influences most of the morphological and physiological traits of host plants like plant height, diameter, growth, plant total fresh and dry weight, leaf water content, etc. (Zhang et al. 2009;

Bolat et al. 2014), depending on the host plant species, and the level, duration and type of stress (Mattson & Haack 1987; Grime & Campbell 1991). In the present study, both host plants showed reduced leaf water potential under water deficit conditions. Water stress also caused a significant reduction in stem growth, which is one of the most obvious, immediate and consistent responses of plants to water deficit (Mattson & Haack 1987; Waring & Cobb 1992).

In this study, despite clear indications of water deficit stress on the host plant (first trophic level), in terms of wilting, yellowing of lower leaves, reduced plant growth, smaller leaf surface area and low leaf/xylem water potential of the stress- treated plants, the stress treatment did not influence *P. xylostella* (second trophic level) development. The findings from the present study do not support the plant stress hypothesis of White (1969, 1974), who proposed that herbivore performance increases on stressed host plants. However, the present results are consistent with those of Slansky & Feeny (1977), Miles et al. (1982) and Wachira et al. (2009). For instance, Slansky & Feeny (1977) and Miles et al. (1982) reported almost the same rate of *P. rapae* development on different water-stressed and non-stressed Brassicaceae species with different levels of nitrogen content. Similarly, Wachira et al. (2009) observed no significant effect of water-stressed host plants on larval development of *P. xylostella*. In the present study, *P. xylostella* appeared to maintain the same rate of development in both stressed and non-stressed plants despite differences in plant architecture and possibly plant quality due to water stress. It may accomplish this by adjusting its food intake like other lepidopteran pests (e.g., *Pieris rapae* L.) (Miles et al. 1982). Moreover, the similar developmental rates of *P. xylostella* on water-stressed and non-stressed plants may reflect the genotypic plasticity of this species that enables it to be among the most successful insect pest species worldwide (Talekar & Shelton 1993; Furlong et al. 2013).

Evaluation of water-stressed plants on the biological parameters of the third trophic level (parasitoid) showed that water treatment and plant genotype on which *P. xylostella* larvae were reared, significantly affected the developmental time of *D. insulare* from egg to pupa and egg to adult. In general, development was more rapid on non-stressed *B. napus* as compared with water-stressed *B. napus* and *S. alba*. Similarly, complete development from egg to adult was one day faster on non-stressed plants regardless of plant species and 1.13 days more rapid on *B. napus* as compared with *S. alba* regardless of water treatment. Sarfraz et al. (2008) evaluated the performance of *D. insulare* when its host larvae were reared on different Brassicaceae species and found that *D. insulare* development varied considerably among different plant species. For instance, egg to pre-pupal development of *D. insulare* was fastest on *B. juncea* and slowest on *B. oleracea* L., whereas complete development from egg to the adult was most rapid on *B. napus* cv. Liberty as compared to *B. napus* cv. Q2. Moreover, plant species could differentially affect the pest and its natural enemy. For instance, pre-pupal to adult development of *P. xylostella* was fastest on *S. alba* and slowest on *B. oleracea* (Sarfraz et al. 2007), while *D. insulare* pre-pupal to adult development was fastest on *B. napus* and *B. oleracea* and slowest on *B. carinata* (Sarfraz et al. 2008). In the present study, overall development of *D. insulare* was fastest on *B. napus* and slowest on *S. alba* regardless of water treatment, a developmental pattern that was opposite to its host *P. xylostella*.

Most of the biological parameters of *P. xylostella* that were evaluated in this study like silk weight, adult weight, and longevity without food were not significantly correlated with pupal weight. In contrast, *D. insulare* pupal, and silk weights were affected by host plant genotype, and heavier pupae were produced on non-stressed *B. napus* plants while heavier silk developed on stressed *S. alba* plants. Furthermore, no significant positive correlations were found between

pupal weight and other biological parameters. Pupal weight is considered as one of the indicators of offspring fitness. Heavier pupae are assumed to produce more silk, and also larger and more fecund adults (Barah & Sengupta 1991; Armbruster & Hutchinson 2002). In fact, besides pupal weight, there are many other aspects like host plant genotype and environmental factors that can influence adult body weight, longevity and wing size of an insect pest (Sarfraz et al. 2007). Thus, it is probable that plant species and various environmental factors had greater effects on *P. xylostella* and *D. insulare* pupal and silk weight than host plant water stress.

Natural enemies development rate, body weight, size, and adult longevity are some of the important factors that determine their fitness, and this fitness is directly linked to host quality and either limit or enhance parasitoid fitness (Romo & Tylianakis 2013). Plant phenology and physiology indirectly influence natural enemies. The food availability for herbivores and natural enemies generally decrease due to lack of synchrony caused by climatic changes (Thomson et al. 2010). Furthermore, the fitness of natural enemies can decline as the quality of their herbivore hosts decreases, and they have to feed on a low quality host, particularly in koinobiont parasitoids whose host continues to feed after parasitization (Harvey et al. 1999; Hoover & Newman 2004; Wang et al. 2007). For instance, oat aphid, *Rhopalosiphum padi* L. development was reported to be altered by water-stressed host plants, and parasitism by the parasitoid wasp *Aphidius ervi* was reduced significantly on water-stressed plants (Aslam et al. 2013). Similarly, larval and pupal development of *P. xylostella* was slower on plants growing in nitrogen deficient soil (Sarfraz et al. 2009a), while *D. insulare* developed more rapidly on host larvae that were reared on highly fertilized plants (Dosdall et al. 2011). In the present study, the development time of *D. insulare* was prolonged, and lighter pupa and females were produced on *P. xylostella* that was reared on water deficient plants, indicating lower fitness of the parasitoid wasp on the stressed host.

Adult longevity is an important characteristic to evaluate the effectiveness of a parasitoid. It can be influenced by many biotic (host and its quality, body size, mating, adult feeding, etc.) and abiotic (temperature, drought, humidity, photoperiod) factors (Jarvis & Copland 1996; Eliopoulos et al. 2005). Research by Sarfraz et al. (2008) demonstrated that *D. insulare* lived for the shortest time on *B. napus* cv. Q2 and longest on *S. alba* when no food was supplied. The present research, however, showed the longest survival without food on *B. napus* compared to *S. alba*, regardless of water treatment. Similarly, body size (hind tibia length, forewing and hindwing length) can influence many biological parameters including longevity (Sarfraz et al. 2008). In the present study, hindwing length was the only parameter affected by plant species. Parasitoids that developed on a host reared on *B. napus* had 1.12 mm larger hindwings than on *S. alba*. Similarly, the parasitoid lived significantly longer on stressed *B. napus* than on stressed *S. alba*. Several previous studies showed a positive correlation between body size and longevity, and also showed that large wasps lived significantly longer than small ones (Hardy et al. 1992; Harvey et al. 1999), but it is not always true that body size and other biological parameters correlate with longevity (Blackburn 1991).

The practice of releasing natural enemies for biological control requires consistent relationships between herbivore and natural enemy performance and host plant stress. However, the results of many studies suggest that responses of herbivores and their natural enemy response to host plant stress can vary greatly and depend on the particular plant-herbivore and its natural enemies system including type and magnitude of host plant stress, and herbivore and parasitoid species (Waring & Cobb 1992; Koricheva et al. 1998; Calatayud et al. 2002; Haile 2002). For instance, cassava mealybug, *P. herreni* development was favored by cassava under water deficit stress. However, development of its associated parasitoid complex showed variable results

depending on parasitoid species (Calatayud et al. 2002).

Environmental factors, particularly moisture deficit, influence plant quality, which in turn may affect herbivore performance positively or negatively (White 1974; Mattson & Haack 1987; Hanks & Denno 1993). These factors can either directly affect distribution and abundance and development of insect pests or indirectly affect their host plants, competitors and natural enemies (Porter et al. 1991). It is evident from the present study that a water deficit stressed first trophic level indirectly influences the development of the third trophic level parasitoids. The slow development of *D. insulare* on water stressed plants might have been due to lack of appropriate and adequate nourishment by its host *P. xylostella,* which may have been directly or indirectly caused by the reduced plant development when the plants were stressed. Natural enemies are more sensitive to climatic changes than their hosts. The fitness of parasitoids declines in response to changes in the quality of their herbivore hosts and this may have unpredicted consequences on the effectiveness of biocontrol. Because of the diverse influences of climatic changes on natural enemies, it is important to have a better understanding of how climatic change impact tritrophic interactions (Thomson et al. 2010). Further detailed laboratory and field studies may help to understand tritrophic interactions between *P. xylostella*, its host plants and natural enemies, and to make useful predictions considering interactions under different stress conditions and ultimately their influence on crop yield. This may eventually result in the design of long-term, efficient integrated pest management plans based on regional climatic change scenarios.

Acknowledgments

Funding for this study is gratefully acknowledged from the Canola Council of Canada, the Alberta Canola Producers Commission, Agriculture and Agri-Food Canada and the Natural Sciences and Engineering Research Council of Canada.

Table 3-I. Mean (±SE) plant morphological characteristics of water-stressed and non-stressed plants of *Brassica napus* and *Sinapis alba* including height, diameter, leaf number, leaf surface area, total plant dry weight and dry weights of leaves, petioles, buds, flowers and stems.

Treatment	Host plant	Plant height (cm)	Plant diameter (mm)	Total number of leaves	Leaf surface area (cm^2)	Total plant dry weight (mg)	Leaf dry weight (mg)	Petiole dry weight (mg)	Bud & flower dry weight (mg)	Stem dry weight (mg)
Stressed	*S. alba*	61.05 ± 3.42^a	4.94 ± 0.59^a	11.41 ± 1.48^a	19.56 ± 4.27^a	3837.9 ± 134.1^a	1134.7 ± 92.2^a	297.9 ± 40.12^a	483.1 ± 23.75^a	1922.3 ± 80.38^a
Non-stressed		80.96 ± 2.85^b	4.39 ± 0.83^a	11.58 ± 1.60^a	40.44 ± 7.27^b	6078.3 ± 123.8^b	2142.3 ± 238.8^b	519.8 ± 62.64^b	916.2 ± 57.08^b	2500.0 ± 101.1^b
Stressed	*B. napus*	26.35 ± 2.79^a	5.13 ± 0.44^a	11.37 ± 1.14^a	28.00 ± 5.59^a	4083.7 ± 537.5^a	2070 ± 287.7^a	285.6 ± 140.7^a	78.72 ± 24.06^a	1280.2 ± 161.4^a
Non-stressed		49.69 ± 6.99^b	4.78 ± 0.39^a	10.50 ± 1.48^a	47.98 ± 2.15^b	6464.1 ± 333.5^b	3324.2 ± 235.1^b	980.9 ± 93.75^b	473.1 ± 102.8^b	2054.4 ± 218.7^b

Column means followed by the same letter are not significantly different ($P = 0.05$) (Student's *t*-test)

Table 3-II. Mean (± SE) development time, silk weight, pupal weight, adult weight and adult longevity without food for *Plutella xylostella* on water-stressed and non-stressed *Brassica napus* and *Sinapis alba* host plants.

Variable	Development (days)			Weight (mg)			Longevity without food (days)
	Larva to pupa	Pupa to adult	Larva to adult	Silk	Pupa	Adult	
A-Water treatment							
1- Stressed	8.0450 ± 0.25	4.4595 ± 0.21	12.5050 ± 0.26	0.2568 ± 0.02	6.6982 ± 0.24	0.8414 ± 0.04	6.6851 ± 0.51
2- Non-stressed	8.4663 ± 0.25	4.7647 ± 0.21	13.0312 ± 0.26	0.2034 ± 0.02	6.4092 ± 0.24	0.7062 ± 0.04	6.3013 ± 0.51
B- Genotype							
1- *B. napus*	8.3125 ± 0.25	4.9073 ± 0.21	13.0163 ± 0.26	0.2183 ± 0.02	6.7636 ± 0.24	0.7984 ± 0.04	6.7031 ± 0.51
2- *S. alba*	8.1988 ± 0.25	4.3169 ± 0.21	12.5200 ± 0.26	0.2419 ± 0.02	6.3438 ± 0.24	0.7492 ± 0.04	6.2833 ± 0.51

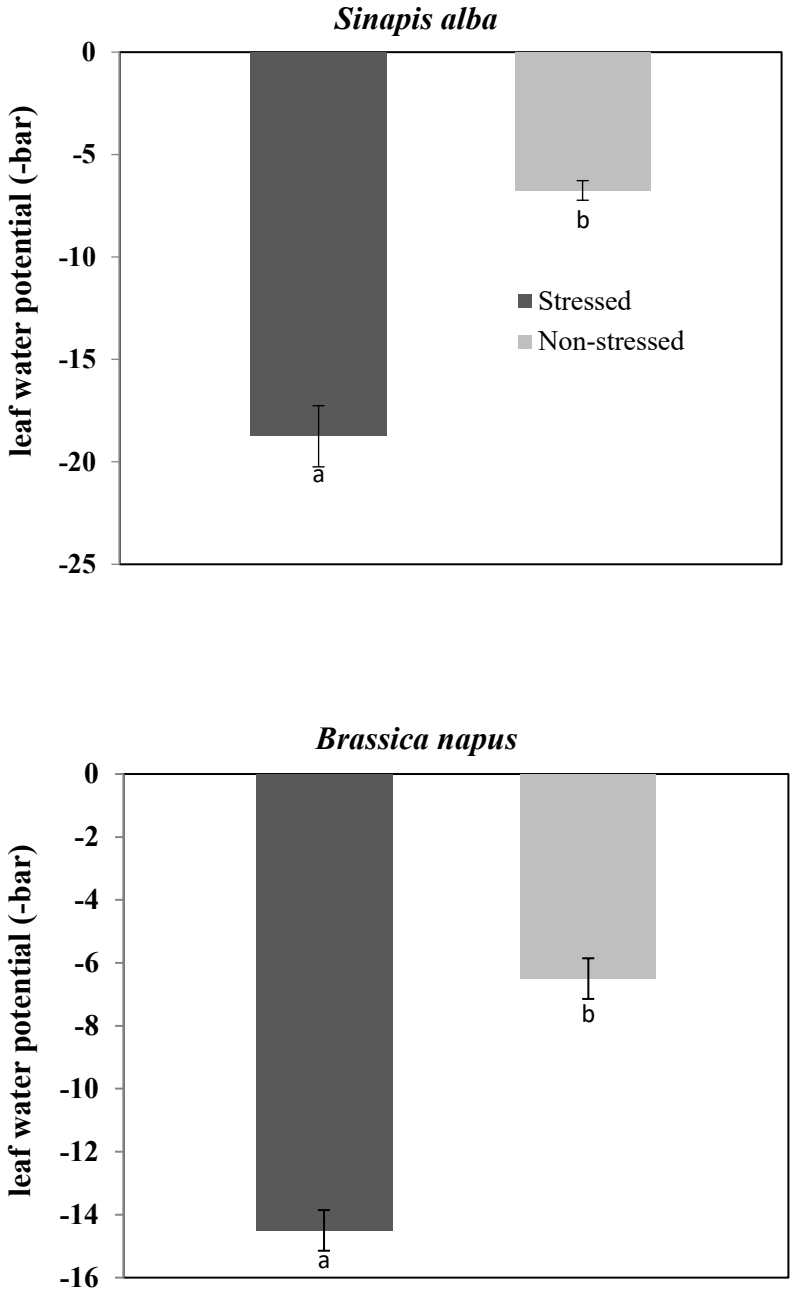


Figure 3-I. Mean (± SE) leaf water potential of water-stressed and non-stressed *Brassica napus* and *Sinapis alba.*

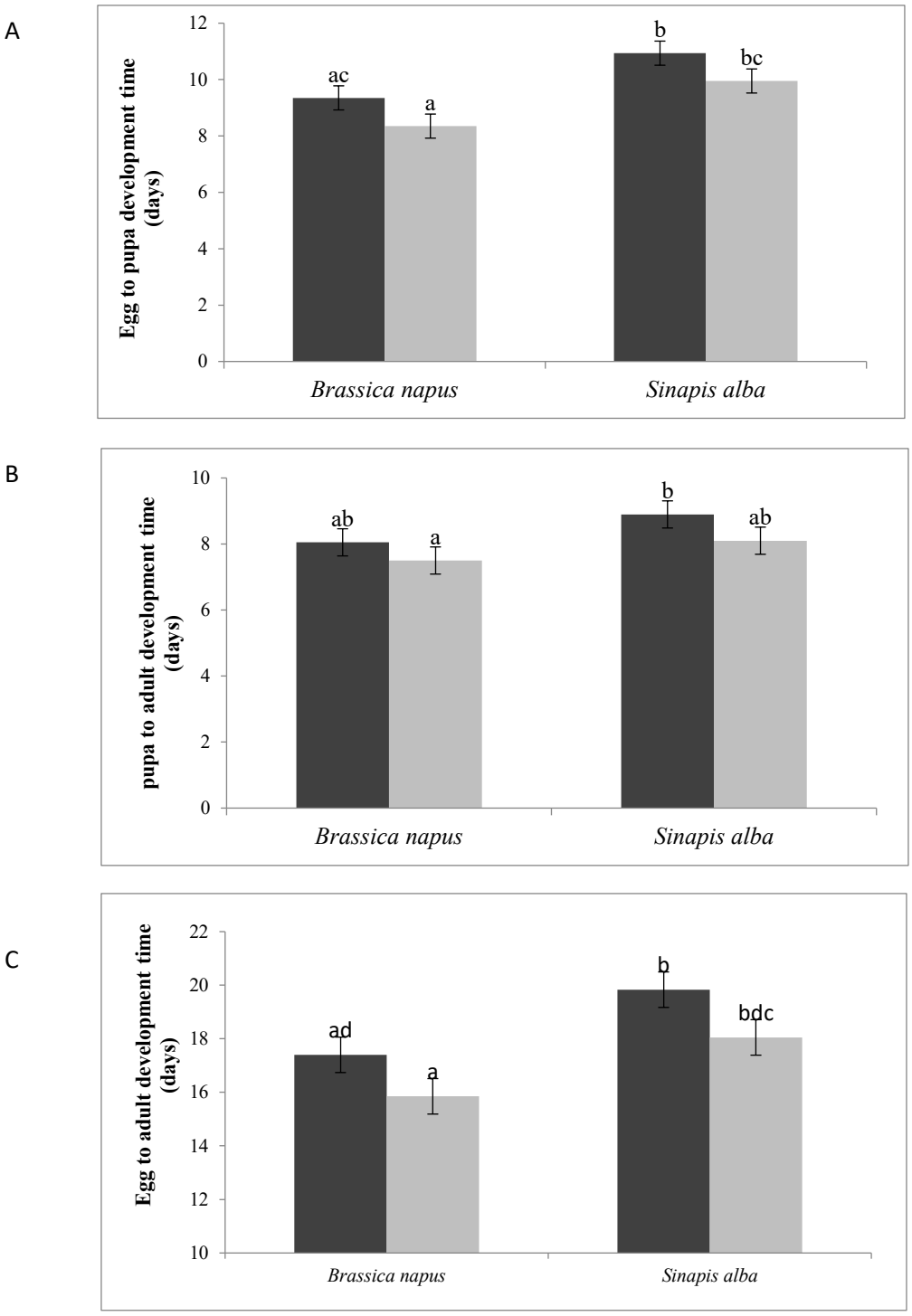


Figure 3-II. Mean (± SE) development time of *Diadegma insulare* on water-stressed (black bars) and non-stressed (gray bars) *Brassica napus* and *Sinapis alba* **(A)** egg to pupa development, **(B)** pupa to adult development, **(C)** egg to adult development. Means followed by the same letter are not significantly different at 5% level (Fisher's PLSD test following ANOVA)

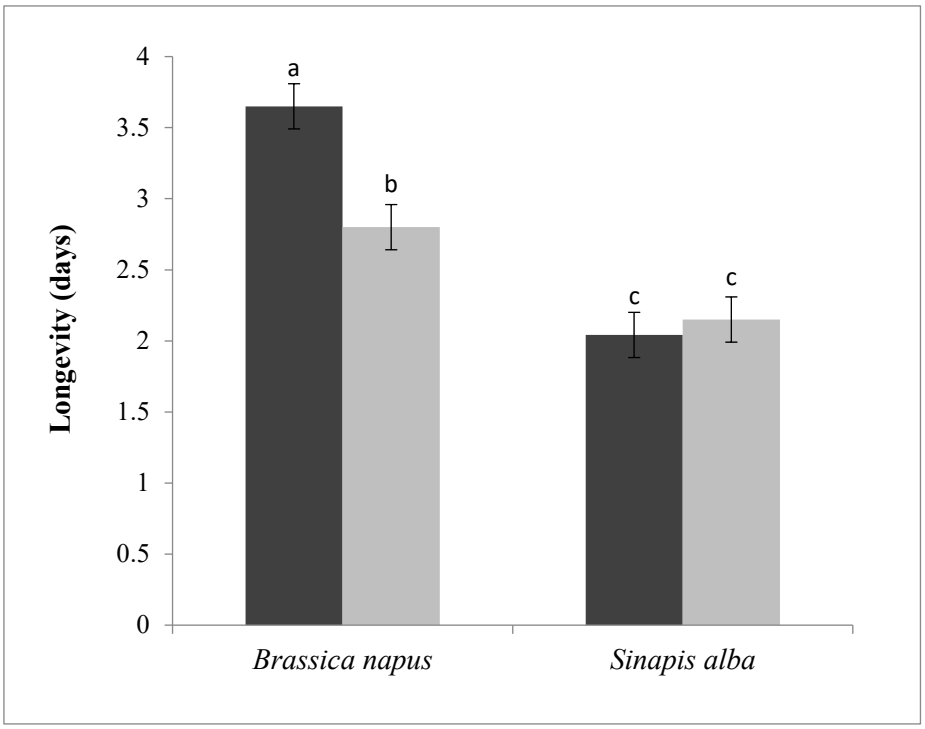


Figure 3-III. Mean (± SE) longevity of *Diadegma insulare* without food on water-stressed (black bars) and unstressed (gray bars) *Brassica napus* and *Sinapis alba.* Means followed by the same letter are not significantly different at 5% level (Fisher's PLSD test following ANOVA)

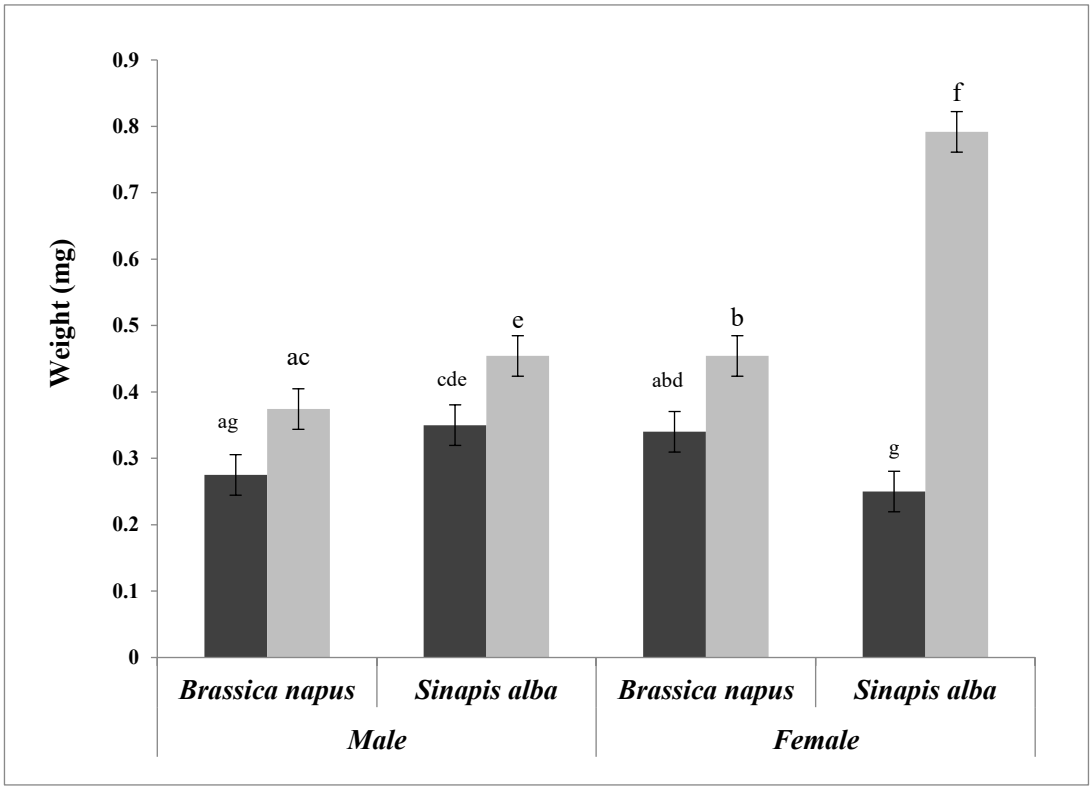


Figure 3-IV. Mean weight (± SE) of male and female of *Diadegma insulare* on water-stressed (black bars) and non-stressed (gray bars) *Brassica napus* and *Sinapis alba.* Means followed by the same letter are not significantly different at 5% level (Fisher's PLSD test following ANOVA)

Chapter 4: Effects of temperature on developmental parameters of *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae)

4.1 Introduction

Temperature is the most important abiotic factor that directly influences population dynamics of insects by affecting their survival, mortality, voltinism, distribution, growth, and development (Hallmann & Denlinger 1998; Huffaker et al. 1999; Bommarco 2001; Roy et al. 2002). Temperature changes can have diverse direct and indirect effects on natural enemies' fitness and effectiveness in controlling pests (Thomson et al. 2010). Therefore, the developmental response of insects and their natural enemies to temperature variations are critical to understand their biology, ecology, and interactions (Frazer & McGregor 1992; Martínez-Castillo et al. 2002). Furlong & Zalucki (2017) reported distinct thermal requirements for parasitoids and their hosts. In general, parasitoids are more sensitive to climatic changes and their responses to temperature variation are significantly different than their hosts (Thomson et al. 2010, Furlong & Zalucki 2017). This can lead to decoupling of synchrony between pests and their natural enemies during the periods of activity resulting in failure or reduction of biological control and ultimately pest outbreak (Read 1962).

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a major destructive pest of brassicaceous crops worldwide (Talekar & Shelton 1993). Development of resistance to a broad range of insecticides, diversity and abundance of host plants, disruption of natural enemies, high reproductive potential, and plasticity to develop rapidly in new environments, are some of the main reasons for the exceptional pest status of *P. xylostella* and control failures in many parts of the world (Talekar & Shelton1993; Mohan & Gujar 2003;

Shelton 2004; Vickers et al. 2004). Biological control is an important alternative for keeping the pest population under economic threshold levels.

More than 135 parasitoid species are reported to attack different life stages of *P. xylostella,* but maximum control is achieved only by few hymenopteran parasitoid species worldwide (Delvare 2004). Among these, species of the genus *Diadegma* are considered to be the most diverse, efficient and economically important worldwide (Lim 1986; Fitton & Walker 1992; Sarfraz et al. 2005a). *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) is a significant biocontrol agent in the Nearctic and Neotropical regions (Harcourt 1963; Furlong et al. 2013). It is an active host searcher (Harcourt 1969, 1986; Sarfraz et al. 2005a), and can parasitize all four larval instars of *P. xylostella* (Putnam 1968). Temperature plays a significant role in the survival, development, reproduction, and parasitism success of *D. insulare* (Bahar et al. 2012). Despite being such an important and useful biological control agent, earlier published reports do not provide information regarding effects of temperature on developmental parameters of this parasitoid. However, the developmental biology of its host *P. xylostella* has been well studied over a wide range of constant and fluctuating temperatures (Liu et al. 2002; Bahar et al. 2012). Until now, only one study on the thermal tolerance of *D. insulare* has been done by Bahar et al. (2012). It is essential to collect the data of the climatic responses on natural enemies along with their hosts. An understanding of thermal regulated development helps in determining the real potential and limitations of koinobiont endoparasitoids as biological control agents and ensure better chances of success in suppressing the pest population (Lim 1986; Dosdall et al. 2012; Saeki & Crowley 2012). The objective of this study was to investigate the developmental responses of *D. insulare* to different constant temperatures when feeding on *P. xylostella* reared on Canola, *B. napus* L. host plant, an economically important crop grown within the geographical

ranges of the pest and parasitoid.

4.2 Materials and methods

4.2.1 Experimental Plants and Insects

Brassica napus L. var. Q2 plants were grown in plastic pots (15 cm diameter) using Metromix-220 (WR Grace & Co. Ajax, ON, Canada) as a potting medium and placed in a growth chamber at a constant temperature of 21 ± 0.5°C, 40-50% r.h., and 16L: 8D photoperiod. Four to six-week-old plants were used for the experiment.

Plutella xylostella and *D. insulare* adults originated from a laboratory colony maintained on *B. napus* plants. Moths and wasps were collected from different commercial fields of *B. napus*, *Brassica juncea* (L.) Czern., and *Sinapis alba* L. throughout Alberta, Canada, and were periodically added to the laboratory colony to maintain genetic diversity. The insects were reared for many generations in the laboratory before experimental use.

4.2.2 Source of third-instar larvae

Third-instar larvae of *P. xylostella* were used for parasitization by *D. insulare.* To get these larvae, 30-40 mature pupae of *P. xylostella* were collected from the laboratory colony and placed in a wooden screened cage with six-week-old *B. napus* host plants. After adult eclosion, they were allowed to mate, and mated females were allowed to oviposit for 24 h then removed from the cage. The host plants were checked daily for egg hatching and larval instars. New plants were added when required. Using this method, third-instar larvae of *P. xylostella* were collected for the study.

4.2.3 Parasitization

For parasitization, 30 to 50 third-instar larvae of *P. xylostella* were carefully transferred to a small cage containing the host plant in a growth chamber maintained at each temperature (10, 15, 20 and 25°C). Six to eight pairs of newly emerged *D. insulare* were obtained from the laboratory colony and released in each of these cages for 48 hrs. Parasitoids were provided with a 10% honey solution, in 30-ml plastic solo cups (Solo, Urbana, Illinois) with plastic lids. A 1-cm hole was placed in the center of the lid, and a cotton wick was inserted to allow the solution to saturate and enable the parasitoids to feed.

After 48 hrs, the parasitoid wasps were removed, and larvae of *P. xylostella* were placed individually in Petri dishes (5-cm-diameter), containing a moistened filter paper, and fresh host plant material. Petri dishes containing *P. xylostella* larvae were incubated at constant temperatures of 10, 15, 20 and 25°C throughout the entire experiment until either adult parasitoid or host emergence. Fresh, excised leaf tissues of the host plant were added to each Petri dish daily until pupation. The host larvae in the Petri dishes were checked daily for development and survival.

4.4.4 Biological parameters measured

Developmental times of *D. insulare* from egg to pupa and pupa to adult were recorded at four constant temperatures in separate growth chambers for each replicate specimen. *Plutella xylostella* larvae that died within 24 h of each temperature treatment were excluded from the calculations.

Parasitoid pupae were removed after 48 h of pupation, weighed on digital scale (Model XS204, Mettler-Toledo, Switzerland) and returned to their respective containers until adult emergence. After adult exclusion, the empty silk cocoons were also weighed. Newly emerged

adults were maintained in the same way in controlled environment chambers in closed Petri dishes with moistened filter paper but without food, and longevity were recorded. Dead specimens were allowed to dry, and their dry weights were recorded after 10 days. The sex of each adult specimen was also identified before drying. Forewing, hindwing and hind tibia lengths of adult *D. insulare* were measured with AxioVision 4.8.2 (Carl Zeiss, Jena, Germany).

Percent parasitism was calculated as (total number parasitized or numbers of *D. insulare* pupae that developed /total number of *P. xylostella* larvae exposed) *100, while percent pupal mortality was calculated as (the difference between the total number pupated and total number emerged) / total pupated*100.

4.2.5 Statistical Analysis

Variables were tested for normality and homoscedasticity before subjecting them to the analysis. Development data were log transformed to achieve normality, but untransformed means are presented. ANOVA (PROC MIXED) was performed to determine the treatment effects on development, parasitism success, pupal mortality, adult longevity, adult dry body weight, pupal weight, cocoon weight, and on the forewing, hindwing and hind tibia length of *D. insulare*. Differences between treatments were assessed using LSMEANS statement with a PDIFF option in PROC MIXED (SAS Institute 2012). Correlations (PROC CORR) were determined between longevity and body size (forewing, hindwing, and hind tibia length), longevity and body weight (pupal weight, adult dry weight, and cocoon weight), pupal weight and cocoon weight, pupal weight and adult dry weight, pupal weight and forewing length, and also pupal weight and hindwing length of *D. insulare*. All data were analyzed by SAS v. 9.3 (SAS Institute 2012).

4.3 Results

Temperature had a significant effect on *D. insulare* development from egg to pupa ($F = 41.87$, $df = 3, 110$; $P < 0.0001$), pupa to adult ($F = 89.01$, $df = 3, 49$; $P < 0.0001$), and egg to adult ($F = 47.05$, $df = 3, 49$; $P < 0.0001$) (Table 4-I). Compared to the other temperature regimes, significantly more time was required to complete egg to pupal development at 15°C, and pupa to adult development at 10°C. Overall, development from egg to adult took longest at 10 and 15°C and the shortest at the higher temperatures of 20 and 25°C. Longevity was also influenced by temperature ($F = 9.58$, $df = 3, 49$; $P < 0.0001$) (Table 4-I). Maximum longevity was observed at 10°C.

Parasitism success did not differ significantly between temperature regimes ($P = 0.4339$). The temperature had a significant effect ($P < 0.0001$) on pupal mortality. The lowest *D. insulare* pupal mortality (4.5%) was recorded at 10°C and the highest (70 &74.3%) at 20 and 25°C, respectively (Fig. 4-I).

Temperature also significantly affected the length of forewing ($F = 10.44$, $df = 3, 49$; $P < 0.0001$), length of hindwing ($F = 12.04$, $df = 3, 49$; $P < 0.0001$), and length of hind tibia ($F = 11.78$, $df = 3, 49$; $P < 0.0001$) (Table 4-II). Both forewing and hindwing length were significantly larger at 10°C compared to all other temperatures. Hind tibia lengths were the longest at 10°C and the shortest at 25°C.

Temperature significantly affected *D. insulare* pupal ($F = 9.38$, $df = 3,61$; $P < 0.0001$) and empty cocoon weights ($F = 4.31$, $df = 3,49$; $P < 0.0089$) (Table 4-II). Pupae were significantly heavier at 10°C than that any other temperatures. Individuals developed at 25°C had heavier cocoon than that developed at other temperatures. However, adult dry weights were not affected significantly by temperature ($F = 1.10$, $df = 3, 49$; $P = 0.3584$).

Longevity was correlated with forewing length (r = 0.32, P = 0.01), hindwing length (r = 0.38, P = 0.004), and hind tibia length (r = 0.28, P = 0.04). Similarly, forewing and hindwing length were correlated (r = 0.31, P = 0.02), as were forewing length and hind tibia length (r = 0.38, P = 0.004). Cocoon weight was correlated with pupal weight (r =0 .31, P=0.02) and adult weight (r = 0.45, P = 0.0005). Pupal weight was also correlated with longevity (r = 0.36, P = 0.006), forewing length (r = 0.48, P = 0.0089), and hindwing length (r = 0.37, P = 0.006).

4.4 Discussion

Although insects are not subjected to constant temperatures in nature, a controlled laboratory study can provide a significant understanding of the population dynamics of a particular species (Satar et al. 2005). The data clearly showed the effects of temperature on the developmental time, body size, body weight, and longevity of *D. insulare*.

The present study revealed that temperature significantly influences the developmental duration of the parasitoid wasp. The parasitoid completed its development at all the temperatures tested. At low temperatures (10 and 15°C), the rate of development was slower compared to higher temperatures (20 and 25°C). It indicates that temperature is inversely related to the rate of development. The same trend of development was observed by Bahar et al. (2012) for the same species *D. insulare*, and for other related species like *Diadegma arunum* (Thomson) and *Diadegma semiclausum* (Hellén) by Golizadeh et al. (2008) and Dosdall et al. (2012), respectively. These results are also consistent with the findings of Ebrahimi et al. (2013), who showed that development time of *D. insulare* from egg to adult was similar to that of present study at 25°C when its host was reared on Chinese cabbage, (*Brassica pekinensis* (Lour.) Rupr.). The same phenomenon of development was also reported in many other endoparasitoids like

Meteorus pulchricornis (Wesmael), *Chelonus murakatae* Munakata, etc. (Liu et al. 2013; Qureshi et al. 2016). Faster development of parasitoids could be explained by the fact that elevated temperatures increase metabolic rate that results in rapid growth, or parasitoids may find the appropriate environment as the temperature increases and grow faster (Davidowitz & Nijhout 2004; Qureshi et al. 2016).

Temperature increase may affect the development and survival of a host and its parasitoids differently (Van & lei 2004). For instance, *P. xylostella* developed successfully from egg to adult at a constant temperature as high as 32°C (Liu et al. 2002), while developmental duration and survival of its parasitoid *Diadegma semiclausum* (Hellén) declined significantly at a constant temperature near 30°C (Yang et al. 1993). Similarly, in the present study, increasing pupal mortality of *D. insulare* was observed with increasing temperature regimes while Bahar et al. (2012) observed that pupal mortality of *P. xylostella* was unaffected at higher temperatures.

The body size of an insect changes with temperature variations and it is an important indicator of parasitoid fitness (Gates 2003; Sarfraz et al. 2008). Body size, an evaluation of the resources available to the developing parasitoid larvae, is measured in terms of length or width of wings, hind tibia, and thorax (Jervis 2005; Riddick 2006; Sarfraz et al. 2008; Fathi et al. 2012). Smaller wing sizes might also influence fitness by affecting dispersal and host searching efficiency of parasitoids (Sarfraz et al. 2008). In the present study, the body size of parasitoids increased with decreasing temperature. Larger adults were produced at 10°C, indicating slower growth rate, thereby increasing the amount of mass that can accumulate. The results coincide with the general statement that adult insects usually are of smaller body size at higher rather than lower temperatures (Gates 2003; Davidowitz & Nijhout 2004; Karl & Fischer 2008).

Body weight is also an important parameter that determines natural enemy fitness (Sarfraz

et al. 2008). Heavier pupae usually produce larger and more productive adults than their lighter counterparts (Barah & Sengupta 1991). The present results indicated that heavier pupae were produced at low temperatures, but the adult dry weight was not influenced by any of the temperatures tested. However, heavier empty cocoons were produced at higher temperatures. The results for pupal and cocoon weights were consistent with those of Bahar et al. (2012), who reported higher *D. insulare* pupal weight at low temperatures, but higher cocoon weight at higher temperatures. This suggests that the heavier pupal case/cocoon may protect the insect from the harmful effects of high temperature. In another study by Dosdall et al. (2012), a reduced pupal weight of *D. semiclausum* at a low temperature of 10°C was observed when its host was reared on *Brassica rapa* L. compared to *B. napus* or *Brassica oleracea* L.

Longevity is one of the most important traits of natural enemies for biological control as oviposition may be increased in the case of extended survival (Qureshi et al. 2016). In the current study, adult longevity was significantly higher at the lower temperature. Earlier studies on *D. insulare* and *D. semiclausum* also indicated increased longevity at lower temperatures (Bahar et al. 2012; Dosdall et al. 2012). This could be due to a decrease in metabolic activity of insects at lower temperatures, and as a result, adults may survive for a longer period (Davidowitz & Nijhout 2004). The same trend was observed in the case of the egg parasitoid *Trichogramma cacoeciae* (Hymenoptera: Trichogrammatidae) and larval endoparasitoid *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) adults, which lived for a shorter period at a higher temperature (Pizzol et al. 2010; Spanoudis & Andreadis 2012).

Global temperatures have risen by approximately 0.6°C in the last century and are expected to increase by 3 to 5°C over the next century (Rosenzweig et al. 1998; Houghton et al. 2001). Higher temperatures may allow rapid development, altered timing of egg hatching and

additional generations per year in multivoltine insect species (Pollard & Yates 1993; Parmesan et al. 1999). For instance, an increase in the cultivated area of brassicaceous crops along with climatic warming, is expected to enhance the *P. xylostella* pest status (Dosdall et al. 2011). With every +2°C increase in average summer temperature, 2-5 more generations of *P. xylostella* and its parasitoid *D. insulare* has been predicted in North America annually (Dosdall et al. 2008; Olfert et al. 2011). *Plutella xylostella* is well adapted and tolerant to wider range of constant temperatures. It can develop effectively from egg to adult at temperatures from 8 to 32°C (Liu et al., 2002). However, the North American population of *P. xylostella* has been observed to develop successfully from the second instar to adult within constant temperatures ranging from 4.0-37°C, which is higher than that of its parasitoid *D. insulare. Diadegma insulare* can complete its egg to adult development within a temperature range of 4.0-33°C (Bahar et al., 2014). These thermal differences are also reported to occur for a parasitoid like *Cotesia marginiventris* Cresson, of lepidopteran pests in North America (Butler & Trumble 2010). The results of the present study showed that despite slower development at the lower temperature, all other parameters increased with the decrease in temperature. This fitness advantage gained by *D. insulare* regarding body size, pupal weight and longevity may be linked to prolonged timing to encounter susceptible stages of the host and ultimately increase parasitism success as earlier reported by Talekar & Yang (1991). Moreover, development and survival may be enhanced at a higher temperature, but those individuals may subsequently have lower fecundity and size (Bale et al. 2002). Moreover, decreased longevity at a higher temperature may not contribute to higher biocontrol efficiency since *D. insulare* females maintain a constant level of oviposition rates in their lifetime (Ebrahimi et al., 2013).

In conclusion, the result showed that at lower temperatures developmental duration of *D.*

insulare is long, larger adults are produced with high survival and longevity. The present research provides fundamental information within the context of climatic warming to understand the effects of temperature on some aspects of the biology of *D. insulare*. The data presented here suggests that *D. insulare* is less tolerant to high temperatures in comparison to its host. *Diadegma insulare* is an important biocontrol agent of *P. xylostella* in North America responsible for more than 90% parasitism in untreated fields (Muckenfuss et al. 1990). The excellent host searching ability of *D. insulare* and high synchrony with its host development makes it a suitable candidate to integrate into *P. xylostella* management system (Idris & Grafius 1993). Additional research with the integration of environmental information is required to anticipate the effects of climate change on host-parasitoid interactions, developmental biology, and biocontrol efficiency of *D. insulare* and other parasitoid fauna of *P. xylostella* in North America. Furthermore, for a more precise evaluation of the influence of temperature on host-parasitoid biology, additional work on other biological parameters, such as lifelong parasitism, population dynamics, distribution and host shifts, is needed, especially under field conditions. Meanwhile, parameters calculated in this experiment in association with other ecological data could be valuable in understanding, developing and facilitating biological control tactics against the pest under climatic change scenarios and predicting the future geographical distribution of *D. insulare*.

Acknowledgments

Funding for this study is gratefully acknowledged from the Canola Council of Canada, the Alberta Canola Producers Commission, Agriculture and Agri-Food Canada.

Table 4-I. Mean (± SE) development time (days) of *Diadegma insulare* at various constant temperatures

Temperature	Egg to pupa (d)	Pupa to adult (d)	Egg to adult (d)	Adult longevity (d)
10°C	7.90± 0.29[a] (n = 22)	13.30 ± 0.28[a] (n = 20)	20.90 ± 0.44[a] (n = 20)	4.10 ± 0.19[a] (n = 20)
15°C	11.34 ± 0.28[b] (n = 23)	9.85 ± 0.33[b] (n =14)	21.00 ± 0.52[a] (n = 14)	3.21 ± 0.23[b] (n = 14)
20°C	7.90 ± 0.24[a] (n = 30)	6.88 ± 0.41[c] (n = 09)	14.44 ± 0.65[b] (n = 09)	2.55 ± 0.05[b] (n = 09)
25°C	7.64 ± 0.21[a] (n = 39)	6.60 ± 0.39[c] (n =10)	14.00 ± 0.62[b] (n = 10)	2.70 ± 0.27[b] (n = 10)

Means in a column followed by the same letter do not differ significantly (P = 0.05). Values in parentheses indicate the number of individuals.

Table 4-II. Mean (±SE) forewing length, hindwing length, hind tibia length, adult body weight, pupal and cocoon weight of *Diadegma insulare* when parasitized *Plutella xylostella* host larvae were reared on leaf tissue of *Brassica napus* under four different temperature regimes.

Temperature	Forewing length (mm)	Hindwing length (mm)	Hind tibia length (mm)	Adult body weight (mg)	Pupal weight (mg)	Cocoon weight (mg)
10°C	3.11 ± 0.06[a]	2.11 ± 0.05[a]	0.98 ± 0.02[a]	0.38 ± 0.03[a]	4.55 ± 0.18[a]	0.72 ± 0.06[ab]
15°C	2.67 ± 0.07[b]	1.75 ± 0.06[b]	0.87 ± 0.03[b]	0.47 ± 0.04[a]	3.38 ± 0.18[b]	0.77 ± 0.07[ac]
20°C	2.74 ± 0.08[b]	1.65 ± 0.08[b]	0.89 ± 0.03[b]	0.37 ± 0.05[a]	3.12 ± 0.27[b]	0.51 ± 0.09[b]
25°C	2.66 ± 0.08[b]	1.67 ± 0.07[b]	0.72 ± 0.03[c]	0.37 ± 0.05[a]	3.67 ± 0.19[b]	0.99 ± 0.09[c]

Means in a column followed by the same letter do not differ significantly (P = 0.05).

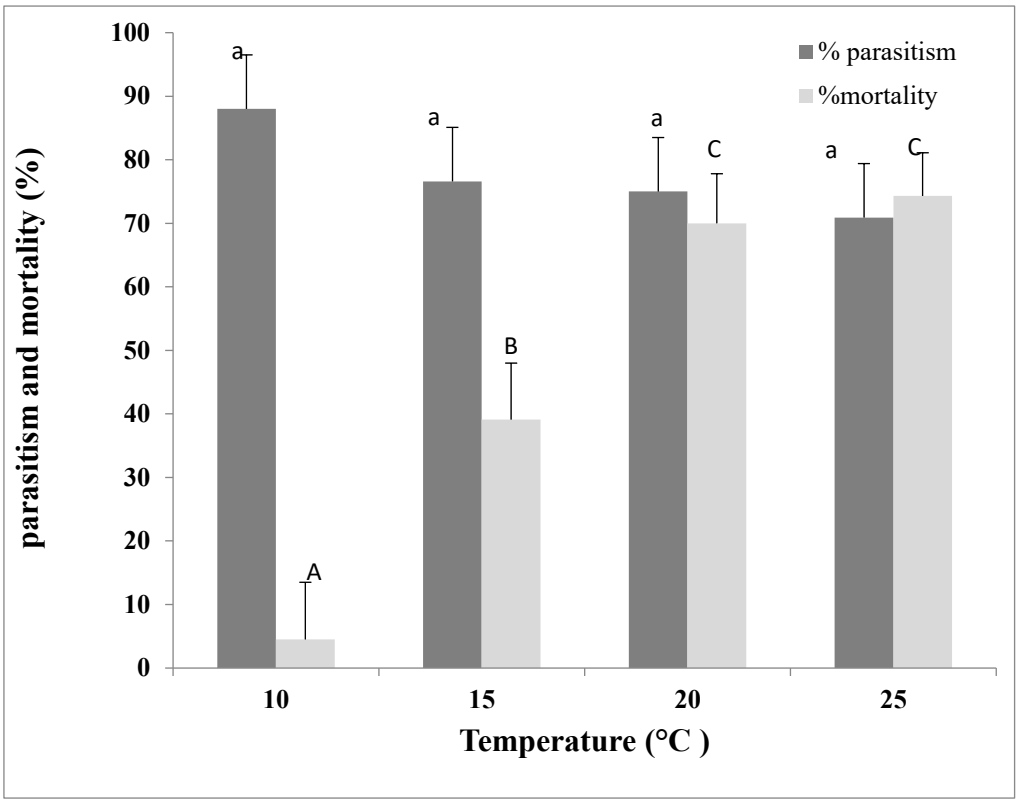


Figure 4-I. Mean (± SE) parasitism and mortality of *Diadegma insulare* at different temperatures. Bars with the same letter do not differ significantly at 5% level of significance

Chapter 5: Selective effects of floral food sources and honey on life-history traits of a pest-parasitoid system

A version of this chapter has been published:
Munir S, Dosdall LM & Keddie A. 2018. Selective effects of floral food sources and honey on life-history traits of a pest-parasitoid system. Entomologia Experimentalis et Applicata.166: 500-507.

5.1 Introduction

The successful growth and development of an insect depend on the fulfillment of its qualitative and quantitative nutritional requirements (Barbehenn et al. 1999). Studies have shown that carbohydrate-rich food is a vital source of energy for many parasitoids and their hosts during the adult stage (Wäckers 2004; Winkler et al. 2005). Planting and maintaining carbohydrate resources as nectar-producing flowering plants near cropping areas are often recommended for the fitness of parasitoids (Gourdine et al. 2003). The provision of floral food sources can be a crucial part in biological control. Feeding on floral resources substantially affects the life-history traits of parasitoids, such as survival, longevity, development, fecundity, and parasitism (Lee et al. 2004; Lee & Heimpel 2008; Tunçbilek et al. 2012). Nectar feeding has been reported to increase the longevity of several hymenopteran parasitoids up to 20-fold under laboratory conditions (Jervis et al. 1996; Fadamiro & Heimpel 2001; Wäckers 2001).

Diadegma insulare (Cresson) (Hymenoptera: Ichneumonidae) is a dominant, solitary, synovigenic, larval parasitoid of diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), a destructive cosmopolitan pest of brassicaceous crops (Harcourt 1986; Sarfraz et al. 2005a; Lee & Heimpel 2008). *Diadegma insulare* is one of the primary *P. xylostella* biocontrol agents in Canada and the USA (Harcourt 1986; Sarfraz et al. 2005a; Wold-Burkness et al. 2005; Young 2013). In North America, parasitism by this wasp varies from 50 to 98% in the field,

depending on host instars (Legaspi et al. 2000; Hutchison et al. 2004). Earlier studies had reported higher parasitism rates and longevity of *D. insulare* when the crop was adjacent to nectar-producing plants (Zhao et al. 1992; Fitton & Walker 1992).

Parasitoids emerge with a limited amount of energy reserves and need sugar solutions as their key source of energy. The importance of sugar feeding for survival has been described for many hymenopteran parasitoid species (Jervis et al. 1996; Wäckers 2001; Wanner et al. 2006). *Diadegma insulare* is not known to feed on pollen or host fluid as an adult but is strongly stimulated to feed on carbohydrate-rich food to satisfy its energy requirements (Idris et al. 1997; Lee et al. 2004). Several studies have demonstrated that feeding on floral nectar of several species like *Brassica oleracea* L., *Barbarea vulgaris* R. Br., *Brassica napus* L., *Lobularia maritima* (L.) (all Brassicaceae), *Daucus carota* L. (Apiaceae), *Fagopyrum esculentum* (Moench) (Polygonaceae), and others, and also on non-floral food such as honey and honeydew, considerably increase the lifespan of *D. insulare* both under laboratory and field conditions (Idris & Grafius 1995,1996ab; Johanowicz & Mitchell 2000; Gourdine et al. 2003; Lee at al. 2004).

In an agroecosystem, the majority of lepidopteran hosts and their hymenopteran parasitoids in their adult stage forage on shared floral resources, and hence increase their fitness and survival (Wäckers 2004; Romeis et al. 2005; Kehrli & Bacher 2008). However, flower species may act selectively and favour one trophic level over the other based on insect morphology, physiology, behaviour, nutritional requirement, preference, floral architecture, and floral nectar composition (Idris & Grafius 1995; Baggen et al. 1999; Winkler 2005; Kehrli & Bacher 2008). For instance, a parasitoid complex of the leafminer *Cameraria ohridella* Deschka & Dimić benefited 8 times more when fed on flowers of *Anthriscus sylvestris* (L.) Hoffm. (Apiaceae) than their host (Kehrli & Bacher 2008). Similarly, two plant species, *Anethum*

graveolens L. (Apiaceae) and *Centaurea cyanus* L. (Asteraceae), were selectively visited in higher numbers by *Diadegma semiclausum* (Hellén) than its herbivore host *P. xylostella*, which was observed in small numbers on both plant species (Winkler et al. 2005).

To date, studies focusing on the impact of floral selectiveness on the pest-parasitoid system are rare. No previous studies on selective floral diets exist for the *P. xylostella* and *D. insulare* system. An understanding of the relative importance of floral nectar selectivity to *D. insulare* is crucial for conservation biological control and to improve its role in long-term *P. xylostella* management. In the present study, we investigated the selective effects of floral diet and honey on life-history traits such as longevity and body weight of a host-parasitoid system consisting of *P. xylostella* and its principal parasitoid *D. insulare.*

5.2 Materials and methods

5.2.1 Insect colonies

Plutella xylostella and D. insulare adults originated from a laboratory colony maintained on *B. napus* plants. Moths and wasps were collected from different commercial fields of *B. napus*, *Brassica juncea* (L.) Czern. and *Sinapis alba* L. throughout Alberta, Canada, and were periodically added to the laboratory colony to maintain genetic diversity. Mature pupae of *P. xylostella* and *D. insulare* were used in the experiment.

5.2.2 Source of floral nectar

Flowering plants of sweet alyssum (*Lobularia maritima* L. cv. Carpet of Snow), volunteer canola (*B. napus* cv. Q2), stinkweed (*Thlaspi arvense* L.), and wild mustard (*Sinapis arvensis* L. cv. AC Pennant; all Brassicaceae) were used as sources of nectar. *Brassica napus, T. arvense,* and *S. arvensis* were chosen because these are important and common weeds of field crops in the

Canadian prairies. Despite providing nectar for adult pest and parasitoid, they are also potential host plants for *P. xylostella* larvae. *Lobularia maritima* is an annual and non-weedy plant. It was selected because natural enemies are attracted to this flowering plant. It flowers within three-weeks of planting and has a long flowering period. Moreover, the nectarines are accessible to parasitoids and may be helpful in enhancing parasitoid longevity at times when few wildflowers are in bloom (Chaney 1998; Johanowicz & Mitchell 2000; Keller & Baker 2002; Hogg et al. 2011; Sivinski et al. 2011).

Plants were grown individually from seeds in plastic pots (15 cm diameter) using Metromix-220 (WR Grace & Co, Ajax, ON, Canada) as a potting medium. Pots were thoroughly watered and placed in a greenhouse at 22°C, 40-50% r.h., and 16 L: 8 D photoperiod. All plants were used for the experiment when they reached the flowering stage. Plants were sown at one-week intervals to ensure synchronous blooming during the experiment.

5.2.3 Source of non-floral food

Distilled water and 10% honey solution were used as a non-floral food source. The honey solution and water were placed in 30-ml plastic solo cups (Solo, Urbana, IL, USA) with plastic lids. A 1-cm hole was placed in the center of the top of the lid, and a cotton wick was inserted to allow the solution to saturate and enable the pest and parasitoid to feed. Cups were replaced every second day to ensure a continuous supply of water and honey solution to pest and parasitoid.

5.2.4 Research Methodology

5.2.4.1 Experiment 1: Effects of floral nectar and honey on *Diadegma insulare*

The effects of the nectar of each of four flowering plant species, a 10% honey solution, and water on the longevity and body weight of adult *D. insulare* were determined in the laboratory at 22 ± 2°C with 16 L: 8 D photoperiod. All treatments (pots of each plant species

when half the plants were flowering, 10% honey solution, and water) were individually placed in wooden screened cages (40 × 40 × 80 cm), arranged on the laboratory bench in a completely randomized design with each cage considered as one replicate. For each treatment, five replicates was conducted. Mature *D. insulare* pupae from the laboratory colony were carefully harvested, and 5-10 pupae were placed in each cage with a food source. This enabled the introduction of adult parasitoids to a potential food source immediately after emergence. Flowering plants were replaced twice a week to ensure a continuous and adequate supply of floral nectar to parasitoids. *Diadegma insulare* pupae were checked daily for adult emergence. After adult exclusion, parasitoid survival was observed and recorded daily until the mortality of the last parasitoid. Longevity was measured in days and individuals that died on the first day were excluded from analysis. Ten days after wasps had died and dried at room temperature, adults were weighed on an electrical balance (Model XS204, Mettler-Toledo, Greifensee, Switzerland).

5.2.4.2 Experiment 2: Effects of floral nectar and honey on *Plutella xylostella*

The same flowering plant species, honey solution and water treatments as described in experiment 1 were used. Food sources were offered in the same way as described in experiment 1 and each *P. xylostella* individual was reared on a single type of food source over its whole lifetime. Longevity data were measured in days, analyzed, and compared to each flowering plant species, honey solution, and water.

5.2.5 Statistical analysis

Diadegma species have complementary sex determination, which often causes a highly male-biased population in the laboratory colonies (Butcher et al. 2000; Khatri et al. 2008). In this study, comparatively small numbers of *D. insulare* females were obtained. Therefore, only data from male *D. insulare* were used in the analysis. Data from both male and female *P. xylostella*

were used. Variables were tested for normality and homoscedasticity before subjecting them to the analysis. Analysis of variance (PROC MIXED) for a completely randomized design was performed to determine the treatment effects on longevity and adult weight of *D. insulare* and *P. xylostella*. If significant treatment effects were indicated, means were compared at the 5% level of significance using the LSMEANS statement with the PDIFF option in PROC MIXED (SAS Institute 2012). Correlation coefficients were determined between longevity and weight of both pest and parasitoid.

5.3 Results

The longevity of *D. insulare* was significantly affected by the diet consumed ($F = 107.09$, $df = 5,24$; $P < 0.0001$) (Fig 5-I). Longevity was shortest (2.8 ± 0.88 days) when fed with water and longest (25.7 ± 0.88 days) when fed on *T. arvense* flowers. Floral nectars of *B. napus*, *L. maritima*, and *S. arvensis* had a similar effect on *D. insulare* longevity.

The weight of *D. insulare* was also affected by the food consumed ($F = 7.14$, $df=5,24$; $P=0.0003$) (Fig 5-II). Weight was highest with *S. arvensis* followed by *T. arvense* and *B. napus,* and lowest with water. Although not significantly different, there was a trend towards greater weight with *L. maritima* and honey compared to water. Longevity of the parasitoid was positively and significantly correlated with the weight gain only when fed with *T. arvense* floral nectar ($r = 0.84$; $P = 0.0357$).

The longevity of *P. xylostella* was also affected by the diet consumed ($F = 33.21$, $df = 5,24$; $P < 0.0001$) (Fig 5-I). All sugar sources (floral nectar and 10% honey) significantly increased longevity compared to the water treatment. *Sinapis arvensis* and *T. arvense* resulted in the highest average longevity. *Brassica napus* resulted in similar longevity as *T. arvense,* but

higher longevity than both *L. maritima* and honey, although longevity was not significantly different when fed on *L. maritima* and 10% honey solution. The sex did not have any effect on the longevity of *P. xylostella* (F= 2.09, df= 1,37; P = 0.16)

Diet consumed by *P. xylostella* adults had an effect on body weight (F = 12.63, df = 5,24; P <0.0001) (Fig. 5-II). The adults tended to be heaviest when fed 10% honey solution (1.24 ± 0.072mg) and lightest on *T. arvense* (0.48 ± 0.072 mg). A significant positive correlation was found between pest longevity and weight only when fed with *S. arvensis* floral nectar (r = 0.83; P = 0.0381). Moreover, the sex did not have any effect on the adult dry weight of *P. xylostella* (F = 1.68, df = 1,37, P = 0.20).

5.4 Discussion

The results revealed that floral and non-floral food act differently on life-history traits of the host-parasitoid system. The biological, ecological, and physiological means by which food resources influence life histories of insects are not entirely known (Casas et al. 2005). In this study, both pest and parasitoid displayed extended longevity on all floral nectars as compared to water, emphasizing the significance of sugar feeding by adult insects as reported by many earlier studies (Idris & Grafius 1995,1996a, b; Gourdine et al. 2003; Winkler 2005; Kehrli & Bacher 2008). Moreover, the longevity of the female moth responded similarly to that of the male. Other studies comparing male and female parasitoid responses to sugar provision showed similar results. For instance, the lifespan of male and female *D. insulare* was not significantly different when fed buckwheat nectar and soybean aphid honeydew (Lee et al. 2004). Similarly, no significant effect of diet (buckwheat flower and 10% honey solution) was recorded on the longevity of male and female *D. semiclausum* (Wratten et al. 2003).

Both the pest and its parasitoid exploited all the floral species tested. However, *D. insulare* survived 7.6 days longer on *L. maritima* than *P. xylostella.* Hence, the floral nectar that is useful for both *D. insulare* and *P. xylostella* may selectively favour the parasitoid's longevity more than that of its host. If the longevity of the female parasitoid responds similarly to that of the male, this selectivity may have important implications for exploitation of the host population. As synovigenic parasitoids can increase fitness by maturing and laying more eggs in their extended lifetime (Jervis et al. 2005; Winkler et al. 2006), this can indirectly promote higher parasitism rates as the time to encounter and parasitize hosts is extended (Thompson & Hagen 1999; Witting-Bissinger et al. 2008). However, the extended longevity of *P. xylostella* may not substantially affect its abundance (Winkler 2005) since it lays 75% of the total number of eggs within the first eight days after emergence (Pivnick et al. 1990). In contrast, *D. insulare* has an average of 13.4 days total pre-oviposition period, followed by a relatively constant oviposition rate (Ebrahimi et al. 2013).

Although 10% honey solution enhanced *D. insulare* longevity compared to the control treatment, it was significantly inferior to all floral nectar resources. However, *P. xylostella* survived better on all floral nectars and honey solution compared to the water control. As in other studies (Johanowicz & Mitchell 2000; Gourdine et al. 2003), *D. insulare* survived only a few days when deprived of any carbohydrate-rich food and consistent with the findings of Gourdine et al. (2003). However, Johanowicz & Mitchell (2000) observed prolonged longevity (27 days) of *D. insulare* on 10% honey solution that may relate to differences in honey composition. When provided with an appropriate concentration, honey may be a good substitute for insect rearing in the laboratory in the absence of floral nectar (Idris & Grafius 1995; Siekmann et al. 2001).

Results indicated that all the flower species tested were fed upon and provided accessible

nectar. However, *P. xylostella* and *D. insulare* differ in their exploitation of floral nectars, mainly depending on flower morphology and their mouthparts (Idris & Grafius 1996b; Wäckers 2004; Vattala et al. 2006). Adult *P. xylostella* have a long proboscis suited for suctorial food intake (Proctor & Yeo 1973). The parasitoids have less specialized mouthparts that restrict their feeding to more exposed carbohydrate sources (Wäckers 2004), as found for *D. semiclausum* (Winkler et al. 2006) and *D. insulare* (Idris & Grafius 1996b). Idris & Grafius (1996b) reported that the parasitoid displayed behavioural flexibility in collecting floral nectar and the longevity differs with the morphological characteristics of the flowering plant species. For instance, *D. insulare* was observed to enter the *T. arvense* corolla either through its opening or by kicking soft petals, whereas it accessed *B. napus* and *S. arvensis* floral nectar by entering the corolla tube and chewing or sucking at the base of the corolla (Idris & Grafius, 1996b). The results suggested that the flower species that are fed upon and accessible may not be the most suitable and rewarding food and might not impact on fitness in the same way. For instance, in this study, the weight of *D. insulare* was highest but not the longevity when fed on *S. arvensis*.

Body weight is an important indicator of parasitoid fitness (Sarfraz et al. 2008). In the present study, *D. insulare* were heavier at death when kept on various floral nectars compared to water alone. Maximum weight was recorded when the parasitoid fed on *S. arvensis* indicating the ability of the parasitoid to access nectar without spending extra effort and energy. In another study, Winkler (2005) found significant weight loss and gains in *D. semiclausum* when exposed to different floral nectars depending on accessibility to nectar. In contrast, *P. xylostella* individuals were heavier when fed on 10% honey, and weight was minimal on *T. arvense* compared to other floral nectars. Moreover, no correlation existed between longevity and weight, suggesting that food sources have an opposing impact on life-history traits of both the herbivore

and its parasitoid.

This study showed that not all the effects of floral nectar feeding on various life-history traits of an insect point in the same direction. For instance, *S. arvensis* additionally enhanced the longevity, but not the weight of *P. xylostella* compared to other floral resources. Idris & Grafius (1995, 1997) reported that *S. arvensis* increased the survival of *D. insulare* in the field. Moreover, parasitism was also significantly higher when *P. xylostella* larvae fed on *S. arvensis* compared to other wild Brassicaceae like *T. arvense* (Idris & Grafius 1996a).

We conclude that floral species have a contrasting effect on various life-history traits. None of the flowering plant species found in the experiment benefitted only the parasitoid. Hence, the nectar-producing plants that are beneficial to both pest and parasitoid may be able to act selectively by favouring the parasitoid more than its host (Winkler et al. 2005; Wäckers et al. 2007). For instance, *D. insulare* benefited considerably more when fed on the floral nectar of *L. maritima* than its host, indicating that *L. maritima* floral nectar may be good food for adult parasitoids. A study by de Groot et al. (2005) also reported the potential of *L. maritima* plant species as a 'trap crop' for *P. xylostella.* These findings emphasize the importance of understanding and studying the selective effects of nectar-producing plants to improve the role and effectiveness of *D. insulare* in *P. xylostella* management (Idris & Grafius 1996b). Choosing particular food plants, which only promote the natural enemy without supporting their host, is harder for *P. xylostella* than for other lepidopteran pests due to its worldwide distribution and exploitation of a broad range of floral nectars (Winkler 2005).

Improvement of biological control has not been reported from the use of floral resources in the field. The influence of floral feeding on the extended longevity and parasitism rates of parasitoids are inconsistent and vague. For instance, parasitism of *P. xylostella* by *D. insulare*

was reported to be higher in broccoli adjacent to floral nectar resources (Zhao et al. 1992), whereas parasitism by *D. insulare* was not affected by the floral borders of buckwheat adjacent to cabbage plots (Lee & Heimpel 2008). However, provision of floral resources in the field is a simple practice to ensure that parasitoids are getting enough food and are likely to be efficient bio-control agents (Heimpel & Jervis 2005; Russell 2015). This study highlights the need to better understand flower architecture and the pest and the parasitoid's phenology for selective food plants that mainly enhance the performance of natural enemies. Further investigation with similar and different flowering species is needed to understand the influence of floral nutrients on female parasitoid life-history traits. The selectivity of floral nectar species has direct implications for conservation biological control. However, for effective biological control of *P. xylostella*, a selective nectar-producing plant for *D. insulare* remains to be recognized. Additional studies with other flowering plant species in the laboratory and the field are warranted to explore compatible, beneficial, and nutritionally selective floral species for parasitoids that should be integrated into management programs for more efficient control of *P. xylostella.*

Acknowledgments

Funding for this study is gratefully acknowledged from the Canola Council of Canada, the Alberta Canola Producers Commission, and Agriculture and Agri-Food Canada.

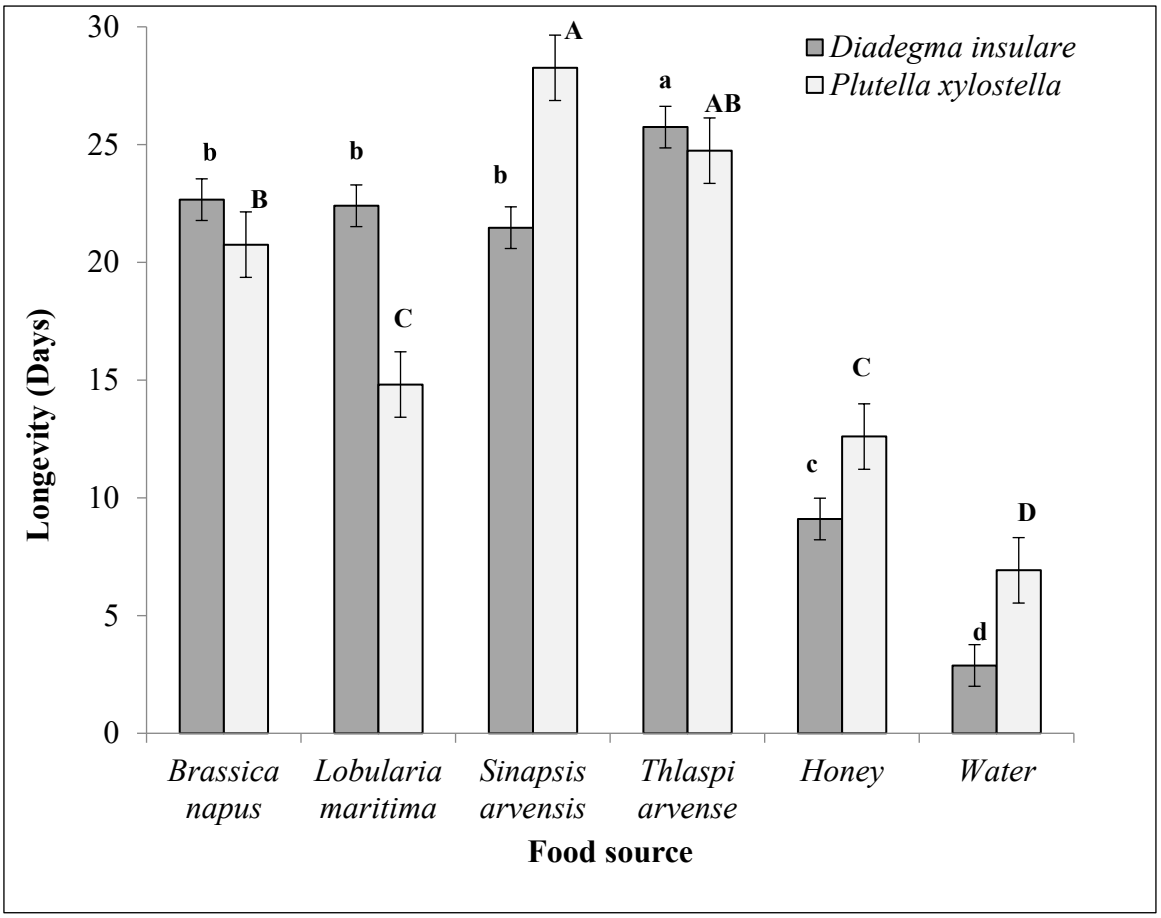


Figure 5-1. Mean (± SE) Longevity (days) of *D. insulare* and *P. xylostella* on various floral food sources, honey and water (control) in the laboratory. Means capped with the same letter are not significantly different at the 0.05 level.

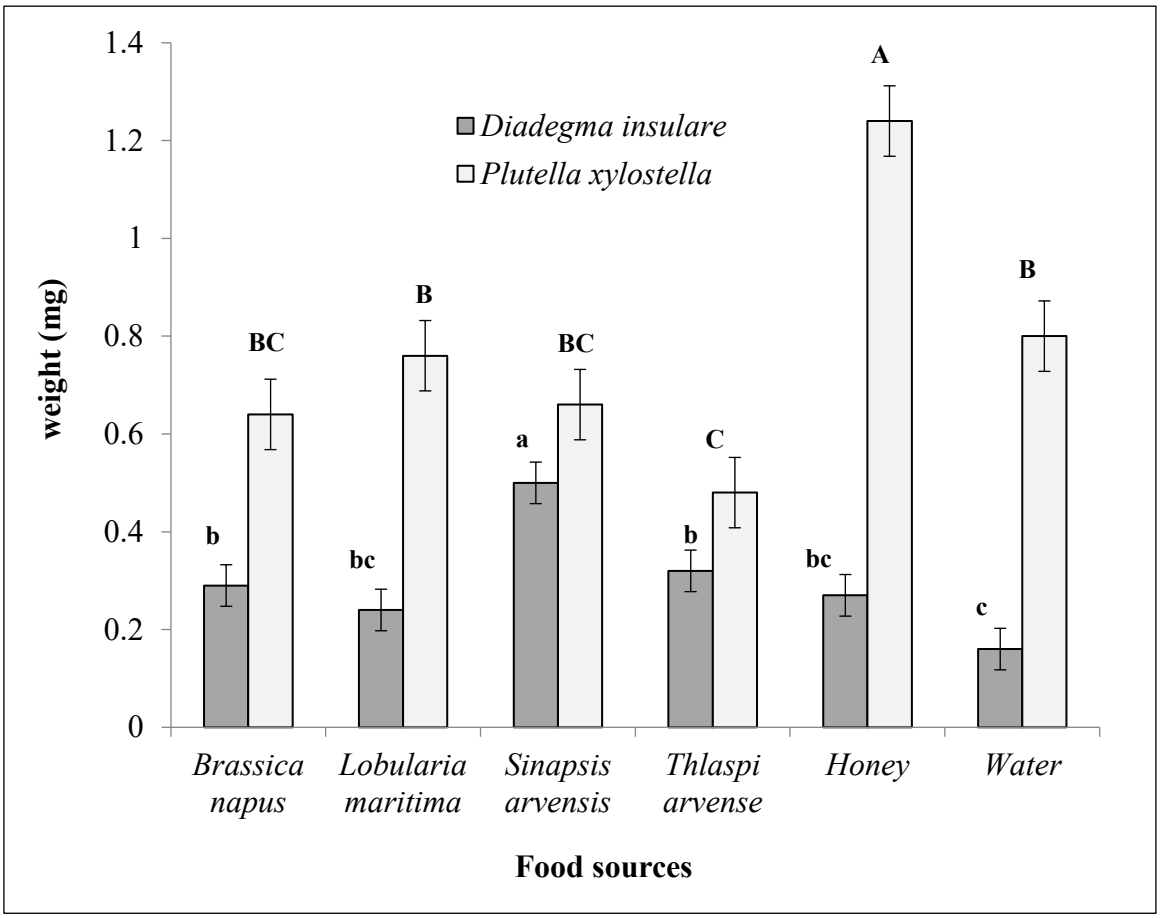


Figure 5-2. Mean (± SE) weight (mg) of *D. insulare* and *P. xylostella* on various floral food sources, honey and water (control) in the laboratory. Means capped with the same letter are not significantly different at the 0.05 level.

Chapter 6: A survey of insect parasitoids of *Plutella xylostella* (L.) (Plutellidae: Lepidoptera) in southern Alberta, Canada

6.1 Introduction

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is a globally distributed and destructive oligophagous pest of Brassicaceae crops that causes significant losses in harvest yield and quality in many regions of the world (Talekar & Shelton 1993; Zalucki et al. 2012). Although *P. xylostella* is believed to have evolved in the Mediterranean area (Harcourt 1954), North American populations are most probably of European origin and were likely introduced about 150 years ago (Hardy 1938).

Plutella xylostella was first reported from western Canada in 1885 (Harcourt 1962), and it now occurs almost annually throughout the Canadian prairies wherever its host plants are cultivated (Anonymous 1996; Dosdall et al. 2004b, 2011). In both eastern and western Canada, *P. xylostella* re-establishes each year from annual immigration of adults borne on northward trajectory winds from the southern USA and Mexico (Dosdall et al. 2004b, 2008; Hopkinson & Soroka 2010). The population densities of *P. xylostella* in any given year are dependent primarily on its arrival time from southern regions of North America, the size of invading populations, the number of population influxes, and environmental and biological conditions in the region of its invasion (Dosdall et al. 2008, 2011; Miluch 2010). *Plutella xylostella* has been reported to survive under mild winter conditions in western Canada (Dosdall 1994), but successful overwintering is considered to be a rare phenomenon (Dosdall et al. 2008).

In western Canada, canola, *Brassica napus* L. and *Brassica rapa* L., and mustard, *Brassica juncea* (L.) Czern. and *Sinapis alba* L. are the primary host crops of *P. xylostella* (Philip

& Mengersen 1989). In most years, *P. xylostella* causes minor economic damage, but in some years, populations reach outbreak densities, and extensive crop losses occur (Dosdall et al. 2011). Outbreaks responsible for economic damage to canola and mustard in western Canada have occurred approximately every two to three years since 1995 (Dosdall et al. 2008).

Once established, *P. xylostella* populations are difficult to manage because of their high reproductive potential, rapid development of resistance to insecticides, diversity and abundance of host plants, tolerance to a broad range of temperatures and a lack of effective natural enemies (Talekar & Shelton 1993; Mohan & Gujar 2003; Sarfraz et al. 2005a). A recent analysis reported a global estimate of total annual costs associated with *P. xylostella* management at US$4 billion (Zalucki et al. 2012). Consequently, this situation has prompted a demand for biological control as an important alternative to keep the pest population under economic threshold levels. Therefore, improved efforts have been undertaken worldwide to develop integrated pest management strategies, primarily based on management, augmentation or preservation of natural enemies of *P. xylostella* (Sarfraz et al. 2005a). More than 135 species of natural enemies are reported to attack different life stages of *P. xylostella,* but maximum control worldwide is achieved only by a few hymenopteran species belonging to the ichneumonid genera *Diadegma* and *Diadromus*, the braconid genera *Microplitis* and *Cotesia*, and the eulophid genus *Oomyzus* (Delvare 2004; Sarfraz et al. 2005a).

In Canada, three hymenopterous parasitoid species, *D. insulare* (Cresson), *M. plutellae* (Muesebeck) and *D. subtilicornis* (Gravenhorst) are known to attack larval, pupal and pre-pupal stages of *P. xylostella* respectively (Harcourt 1986; Anonymous 1996; Braun et al. 2004). Overall, little is known about the effect of these parasitoids on the population dynamics of *P. xylostella* in western Canada. Surveys conducted in this region in the early 1990's and 2012

indicated potential roles of *D. insulare* and *M. plutellae* and a lesser impact of *D. subtilicornis* for reducing populations of *P. xylostella* (Braun et al. 2004; Bahar et al. 2013).

No detailed multiyear studies have been conducted in southern regions of Alberta to determine the parasitoid communities associated with *P. xylostella*. The main objective of this study was to catalog the parasitoid species associated with *P. xylostella* in canola and mustard.

6.2 Materials and Methods

Species composition and abundance of important parasitoid species of *P. xylostella* in commercial fields of canola and mustard in southern Alberta, Canada from 2010 to 2013 were investigated. Surveys were conducted each year by collecting potential hosts, *P. xylostella* larvae and pupae, from late August in 2010, or from early July to late August while in 2011 to 2013. Canola and mustard fields close to major highways were chosen on the basis of accessibility (unfenced/ungated). Global positioning system (Garmin GPSMAP 64st) coordinates were used to record the locations. Insect samples were taken in a 180° arc by using a standard 38cm diameter insect sweep net while walking from the edge of the fields towards the center. Populations of hosts were not uniformly distributed, so once selected, several locations within each field were sampled by taking fifty sweeps per location for larvae while pupal samples were carefully hand-picked from host plants when available. In the field, all larval and pupal samples were placed in small plastic containers with lids with screened aeration holes, then brought to the laboratory and enumerated. Pupal samples were collected at only a few locations, so they were kept singly in Petri dishes. Fifteen *P. xylostella* larvae per Petri dish were placed with moistened filter paper and host plant material until pupation. *Plutella xylostella* pupae and parasitoid pupae were then kept singly in Petri dishes until adult emergence. Adult parasitoids were identified by visual

examination. However, some parasitoids from each site were preserved in 70% alcohol and a few were mounted on pins in boxes and kept for future species identification confirmation by specialists.

6.3 Results and Discussion

During the four years (2010-2013) of this study, a total of 59 localities consisting of 116 fields of canola (*B. napus*) and 22 fields of mustard (including four of *B. juncea* and 18 of *S. alba*) were surveyed (Fig. 6-I). *Plutella xylostella* was widespread in canola/mustard growing areas of southern Alberta. However, fewer larval samples were collected from fewer locations in 2012, despite collection efforts, due to adverse weather conditions.

Overall, 3288 larval and 370 pupal *P. xylostella* samples were field-collected and reared in the laboratory (Table 6-I). Parasitoids were not obtained from all the locations sampled (Table 6-I). The reason might be that too few samples were collected due to lower pest densities in 2012 and 2013 due to weather conditions, or sampling before parasitism occurred, or uneven distribution of parasitoids at a location. Moreover, several factors other than parasitoids may have affected *P. xylostella* abundance, such as heavy rain, high temperature, the suppressive effect of predators, size of the immigrant population and host plant quality (Talekar & Lee 1985; Campos et al. 2006, Mauduit 2012).

6.3.1 Species of parasitoids

Primary parasitoids

At least five species of hymenopteran larval parasitoids belonging to three genera (*Diadegma, Cotesia,* and *Microplitis*) and one of prepupal /pupal species (*Diadromus*) were associated with *P. xylostella* (Table 6-II). Most of the Ichneumonid wasps reared from *P.*

xylostella larvae were identified as *Diadegma insulare*. However, a few specimens were not identified to species as they were unusual, or the diagnostic characters were either obscure or body parts were missing. For instance, six specimens identified as *Diadegma* were unlikely to be *insulare*.

Hyperparasitoids

A total of four species of hyperparasitoids belonging to four genera (*Conura*, *Cataloccus*, *Pteromalus,* and *Mesochorus*), were recorded from primary parasitoids of *P. xylostella* (Table 6-II).

Rate of parasitism of *P. xylostella* by larval parasitoids

Parasitization rates and timing varied significantly among these parasitoid species. Substantial differences were documented among fields of the same crop and different crops, at the same time of the year. This may have been due to wide variations in the application of pesticides in various canola/mustard fields by different farmers, which interrupted both *P. xylostella* and parasitoid communities (Bahar et al. 2013).

In general, more *P. xylostella* larvae were collected and reared in August and few or no larvae collected in July 2010-2012. Parasitism rates also were higher in August in 2010 (30.4%), 2011 (23.7%), and 2012 (45%). However, more larval samples were collected in July than August during 2013, and percentage parasitism was also higher in July (37.2%) than August (32.9%). Comparison between crops indicated that parasitization rates by all larval parasitoid species in mustard (*S. alba)* were higher than canola (*B. napus*) in 2012 and 2013, but lower than canola in 2011. Moreover, the parasitism rates were higher in all three crops surveyed in 2012 as compared with 2010, 2011 and 2013 (Table 6-III). Compared to *Cotesia* spp., parasitism by *D. insulare* was highest in *B. napus* from 2010 to 2012. Parasitism *by M. plutellae* was lowest in all

crops in all four years (Table 6-III). In 2010, data was obtained from 11 locations in southern Alberta, and two parasitoid species, *D. insulare* and *Cotesia* spp., were the dominant species. Collectively, parasitism by these two species was 0.4% (Table 6-IV). In 2011, a survey of *P. xylostella* parasitism was conducted at 14 locations in southern Alberta. Collective parasitism by the three larval parasitoid species *D. insulare, Cotesia* sp., and *M. plutellae* was 23.2%. The highest parasitism was recorded from the fields near Oyen (80%) and Medicine Hat (58%). The dominant parasitoid species were *D. insulare* and *Cotesia* sp. (Table 6-IV).

Data were obtained from 19 locations in 2012 and 15 in 2013 from southern Alberta (Table 6-I). The collective parasitism by all larval species was recorded as 44.6% and 35.4%, respectively. The dominant larval parasitoid species was *D. insulare* in 2012 and *Cotesia* spp. in 2013. These were responsible for 20.6 and 29.1% parasitism of *P. xylostella* larvae, respectively (Table 6-IV). In 2012, highest parasitism by *D. insulare* was recorded from the fields near Grassy Lake (100%) and Hilda (57.8%). However, in 2013, highest parasitism was recorded from the fields near Oyen (66%) and Seven Persons (55.5%), and the dominant parasitoid species was *Cotesia* sp. In general, *D. insulare* was recorded as the dominant larval parasitoid species in 2010-2012, followed by *Cotesia* sp. and *M. plutellae*. *Cotesia* sp. was dominant in 2013, followed by *D. insulare* and *M. plutellae.*

Diadegma insulare is native to Central America (Lee et al. 2004). *Diadegma insulare's* origin in western Canada is unknown, but it likely migrates northward in spring along with its host rather than overwintering (Monnerat et al. 2002). It can parasitize all four larval instars of *P. xylostella* (Monnerat et al. 2002). In the absence of insecticide application, *D. insulare* is one of the most abundant species in brassicaceous crops in North America (Biever et al. 1992). In various regions of North America, parasitism has been reported sometimes to surpass 50–80% for

3rd and 4th instar larvae, respectively (Lee et al. 2003; Hutchison et al. 2004). *Diadegma insulare* was recorded as the principal parasitoid in Alberta and Saskatchewan in 1992-1993, accounting for 45% and 30% mortality of its host, respectively (Braun et al. 2004). A survey conducted in 2012 in Saskatchewan reported significantly higher parasitism by *D. insulare* (61.87%) than *M. plutellae* (38.13%) in canola (Bahar et al. 2013).

In this study, another larval parasitoid species of braconid, believed to be *Cotesia vestalis* (Haliday) [= *C. plutellae* (Kurdjumov)] (Hymenoptera: Braconidae), was responsible for a very substantial level of the total parasitism of *P. xylostella*. In the most recent checklist of *Cotesia* species in North America, Fernández-Triana (2010) reported 55 species with the expectation that many more species in this genus are unreported. *Cotesia plutellae* is a primary solitary larval endoparasitoid responsible up to 90% parasitism of *P. xylostella* in brassica crops when released in large numbers (Moralla-Rejesus & Sayavoc 1991; Shi et al. 2002; CABI 2005). *It* can parasitize all four larval instars of *P. xylostella but* prefers 2nd and 3rd instars for development (Shi et al. 2002).

Microplitis plutellae is a primary larval endoparasitoid with a transcontinental distribution in North America (Harcourt 1960; Braun et al. 2004; Sarfraz et al. 2005a). Females can parasitize all four larval instars of *P. xylostella* (Sarfraz et al. 2005a). *Microplitis plutellae* can overwinter in western Canada and is present early in the season to parasitize *P. xylostella* (Putnam 1978). *Microplitis plutellae* was found to perform best at low pest densities and considered a better parasitoid for small-scale pest infestations (Young 2013).

The study results have shown the presence and effective parasitism by the larval parasitoid complex of *P. xylostella*. Parasitism was one of the main factors regulating *P. xylostella* populations; revealing the significance of the occurrence and action of natural enemies.

The diversity of the larval parasitoids found in different locations in southern Alberta is quite similar. However, variations in the level of parasitism in fields of the same crop at different locations or of different crops at the same location, at the same time of the year were noticed. This may have been due to many reasons. Sarfraz et al. (2010a) reported that *D. insulare* distribution is generally associated with its host abundance and showed an aggregated distribution with *P. xylostella* within canola fields. Moreover, parasitism was also favored by host plant nutrient content and number of host population available (Bolter & Laing 1984; Sarfraz et al. 2009b). For instance, parasitism of *D. insulare* was highest when *P. xylostella* larvae were reared on the plant grown with 3.0 g fertilizer as compared to unfertilized plants (Sarfraz et al. 2009b). Similarly, a higher rate of parasitism by *D. insulare* was recorded on high-nitrogen *Brassica oleracea* L. var. *acephala* than on low-nitrogen plants (Fox et al. 1990). Overall, low parasitism rates by *M. plutellae* may reflect less abundance of this species in canola fields compared to *D. insulare* or relatively less parasitism later in the season due to the high proportion of host available since this species reported to perform best at low host densities (Young 2013). *Microplitis plutellae* overwinters in western Canada and is available early in the season to parasitize its hosts (Putnam 1978). Bahar et al. 2013 reported higher parasitism by *M. plutellae* when hosts were present at low densities early in the season. In this study, the samples were collected during the mid-and late season, when *D. insulare* is more active.

The data collected in this study indicated that *D. insulare* and *C. plutellae* were active and prominent in the fields during all four years in most of the locations surveyed. This also suggests that these species have stable populations in southern Alberta in most years. However, early season crop data should be collected to know more about *M. plutellae* distribution and natural parasitism. In 2011 and 2013 rates of parasitism by *C. plutellae* were higher in almost all of the

crops surveyed. This may be attributed to temperature variation during sample collecting time in these years. Field and laboratory observation of *C. plutellae* showed that this parasitoid is more active at higher temperatures (Talekar & Yang 1991) while cooler temperatures of 22°C and lower are favorable for the survival and parasitism of *D. insulare* (Bahar et al. 2012). Secondly, unlike *D. insulare*, *C. plutellae* has poor interspecific discrimination, so multiparasitism is common in this species. It oviposits in hosts containing larvae of other parasitoids such as *Diadegma* species when unparasitized *P. xylostella* larvae are not available (Lloyd 1940).

Rate of parasitism of *P. xylostella* pupae

Diadromus subtilicornis is a prepupal and pupal solitary parasitoid (Harcourt 1960; Anonymous 1996; Braun et al. 2004), but little is known about its biology in western Canada (Dosdall et al. 2011). In the early 1990's in western Canada, parasitism by *D. subtilicornis* accounted for 15% of the total (Braun et al. 2004). A total of 370 host pupae were collected during 2011to 2013 from 12 locations of southern Alberta. The only pupal parasitoid species observed was *D. subtilicornus.* The highest number of host pupae was collected in 2011 followed by 2012 (Table 6-V). Parasitism was highest in 2011(40.84%), while no parasitism was recorded in 2013. In 2011*, D. subtilicornus* accounted for 65, 40, 13.2, and 3.7% parasitism in fields near Medicine Hat, Orion, Etzikom and Seven Persons, respectively. However, a total of 30.3% parasitism of *P. xylostella* pupae was observed in 2012 with a highest parasitism in fields near Skiff (66.6%) and Bow Island (60%). The parasitism was higher in canola (44.4 & 50 %) than in mustard (13.2 & 15.7%) in 2011 and 2012, respectively.

Hyperparasitoids

Some species of Chalcidoidea have been associated with *P. xylostella* in western Canada, but it is unclear whether these are primary parasitoids or hyperparasitoids. *Conura*

albifrons (Walsh) and *Conura torvina* (Cresson) (Hymenoptera: Chalcididae) were recorded from *P. xylostella* in Saskatchewan and Alberta, respectively (Braun et al. 2004). Some other studies like Okine et al. (1996); Gaines (1997) and Pitkin (2004) reported a few species of *Conura*, including *C. torvina* (Cresson) and *C. side* (Walter) as hyperparasitoids of *Diadegma* and *Cotesia* species, that are common parasitoids in brassicaceous crops. A *Conura* sp. was also obtained in this study in 2011 from *P. xylostella* pupae responsible for a low level of parasitism (2%) from southern Alberta, but it is not clear whether it actually emerged from the *P. xylos*tella or from the primary parasitoid *D. insulare* since it was not determined initially whether the pupae were parasitized by *D. insulare*. It is difficult to differentiate larvae or pre-pupae that are parasitized from a primary parasitoid than from those that are not (Lee et al. 2004).

In 2011 in Alberta, a *Pteromalus sp.* (Hymenoptera: Pteromalidae) and a hyperparasitoid of *D. insulare, Catolaccus aeneoviridis* (Girault) (Hymenoptera: Pteromalidae) also were recorded. Previously, *Pteromalus semotus* Walker was obtained from Alberta in 2001 (Braun et al. 2004). Two hyperparasitoids of *D. insulare*, *Catolaccus cyanoideus* Burks and *Catolaccus aeneoviridis* (Girault) (Hymenoptera: Pteromalidae), were also identified in 2003 from canola in Alberta (Ulmer et al. 2005).

A facultative hyperparasitoid of ichneumonids and tachinids, *Mesochorus bilineatus* Thomson (Hymenoptera: Ichneumonidae), was also identified in 2011. There are over 100 species described in North America. The *Mesochorus* sp. has been reared previously from a primary larval parasitoid *C. plutellae* of *P. xylostella*. *Mesochorus* sp. started to feed after the primary parasitoids completed their development and formed cocoons. It pupated inside the cocoon of its host and later emerged from it (Kfir 1997). Hyperparasitoids could play an important role in reducing the primary parasitoid population and ultimately their impact on *P.*

xylostella densities.

Acknowledgments

Sincere appreciation is extended to Dr. Gary Gibson and Dr. A. Bennett of Agriculture and Agri-Food Canada for identifying the Braconidae and Ichneumonidae specimens. The Canola Council of Canada and Agriculture and Agri-Food Canada through the Canola Cluster Program provided funding for the *P. xylostella* parasitoid surveys.

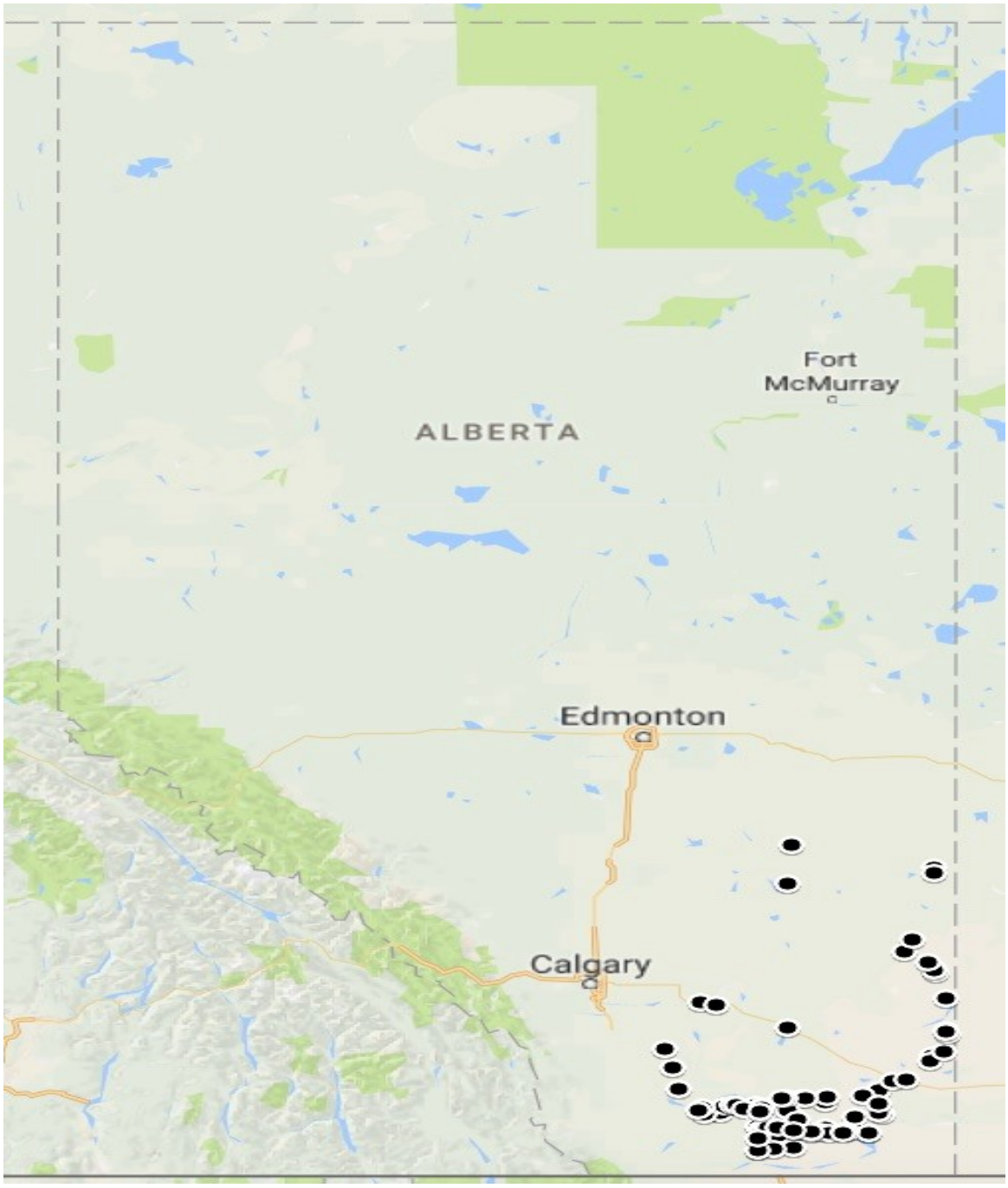


Figure 6-I. Map showing localities surveyed for *Plutella xylostella* and parasitoids in southern Alberta, Canada from 2010 to 2013.

Table 6-I. Numbers of localities in southern Alberta, Canada, surveyed in 2010-2013 and total numbers of pest (host) and parasitoids sampled.

	2010	2011	2012	2013
Total number of locations surveyed	11	14	19	15
Total fields surveyed	29	32	44	33
Number of locations with *P. xylostella* present	10	12	14	13
Total *P. xylostella* larvae collected	1284	1527	261	216
Number of locations with *P. xylostella* larvae	10	11	11	13
Number of locations with larval parasitoids present	10	11	11	10
Total *P. xylostella* pupae collected	0	333	33	4
Number of locations with *P. xylostella* pupae	0	4	5	3
Number of locations with pupal parasitoids present	0	4	4	0

Table 6-II. Hymenopterous parasitoids of *P. xylostella* recorded from southern Alberta, Canada

Species	*Plutella xylostella* stage(s) attacked	Parasitoid status	Host
Ichneumonidae: Campopleginae			
Diadegma spp.	Larva	Primary parasitoid	*P. xylostella*
Diadegma insulare (Cresson)	Larva	Primary parasitoid	
Ichneumonidae: Ichneumoninae			
Diadromus subtilicornis (Gravenhorst)	Prepupa/Pupa	Primary parasitoid	*P. xylostella*
Braconidae: Microgastrinae			
Cotesia plutellae	Larva	Primary parasitoid	*P. xylostella*
Microplitis plutellae (Muesbeck)	Larva	Primary parasitoid	*P. xylostella*
Chalcididae: Chalcidinae			
Conura sp.		Primary parasitoid hyperparasitoid	*P. xylostella* Ichneumonoids
Pteromalidae: Asaphinae			
Pteromalus sp.		Hyperparasitoid	Ichneumonoids
Cataloccus aeneoviridis (Girault)		Hyperparasitoid	
Ichneumonidae: Mesochorinae			
Mesochorus bilineatus Thomson		Hyperparasitoid	Ichneumonoids & Techinids

Table 6-III. Rates of parasitization of *P. xylostella* larvae in canola and mustard in southern Alberta, Canada

Date (month/year)	Crop	Total no. of larvae sampled	% parasitism by all species	% parasitism by major species			No. of larval parasitoid species
				Diadegma insulare	*Cotesia* sp.	*Microplitis plutellae*	
July/August 2013	*Brassica napus*	136	34.5	6.61	25.7	2.2	3
	Brassica juncea	7	28.57	0	28.57	0	1
	Sinapis alba	73	38.35	2.7	35.6	0	2
July/August 2012	*Brassica napus*	228	46	21.49	17.1	7.4	3
	Brassica juncea	20	30	5	10	15	3
	Sinapis alba	13	46.15	30.76	15.38	0	2
July/August 2011	*Brassica napus*	962	24.5	15.9	8.0	0.62	4
	Brassica juncea	215	27.9	8.83	18.1	0.93	3
	Sinapis alba	330	15.15	2.7	11.5	0.9	3
August 2010	*Brassica napus*	1284	30.46	16.40	14.06	0	2
	Brassica juncea	0	0	0	0	0	0
	Sinapis alba	0	0	0	0	0	0

Table 6-IV. Total parasitism by major larval parasitoid species

	% parasitism during the years of			
	2010	2011	2012	2013
Diadegma insulare	16.40	12	20.6	5
Cotesia sp.	14	10.8	16.4	29.1
Microplitis plutellae	0	0.7	7.6	1.3
Total % parasitism	30.4	23.5	44.8	35.6

Table 6-V. Number of host pupae and pupal parasitoid collected in canola and mustard in southern Alberta, Canada

Year	Crop	*P. xylostella* pupae collected	Pupal parasitoid emerged
2011	*Brassica juncea*	38	5
	Brassica napus	295	131
	Sinapis alba	0	0
2012	*Brassica juncea*	0	0
	Brassica napus	14	7
	Sinapis alba	19	3
2013	*Brassica juncea*	0	0
	Brassica napus	4	0
	Sinapis alba	0	0

Chapter 7: General Discussion/ Summary

This thesis elaborates on investigations of various bioecological aspects of *P. xylostella* and its major larval parasitoid *D. insulare* in western Canada. Through this research, I have attempted to explore understudied or unstudied fundamental aspects of the biology and ecology of both pest and parasitoid. Overall, this thesis establishes baseline ecological parameters (development under climatic change, bitrophic and tritrophic interactions, parasitism rate, fitness traits, floral nectar diet, etc.) for *D. insulare* and compares them with other previously published studies.

Plutella xylostella is seasonal in western Canada, and its population varies considerably from year to year, primarily depending on the arrival time and number of migrants from the southern or western United States in the spring (Dosdall et al. 2004b, 2011; Bahar et al. 2013). Natural enemies are known to keep most *P. xylostella* infestations below economically damaging levels. For instance, the outbreak of *P. xylostella* in brassica crops in western Canada in 2001 was terminated by its natural enemies (Dosdall et al. 2004b). However, to design a sustainable management framework applicable to western Canada, and to facilitate effective implementation of biocontrol and other pest management practices, an understanding of the life histories and host-parasitoid interactions with ecological factors is critical. Thus, I focused on investigating unknown significant life history traits of *P. xylostella* and *D. insulare* in relation to climatic factors. Thorough studies on the developmental biology of both pest and parasitoid with reference to host plant water stress and temperature were conducted thereby facilitating a better understanding of tritrophic interactions under climatic changes scenarios (Chapter 2-4).

I further extended my study on more bioecological traits and attempted to investigate the selective effect of various floral nectar diets on the host-parasitoid system (Chapter 5).

Furthermore, surveys in southern Alberta were conducted to explore the distribution and abundance of *P. xylostella,* and its associated parasitoid fauna over time (Chapter 6).

A substantial volume of research literature has been published on the biology and development of *P. xylostella* in different regions of the world. However, studies on tritrophic interactions involving host plants, pests, and their natural enemies are lacking. Moreover, very little research has been done on the effects of climate change on pests, and particularly their biocontrol agents, despite their tremendous economic importance in agroecosystems. Biological control programs can be improved substantially and implemented successfully through an in-depth understanding of the bioecology of both natural enemies and their hosts (Mommott et al. 1998; Martínez- Castillo et al. 2002). In this regard, *P. xylostella* and *D. insulare* are understudied. This formed the basis of my investigation on oviposition preferences of *P. xylostella*, and on the development and life history traits of *P. xylostella* and *D. insulare* under water deficit stressed host plants. The importance of host plants (first trophic level) in mediating ecological interactions between host-parasitoid systems is well documented (Takabayashi et al. 1998; Verkerk et al. 1998). To the best of my knowledge, there is no study that has reported the development of *D. insulare* and its host under climatic stress. My study reports for the first time tritrophic interactions and development of host and parasitoid under water deficit conditions (Chapter 3).

Ovipositional preferences of *P. xylostella* indicated that oviposition was significantly affected by water deficit stress and host plant (*B. napus*) age (Chapter 2). These findings support the preference-performance hypothesis stating that oviposition preference should correspond with host suitability. Thus, female phytophagous insects select to oviposit on host plants that optimize the fitness of their off springs (Jaenike 1978). The present study results confirmed that *P.*

xylostella females preferred to deposit eggs on vigorous plants not under water stress to ensure the successful development and survival of their offspring (Chapter 2). However, my investigation indicated a complex set of bitrophic and tritrophic interactions, and also revealed variable effects of stressed hosts on different trophic levels (Chapter 3). My research findings support neither the host plant stress nor plant vigor hypothesis as *P. xylostella* appeared to maintain the same rate of development on both stressed and non-stressed host plants. It may have been due to the genotypic plasticity of this species, which enables it to be among the most successful insect pest species worldwide (Talekar & Shelton 1993; Furlong et al. 2013). This trait allows *P. xylostella* to develop at the same rate on both stressed and non-stressed plants, as previously reported for some other lepidopteran pests (e.g. *Pieris rapae* L.) (Miles et al. 1982).

Investigation of tritrophic interactions confirmed that herbivores and their natural enemies respond to plants under stress in diverse and variable ways. These responses depend on the particular plant-herbivore and its natural enemies system, and also the nature, magnitude and duration of host plant stress (Waring & Cobb 1992; Koricheva et al. 1998; Calatayud et al. 2002; Haile 2002). For instance, unlike *P. xylostella*, the development and fitness of *D. insulare* were influenced by both water stress and host plant genotype, independently (Chapter 3). Several parameters (development, adults, and pupal weight, etc.) indicated lower fitness of *D. insulare* when it was reared on *P. xylostella* larvae that fed on water stressed host plants, suggesting water stressed hosts were less suitable for the parasitoid. Similarly, development varied considerably on different plant genotype regardless of water treatment. For instance, the fastest development of *D. insulare* was noticed on *B. napus* and the slowest on *S. alba,* a developmental pattern opposite to its host. These deviations under climatic stress may lead to disruption of synchronization, thereby increasing the chances of pest outbreak (Hence et al. 2007). The results provide a basic

understanding of tritrophic interactions and responses of trophic levels to abiotic stress. However, additional field and laboratory trials with different plant genotypes, magnitudes, and durations of water stress are warranted to investigate and validate their impact on a host-parasitoid system.

Biological control is facilitated when the responses of biocontrol agents to temperature and other climatic factors are known (Roy et al. 2002). Complementary studies on developmental rates of natural enemies and their hosts at different temperatures and the estimation of thermal requirements are helpful for improving the efficiencies of biocontrol strategies (Dosdall et al. 2012). This formed the basis of my investigation on development and fitness traits of *D insulare* at various temperatures (Chapter 4). My study reports that most of the parameters studied were proportional to temperature. Overall, parasitism increased with decreasing temperature and the developmental time decreased significantly with increasing temperature. The shortest developmental time was observed at 20 and 25°C while the longest was at 10°C. Short developmental time of biological control agents is critical to pest management plans as this can regulate how quickly and efficiently a natural enemy can track an increase in pest populations (Tran et al. 2012). The Results suggested that *D. insulare* is less tolerant to higher temperatures. Bahar et al. (2012) reported that the wasp is most likely suitable and efficient biocontrol agent at lower temperatures. This Information would be useful in extrapolating the potential effects of constant temperature on some aspects of *D. insulare* biology under laboratory conditions.

Combined results reported in Chapters 2 and 3 (e.g., developmental times, pupal and adult weights, adult body size, longevities in the absence of food, and the plant on which herbivore host was reared) linked with several fitness correlates of the parasitoid *D. insulare* under water deficit stress and various temperatures. These results have facilitated a better understanding of bi and tritrophic interactions with different climatic conditions. These findings are only a step toward

growing our understanding of how changes in moisture and temperature affect host-parasitoid responses and interactions.

These comprehensive analyses of tritrophic relationships are rarely integrated into pest management schemes. However, the study data (Chapter 2-4) indicated that without an understanding of the complexities and interactions that occur in these systems, significant management aspects can be ignored or miscalculated (Sarfraz et al. 2008). For instance, the development of *P. xylostella* was unaffected when reared on the water-stressed host. However, *D. insulare* development was slow while the longevity was high on the stressed host. Because of the diverse influence of changes in climatic factors on species interactions across trophic levels, a more comprehensive research into these relationships holds promise for a better understanding of multitrophic interactions. This will also provide a realistic view and further insights into interconnected climatic stressors like temperature and moisture, and their impact on the community and ecosystem-level processes, and also on biological control programes. (Thomson et al. 2010; Jamieson et al. 2012).

Numerous studies have shown the importance of floral nectar/sugar feeding for insects to increase their survival and fitness (Jervis & Kidd 1996; Wäckers et al. 2007). Improving the effectiveness of natural enemies by providing suitable nectar sources is an important tool in the conservation of biocontrol agents within sustainable agroecosystem management (Gurr et al. 1998; Landis et al. 2000). However, basic knowledge of the selective effects of nectar feeding on both pest and parasitoid's longevity is scarce. This formed the basis of my investigation on the differential effects of floral and non-floral feeding on *D. insulare* and its host *P. xylostella* (Chapter 5). My study reports for the first time the selective effects of nectar/sugar feeding on the longevity, body weight and size of *P. xylostella* and *D. insulare*. Results confirmed that

carbohydrate sources prolonged the lifespan of *D. insulare* and *P. xylostella*. Floral nectars of all the plant species tested were accessible to both the pest and its parasitoid. None of the nectar-producing plants was selective towards *D. insulare* relative to its host *P. xylostella*. However, selectivity in terms of floral nectar suitability and their impact on longevity were obvious in the case of *L. maritima* and *S. arvensis* for both the parasitoid and its host. Results showed that different diet (floral and non-floral) could selectively impact fitness and other life history traits of a pest -parasitoid system. For instance, *D. insulare* gained considerably more weight while feeding on floral nectar as compared to water alone. Furthermore, hind tibia length was significantly increased when *D. insulare* was fed on *B. napus* and *S. arvensis*. On the contrary, *P. xylostella* individuals gained more weight when fed on 10% honey compared to any of the floral nectars or water. However, floral and non-floral food sources did not have any impact on hind tibia length of *P. xylostella.* The food sources may only support one trophic level over the other depending on insect behavior, mouthpart morphology, nectar availability, accessibility, suitability, composition and concentration, and flower architecture and attractiveness (Idris & Grafius 1995; Wäckers 2001; Winkler et al. 2005; Carrillo et al. 2006; Kehrli & Bacher 2008; Lee & Heimpel 2008; Tunçbilek et al. 2012). The results obtained in this study underline the importance and potential for application of selective floral plant species in terms of their suitability and impact on the life history traits of pests and their parasitoids to improve biological control. From a conservation point of view, the needs of natural enemies as well as pest species must be taken into account. However, careful choice of floral resources that promotes natural enemies' performance without supporting pest species is critical (Winkler 2005). Field and laboratory research on floral nectar species that are common in canola fields of western Canada should continue to explore selective suitable, attractive, and nutritional floral species with

accessible nectar, and their role in mediating herbivore-natural enemy ecological interactions.

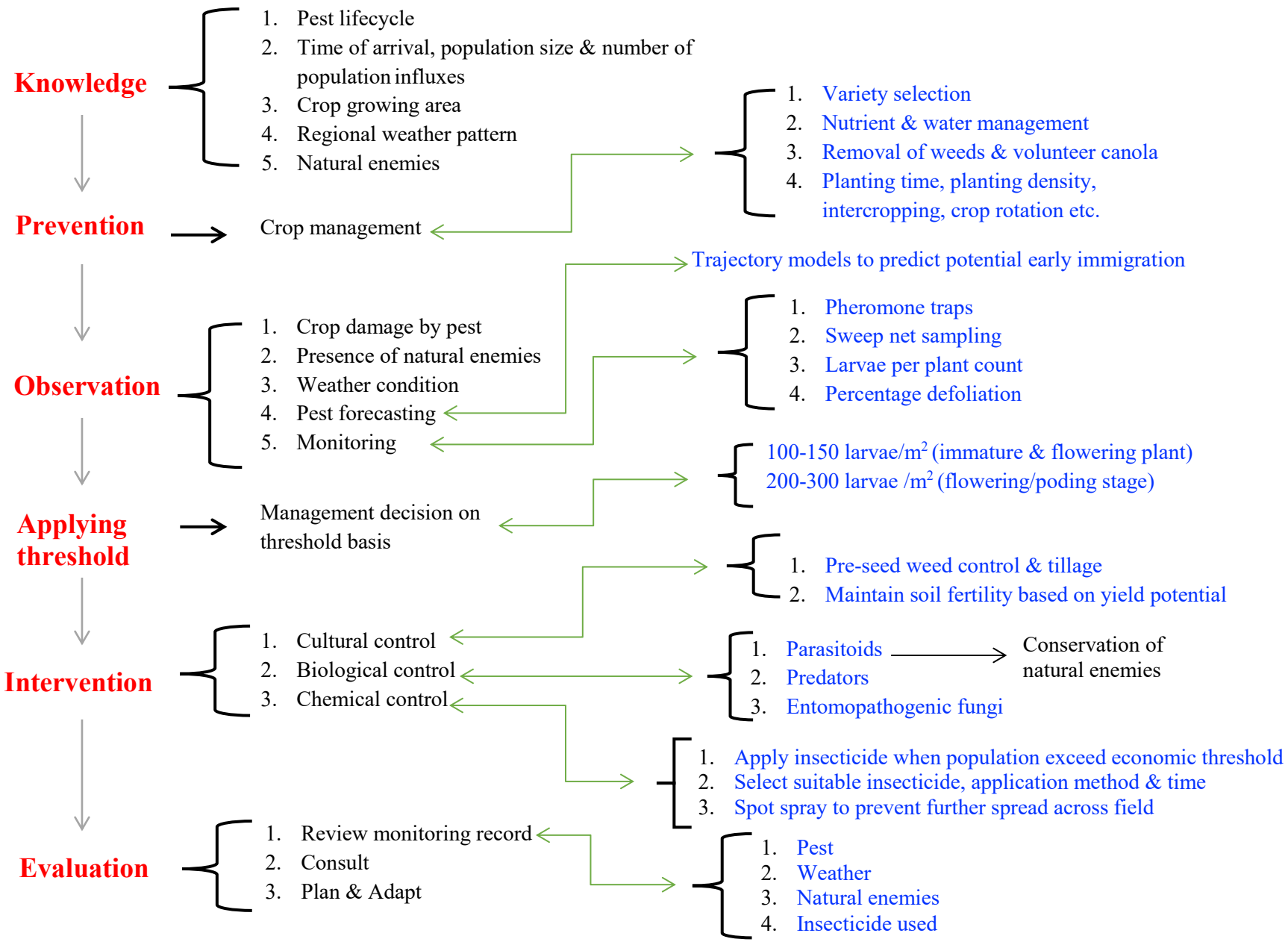
Surveys of commercial fields of canola and mustard from 2010 to 2013 in southern Alberta, showed the association of almost six species of primary hymenopteran parasitoids belonging to four genera (*Diadegma, Cotesia, Microplitis, and Diadromus)* with *P. xylostella. Moreover,* four species of hyperparasitoids belonging to four genera (*Conura*, *Cataloccus*, *Pteromalus,* and *Mesochorus*) were also recorded from primary parasitoids of *P. xylostella.* The data collected in this study indicated that larval parasitoids were present and active in the fields during all four years of the survey. However, rates of parasitization varied greatly among species, fields of same crop, and fields of different crops in the same or different years. In general, *D. insulare* was recorded as the most abundant species in 2010-2012, followed by *Cotesia* sp. and *M. plutellae*. *Cotesia* sp. was dominant in 2013, followed by *D. insulare* and *M. plutellae.* The existing larval parasitoid species appeared to provide considerable collective parasitism (e.g., 44.6% in 2012 & 35.4% in 2013), Similarly, a total of 30.3% parasitism in 2012 by the pupal parasitoid *D. subtilicornis* was observed, suggesting the importance of parasitoids in regulating the *P. xylostella* population. Hence, this study provides a valuable contribution to the knowledge about the parasitism levels and parasitoid communities associated with *P. xylostella* in southern Alberta.

However, regular annual and seasonal monitoring of different host crops in different geographical areas should be done to determine changes in parasitoid species composition, parasitism, and population densities over time and space. It is also critical to get in-depth knowledge and understanding of the biology of primary and hyperparasitoids of *P. xylostella* in western Canada. Conducting a regular survey of insect pests to detect any potential risk to the

cultivated crops early in the growing season is important because implementing control measures without considering the pest density may not be economically feasible.

Despite the limitations to the present study from drawing broader conclusions regarding the effect of climatic change and floral nectar diet on pest-parasitoid system, the study will help to understand bioecological foundation of host plant, and pest-parasitoid relationships. The study findings add to the growing literature highlighting the importance of incorporating climatic factors, floral nectar resouces, and natural enemies to develop an integrated *P. xylostella* management model of continual improvement (Fig. 7-I). Future research should consider long-term monitoring of the demographics of *P. xylostella* and its parasitoids. Thorough studies that include a wider range of host-parasitoid fitness traits and the potential effects of multiple biotic and abiotic stress factors on these traits and multitrophic relationships are warranted. Careful evaluation of the responses of a pest-parasitoid system to multiple climatic stressors are critical. This will eventually improve our understanding to enhance sustainable management of *P. xylostella.*

Figure 7-I: IPM Strategies for *Plutella xylostella*



Literature cited

Abbas MST. 1988. Biological and ecological studies on *Diadegma semiclausum* Hellen (Hym., Ichneumonidae), a larval parasite of the diamondback moth, *Plutella xylostella* (L.) (Lep., Plutellidae) in Egypt. Anzeiger fur Schadlingskunde, Pflanzenschutz, Umweltschutz 61: 1-2.

Abro GH, Jayo AL, Syed TS. 1994. Ecology of diamondback moth, *Plutella xylostella* (L.) in Pakistan. Host plant preference. Pakistan Journal of Zoology 26: 35-38.

Abro GH. 1985. Varietal resistance and insecticide efficacy against the diamondback moth, *Plutella xylostella* L. Ph.D. Thesis. The University of London. Pp. 159.

Abuzid MN, Mohamad Roff MN, Mansour S, Idris AB. 2011. Olfactory responses of *Plutella xylostella* to Chinese mustard volatiles. The 6th International Workshop on Management of the Diamondback Moth and other Crucifer Insect Pests. The World Vegetable Center. Pp. 66-69.

Agerbirk N, Olsen CE, Bibby BM, Frandsen HO, Brown LD, Neilsen JK, Renwick JAA. 2003. A saponin correlated with variable resistance of *Barbarea vulgaris* to the diamondback moth, *Plutella xylostella*. Journal of Chemical Ecology 29: 1417-1433.

Ahuja I, Borgen BH, Hansen M, Honne BI, Caroline M, Rohloff J, Rossiter JT, Bones AM. 2011. Oilseed rape seeds with ablated defense cells of the glucosinolate–myrosinase system. Production and characteristics of double haploid MINELESS plants of *Brassica napus* L. Journal of Experimental Botany 62: 4975-4993.

Alam MM. 1992. Diamondback moth and its natural enemies in Jamaica and some other Caribbean Islands. In: Talekar NS (ed) Diamondback moth and other crucifer Pests.

Proceedings of the Second International Workshop. Asian Vegetable Research and Development Center, Shanhua, Taiwan. Pp. 233-243.

Alizadeh M, Rassoulian GR, Karimzadeh J, Hosseini-Naveh V, Farazmand H. 2011. Biological study of *Plutella xylostella* (L.) (Lep: Plutellidae) and its solitary endoparasitoid, *Cotesia vestalis* (Haliday) (Hym: Braconidae) under laboratory conditions. Pakistan Journal of Biological Sciences 14: 1090-1099.

Ankersmit GW. 1953. DDT resistance in *Plutella maculipennis* (Curtis) (Lep.) in Java. Bulletin of Entomological Research 44: 421-425.

Anonymous 1971. Outbreaks and new records. FAO Plant Protection Bulletin 19: 89-92.

Anonymous 1996. Diamondback moth. Canada's Green Plan. http://www.agr.gov.sk.ca/docs/crops/.

Anuradha M. 1997. Possibility of the integration of bio-agent for the management of diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Yponumeutidae). Ph.D. Thesis. University of Agricultural Sciences, Bangalore. Pp.117.

Anwar MR, O'Leary G, McNeil D, Hossain H, Nelson R. 2007. Climate change impact on rainfed wheat in south-eastern Australia. Field Crop Research 104: 139-147.

Armbruster P, Hutchinson RA. 2002. Pupal mass and wing length as indicators of fecundity in *Aedes albopictus* and *Aedes geniculatus* (Diptera: Culicidae). Journal of Medical Entomology 39: 669-704.

Aslam TJ, Johnson SN, Karley AJ. 2013. Plant-mediated effects of drought on aphid population structure and parasitoid attack. Journal of Applied Entomology 137: 136-145.

Ayalew G, Lohr B, Baumgartner J, Ogol CKPO. 2004. Diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) and its parasitoids in Ethiopia. In: Kirk AA, Bordat D (eds)

Improving biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp. 140-143.

Azidah AA, Fitton MG, Quicke DLJ. 2000. Identification of the *Diadegma* species (Hymenoptera: Ichneumonidae, Campoleginae) attacking the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Bulletin of Entomological Research 90: 375-389.

Badenes-Pérez F, Nault BA, Shelton AM. 2005. Manipulating the attractiveness and suitability of hosts for diamondback moth (Lepidoptera: Plutellidae). Journal of Economic Entomology 98: 836-844.

Badenes-Pérez FR, Reichelt M, Gershenzon J, Heckel DG. 2011. Phylloplane location of glucosinolates in *Barbarea* spp. (Brassicaceae) and misleading assessment of host suitability by a specialist herbivore. New Phytologist 189: 549-556.

Badenes-Perez FR, Reichelt M, Gershenzon J, Heckel DG. 2014. Using plant chemistry and insect preference to study the potential of *Barbarea* (Brassicaceae) as a dead-end trap crop for DBM. Phytochemistry 98: 137-144.

Badenes-Perez FR, Shelton AM, Nault BA. 2004. Evaluating trap crops for diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Journals of Economic Entomology 97: 1365-1372.

Baggen LR, Gurr GM, Meats A. 1999. Flowers in tri-trophic systems: Mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. Entomologia Experimentalis et Applicata 91: 155-161.

Baggen LR, Gurr GM. 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance

biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Biological Control 11: 9-17.

Bahar MH, Soroka JJ, Dosdall LM, Olfert OO. 2013. Occurrence of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), and its larval parasitoid across Saskatchewan, Canada. Biocontrol Science and Technology 23:724-729.

Bahar MH, Soroka JJ, Dosdall LM. 2012. Constant versus fluctuating temperatures in the interactions between *Plutella xylostella* (Lepidoptera: Plutellidae) and its larval parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). Environmental Entomology 41: 1653-1661.

Bahar MH, Soroka JJ, Grenkow L, Dosdall LM. 2014. New threshold temperatures for the development of a North American diamondback moth (Lepidoptera: Plutellidae) population and its larval parasitoid, *Diadegma insulare* (Hymenoptera: Ichneumonidae). Environmental Entomology 43: 1443-1452.

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8: 1-16.

Barah A, Sengupta AK. 1991. Correlation and regression studies between pupal weight and fecundity of muga silkworm *Antherae assama* Westwood (Lepidoptera: Saturniidae) on four different food plants. Acta Physica Hungarica 78: 261-264.

Barbehenn RV, Reese JC, Hagen KS. 1999. The food of insects. Ecological Entomology, 2nd edn. In: Huffaker CB, Gutierrez AP (eds). John Wiley and Sons, New York, NY, USA. Pp. 83-122.

Bauer LS. 1995. Resistance: A threat to the insecticidal crystal proteins of *Bacillus thuringiensis*. Florida Entomologist 78: 414-443.

Baur ME, Kaya HK, Tabashnik BE, Chilcutt CF. 1998. Suppression of diamondback moth (Lepidoptera: Plutellidae) with an entomopathogenic nematode (Rhabditida: Steinernematidae) and *Bacillus thuringiensis* Berliner. Journal of Economic Entomology 91: 1089-1095.

Beck EH, Fettig S, Knake C, Hartig K, Bhattarai T. 2007. Specific and unspecific responses of plants to cold and drought stress. Journal of Bioscience 32: 501-510.

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

Bidart-Bouzat MG, Kliebenstein DJ. 2008. Differential levels of insect herbivory in the field associated with genotypic variation in glucosinolates in *Arabidopsis thaliana*. Journal of Chemical Ecology 34: 1026-1037.

Biever KD, Chauvin RL, Reed GL, Wilson RC. 1992. Seasonal occurrence and abundance of lepidopterous pests and associated parasitoids on collards in the north western United States. Journal of Entomological Science 27(1): 5-18.

Blackburn TM. 1991. A comparative examination of life-span and fecundity in parasitoid Hymenoptera. Journal of Animal Ecology 60: 151-164.

Bolat I, Dikilitas M, Ercisli S, Ikinic A, Tonkaz T. 2014. The effect of water stress on some morphological, physiological, and biochemical characteristics and bud success on Apple and Quince rootstocks. The Scientific World Journal. doi.org/10.1155/2014/769732

Bolter CJ, Laing JE. 1983. Competition between *Diadegma insulare* (Hymenoptera: Ichneumonidae) and *Microplitis plutellae* (Hymenoptera: Braconidae), for larvae of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Proceedings of Entomological Society of Ontario 14: 1-10.

Bommarco R. 2001. Using matrix models to explore the influence of temperature on population growth of arthropod pests. Agricultural and Forest Entomology 3: 275-283.

Bonebrake TC, Boggs CL, McNally JM, Ranganathan J, Ehrlich PR. 2010. Oviposition behavior and offspring performance in herbivorous insects: consequences of climatic and habitat heterogeneity. Oikos 119: 927-934.

Braun L, Olfert O, Soroka J, Mason P, Dosdall LM. 2004. Diamondback moth biocontrol activities in Canada. In: Kirk AA, Bordat D (eds) Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp. 144-146.

Bretherton RF. 1982. Lepidoptera immigration to the British Isles, 1969 to 1977. Proceedings and Transactions of the British Entomological and Natural History Society 15: 98-110.

Brodeur J, Boivin G. 2004. Functional ecology of immature parasitoids. Annual Review of Entomology 49: 27-49.

Brown J, McCaffrey JP, Harmon BL, Davis JB, Brown AP, Erickson DA. 1999. Effect of late season insect infestation on yield, yield components and oil quality of *Brassica napus, B. rapa, B. juncea* and *Sinapis alba* in the Pacific Northwest region of the United States. Journal of Agricultural Science 132: 281-288.

Buchholtz KP, Grigsby B, Lee OC, Slife FW, Willard CJ, Volk NJ. 1981. Weeds of the North Central states. National Center Registration and Publications. Pp. 281.

Bukovinszky T, Potting RPJ, Clough Y, van Lenteren JC, Vet LEM. 2005. The role of pre- and post-alighting detection mechanisms in the responses to patch size by specialist herbivores. Oikos 109: 435-446.

Buntin GD. 1990. Canola insect issues in the southeast. Proceedings of Canola Crop Protection Symposium, University of Tennessee, Memphis, TN. Pp. 28-33.

Burgess AJ, Warrington S, Allen-Williams L. 1994. Cabbage aphid (*Brevicoryne brassicae* L.) 'Performance' on oilseed rape (*Brassica napus* L.) experiencing water deficiency: roles of temperature and food quality. Acta Horticulturae 407: 16-19.

Butcher RDJ, Whitfield WGF, Hubbard SF. 2000. Complementary sex determination in the genus *Diadegma* (Hymenoptera: Ichneumonidae). Journal of Evolutionary Biology 13: 593-606.

Butler CD, Trumble JT. 2010. Predicting population dynamics of the parasitoid *Cotesia marginiventris* (Hymenoptera: Braconidae) resulting from novel interactions of temperature and selenium. Biocontrol Science and Technology 20: 391-406.

CABI (Centre for Applied Biosciences International). 2005. Crop Protection Compendium. Wallingford, UK. CAB International. Pp: s/n.

Calatayud PA, Polanía MA, Seligmann CD, Bellotti AC. 2002. Influence of water-stressed cassava on *Phenacoccus herreni* and three associated parasitoids. Entomologia Experimentalis et Applicata 102: 163-175.

Campos WG, Schoereder JH, Sperber CF. 2004. Does the age of the host plant modulate migratory activity of *Plutella xylostella*? Entomological Science 7: 323-329.

Campos WG, Schoereder LH, DeSouza OF. 2006. Seasonality in neotropical populations of *Plutella xylostella* (Lepidoptera): resource availability and migration. Population Ecology 48: 151-158.

Canola Council of Canada 2014. The economic impact of canola industry. http://www.canolacouncil.org/markets-stats/industry-overview/economic-impact-of-the-canola-industry/

Canola Council of Canada 2016. What is Canola? http://www.canolacouncil.org/oil-and-meal/what-is-canola/

Canola Council of Canada 2017. Industry overview. http://www.canolacouncil.org/markets-stats/industry-overview/

Carrillo I, Serrano HS, Torrado-León E. 2006. Effects of nectar producing on the reproduction of *Diadegma aff insulare* Cresson (Hymenoptera: Ichneumonidae), parasitoid of *Plutella xylostella* L. (Lepisoptera: Plutellidae). Revista Cotomhiana de Etttoiiiología. 32: 18-23.

Casas J, Pincebourde S, Mandon N, Vannier F, Poujol R, Giron D. 2005. Lifetime nutrient dynamics reveal simultaneous capital and income breeding in a parasitoid. Ecology 86: 545-554.

Chaney WE. 1998. Biological control of aphids in lettuce using in-field insectaries. In: Pickett CH, Bugg RL (eds) Enhancing biological control: Habitat management to promote natural enemies of agricultural pests. University of California Press, Berkeley, CA, USA. Pp. 73-83.

Chapman JW, Reynolds DR, Smith AD, Riley JR, Pedgley DE, Woiwod IP. 2002. High altitude migration of the diamondback moth *Plutella xylostella* to the U.K. A study using radar, aerial netting, and ground trapping. Ecological Entomology 27: 641-650.

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

Charron CS, Sams CE. 2004. Glucosinolate content and myrosinase activity in rapid-cycling *Brassica oleracea* grown in a controlled environment. Journal of the American Society for Horticultural Science 129: 321-330.

Chauhan U, Sharma KC. 2004. Status of biocontrol agents of *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae) in hilly areas of the north-west Himalayas, India. In: Kirk AA, Bordat D (eds) Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp. 153-157.

Cherry AJ, Mercadier G, Meikle W, Castelo-Blanco M, Schroer S. 2004a. The role of entomopathogens in DBM biological control. In: Kirk AA, Bordat D (eds) Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp. 51-70.

Cherry AJ, Osae M, Djegui D. 2004b. Relative potency, yield, and transmission of a Kenyan isolate of *Plutella xylostella* granulovirus in a population of diamondback moth from Benin, West Africa. In: Kirk AA, Bordat D (eds) Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp. 158-162.

Chew FS, Robbins RK. 1984. Egg-laying in butterflies. In: Vane-Wright RJ, Ackery PR (eds) The biology of butterflies. Academic Press, New York. Pp. 65-80.

Craig TP, Itami JK, Price PW. 1989. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. Ecology 70: 1691-1699.

Curtis J. 1860. Farm Insects. London: Blackie and Son. Pp. 528.

Daane KM, Williams LE. 2003. Manipulating vineyard irrigation amounts to reduce insect pest damage. Ecological Applications 13: 1650-1666.

Davidowitz G, Nijhout HF. 2004. The physiological basis of reaction norms: the interaction between growth rate, the duration of growth and body size. Integrative and Comparative Biology 44: 443-449.

De Bortoli SA, Polanczyk RA, Vacari AM, De Bortoli CP, Duarts RT. 2013. *Plutella xylostella* (Lepidoptera: Plutellidae): Tactics for Integrated Pest Management in Brassicaceae. DOI:10.5772/54110

De Bortoli SA, Vacari AM, Goulart RM, Santos RF, Volpe HXL, Ferraudo AS. 2011. Reproductive capacity and preference of the diamondback moth feeding on different Brassicaceae. Horticultura Brasileira 29: 187-192.

De Groot M, Winkler K, Potting R. 2005. Testing the potential of white mustard (*Sinapis alba*) and sweet alyssum (*Lobularia maritima*) as trap crops for the diamondback moth *Plutella xylostella*. Proceedings of the Netherlands Entomological Society Meeting 16: 117-123.

De Sassi C, Tylianakis JM. 2012. Climate change disproportionately increases herbivore over the plant or parasitoid biomass. PLoS ONE 7: e40557

Delvare G. 2004. The taxonomic status and role of Hymenoptera in biological control of DBM, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). In: Kirk AA, Bordat D (eds) Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp. 17-49.

Dewar RC, Watt AD. 1992. Predicted changes in the synchrony of larval emergence and budburst under climatic warming. Oecologia 89: 557-559.

Diaz-Gomez O, Rodriguez JC, Shelton AM, Lagunes A, Bujanos R. 2000. Susceptibility of *Plutella xylostella* populations in Mexico to commercial formulations of *Bacillus thuringiensis*. Journal of Economic Entomology 93: 963-970.

Dijkerman HJ. 1990. Suitability of eight *Yponomeuta*-species as hosts of *Diadegma armillata*. Entomologia Experimentalis et Applicata 54: 173-180.

Dixon GR. 2006. Origins and diversity of Brassica and its relatives. Vegetable brassicas and related crucifers.1-33.

Dosdall LM, Clayton GW, Harker KN, O'Donovan JT, Stevenson FC. 2004a. The effects of soil fertility and other agronomic factors on infestations of root maggots (*Delia* spp.) (Diptera: Anthomyiidae) in canola. Agronomy Journal 96: 1306-1313.

Dosdall LM, Mason PG, Olfert O, Kaminski L, Keddie BA. 2004b. The origins of infestations of diamondback moth, *Plutella xylostella* (L.), in canola in western Canada. In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment. Pp. 95-100.

Dosdall LM, Mason PG. 2010. Key pests and parasitoids of oilseed rape or canola in North America and the importance of parasitoids in integrated management. In: Williams IH (ed) Biocontrol-based integrated management of oilseed rape pests. Dordrecht/London: Springer 167- 213.

Dosdall LM, Soroka JJ, Olfert O. 2011. The diamondback moth in canola and mustard: current pest status and future prospects. Prairie Soils and Crops Journal 4: 66-76.

Dosdall LM, Weiss RM, Olfert O, Mason PG, Soroka JJ. 2008. Diamondback moth, *Plutella xylostella* (L.), as a pest of canola in Canada: Its historical impact on the crop and predicted

effects of climate change on its pest status. In: Shelton AM, Collins HL, Zhang Y, Wu Q (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fifth International Workshop, 24-27 October 2006. Beijing, China. Pp. 112-121.

Dosdall LM, Zalucki MP, Tansey JA, Furlong MJ. 2012. Developmental responses of the diamondback moth parasitoid *Diadegma semiclausum* (Hellen) (Hymenoptera: Ichneumonidae) to temperature and host plant species. Bulletin of Entomological Research 102: 373-384.

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

Dosdall LM. Soroka JJ, Olfert O. 2011. The diamondback moth in canola and mustard: current pest status and future prospects. Prairie Soils and Crops Journal 4: 66-76.

Downey RK. 1983. The origin and description of the Brassica oilseed crops. In: Kramer JKG, Sauer FD, Pigden WJ (ads) High and low erucic acid rapeseed oils: production, usage, chemistry, and toxicological evaluation, Academic Press. London and New York. Pp. 1-20.

Ebrahimi M. Ahad S, Talaei-Hassanloui R, Aurang K, Hsin C. 2013. The life table and parasitism rate of *Diadegma insulare* (Hymenoptera: Ichneumonidae) reared on larvae of *Plutella xylostella* (Lepidoptera: Plutellidae), with special reference to the variable sex ratio of the offspring and comparison of jackknife and bootstrap techniques. Annals of the Entomological Society of America 106: 279-287.

Edward J, Grafius I. 1997. Know your friends: *Diadegma insulare*, Parasite of Diamondback moth, Midwest Biological Control News Online. Vol. IV, No.1 http://www.entomology.wisc.edu/mbcn/kyf401.html

Eliopoulos PA, Stathas GJ, Bouras SL. 2005. Effects and interactions of temperature, host deprivation and adult feeding on the longevity of the parasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae). European Journal of Entomology 102: 181-187.

Fadamiro HY, Heimpel GE. 2001. Effects of partial sugar deprivation on lifespan and carbohydrate mobilization in the parasitoid *Macrocentrus grandii* (Hymenoptera: Braconidae). Annals of Entomology Society of America 94: 909-916.

Farooq M, Wahid A, Kobayashi N, Fujita D, Basra SMA. 2009. Plant drought stress: effects, mechanisms and management. Agronomy for Sustainable Development, Springer-Verlag (Germany), 29 (1): 185-212.

Fathi SAA, Bozorg-Amirkalaee M. Sarfraz M, Rafiee-Dastjerdi H. 2012. Parasitism and developmental parameters of the parasitoid *Diadegma majale* (Gravenhorst) in control of *Plutella xylostella* (L.) on selected cultivars of canola. Bio Control 57:49-59.

Fernandez-Triana J, Shaw M, Cardinal S, Dosdall L. 2014. First Nearctic record of *Diolcogaster claritibia* (Hymenoptera: Braconidae: Microgastrinae), with notes on taxonomic status and natural history. The Canadian Entomologist 146: 609-620.

Fernández-Triana J. 2010. Eight new species and an annotated checklist of Microgastrinae (Hymenoptera: Braconidae) from Canada and Alaska. Zookeys 63: 1-53.

Fitton M, Walker A. 1992. Hymenopterous parasitoids associated with diamondback moth: taxonomic dilemma. In: Talekar NS (ed) Diamondback moth and other crucifer pests.

Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 225-232.

Foster MA, Ruesink WG. 1984. Influence of flowering weeds associated with reduced tillage in corn on a black cutworm (Lepidoptera: Noctuidae) parasitoid, *Meteorus rubens* (Nees von Esenbeck). Environmental Entomology 13: 664-668.

Fox LR, Kester KM, Eisenbach J. 1996. Direct and indirect responses of parasitoids to plants: sex ratio, plant quality and herbivore diet breadth. Entomologia Experimentalis et Applicata. 80: 289-292.

Fox LR, Letourneau DK, Eisenbach J, Nouhuys SV. 1990. Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. Oecologia 83: 414-419.

Frazer BD, McGregor RR. 1992. Temperature-dependent survival and hatching rate of eggs of seven species of Coccinellidae. Canadian Entomologist. 124: 305-312.

Freitas AVL, Oliveira PS. 1996. Ants as selective agents on herbivore biology: effect on the behavior of a non-myrmecophilous butterfly. Journal of Animal Ecology 65: 205-210.

French RA. 1967. Long distance movement of two migrants Lepidoptera in relation to synoptic weather conditions. Biometeorology 2: 565-69.

Furlong MJ, Ju KH, Su PW, Chol JK, II R, Zalucki MP. 2008b. Integration of endemic natural enemies and *Bacillus thuringiensis* to manage insect pests of brassica crops in North Korea. Agriculture Ecosystems and Environment 125: 233-238.

Furlong MJ, Shi ZH, Liu SS, Zalucki MP. 2004. Evaluation of the impact of natural enemies on *Plutella xylostella* L. (Lepidoptera: Yponomeutidae) populations on commercial Brassica farms. Agricultural and Forest Entomology 6: 311-322.

Furlong MJ, Spafford H, Ridland PM. Endersby NM. Edwards OR, Baker GJ, Keller MA, Paull CA. 2008a. Ecology of diamondback moth in Australian canola: Landscape perspective and the implications for management. Australian Journal of Experimental Agriculture 48: 1494-1505.

Furlong MJ, Wright DS, Dosdall LM. 2013. Diamondback moth ecology and management: problems, progress, and prospect. Annual Review of Entomology 58: 517-541.

Furlong MJ, Zalucki MP. 2007. Parasitoid complex of diamondback moth in south- east Queensland: First records of *Oomyzus sokolowskii* (Hymenoptera: Eulophidae) in Australia. Australian Journal of Entomology 46: 167-75.

Furlong MJ, Zalucki MP. 2010. Exploiting predators for pest management: the need for sound ecological assessment. Entomologia Experimentalis et Applicata 135: 225-236.

Furlong MJ, Zalucki MP. 2017. Climate change and biological control: the consequences of increasing temperatures on host-parasitoid interactions. Current Opinion in Insect Science 20: 39-44.

Futuyma DJ, Agrawal AA. 2009. Macroevolution and the biological diversity of plants and herbivores. Proceedings of the National Academy of Sciences USA. 106: 18054-18061.

Gabriela LV. 2011. Interactions between *Plutella xylostella, Diadegma semiclausum* and some generalist predators of brassica crops. Ph.D. Thesis. University of Adelaide, School of Agriculture, Food and Wine. http://digital.library.adelaide.edu.au/dspace/handle/2440/65487

Gaines DN. 1997. Studies on *Conura torvina* (Hymenoptera: Chalcididae) reproduction and biology in relation to hosts in Brassica Crops. http://scholar.lib.vt.edu/theses/

Gates DM. 2003. Biophysical Ecology. Chapter 15. Temperature and organisms. Temperature effects on insects. Dover Publications Inc., N.Y. P 561.

Gathu RK, Lohr B, Poehling HM. 2008. Development and reproductive potential of diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) on cultivated and wild crucifer species in Kenya. International Journal of Tropical Insect Science 28: 19-29.

Georghiou GP, Lagunes-Tejeda A. 1991. The occurrence of resistance to pesticides in arthropods. An index of cases reported through 1989. FAO, Rome.

Gharuka M, Talekar NS, Lai PY. 2004. Biological studies on *Microplitis plutellae* (Hymenoptera: Braconidae), a larval parasitoid of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Formosan Entomologist 24: 1-13.

Godfray HCJ. 1994. Parasitoids: Behavioural and evolutionary ecology. Princeton University Press, Princeton.

Godfray HCJ. 1994. Parasitoids. Behavioral and evolutionary ecology. Princeton University Press, Princeton, New Jersey.

Golizadeh A, Kamali K, Fathipour Y, Abbasipour H. 2008. Life table and temperature-dependent development of *Diadegma anurum* (Hymenoptera: Ichneumonidae) on its host *Plutella xylostella* (Lepidoptera: Plutellidae). Environmental Entomology 37: 38-44.

Golizadeh A, Kamali K, Fathipour Y, Abbasipour H. 2009. Life table of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) on five cultivated brassicaceous host plants. Journal of Agricultural Science and Technology 11: 115-124

Gols R, Harvey JA. 2009. The effect of host developmental stage at parasitism on sex- related size differentiation in a larval endoparasitoid. Ecological Entomology 34:755-762.

Goodwin S, Danthanarayana W. 1984. Flight activity of *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae). Australian Journal of Entomology 23: 235-240.

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

Goulet H, Huber JT. 1993. Hymenoptera of the world: An identification guide to families. Agriculture Canada. Publication 1894/E. Pp. 668.

Gourdine JS, Gloria SM, Alvin MS, Leibee GL. 2003. Kale floral nectar and honey as food sources for enhancing longevity and parasitism of *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Journal of Agricultural and Urban Entomology 20: 1-6.

Gray RAH. 1915. Prevention of egg laying on turnip by the diamondback moth. J. Board Agric. 23: 222- 26.

Grime JP, Compbell BB. 1991. Growth rate, habitat productivity, and plant strategy as predictors of stress response. In: Mooney HH, Winner WE, Pell EJ (eds) Response of plant to multiple stresses. Academic Press, San Diego, USA. Pp. 143-159.

Griswold MW, Lounibos LP. 2006. Predator identity and additive effects in a tree hole community. Ecology 87: 987-995.

Gu H, Fitt GP, Baker GH. 2007. Invertebrate pests of canola and their management in Australia: A review. Australian Journal of Entomology 46: 231-243.

Gupta JC. 1971. Okra, a new host of diamondback moth. FAO Plant Protection Bulletin 19: 89-90.

Gurr GM, Van Emden HF, Wratten SD. 1998. Habitat manipulation and natural enemy

efficiency: implication for the control of pests. In: Barbosa P. (ed) Conservation biological control. San Diego, CA. Academic Press. Pp. 155-183.

Gutbrodt B, Mody K, Dorn S. 2011. Drought changes plant chemistry and causes contrasting response in lepidopteran herbivores. Oikos 120:1732-1740.

Haile FJ. 2002. Drought stress, insects and yield loss. In: Peterson RKD, Higley LG (eds) Biotic stress and yield loss. CRC Press, Boca Raton FL, USA. Pp. 117-134.

Hallmann GJ, Denlinger DL. 1998. Introduction: temperature sensitivity and integrated pest management. In: Hallman GJ, Denlinger DL (eds) Temperature sensitivity in insects and application in integrated pest management. Westview Press, Boulder. Pp. 1-5.

Hance T, van Baaren J, Vernon P, Boivin G. 2007. Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology 52: 107-12.

Hanks LM, Denno RF. 1993. Natural enemies and plant water relations influence the distribution of an armored scale insect. Ecological Society of America. Ecology 74: 1081-1091.

Harcourt DG. 1954. The biology and ecology of the diamondback moth, *Plutella maculipennis*, Curtis, in Eastern Ontario. Ph.D. Thesis. Cornell Univ., Ithaca, N.Y. Pp. 107.

Harcourt DG. 1957. Biology of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae), in Eastern Ontario. II. Life-history, behavior, and host relationship. The Canadian Entomologist 12: 554-564.

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

Harcourt DG. 1962. Biology of cabbage caterpillars in Eastern Ontario. Proceedings of the Entomological Society of Ontario 93: 61-75.

Harcourt DG. 1963. Major mortality factors in the population dynamics of the diamondback moth, *Plutella maculipennis* (Curt.) (Lepidoptera: Plutellidae). Memoirs of the Entomological Society of Canada 32: 55-56.

Harcourt DG. 1969. The development and the use of life tables in the study of natural insect populations. Annual Review of Entomology 12: 175-196.

Harcourt DG. 1986. Population dynamic of the diamondback moth in southern Ontario. In: Talekar NS, Griggs TD (eds) Diamondback moth management. Proceedings of the First International Workshop, 11–15 March 1985. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 1-15.

Hardy ICW, Griffiths NT, Godfray HCJ. 1992. Clutch size in a parasitoid wasp: A manipulation experiment. Journal of Animal Ecology 61: 121-129.

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

Harvey JA, Jervis MA, Gols R, Jiang N, Vet LEM. 1999. Development of the parasitoid, *Cotesia rubecula* (Hymenoptera: Braconidae) in *Pieris rapae* and *Pieris brassicae* (Lepidoptera: Pieridae): evidence for host regulation. Journal of Insect Physiology 45: 173-182.

Hawkins BA, Shaheen W. 1994. Parasitoid community ecology. Oxford University Press. Pp. 516.

Heimpel GE, Jervis MA. 2005. Does floral nectar improve biological control by parasitoids? Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications. In: Wäckers FL, van Rijn PCJ, Bruin J (eds). Cambridge University Press, Cambridge, UK. Pp. 267-304.

Henniges-Janssen K, Reineke A, Heckel DG, Groot AT. 2011a. Complex inheritance of larval adaptation in *Plutella xylostella* to a novel host plant. Heredity 107: 421-432.

Henniges-Janssen K, Schoefl G, Reineke A, Heckel DG, Groot AT. 2011b. Oviposition of diamondback moth in the presence and absence of a novel host plant. Bulletin of Entomological Research 101: 99-105.

Hillyer RJ, Thorsteinson AJ. 1969. The influence of the host plants or males on ovarian development or oviposition in diamondback moth, *Plutella maculipennis* (Curt.). Canadian Journal of Zoology 47: 805-816.

Hogg BN, Nelson EH, Mills NJ, Daane KM. 2011. Floral resources enhance aphid suppression by a hoverfly. Entomologia Experimentalis et Applicata 141: 138-144.

Holtzer TO, Archer TL, Norman JM. 1988. Host plant suitability in relation to water stress. In: Heinrichs EA (ed) Plant stress-insect interactions. John Wiley and Sons, New York, USA. Pp. 111-138.

Hoover JK, Newman JA. 2004. Tritrophic interactions in the context of climate change: a model of grasses, cereal aphids, and their parasitoids. Global Change Biology 10: 1197-1208.

Hopkins RJ, van Dam NM, van Loon JJA. 2009. Role of glucosinolates in insect-plant relationships and multitrophic interactions. Annual Review of Entomology 54: 57-83.

Hopkinson RF, Soroka JJ. 2010. Air trajectory model applied to an in-depth diagnosis of potential diamondback moth infestations on the Canadian Prairies. Agricultural and Forest Meteorology 150: 1-11.

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Xiaosu D, Maskell K, Johnson CA. 2001. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge.

Hsiao TC. 1973. Plant responses to water stress. Annual Review of Plant Physiology 24: 519-570.

Huffaker CB, Berryman A, Turchin P. 1999. Dynamics and regulation of insect populations. In: Huffaker CB, Gutierrez AP (eds) Ecological Entomology, 2nd ed. Wiley, New York. Pp. 269-305.

Hutchison WD, Burkness EC, Pahl G, Hurley TM. 2004. Integrating novel technologies for cabbage IPM in the USA: value of on-farm research. In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26- 29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment. Pp. 371-379.

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

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

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

Idris AB, Grafius E. 1996b. Effects of nectar-producing plants on *Diadegma insulare* (Cresson), a biological control agent of diamondback moth, *Plutella xylostella* (L.). The management of diamondback moth and other crucifer pests. Proceedings of the Third International Workshop, Kuala Lumpur, Malaysia. Pp. 90-96.

Idris AB, Grafius E. 1997. Nectar-collecting behavior of *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Plutellidae), in the field. Environmental Entomology 26: 114-120.

Idris AB, Grafius E. 2001. Evidence of *Diadegma insulare* (Cresson), a parasitoid of diamondback moth, *Plutella xylostella* (L.), present in various habitats. Pakistan Journal of Biological Sciences 1: 742-743.

Idris AB, Norhayati AM, Grafius E. 1997. Is *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) nectar or a pollen feeder? Malaysian Applied Biology 26: 101-103.

Idris AB, Zainal-Abidin BAH, Sajap AS, Noran AM, Hussan AK. 2004. Some studies on Nosema infecting DBM in Malaysia. In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment. Pp. 295-303.

Inbar M, Doostdar H, Mayer RT. 2001. Suitability of stressed and vigorous plants to various insect herbivores. Oikos 94: 228-235.

Jaenike J. 1978. Optimal oviposition behavior in phytophagous insects. Theoretical Population Biology 14:350-356.

Jamieson MA, Trowbridge AM, Raffa KF, Lindroth RL. 2012. Consequences of Climate Warming and Altered Precipitation Patterns for Plant-Insect and Multitrophic Interactions Plant Physiology 160: 1719-172.

Jervis MA, Copland MJW, Harvey JA. 2005. The life-cycle. In: Jervis MA (ed) Insect natural enemies: a practical perspective. Springer. The Netherlands. Pp. 73-165.

Jervis MA, Copland MJW. 1996. The life cycle. In: Jervis M, Kidd N (eds) Insect natural enemies: practical approaches to their study and evaluation. Chapman & Hall, London. Pp. 63-161.

Jervis MA, Kidd NAC, Heimpel GE. 1996. Parasitoid adult feeding behavior and biocontrol-a review. Biocontrol News Information 17: 11N-26N.

Jervis MA. 2005. Insects as natural enemies; a practical perspective. Springer, The Netherlands.

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

Johnson DR. 1953. *Plutella maculipennis* resistance to DDT in Java. Journal of Economic Entomology 46:176.

Justus KA, Dosdall LM, Mitchell BK. 2000. Oviposition by *Plutella xylostella* (Lepidoptera: Plutellidae) and effect of phylloplane waxiness. Journal of Economic Entomology 93: 1152-1159.

Kareiva P. 1987. Habitat fragmentation and stability of predator-pray interaction. Nature 326: 388-390.

Karl I, Fischer K. 2008. Why get big in the cold? Towards a solution to a life-history puzzle. Oecologia 155: 215-225.

Kehrli P, Bacher S. 2008. Differential effects of flower feeding in an insect host–parasitoid system. Basic and Applied Ecology 9: 709-717.

Keller MA, Baker G. 2002. Impact of conservation biological control practices on natural enemies: a case study of diamondback moth and its parasitoids. In 1st International Symposium on Biological Control of Arthropods. Pp. 215-219.

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

Kfir R. 1997. The diamondback moth with special reference to its parasitoids in South Africa. In: Sivapragasam A, Loke WH, Hussan AK, Lim GS (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Third International Workshop, 29 October - 1 November 1996. Kuala Lumpur, Malaysia: Malaysian Agricultural Research and Development Institute. Pp. 54-60.

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

Khan MFR, Griffin RP, Carner GR, Gorsuch CS. 2005. Diamondback moth (Lepidoptera: Plutellidae) population density and parasitism by Diadegma insulare on collard in South Carolina. Journal of Agriculture and Urban Entomology. 21: 164-170.

Khatri D, Wang Q, He XZ. 2008. Development and reproduction of *Diadegma semiclausum* (Hymenoptera: Ichneumonidae) on diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). New Zealand Plant Protection 61: 322–327.

Kirk AA, Mercadier G, Bordat D, Delvare G, Pichon A, Arvanitakis L, Goude´gnon AE, Rincon C. 2004. Variability in *Plutella xylostella* and its natural enemies: implications for biological control. In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-/29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment. Pp. 71-77.

Knolhoff LM, Heckel DG. 2011. Behavioral and genetic components of a host range expansion in the diamondback moth. In: Srinivasan R, Shelton AM, Collins HL (eds) Proceedings

of the Sixth International Workshop on Management of the Diamondback Moth and Other Crucifer Insect Pests, 21-25 March 2011, Kasetsart University, Nakhon Pathom, Thailand. The World Vegetable Center Taiwan. Pp. 321.

Koricheva J, Larsson S, Haukioja J. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. Annual Review of Entomology 43: 195-216.

Landis DA, Wratten SD, Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45: 175-201.

Lee JC, Carrillo MA, Hutchison WD. 2003. *Diadegma insulare*. VegEdge Fact Sheet, University of Minnesota Extension Service. University of Minnesota, St. Paul, MN.

Lee JC, Heimpel GE, Leibee GL. 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. Entomologia Experimentalis et Applicata 111: 189-199.

Lee JC, Heimpel GE. 2008. Effect of floral nectar, water, and feeding frequency on *Cotesia glomerata* longevity. Biological Control 53: 289-294.

Lee JC, Heimpel GE. 2008. Floral resources impact longevity and oviposition rate of a parasitoid in the field. Journal of Animal Ecology 77: 565-572.

Lee JH, Kim S-T. 2001. Use of spiders as natural enemies to control rice in Korea. Entomology Program, School of Agricultural Biotechnology, Seoul National University, Suwon, Korea. Pp. 441-744.

Legaspi B, Liu TX, Sparks AN, Jr. 2000. Occurrence of the diamondback moth and its parasitoids in the Lower Rio Grande Valley of Texas. Subtropical Plant Science 52: 47-51.

Li Q, Eigenbrode SD, Stringam GR, Thiagarajah MR. 2000. Feeding and growth of *Plutella xylostella* and *Spodoptera eridania* on *Brassica juncea* with varying glucosinolate concentrations and myrosinase activities. Journal of Chemical Ecology 10: 2401-2419.

Lim GS. 1986. Biological control of diamondback moth. In: Talekar NS (ed) Diamondback moth and other crucifer pests. Proceedings of the First International Workshop, 11-15 March 1985. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 159-171.

Lim GS. 1992. Integrated pest management of diamondback moth. In: Talekar NS (ed) Diamondback moth and other crucifer pests: Proceedings of the Second International Workshop,10-14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 565-576.

Liu S, Chen FZ, Zalucki MP. 2002. Development and survival of the diamondback moth (Lepidoptera: Plutellidae) at constant and alternating temperatures. Environmental Entomology 31: 221-231.

Liu S, Jiang L. 2003. Differential parasitism of *Plutella xylostella* (Lepidoptera: Plutellidae) larvae by the parasitoid *Cotesia plutellae* (Hymenoptera: Braconidae) on two host plant species. Bulletin of Entomological Research 93: 65-72.

Liu S, Li Y, Tang Z. 2004. Host resistance to an insecticide and selection at larval stage favor the development of resistance in the parasitoid, *Cotesia plutellae*. In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26- 29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment. Pp. 227-233.

Liu SS, Wang XG, Guo SJ, He JH, Shi ZH. 2000. Seasonal abundance of the parasitoid complex associated with the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in Hangzhou, China. Bulletin of Entomological Research 90: 221-231.

Liu YH, Li BP, ZH X. 2013. Effect of host instar and temperature on fitness-related traits in the solitary endoparasitoid, *Meteorus pulchricornis*. Phytoparasitica 41:1-7.

Lloyd DC. 1940. Host selection by hymenopterous parasites of the moth Plutella maculipennis Curtis. Proceedings of the Royal Society of London, Series B. Biological Sciences 128:451-484.

Lohr B, Gathu R. 2002. Evidence of adaptation of diamondback moth, *Plutella xylostella* (L.), to pea, *Pisum sativum* L**.** Insect Science and its Application 22: 161-173

Lohr B, Kfir R. 2004. Diamondback moth *Plutella xylostella* (L.) in Africa. A review with emphasis on biological control. Improving Biocontrol of *Plutella xylostella.* In: Kirk AA, Bordat D (eds) CIRAD, Montpellier, France. Pp. 71-83.

Lohr B. 2001. Diamondback moth on peas, really. Biocontrol News and Information 19: 38N-39N.

Ma J, Li D, Keller M, Schmidt O, Feng X. 2005a. A DNA marker to identify predation of *Plutella xylostella* (Lepidoptera: Plutellidae) by *Nabis kinbergii* (Hem., Nabidae) and *Lycosa* sp. (Araneae, Lycosidae). Journals of Applied Entomology 129: 330-335.

Ma J, Li YZ, Keller M, Ren SX. 2005b. Functional response and predation of *Nabis kinbergii* (Hemiptera: Nabidae) *to Plutella xylostella* (Lepidoptera: Plutellidae). Insect Science 12: 281-286.

Madore L. 2010. Diamondback moth in cole crops and corn earworm and European corn borer in the sweet corn Integrated pest management projects final report. Forestry and Agrifoods

Agency, Newfoundland and Labrador. http://www.faa.gov.nl.ca/publications/pdf/corn_pests_10.pdf

Marazzi C, Patrian B, Städler E. 2004. Secondary metabolites of the leaf surface affected by sulfur fertilization and perceived by the diamondback moth. Chemoecology 14: 81-86.

Martínez-castillo M, Leyva JL, Cibrián-tovar J, Bujanos-muñiz R. 2002. Parasitoid diversity and impact on populations of the diamondback moth *Plutella xylostella* (L.) on Brassica crops in central Mexico. Bio Control 47: 23-31.

Mason JM, Matthews GA, Wright DJ. 1999. Evaluation of spinning disc technology for the application of entomopathogenic nematodes against a foliar pest. Journal of Invertebrate Pathology 73:282-88.

Mattson WJ, Haack RA. 1987. Role of drought in outbreaks of plant-eating insects. Bioscience 37: 110-118.

Mattson WJ, Haack RA. 1987. The role of drought in provoking outbreaks of phytophagous insects. In: Barbosa P, Schultz JC (eds) Insect outbreaks. Academic Press, New York. Pp. 365-407.

Mattson WR. 1980. Herbivory in relation to plant nitrogen. Annual Review of Ecology and Systematics 11: 119-161.

Mauduit A. 2012. First assessment of predation by the arthropod natural enemy complex on the insect pests of canola-cropping systems in Southern Alberta in Canada: example of the diamondback moth (*Plutella xylostella*). Msc Thesis. University of Alberta, Canada

Meyer GA, Root RB. 1996. Influence of feeding guild on insect response to host plant fertilization. Ecological Entomology 21: 270-278.

Miles HW. 1924. The diamondback moth, *Plutella maculipennis* Curt. Kirton Agricultural Institute. Annual Report 1923-24. Pp. 45-48.

Miles PW, Aspinall D, Correll AT. 1982. The performance of two chewing insects on water-stressed food plants in relation to changes in their chemical composition. Australian Journal of Zoology 30: 347-355.

Miles PW, Aspinall D, Correll AT. 1982. The performance of two chewing insects on water-stressed food plants in relation to changes in their chemical composition. Australian Journal of Zoology 30: 347-355.

Miluch CE. 2010. Development of a semiochemical based monitoring system for diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), in canola in Alberta. MSc Thesis. The University of Alberta, Edmonton.

Mitchell ER, Hu GY, Okine JS. 1997. Diamondback moth (Lepidoptera: Plutellidae) infestation and parasitism by *Diadegma insulare* (Hymenoptera: Ichneumonidae) in collards and adjacent cabbage fields. Florida Entomologist 80: 54-62.

Mitchell-Olds T, Siemens D, Pedersen D. 1996. Physiology and costs of resistance to herbivory and disease in Brassica. Entomologia Experimentalis et Applicata 80:231–237.

Mohan M, Gujar GT. 2003. Local variation in susceptibility of the diamondback moth, *Plutella xylostella* (L.) to insecticides and detoxification enzymes. Crop Protection 22: 495-504.

Mommott J, Flwler SV, Hill RL. 1998. The effect of release size on the probability of establishment of biological control agents: gorse thrips (*Sericothrips staphylinus*) released against gorse (*Ulex europaeus*) in New Zealand. Biocontrol Science and Technology 8:103-115.

Monnerat RG, Kirk AA, Bordat D. 2002. Biology of *Diadegma* sp. (Hymenoptera:

Ichneumonidae), a parasitoid of *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), from Reunion Island. Neotropical Entomology 31(2): 271-274.

Moon DC, Rossi AM, Stiling P. 2000. The effects of abiotically induced changes in host plant quality and morphology on a salt marsh planthopper and its parasitoid. Ecological Entomology 25: 325-331.

Morallo-Rejesus B, Sayaboc A. 1992. Management of diamondback moth with *Cotesia plutellae*: prospects in the Philippines. In: Talekar NS (ed) Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 279-286.

Morallo-Rejesus B, Sayavoc AS. 1991. Management of diamondback moth with Cotesia plutellae: Prospects in the Philippines. In: Talekar NS (ed) Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, Shanhua, Taiwan: Asian Vegetable Research and Development Center. Pp. 279-286.

Morallo-Rejesus B. 1986. Botanical insecticides against the diamondback moth. In: Talekar NS (ed) Diamondback moth management. Proceedings of the First International Workshop, 11–15 March 1985. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 241-255.

Moran PJ, Showler AL. 2005. Plant responses to water deficit and shade stresses in pigweed and their influence on feeding and oviposition by the beet armyworm (Lepidoptera: Noctuidae). Environmental Entomology 34:929-937.

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

Mukenfuss AE, Sheppard BM, Ferrer ER. 1990. Natural mortality of diamondback moth in coastal South Carolina. In: Talekar NS (ed) Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 27-36.

Mukenfuss AE, Sheppard BM, Ferrer ER. 1992. Natural mortality of diamondback moth in coastal South Carolina. In: Talekar NS (ed) Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 27-36.

Mustata G. 1992. Role of parasitoid complex in limiting the population of diamondback moth in Moldavia, Romania. In: Talekar NS (eds) Diamondback moth and other crucifer pests. Proceedings of the Second International Workshop, 10-14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 203-212.

Nayar JK, Thorsteinson AJ. 1963. Further investigations into the chemical basis of insect-host plant relationship in an oligophagous insect *Plutella maculipennis* (Curtis) (Lepidoptera: Plutellidae). Canadian Journal of Zoology 41: 923-929.

Ninsin KD. 2004. Acetamiprid resistance and cross-resistance in the diamondback moth, *Plutella xylostella.* Pest Management Science 60: 839-841.

Okine JS, Mitchell ER, Hu GY. 1996. Low temperature effect on the viability of *Diadegma insulare* (Hymenoptera: Ichneumonidae) pupae and effect of this parasitoid on feeding rate of diamondback moth larvae (Lepidoptera: Plutellidae). Florida Entomologist 79: 503-509.

Olfert O, Weiss RM, Soroka JJ. 2011. Modeling tools provide advance warnings of potential distribution of diamondback moth and risk – A team approach

http://www.oecd.org/env/ehs/pesticides-biocides/49990901.pdf

Ooi PAC, Kelderman W.1979. The biology of three common pests of cabbage in Cameron Highlands, Malaysia. Malaysian Agriculture Journal 52: 85-101.

Ooi PAC, Lim GS. 1989. Introduction of exotic parasitoids to control diamondback moth in Malaysia. Journal of Plant Protection in the Tropics 6: 103-111.

Ormerod EA. 1891. The diamondback moth. Journal of Agriculture Society. II1 Ser. 2: 596-630.

Ortiz FM. 2011. Biological control of diamondback moth. The role of predators, parasitoids, and insecticides. Ph.D. Thesis. The Faculty of Natural Resources and Agriculture Sciences. Department of Ecology. Uppsala. http://pub.epsilon.slu.se/8073/1/miranda_f_110414.pdf

Oswald CJ, Brewer MJ. 1997. Aphid-barley interactions mediated by water stress and barley resistance to Russian wheat aphid (Homoptera: Aphididae). Environmental Entomology 26:591-602.

Palaniswamy PC, Gillott C, Slater GP. 1986. Attraction of diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), by volatile compounds of canola, white mustard and faba bean. Canadian Journal of Entomology 118: 1279-1285.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579-583.

Parmesan C. 2007. Influences of species, latitudes, and methodologies on estimates of phenological response to global warming. Global Change Biology 13: 1860-1872.

Pathak MR, J.A. Da Silva JAT, Wani SH. 2014. Polyamines in response to abiotic stress tolerance through transgenic approaches. GM Crops & Food 5: 87-96.

Philip H, Mengersen E. 1989. Insect pests of the Prairies. University of Alberta, Edmonton, AB. Pp.122.

Pichon LA, Roux O, Kirk AA, Alauzet C, Bordat D, Legal L. 2006. Genetic differentiation among various populations of the DBM, *Plutella xylostella* (Lepidoptera: Yponomeutidae). Bulletin of Entomological Research 96: 137-144.

pitkin BR. 2004. Notes on Families Chalcidoidea. Natural History Museum, London. http://www.nhm.ac.uk/research-curation/ projects/chalcidoids/chalcididae.html.

Pivnick KA, Jarvis BJ, Gillott C, Slater GP, Underhill EW. 1990. Daily patterns of reproductive activity and the influence of adult density and exposure to host plants on reproduction in the diamondback moth (Lepidoptera: Plutellidae). Environmental Entomology 19: 587-593.

Pivnick KA, Jarvis BJ, Slater GP, Gillott C, Underhill EW. 1990a. Attraction of diamondback moth (Lepidoptera: Plutellidae) to volatiles of oriental mustard; the influence of age, sex and prior exposure to males and host plants. Environmental Entomology 19: 704-709.

Pizzol J, Pintureau B, Khoualdia O, Desneux N. 2010. Temperature dependent differences in biological traits between two strains of *Trichogramma cacoeciae* (Hymenoptera: Trichogrammatidae). Journal of Pest Science 83: 447-452.

Polis GA, Myers CA, Holt RD. 1989. The ecology and evolution of intrigued predation: potential competitors that eat each other. Annual Review of Ecology, Evolution and Systematics 20: 297-330.

Pollard E, Yates TJ. 1993. Monitoring Butterflies for Ecology and Conservation. Chapman & Hall, London.

Popov C, Trotus E, Vasilescu S, Barbulescu A, Rasnoveanu L. 2006. Drought effect on pest attack in field crops. Romanian Agricultural Research 23: 43-52.

Porter JH, Parry ML, Carter TR. 1991. The potential effects of climatic change on agricultural insect pests. Agriculture and Forest Meteorology 57: 221-240.

Prakash S. 1980. Cruciferous oilseeds in India. In: Tsunoda S, Hinata K, Gomez-Campo C (eds) Brassica crops and wild allies. Biology and Breeding. Japan Scientific Society Press, Tokyo. Pp. 151-163.

Price PW, Roininen H, Tahvanainen J. 1987. Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? Oecologia 74:1-6.

Price PW. 1991. The plant vigor hypothesis and herbivore attack. Oikos 62: 244-251.

Pritchard J, Griffiths B, Hunt EJ. 2007. Can the plant-mediated impacts on aphids of elevated CO_2 and drought be predicted? Global Change Biology 13: 1616-1629.

Proctor M, Yeo P. 1973. The pollination of flowers. Collins, London.

Putnam LG. 1968. Experiments in the quantitative relationships between *Diadegma insularis* (Hymenoptera: Ichneumonidae) and *Microplitis plutellae* (Hymenoptera: Braconidae) with their host *Plutella maculipennis* (Lepidoptera: Plutellidae). The Canadian Entomologist 100: 11-16.

Putnam LG. 1978. Diapause and cold hardiness in *Microplitis plutellae*, a parasite of the larvae of the diamondback moth. Canadian Journal of Plant Science 58: 911-913.

Quan X, WU L, Zhou Q, Yun Y, Peng Y, Chen J. 2011. Identification of predation by spiders on the diamondback moth *Plutella xylostella*. Bulletin of Insectology 64: 223-227.

Qureshi SR, Quan WL, Zhou RQ. 2016. Thermal effects on development and adult longevity of endoparasitoid *Chelonus murakatae* Munakata (Hymenoptera: Braconidae) Environmental Science and Pollution Research. Pp. 1-6.

Rabia S, Sayyed AH, Sarfraz A, Zaka SM. 2010. Effect of different host plants on the fitness of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Crop Protection 29: 178-182.

Ramachandran S, Buntin GD, All JN. 2000. Response of canola to simulated diamondback moth (Lepidoptera: Plutellidae) defoliation at different growth stages. Canadian Journal of Plant Science 80: 639-646.

Rask L, Andreasson E, Ekbom B, Eriksson S, Pontoppidan B, Meijer J. 2000. Myrosinase: gene family evolution and herbivore defense in Brassicaceae. Plant Molecular Biology 42: 93-113.

Ratzka A, Vogel H, Kliebenstein DJ, Mitchell-Olds T, Kroymann J. 2002. Disarming the mustard oil bomb. Proceedings of the National Academy of Sciences USA. 99: 11223-11228.

Raymer PL. 2002. Canola: An emerging oilseed crop. In: Janick J, Whipkey A (eds) Trends in new crops and new uses. ASHS Press, Alexandria, VA. Pp. 122-126.

Read DC. 1962. Notes on the life history of *Aleochara bilineata* (Gyll.) (Coleoptera: Staphylinidae), and on its potential value as a control agent for the cabbage maggot, *Hylemya brassicae* (Bouché) (Diptera: Anthomyiidae). The Canadian Entomologist 94: 417-424.

Reay-Jones FPF, Wison LT, Showler AT, Reagan TE, Way MO. 2007. Role of oviposition preference in an invasive crambid impacting two graminaceous host crops. Environmental Entomology 36: 938-951.

Reddy GVP, Guerrero A. 2000. Behavioral responses of diamondback moth, *Plutella xylostella*, to green leaf volatiles of *Brassica oleracea* subspecies capitata. Journal of Agriculture and Food Chemistry 48: 6025-6029.

Reddy GVP, Tabone E, Smith MT. 2004. Mediation of host selection and oviposition behavior in the diamondback moth, *Plutella xylostella* and its predator, *Chrysoperla carnea* by chemical cues from cole crops. Biological Control 29:270-277.

Reinhardt D, Kuhlemeier C. 2002. Plant architecture. EMBO Reports. 9: 846-851. doi: 10.1093/embo-reports/kvf177

Renwick JAA, Haribal M, Gouinguene S, Stadler E. 2006. Isothiocyanates stimulating oviposition by the diamondback moth, *Plutella xylostella*. Journal of Chemical Ecology 32: 755-766.

Renwick JAA, Radke CD. 1990. Plant constituents mediating oviposition by the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). Phytophaga 3: 37-46.

Renwick JAA. 1989. Chemical ecology of oviposition in phytophagous insects. Experientia 45: 223-228.

Riddick EW. 2006. Egg load and body size of lab-cultured *Cotesia marginiventris*. Bio Control 51: 603-610.

Romeis J, Städler E, Wäckers FL. 2005. Nectar and pollen feeding by adult herbivorous insects. In: Wäckers FL, Van Rijn PCJ, Bruin J (eds) Plant-provided food for carnivorous insects: a protective mutualism and its applications. Cambridge University Press, Cambridge, UK. Pp. 178-219.

Romo CM, Tylianakis JM. 2013. Elevated temperature and drought interact to reduce parasitoid effectiveness in suppressing hosts. PLoS ONE 8(3): e58136.

Rosenzweig C, Hillel D. 1998. Climate change and the global harvest: Potential Impacts of the Greenhouse Effect on Agriculture. Oxford University Press. New York. Pp. 324.

Rossbach, Lohr B, Vidal S. 2006. Host shift to peas in the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) and response of its parasitoid *Diadegma mollipla* (Hymenoptera: Ichneumonidae). Bulletin of Entomological Research 96: 413-419.

Rouault G, Candau J, Lieutier F, Nageleisen L, Martin J, Warzee N. 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Annals of Forest Science 63: 613-624.

Roy M, Brodeur J, Cloutier C. 2002. Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). Environmental Entomology 31: 177-187.

Rubberson J. 1996. Environmental conditions and biological control of the beet armyworm. In: Council NC (ed) Beltwide Cotton Conference, Memphis, TN. Pp. 116-118.

Russell M. 2015. A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers of individual plant species. Biological Control 82: 96-103

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126: 543-562.

Saeki Y, Crowley PH. 2012. Temperature effects during development on a poly embryonic parasitoid and its host. Journal of Thermal Biology 37: 602-607.

Sanghera GS, Wani SH, Hussain W, Singh NB. 2011. Engineering cold stress tolerance in crop plants. Current Genomics 14: 30-43.

Saranga Y, Menz M, Jiang C-X, Wright RJ, Yakir D, Paterson AH. 2001. Genomic dissection of genotype x environment interactions affecting adaptation of cotton to arid conditions. Genome Research 11: 1988-1995.

Sarfraz M, Dosdall LM, Black AJ, Keddie BA. 2010a. Leaf nutrient levels and the spatio-temporal distributions of *Plutella xylostella* and its larval parasitoids *Diadegma insulare* and *Microplitis plutellae* in canola. Biological Control 55: 229-244.

Sarfraz M, Dosdall LM, Keddie BA, Myers J. 2011. Larval survival, host plant preferences and developmental responses of the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae) on wild brassicaceous species. Entomological Science 14: 20-30.

Sarfraz M, Dosdall LM, Keddie BA. 2005a. Biological control of the diamondback moth, *Plutella xylostella* (L.): a review. Biocontrol Science and Technology 15: 763-789.

Sarfraz M, Dosdall LM, Keddie BA. 2005b. Effects of the host plant nutrient regime on diamondback moth, *Plutella xylostella* (L.). In: Entomology – A Celebration of Life's Little Wonders. Proceedings of the Joint Annual Meeting of Entomological Society of Canada and Entomological Society of Alberta, 2–5 November 2005, Canmore, Alberta, Canada.

Sarfraz M, Dosdall LM, Keddie BA. 2005c. Evidence for behavioral resistance by the diamondback moth, *Plutella xylostella* (L.). Journal of Applied Entomology 129: 340-341.

Sarfraz M, Dosdall LM, Keddie BA. 2006. Diamondback moth–host plant interactions: implications for pest management. Crop Protection 25: 625-639.

Sarfraz M, Dosdall LM, Keddie BA. 2007. Resistance of some cultivated Brassicaceae to infestations by *Plutella xylostella* (Lepidoptera: Plutellidae). Journal of Economic Entomology 1: 215-224.

Sarfraz M, Dosdall LM, Keddie BA. 2008. Host plant genotype of the herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) affects the performance of its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). Biological Control 44: 42-51.

Sarfraz M, Dosdall LM, Keddie BA. 2009a. Bottom-up effects of host plant nutritional quality on *Plutella xylostella* (Lepidoptera: Plutellidae) and top-down effects of herbivore attack on plant compensatory ability. European Journal of Entomology 106: 583-594.

Sarfraz M, Dosdall LM, Keddie BA. 2009b. Host plant nutritional quality affects the performance of the parasitoid *Diadegma insulare*. Biological Control 51: 34-41.

Sarfraz M, Dosdall LM, Keddie BA. 2010b. Performance of the specialist herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) on Brassicaceae and non-Brassicaceae species. The Canadian Entomologist 142: 24-35.

Sarfraz MR, Dosdall LM, Keddie BA. 2012. Influence of the herbivore host's wild food plants on parasitism, survival, and development of the parasitoid *Diadegma insulare.* Biological Control 62: 38-44.

SAS Institute Inc. 2012. SAS 9.3 User's Guide. Cary, NC, USA.

Satar S, Kersting U, Uygun N. 2005. Effect of temperature on development and fecundity of *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumber. Journal of Pest Science. 78:133-137.

Satpathy S, Shivalingaswamy TM, Kumar A, Rai AM, Rai M. 2010. Potentiality of Chinese cabbage (*Brassica rapa* subsp. *Pekinensis*) as a trap crop for diamondback moth (*Plutella xylostella*) management. Indian Journal of Agricultural Sciences 80: 240-243.

Sayyed AH, Omar D, Wright DJ. 2004. Genetics of spinosad resistance in a multi-resistant field selected population of *Plutella xylostella*. Pest Management Science 60: 827-832.

Scheirs J, De Bruyn L. 2005. Plant-mediated effects of drought stress on host preference and performance of a grass miner. Oikos 108: 371-385.

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA. 1965. Sap pressure in vascular plants. Science. 148: 339-346.

Schoonhoven LM, Van Loon JJM, Dicke M. 2005. Insect-plant Biology. Oxford University Press, New York.

Seagraves MP, Riedell WE, Lundgren JG. 2011. Oviposition preference for water-stressed plants in *Orius insidiosus* (Hemiptera: Anthocoridae). Journal of Insect Behaviour 24: 132-143.

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

Shelton AM, Nault BA. 2004. Dead-end trap cropping: a technique to improve management of the diamondback moth. Crop Protection 23: 497-503

Shelton AM, Roush RT. 2000. Resistance to insect pathogens and strategies to manage resistance. In: Lacey LA, Kaya HK (eds) Field manual of techniques in invertebrate pathology. Kluwer Academic Press. Pp. 829-846.

Shelton AM, Wyman JA. 1992. Insecticide resistance of diamondback moth in North America. In: Talekar NS (ed) Diamondback moth and other crucifer pests. Proceedings of the

Second International Workshop, 10–14 December 1990. Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 447-454.

Shelton AM. 2001. Management of the Diamondback moth: déjà vu all over again? In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop. Melbourne, Australia. Pp. 3-8.

Shelton AM. 2004. Management of diamondback moth: déjà vu all over again? In: Endersby, NM, Ridland PM (eds.) The management of diamondback moth and other crucifer pests. Proceedings of the 4th International Workshop, 26-29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment Pp. 3-8.

Shi Z, Li Q, Li X, Liu S. 2004. Interspecific competition between *Diadegma semiclausum* and *Oomyzus sokolowskii*, parasitoids of diamondback moth, *Plutella xylostella*. In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment. Pp. 243-248.

Shi Z, Liu S, Li Y. 2002 *Cotesia plutellae* parasitizing *Plutella xylostella*: Host-age dependent parasitism and its effect on host development and food consumption BioControl 47: 499-511.

Shinoda T, Nagao T, Nakayama M, Serizawa H, Koshioka M, Okabe H, Kawai A. 2002. Identification of a triterpenoid saponin from a crucifer, *Barbarea vulgaris*, as a feeding deterrent to the DBM, *Plutella xylostella*. Journal of Chemical Ecology 28: 587-599.

Showler AT, Moran PJ. 2003. Effects of drought-stressed cotton, *Gossypium hirsutum* L., on beet armyworm, *Spodoptera exigua* (Hubner), oviposition, and larval feeding preferences and growth. Journal of Chemical Ecology 29: 1997-2011.

Showler AT. 2012. Drought and arthropod pests of crops. In: Neves DF, Sanz JD (eds) Drought: New research. Nova Science, Hauppauge, New York, USA. Pp. 131-154.

Siekmann G, Tenhumberg B, Keller MA. 2001. Feeding and survival in parasitic wasps: sugar concentration and timing matter. Oikos 95: 425-430.

Siemens DH, Mitchell-Olds T. 1996. Glucosinolates and herbivory by the specialist (Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae): consequences of concentration and induced resistance. Environmental Entomology 52: 1344-1353.

Silva R, Furlong MJ. 2012. Diamondback moth oviposition: effects of host plant and herbivory. Entomologia Experimentalis et Applicata 143: 218-230.

Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions 1: 21-32.

Singer MC. 2003. Spatial and temporal patterns of checkerspot butterfly–host plant association: the diverse roles of oviposition preference. In: Boggs CL, Watt WB, Erlich PR (eds) Butterflies: Ecology and evolution taking flight. University of Chicago Press, Chicago. Pp. 207-228.

Singer MC. 2004. Measurement correlates, and the importance of oviposition preference in the life of checkerspots. In: Ehrlich PR, Hanski I (eds) On the wings of checkerspots. Oxford University Press, New York. Pp. 112-137.

Sivinski J, Wahl D, Holler T, Al Dobai S, Sivinski R. 2011. Conserving natural enemies with flowering plants: Estimating floral attractiveness to parasitic Hymenoptera and attraction's relationship to flower and plant morphology. Biological Control 58: 208-214.

Slansky F, Feeny P. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage white butterfly on wild and cultivated food plants. Ecological Monographs 47: 209-228.

Slosser J. 1980. Irrigation timing for bollworm management in cotton. Journal of Economic Entomology 73: 346-349.

Smith DB, Sears MK. 1982. Evidence for dispersal of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), into southern Ontario. Proceedings of Entomological Society Ontario. 113: 21-28.

Smith TJ, Villet MH. 2004. Parasitoids associated with the diamondback moth, *Plutella xylostella* (L.), in the Eastern Cape, South Africa. In: Endersby NM, Ridland PM (eds) The management of diamondback moth and other crucifer pests. Proceedings of the Fourth International Workshop, 26-29 November 2001. Melbourne, Australia: Department of Natural Resources and Environment. Pp. 249-253.

Soufbaf M, Fathipour Y, Karimzadeh J, ZaluckI MP. 2010. Development and age-specific mortality of diamondback moth on brassica host plants: pattern and causes of mortality under laboratory conditions ecology and population biology. Annals of the Entomological Society of America 103: 574-579.

Sourakov A, Mitchell ER. 2000. Featured Creatures. USDA Available: http//creatures.ifas.edu/wasps/diadegma_insulare.html

Soyatech 2017. Soyatech growing opportunities. Canola facts. http://www.soyatech.com/canola_facts.htm

Spanoudis CG, Andreadis SS. 2012. Temperature-dependent survival, development, and adult longevity of the koinobiont endoparasitoid *Venturia canescens* (Hymenoptera:

Ichneumonidae) parasitizing *Plodia interpunctella* (Lepidoptera: Pyralidae). Journal of Pest Science 85: 75-80.

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

Statistics Canada 2016. Principle field crop areas, June 2016. http://www.statcan.gc.ca/daily-quotidien/160629/dq160629a-cansim-eng.htm

Sumerford DV, Abrahamson WG, Weis AE. 2000. The effects of drought on the *Solidago altissima–Eurosta solidaginis–* natural enemy complex: population dynamics, local extirpations, and measures of selection intensity on gall size. Oecologia 122: 240-248.

Symondson WO, Sunderland KD, Greenstone MH. 2002. Can generalist predators be effective biocontrol agents? Annual Review of Entomology 47: 561-594.

Takabayashi J, Santo Y, Horikoski M, Yamaoka R, Yano S, Ohsaki N, Dicke M. 1998. Plant effects on parasitoid foraging, differences between two trophic systems. Biological Control 11: 97-103.

Talekar NS, JC Yang 1991. Characteristics of parasitism of diamondback moth by two larval parasites. Entomophaga 36: 95-104.

Talekar NS, Lee ST. 1985. Seasonality of insect pests of Chinese cabbage and common cabbage in Taiwan. Plant Protection Bulletin 27: 47-52.

Talekar NS, Liu S, Chen C, Yiin Y. 1994. Characteristics of oviposition of diamondback moth (Lepidoptera: Yponomeutidae) on cabbage. Zoological Studies 33:72-77.

Talekar NS, Shelton AM. 1993. Biology, ecology and management of diamondback moth. Annual Review of Entomology 38: 275-301.

Talekar NS, Yang HC, Lee ST, Chen BS, Sun LY. 1985. Annotated bibliography of diamondback moth. Taipei, Taiwan: Asian Vegetable Research and Development Center. Pp. 469.

Talekar NS, Yang JC, Lee ST. 1992. Introduction of Diadegma semiclausum to control diamondback moth in Taiwan. In: Talekar NS (ed) Diamondback Moth and Other Crucifer Pests. Proceedings of the Second International Workshop, Tainan, Taiwan: Asian Vegetable Research and Development Center. Pp. 263-270.

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

Talekar NS. 1992. Management of diamondback moth and other crucifer pests: Proceedings of the Second International Workshop. Shanhua, Taiwan: Asian Vegetable Research and Development Center. Pp. 603.

Talekar NS. 1997. Characteristics of parasitism of diamondback moth by *Oomyzus sokolowskii* (Hymenoptera: Eulophidae). In: Sivapragasam A, Loke WH, Hussan AK, Lim GS (eds) The management of diamondback moth and other crucifer pests: Proceedings of the Third International Workshop, October 1996. Kuala Lumpur, Malaysia: Malaysian Agricultural Research Institute. Pp. 97-103.

Teder T, Tammaru T. 2002. Cascading effects of variation in plant vigor on the relative performance of insect herbivores and their parasitoids. Ecological Entomology 27: 94-104.

Textor S, Gershenzon J. 2009. Herbivore induction of the glucosinolates-myrosinase defense system: major trends, biochemical basis, and ecological significance. Phytochemistry Reviews 8: 149-170.

Thompson JN, Pellmyr O. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. Annual Review of Entomology 36: 65-89.

Thompson SN, Hagen KS. 1999. Nutrition of entomophagous insects and other arthropods. In: Bellows TS, Fisher TW (eds) Handbook of biological control. Academic Press, San Diego, CA, USA. Pp. 594-652.

Thomson LJ, Macfadyen S, Hoffmann AA. 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control 52: 296-306.

Todd DH. 1959. Incidence and parasitism of insect pests of cruciferous crops in the North Island, evaluation of data, 1955-58 seasons. New Zealand Journal of Agricultural Research 2: 613-622.

Tran DH, Le KP, Ueno T, Takagi M. 2012. Effects of Temperature and Host on the Immature Development of the Parasitoid *Neochrysocharis okazakii* (Hymenoptera: Eulophidae) Journal of Faculty of Agriculture, Kyushu University, Japan. 57: 133-137.

Trnka M, Muškab F, Semerádováa D, Dubrovsky´CM, Kocmánkováa E, Zaluda Z. 2007. European corn borer life stage model: regional estimates of pest development and spatial distribution under present and future climate. Ecological Modeling 207: 61-84.

Tunçbilek A, Çinar AS, Canpolat ÜA. 2012. Effects of artificial diets and floral nectar on longevity and progeny production of *Trichogramma euproctidis* Girault (Hymenoptera: Trichogrammatidae). Türkiye Entomoloji Dergisi 36: 183-191

Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11: 1351-1363.

Ulmer BJ, Dosdall LM, Gibson GAP. 2005. Spatio-temporal distribution patterns of the diamondback moth and its principal parasitoid, *Diadegma insulare*, in canola crops and the occurrence of hyperparasitism. Brassica 6: 63-69.

Valkama E, Koricheva J, Oksanen E. 2007. Effects of elevated O_3, alone and in combination with elevated CO_2, on tree leaf chemistry and insect herbivore performance: a meta-analysis. Global Change Biology 13: 184-201.

Van Emden HF. 1964. The role of uncultivated land in the biology of crop pests and beneficial insects. Pp. 121-136.

Van Nouhuys S, Lei GC. 2004. Parasitoid-host meta population dynamics: the causes and consequences of phenological asynchrony. Journal of Animal Ecology 73: 526-535.

Vandenberg JD, Shelton AM, Wilsey WT, Ramos M. 1998. Assessment of *Beauveria bassiana* sprays for control of diamondback moth (Lepidoptera: Plutellidae) on crucifers. Journal of Economic Entomology 91: 624-630.

Vattala HD, Wratten SD, Phillips CB, Wäckers FL. 2006. The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. Biological Control 39:179-185

Verkerk RHJ, Leather SR, Wright DJ. 1998. The potential for manipulating crop-pest-natural enemy interactions for improved insect pest management. Bulletin of Entomological Research 88: 493-501.

Verkerk RHJ, Wright DJ. 1996. Multitrophic interactions and management of the diamondback moth: a review. Bulletin of Entomological Research 86: 205-216.

Vet LEM, Dick M. 1992. Ecology of infochemical uses by natural enemies in tritrophic contest. Annual Review of Entomology 37: 141-172.

Vickers RA, Furlong MJ, White A, Pell JK. 2004. Initiation of fungal epizootics in diamondback moth populations within a large field cage: proof of concept of auto-dissemination. Entomologia Experimentalis et Applicata 111: 7-17.

Wachira JM, Poehling H-M, Meyhoefer R. 2009. Impacts of climate change on insect pests; A case study of effects of high-temperature pulses and drought stress on *Plutella xylostella*. Tropentag, October 6-8, 2009, Hamburg. http://www.tropentag.de/2009/proceedings/node68.html\

Wäckers FL, Romeis J, Van Rijn PCJ. 2007. Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. Annual Review of Entomology 52: 301-323.

Wäckers FL, van Rijn PCJ, Bruin J. 2005. Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and its Applications. Cambridge University Press, Cambridge, UK.

Wäckers FL. 2001. A comparison of nectar and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. Journal of Insect Physiology 47: 1077-1084.

Wäckers FL. 2004. Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. Biological Control 29: 307-314.

Wäckers FL., Romeis J, van Rijn PCJ. 2007. Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. Annual Review of Entomology 52: 310-323.

Wagener B, Reineke A, Lohr B, Zebitz CPW. 2004. Molecular identification of *Diadegma* species (Ichneumonidae) parasitizing diamondback moth, *Plutella xylostella* (Plutellidae) in eastern and southern Africa. In: Kirk AA, Bordat D (eds) Improving Biocontrol of

Plutella xylostella. Proceedings of the International Symposium, 21/24 October 2002. Montpellier, France. Pp. 252-257.

Wang XG, Keller MA. 2002. A comparison of host searching efficiency of two larval parasitoids of *Plutella xylostella.* Ecological Entomology 27: 105-114.

Wang XG, Keller MA. 2002. A comparison of host searching efficiency of two larval parasitoids of *Plutella xylostella*. Ecological Entomology 27: 105-114.

Wang XY, Yang ZQ, Wub H, Gould JR. 2007. Effects of host size on the sex ratio, clutch size, and size of adult *Spathius agrili*, an ectoparasitoid of emerald ash borer. Biol. Control 44: 7-12.

Wanner H, Gu H, Dorn S. 2006. Nutritional value of floral nectar sources for flight in the parasitoid wasp, *Cotesia glomerata*. Physiological Entomology 31: 127-133.

Waring GL, Cobb NS- 1992. The impact of plant stress on herbivore population dynamics. In: Bernays EA (ed) Insect-plant interactions. Volume 4. CRC Press, Boca Raton, Florida, USA. Pp.167-226.

Warwick SI, Francis A, Mulligan GA. 2003. Brassicaceae of Canada. The Government of Canada. http://www.cbif.gc.ca/spp_pages/brass/index_e.php.

Warwick SI, Francis A, Shehbaz IA. 2006. Brassicaceae: Species checklist and database on CD-Rom. Plant Systematics and Evolution 259: 249-258.

Weiss UJ, Knodel JJ, Olson D. 2009. Insect pests of Canola. Redcliff's IPM textbook, University of Minnesota. http://ipmworld.umn.edu/chapters/Weiss_et_al_canola.htm.

White TCR. 1969. An index to measure the weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology 50: 905-909.

White TCR. 1974. A hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. Oecologia 16: 279-301.

Whittaker JB, Tribe NA. 1996. An altitudinal transect as an indicator of responses of insects to climate change. European Journal of Entomology 93: 319-324.

Whittaker JB, Tribe NP. 1998. Predicting numbers of an insect (*Neophilaenus lineatus*: Homoptera) in a changing climate. Journal of Animal Ecology 67: 987-991.

Winkler K, Wäckers FL, Buitriago L, van Lenteren JC. 2005. Herbivores and their parasitoids show differences in abundance on eight different nectar producing plants. Proceedings of the Netherlands Entomological Society Meeting. Pest control 16: 125-130.

Winkler K, Wäckers FL, Bukovinszkine-Kiss G, Van Lenteren JC, 2006. Sugar resources are vital for *Diadegma semiclausum* fecundity under field conditions. Basic and Applied Ecology 7: 133-140.

Winkler K, Wäckers FL, Pinto DM. 2009. Nectar-providing plants enhance the energetic state of herbivores as well as their parasitoids under field conditions. Ecological Entomology 34: 221-227.

Winkler K, Wackers FL, Stingli A, Van Lenteren JC. 2005. *Plutella xylostella* (Diamondback moth) and its parasitoid *Diadegma semiclausum* show different gustatory and longevity responses to a range of nectar and honeydew sugars. Entomologia Experimentalis et Applicata 115:187-192.

Winkler K, Wäckers FL. Termorshuizen AJ, van Lenteren JC. 2010. Assessing risks and benefits of floral supplements in conservation biological control. BioControl 55: 719-727.

Winkler K. 2005. Assessing the risks and benefits of flowering field edges: Strategic use of

nectar sources to boost biological control. Ph.D. Thesis. Wageningen University, Netherland.

Witting-Bissinger BE, Orr DB, Linker HM. 2008. Effects of floral resources on the fitness of the parasitoids *Trichogramma exiguum* (Hymenoptera: Trichogrammatidae) and *Cotesia congregata* (Hymenoptera: Braconidae). Biological Control 47: 180-186.

Wold-Burkness SJ, Hutchison WD, Lee JC, Hines RL, Bolin PC, Heimpel GE. 2005. A long-term survey of parasitoid species composition and parasitism of *Trichoplusia ni* (Lepidoptera: Noctuidae), *Plutella xylostella* (Lepidoptera: Plutellidae), and *Pieris rapae* (Lepidoptera: Pieridae) in Minnesota cabbage. Journal of Entomological Science 40: 211-221.

Wolfson JL. 1980. Oviposition response of *Pieris rapae* to environmentally induced variation in *Brassica nigra*. Entomologia Experimentalis et Applicata 27: 223-232.

Woodward DT, Grzywacz D, Winstanely D. 2004. Biological and molecular characterization of granuloviruses isolated from diamondback moth (*Plutella xylostella*, Plutellidae) in Kenya. In: Kirk AA, Bordat D (eds). Improving Biocontrol of *Plutella xylostella*. Proceedings of the International Symposium, 21-24 October 2002. Montpellier, France. Pp. 263-266.

Wratten SD, Lavandero BI, Tylianakis J, Vattala D, Cilgi T, Sedcole R. 2003. Effects of flowers on parasitoid longevity and fecundity. New Zealand Plant Protection 56: 239-245.

Xu J, Shelton AM, Cheng X. 2001. Comparison of *Diadegma insulare* (Hymenoptera: Ichneumonidae) and *Microplitis plutellae* (Hymenoptera: Braconidae) as biocontrol agents of *Plutella xylostella* (Lepidoptera: Plutellidae): Field parasitism, insecticide susceptibility, and host searching. Journal of Economic Entomology 94: 14-20.

Xu J, Shelton AM, Cheng X. 2001. Variation in susceptibility of *Diadegma insulare* to permethrin. Journal of Economic Entomology 94: 541-546.

Yan Z. 1990. Overview of rapeseed production and research in China. Proceedings of the International Canola Conference. Potash and Phosphate Institute, Atlanta. Pp. 29-35.

Yang YC, Chu YI, Talekar NS. 1993. Biological studies of *Diadegma semiclausum* (Hymenoptera: Ichneumonidae), a parasite of diamondback moth. Entomophaga 38: 579-586.

You M, Yue Z, He W, Yang X, Yang G et al. 2013. A heterozygous moth genome provides insights into herbivory and detoxification. Nature Genetics 45: 220-225

Young A. 2013. War of the wasps: is *Diadegma insulare* or *Microplitis plutellae* a more effective parasitoid of the Diamondback Moth, *Plutella xylostella*? Canadian Field Naturalist 127(3): 211-215.

Yu S, Horstmann K. 1997. A catalogue of world Ichneumonidae (Hymenoptera). Memoirs of the American Entomological Institute 58:1-1558.

Yu S, Nguyen S.1992. Detection and biochemical characterization of insecticide resistance in the diamondback moth. Pesticide Biochemistry and Physiology 44: 74-81.

Zalucki MP, Shabbir A, Silva R, Adamson D, Shu-Sheng L, Furlong MJ. 2012. Estimating the economic cost of one of the world's major insect pests, *Plutella xylostella* (Lepidoptera: Plutellidae): just how long is a piece of string? Journal of Economic Entomology 105: 1115-1129.

Zhang PJ, Lu YB, Zalucki MP, Liu SS. 2012. Relationship between adult oviposition preference and larval performance of the diamondback moth, *Plutella xylostella.* Journal of Pest Science 85: 247-252.

Zhang SW, Li CH, Cao J, Zhang YC, Zhang SQ, Xia YF, Sun DY, Sun Y. 2009. Altered architecture and enhanced drought tolerance in Rice via the down-regulation of indole-3-acetic acid by TLD1/OsGH3.13 activation. Plant Physiology 151: 1889-1901.

Zhao JZ, Ayers GS, Grafius EJ, Stehr FW. 1992. Effects of neighboring nectar-producing plants on populations of pest Lepidoptera and their parasitoids in broccoli plantings. Great Lakes Entomologist 25: 253-258.

Zvereva EL, Kozlov MV. 2006. Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a meta-analysis. Global Change Biology 12: 27-41.