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Insect and Agronomic Responses in Canola and Wheat Intercrops

by

Jeremy Dean Hummel

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Examining Committee

Dr. Lloyd M. Dosdall, Agricultural, Food and Nutritional Science

Dr. B. Andrew Keddie, Biological Science

Dr. George W. Clayton, Agricultural, Food and Nutritional Science

Dr. Dean Spaner, Agricultural, Food and Nutritional Science

Dr. Vic Lieffers, Renewable Resources

Dr. Guy Boivin, Horticulture Research and Development Centre, Agriculture and Agri-Food Canada, Saint-Jean-sur-Richelieu, Québec

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Abstract

Intercropping systems offer potential benefits relative to monocultures of increased crop yields and improved pest control through physical, chemical, or behavioural interference and the enhancement of natural enemy populations, prompting increased predation and parasitism. Intercrops of canola (*Brassica napus* L.) and wheat (*Triticum aestivum* L.) in various proportions were investigated at three sites in Alberta, Canada, in 2005 and 2006, to determine effects on 1) agronomic parameters, including crop grain and biomass yields, crop quality (canola oil and canola and wheat protein), lodging, soil microbial communities, and wheat leaf diseases; 2) pest insects, including flea beetle (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae) damage to seedling canola and root maggot (*Delia* spp.) (Diptera: Anthomyiidae) adult collection numbers, egg populations, and canola taproot damage; and 3) beneficial insects, including ground beetles (Coleoptera: Carabidae) and the predator-parasitoid *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae). Crop yields were similar in intercrops and monocultures, and benefits of intercropping were observed in enhanced crop quality characteristics in some site-years. Neither soil microorganisms nor wheat leaf diseases generally responded to intercropping regimes. Intercropping did not reduce flea beetle damage to canola seedlings. Flea beetle damage was greatest at the first true-leaf stage of canola development. Although a thiamethoxam seed treatment reduced flea beetle herbivory, untreated plots generally did not sustain greater than 20% damage, suggesting that seed treatments were usually unnecessary. Adult *Delia* did not respond to intercropping canola with wheat, but egg populations were lower in intercrops on a land area basis. Canola taproot damage was as much as 13% reduced in intercrops compared to monocultures. Carabid beetles appeared to respond to qualities of the intercrops and monocultures, such as ground cover, rather than to the level of vegetational diversity itself, but carabid diversity was enhanced in diverse intercrops compared to canola monocultures in one site-year. *Aleochara bilineata* adult populations and parasitism rates were favoured in canola monocultures, but a temporal shift in *A. bilineata* adult collection numbers suggests reduced preference for canola monocultures in early summer. Benefits of canola-wheat intercrops identified in this study do not appear sufficient to recommend these cropping systems for widespread adoption in western Canada.

Table of Contents

List of Tables

List of Figures

1. Chapter 1 – Introduction

1.1. Diversity in natural and agricultural systems

Natural plant communities tend to consist of numerous species representing several unrelated families and genera in complex associations (Pimentel 1961; Altieri 1994). Interactions occur not only among plant species and individuals in natural communities, but they also encompass soil organisms, pathogens, arthropods, and higher animals. Pimentel (1961) referenced several reports in which complex natural systems maintained a level of stability in the populations comprising them, and in which few outbreaks of any one species occurred. Conversely, natural communities that are not comparatively diverse, such as many in the Arctic (Pimentel 1961) or on islands (Dempster and Coaker 1974), often have greater instability and as a result do incur outbreaks or dramatic fluctuations of single species.

Agricultural systems dominate large areas of the planet and also consist of different populations in association with each other. Typically, modern agriculture strives for a limited diversity of plant and animal species (Pimentel 1961; Tahvanainen and Root 1972; Dempster and Coaker 1974; Altieri and Letourneau 1982; Andow 1991; Altieri 1994). Modern cropping systems usually involve monocultures, which are plantings of a single cultivar of a species typically over large tracts of land (Andrews and Kassam 1976). In monocultures, plant species that occur in addition to the crop are considered weeds and are subject to attempted eradication because of the competition they exert against the crop (Liebman 2001). Herbivorous arthropods, in most cases insects, and other organisms that feed on the crop are considered pests and are also often the targets of systematic eradication efforts.

The limited diversity of agricultural crop monocultures makes them much more susceptible to pest outbreaks and thus highly reliant upon chemical controls and other human interventions (Tahvanainen and Root 1972; Altieri 1994). Such controls, especially the use of chemicals, can be costly and environmentally unsustainable. Because of these and other considerations, studies in the past half century have begun to explore the incorporation of increased vegetational diversity into agricultural systems (Andow 1991; Altieri 1994). Widespread acceptance of diversified agroecosystems and of intercropping systems specifically has not occurred because modern crop cultivars, agricultural technology, government farm policies, and research efforts are focused on the production of monocultures, not of polycultures (Vandermeer 1989; Kirschenmann 2007). An increasing recognition that significant drawbacks exist in modern agricultural systems continues to stimulate interest in intercropping and other methods of agroecosystem diversification for the production of food and fiber (Kirschenmann 2007).

1.2. Intercropping

Intercropping is the simultaneous production of two or more crops on the same field (Andrews and Kassam 1976). Because the multiple crops are produced at the same time, sometimes in close association, intercrops are usually subject to some degree of interspecific competition, which varies by the type of intercropping system and the plant species cropped together.

Intercropping can be divided into four types (Andrews and Kassam 1976) depending on the degree of crop mixture in the field. Mixed intercropping, as the name implies, is the complete mixture of two or more crops grown simultaneously, with the crops grown together in the same rows, or without any distinguishable row arrangement. This is a common cropping system in the traditional farming of peoples in Central and South America (Altieri 1991) and other tropical regions. The extreme nature of the mixture is reduced in row intercropping, where crops are grown in alternating rows, and further reduced in strip intercropping, where crops are planted in larger strips in the field. Vandermeer (1989) noted that strip intercropping easily facilitates the use of machinery and modern, mechanized agricultural practices. Strips allow independent cultivation of each crop, but strips must be sufficiently narrow that the agronomic interactions characteristic of intercrops continue to occur (Andrews and Kassam 1976). A fourth form of intercropping incorporates temporal diversity into the system. Relay cropping is the production of two or more crops that have only part of their life cycles occurring simultaneously in the field (Andrews and Kassam 1976). Subsequent crops are planted following the establishment or onset of the reproductive stage of the first crop.

1.2.1. History

The origins of intercropping cannot be traced to any particular place or point in time. Instead, intercropping evolved independently in numerous places as it was, and still is, the method of agriculture used by indigenous peoples in traditional farming situations around the world (Vandermeer 1989; Altieri 1991). Altieri (1991, 1994) indicated that such systems developed over centuries as traditional farmers learned about the complexities of the natural systems around them and discovered how to produce crops in ways that reflected and utilized those natural complexities. Indigenous agricultural systems were designed to fulfill various needs of farmers such as the production of varied foods for personal consumption, the production of a diversified source of income, the use of available labour and plant nutrient sources, and the natural control of pests. Historical intercropping systems that developed in Latin America are still very much in use there, especially intercrops involving beans and maize (Altieri 1991).

Intercropping was used in the production of field crops in North America even into the early 1900's, until modern agricultural technologies replaced intercrops with large expanses of monocultures (Vandermeer 1989). Even in the earlier part of the last century, some observers recognized serious drawbacks in the monocultural systems that were developing (Pimentel 1961), and these realizations have since rekindled interest in intercropping and multiple cropping systems (Vandermeer 1989).

Numerous reviews provide examples of intercropping around the world (Pimentel 1961; Altieri and Letourneau 1982; Altieri 1991, 1994; Andow 1991; Theunissen 1994), including reviews of specific systems in the tropical regions of Asia, Africa, and the Americas (Harwood and Price 1976; Okigbo and Greenland 1976; Pinchinat et al. 1976).

1.2.2. Intercropping in western Canada and the midwestern U.S.A.

Especially since the late 1980's, investigations of intercropping regimes for field crop production in the North American plains and prairies have increased as the potential benefits of these cropping systems have been recognized. Izaurralde et al. (1990) explored a barley-pea intercrop in central Alberta. When both field pea and barley were seeded at more than one-half of their optimal monoculture rates, a significant yield benefit was not achieved and crop lodging increased, but N yield in the grain and N returned to the soil were significantly greater for the intercrop than for barley monocultures. Crop competitiveness against weeds was also greater in the intercrop. Higher rates of N-fixation were observed in intercrops compared to monocropped legumes in Saskatchewan, and yields were greater in intercrops relative to yields from monocultures at sites with poor growing conditions (Cowell et al. 1989).

Carr et al. (1993, 1995) revisited wheat-flax and wheat-lentil intercrops conducted in the 1920's and 1960's in the upper midwest United States. Wheat-flax intercrops failed to produce wheat yields equivalent to those achieved in wheat monocultures and failed to add an economical yield of flax; Carr et al. (1993) concluded that unless grain separation costs could be defrayed by on-farm separating, the intercrop was not profitable. Wheat-lentil intercrops consisting of nearly complete monoculture seed rates of both wheat and lentil produced wheat yields at monoculture levels, but resulting lentil yields were significantly depressed in intercrops from those of the monocultures (Carr et al. 1995). Intercropping reduced weed biomass and made lentils easier to harvest because pods developed farther above the ground; however, incidences of ascochyta and sclerotinia plant diseases in the lentils were sometimes greater in intercrops (Carr et al. 1995), likely because the wheat formed a more enclosed and hospitable environment for disease development. Carr et al. (1995) concluded that an intercrop of wheat and lentil would be most useful in situations where a producer sought to reduce or eliminate herbicide inputs.

Weiss et al. (1994) found that field pea-oilseed rape intercrops did not have higher relative yields (see discussion of LER in section 1.3. Yield and agronomic effects) compared to monocultures of either species, and intercrops failed to reduce populations of a specialist herbivore, the crucifer flea beetle, *Phyllotreta cruciferae* (Goeze) (Coleoptera: Chrysomelidae), on a per-plant and per-area basis. However, the intercrop increased the harvestability of the peas because the rape provided support onto which the peas could climb, and the intercrop could also reduce the incidence of disease by keeping the peas above the ground and thus maintaining a drier environment within the crop canopy (Weiss et al. 1994).

Although not investigating intercropping, studies by O'Donovan (1992) and O'Donovan et al. (1988, 1989) of effects of volunteer cereals in canola crops in Alberta and Saskatchewan add to the body of knowledge regarding intercropping. Although volunteer barley and wheat decreased canola yields, when the volunteer cereals were considered to have marketable value, costs due to canola yield losses could be partially to completely alleviated depending on the respective market prices of canola and cereals (O'Donovan et al. 1988, 1989).

Intercrops in Manitoba experienced greater relative yields (LER > 1) for grain and biomass in the presence and absence of in-crop herbicides, enhanced weed suppression, and greater yield stability compared to monocultures (Szumigalski and Van Acker 2005, 2006). Szumigalski and Van Acker (2006) suggested that intercrops more efficiently utilized the available sunlight than monocultures of any one of the species. Under organic management, however, wheat intercrops with other cereals, flax, pea, and mustard usually did not provide yield advantages (Pridham and Entz 2008).

1.3. Yield and agronomic effects

Intercropping can provide yield benefits by stabilizing yields or increasing them (Andrews and Kassam 1976; Willey 1979; Liebman 1988; Fukai and Trenbath 1993). For any intercropping system to be viable, crop yield must be considered of significant importance; focus on fewer inputs or enhanced pest control must not neglect crop yield (Altieri and Letourneau 1982). Instead, intercrops should be designed to enhance the profitability of the agroecosystem through yield benefits working alongside pest control.

Two approaches can be taken in the design of an intercropping system for the pursuit of enhanced yields. First, a producer can plant an intercrop using an additive design, with the intention that one of the component crops provide an equivalent or better yield than if it was planted in an optimal monoculture (Vandermeer 1989). In such a system, a full yield of the principal crop and an economically viable yield of the secondary crop could be sought. In intercrops with additive designs, the secondary crop is incorporated for various reasons, including benefits to soil fertility, erosion control, and pest management (Liebman 1988).

The second intercropping design does not require that any one of the intercropped species attain monoculture-level yields, but that the combined yield of all component crops meets or exceeds the optimal yield of any one of the crops in monoculture (Vandermeer 1989). Vandermeer (1989) pointed out the value of this replacement design approach for those seeking to obtain multiple nutrient sources from a single field, or the value in light of unpredictable commodity markets. Both Vandermeer (1989) and Altieri (1991) noted that this approach minimizes risk, such that if one crop is lost to disease, insects, or for some other reason, the other component crops may still provide economic returns.

The combined yields of the species comprising an intercrop can only be compared effectively to monocultures on a crop equivalence basis (Liebman 1988). Several methods have been developed to evaluate relative intercrop yields compared to monoculture yields, but the land equivalency ratio (LER) is most commonly used (Vandermeer 1989). The concept of LER was developed in the mid 1970's, and Trenbath (1976) provided a detailed discussion of its underlying concepts and assumptions. Basically, LER is the sum of the proportion of monoculture production for each component in the intercrop. If the optimal yield of a canola monoculture under certain conditions is 2500 kg/ha, the LER of that monoculture in that situation is LER = 2500 kg/ha ÷ 2500 kg/ha = 1. This demonstrates why any relative value obtained for an intercrop is compared to a monoculture LER value of 1. Applying this to an intercrop, we arrive at (after Vandermeer 1989):

$$\text{LER} = \frac{\text{(yield of crop A in intercrop)}}{\text{(yield of A in monoculture)}} + \frac{\text{(yield of crop B in intercrop)}}{\text{(yield of B in monoculture)}}$$

Consider a hypothetical case in which we intercrop canola and wheat and receive yields of 2000 kg/ha and 500 kg/ha, respectively. Monocultures of canola and wheat in this situation yield 2500 kg/ha and 3000 kg/ha, respectively. The LER of this intercrop can be calculated as:

$$\text{LER} = \frac{2000\ \text{kg/ha}}{2500\ \text{kg/ha}} + \frac{500\ \text{kg/ha}}{3000\ \text{kg/ha}} = 0.97$$

Since the LER is 0.97, which is less than 1, the intercrop does not outperform the monocultures.

In many cases actual yields may not be as important to producers as the economic value of the crops coming off the land. Vandermeer (1989) presents several methods of determining value equivalents for intercrops, where the total market value of an intercrop is compared against the monoculture of the component with the highest value.

Two component crops in an intercrop influence each other in many ways. The nature of these influences determines the viability of that intercrop. Light, water, and soil nutrients can all be limiting in agricultural systems, and intercropped species compete for these resources. Intercrops designed with consideration of above- and below-ground plant growth habits, specific crop resource needs, different resource needs over time, and possible facilitative interactions among crop species can reduce competition and enhance resource use and, potentially, crop yield (Andrews and Kassam 1976; Trenbath 1976; Altieri 1991; Fukai and Trenbath 1993; Liebman and Dyck 1993; Callaway 1995; Hauggaard-Nielsen and Jensen 2005). A facilitative interaction commonly considered for intercropping systems is when a component species makes available nutrients required by another species (Trenbath 1976; Altieri 1991), such as plant-available nitrogen through N_2-fixation by legumes. Because of such interactions and the diverse resource requirements of multiple crop species, intercrops are sometimes more productive than monocultures under conditions of low fertility or water stress compared to when these resources are not limiting (Cowell et al. 1989; Fukai and Trenbath 1993; Hauggaard-Nielsen and Jensen 2005). Yield benefits under poor growing conditions reinforce observations of greater yield stability in intercropping systems.

Other benefits of an intercrop may include enhanced structural support of lodging-prone crops (Trenbath 1976; Cowell et al. 1989), enhanced harvesting ease of one or more of the components (Cowell et al. 1989; Weiss et al. 1994; Carr et al. 1995), enhanced protection of delicate plants (Trenbath 1976), and benefits in the control of pests, be they weeds (Liebman and Dyck 1993; Szumigalski and Van Acker 2005), diseases (Vandermeer 1989; Hauggaard-Nielsen et al. 2008), or arthropods. Even genotypic diversity within a field, which is uncommon in many modern monocultures, can have benefits, such as for disease control (Garrett and Mundt 1999; Zhu et al. 2000).

For an intercrop to be successful, certain practical considerations must be addressed from the onset. This is especially true of harvesting the intercrop, because of specific harvesting requirements that each component may have. If two crops in a mixture will be harvested separately, as they are in smaller traditional farming situations, crop maturity need not occur at the same time for all species in the mixture (Andrews and Kassam 1976) since the mature crop can be removed with minimal damage to the remaining crops. Larger-scale, mechanized intercrops, as would more likely occur in the Canadian Prairie Provinces or the U.S. Midwest, require crops in a mixture to have synchronized maturities (Andrews and Kassam 1976; Carr et al. 1995). Failure to effectively synchronize plant maturity may result in one or more of the component crops not being harvestable.

The establishment of an intercropping regime must also take into account weed control issues. Not all intercropping systems dramatically outperform weeds, particularly if a field had previously uncontrolled or insufficiently controlled weed populations. Provided organic production is not a priority, crop cultivars of different species may be available that are similarly herbicide tolerant, providing a weed control option for mechanized crop production even in a mixed intercrop.

1.4. Intercropping and entomology

Among the potential benefits of intercrops are effects on arthropod, especially insect, pest populations. Maintenance of pest populations below economically significant levels is the goal of agroecosystem diversification with regard to pests (Dempster and Coaker 1974; Altieri 1994); the complete elimination of pests is not an aim of intercropping. Although many studies demonstrate reduced pest attack in intercropped systems (Vandermeer 1989; Trenbath 1993), cases of equivalent or greater insect populations and damage in intercrops compared to monocultures are also documented (Altieri and Letourneau 1982; Helenius 1989; Andow 1991; Altieri 1994; Theunissen 1994).

Many efforts have been made to identify the mechanisms responsible for insect pest management in intercropping systems. Two hypotheses are most common and extensively referenced: the natural enemy and resource concentration hypotheses (Root 1973).

The natural enemy hypothesis has been addressed in numerous reviews (Root 1973; Altieri and Letourneau 1982; Helenius 1989; Andow 1991; Trenbath 1993; Theunissen 1994). The hypothesis states that natural enemies of pest insects will be more abundant and more diverse in polycultures, such as intercrops, than in monocultures (Root 1973). There are several reasons for this proposed increase in predator and parasitoid populations. Polycultures support a wider array of herbivorous arthropods in a variety of microhabitats, and predators can take advantage of these alternate prey species when their principal prey are not locally abundant or are out of season (Altieri and Letourneau 1982). Because the complex and fractured microclimates in polycultures provide more refuges for small populations of herbivores than the uniform conditions in monocultures, it is unlikely that predators and parasitoids will completely decimate herbivore populations and thus deprive themselves of prey or hosts (Altieri and Letourneau 1982). Systems with diversified vegetation, particularly those with flowering plants, also provide nectar or pollen needed by the adults of many parasitoid species (Altieri and Whitcomb 1979; Altieri and Letourneau 1982; Idris and Grafius 1995).

Although some authors distinguish aspects of the resource concentration hypothesis as fully separate mechanisms, the validity of a single mechanism with numerous manifestations has been argued (Root 1973; Helenius 1989; Andow 1991). In its basic form, the resource concentration hypothesis states that many herbivores tend to easier locate and preferentially remain among concentrated host plants such as those in the pure, dense stands of modern monocultures (Root 1973). Altieri and Letourneau (1982) explained that reduction of natural plant defences in modern crop cultivars, along with the concentration of attractive stimuli arising from numerous similar plants grown together to the exclusion of all others, have caused monocultures to become more “visible” to pest insects. This increase in “plant apparency” increases the potential for damaging outbreaks (Altieri and Letourneau 1982). Theunissen (1994) described a “host-plant quality hypothesis,” wherein he explained that plants in intercrops may have reduced nutritional quality due to interspecific competition, and therefore such plants are less desirable to pest insects. Polycultures tend to be more structurally and chemically complex than monocultures, and the smaller size and fracturing of microclimates makes polycultures inhospitable to large populations of herbivores, a quality known as associational resistance (Tahvanainen and Root 1972). Altieri and Letourneau (1982) explained that herbivorous insects have increased difficulty finding suitable areas in which to remain and flourish within environments with fractured microclimates, so complex plant communities, as may occur in intercrops, inhibit the widespread success of any one insect species, success which is otherwise characteristic of pest infestations in large monocultures.

Mechanisms responsible for pest responses to intercropping cannot always be easily distinguished (Trenbath 1993), and some authors have proposed holistic intercrop pest management theories (Tahvanainen and Root 1972; Dempster and Coaker 1974). These theories generally suggest that insect responses to any multiple cropping system are products of determinative and limitative forces in the immediate environment. Determinative forces are be those that set the normal maximum population limits of an insect (such as climate, habitat structure, and availability of food), whereas limitative forces are those that reduce the population from its potential maximum (such as predation, parasitism, and adverse weather conditions).

Because of the complex and varied factors affecting different intercropping systems, no mechanism or hypothesis can perfectly explain the effects of intercropping on insect pests in every situation (Andow 1991). Instead, for an effective understanding of the arthropod ecology of intercrops, it is necessary to consider each system or population individually.

1.5. Root maggots

Certain species of *Delia* Robineau-Desvoidy (Diptera: Anthomyiidae) are known as root maggots and their larvae are responsible for damage to the root systems of various cultivated plants. One group of root maggots in particular is well known as pests of brassicaceous crops and weeds (Griffiths 1991a) and can cause significant yield losses to canola crops (Griffiths 1991b, Soroka et al. 2004). Larvae of crucifer-infesting *Delia* species feed on roots. Adults of most Anthomyiidae, including *Delia*, feed on nectar, honeydew, or sap, and as such *Delia* adults are not damaging to cruciferous crops (Griffiths 1997).

Root maggots are dispersed throughout the temperate regions of the Holarctic (Hill 1987; Finch 1988; Griffiths 1997). Although Hill (1987) indicated that widespread damage to cruciferous vegetables is common, he did not list *Delia* as noteworthy pests of crucifers grown for seed, namely mustards and oilseed rape or canola. Similarly, Griffiths (1986a) alluded to extensive investigations of root maggot biology and control in European and North American market garden situations, but indicated that little was known about this pest in rape crops prior to his investigations. A report of *Delia floralis* (Fallén) destroying stinkweed (*Thlaspi arvense* L.) in the Peace River Region of Alberta was one of the first published accounts of root maggot – host plant interactions in this province (Griffiths 1986b). Lists of suitable host plants for various *Delia* species in North America have been compiled (Griffiths 1991a).

1.5.1. Impact and biology in Alberta canola

Although root maggots have been known from Alberta for some time (Griffiths 1986b), they were first reported to be infesting canola in the province in 1981 (Liu and Butts 1982). Four species were initially identified infesting canola roots in a province-wide survey (Liu and Butts 1982): *Delia radicum* (L.), *Delia planipalpis* (Stein), *Delia platura* (Meigen), and *Delia florilega* (Zetterstedt). Griffiths (1986a, 1986b) determined that the cabbage maggot, *D. radicum*, was the primary root maggot of economic importance in the northwestern agricultural region of Alberta. Broatch et al. (2006) confirmed that *D. radicum* is abundant in central Alberta but also found considerable populations of the seedcorn maggot, *D. platura*, in collections of adult *Delia* from canola fields. Root maggot infestations in the Peace River and northeastern agricultural regions, where mean mid-summer precipitation is somewhat lower, were due primarily to *D. floralis*, the turnip maggot (Griffiths 1986b; 1991b).

Root maggot attack is most severe in central Alberta (Liu and Butts 1982; Soroka et al. 2004), where cooler temperatures and high mid-summer rainfall provide favourable climatic conditions for the pests (Liu and Butts 1982; Griffiths 1986b, 1991b). Root maggots may be adapting to the hot, dry conditions of southern Alberta, as Soroka et al. (2004) found more extensive damage than was reported in the earlier survey (Liu and Butts 1982).

Root maggot larvae feed on the parenchyma tissues of the canola root, often forming deep channels in the taproot and limiting the effect of lateral roots; larvae therefore reduce water and nutrient uptake and storage by the plant (McDonald and Sears 1992). Feeding damage provides access by which root rot fungi, particularly species of *Fusarium*, can invade the plant (Griffiths 1986a, 1991b). Crop lodging can result from the loss of the lateral roots that stabilize the canola plant, and from decreased plant vigour (Griffiths 1991b; McDonald and Sears 1992). Plant damage from the compounded effects of maggot feeding and *Fusarium* root rot cause decreased canola seed yields, decreased seed size, and premature plant death (Griffiths 1991b; McDonald and Sears 1991), costing Alberta canola producers millions of dollars in lost yields (Soroka et al. 2004). Griffiths (1991b) estimated that yield losses for *Brassica napus* L. and *Brassica rapa* L. under conditions experienced in Alberta could be about 20% and 50%, respectively, due to the combined effects of root maggot infestations and *Fusarium* infections.

In Alberta, both *D. radicum* and *D. floralis* are primarily univoltine, though a small second generation of *D. radicum* may sometimes occur; this second generation does not successfully reproduce before the onset of winter (Griffiths 1986a, 1986b). *Delia platura* is bivoltine in Alberta (Broatch et al. 2006). Root maggots overwinter as pupae within the cuticle of their last (3rd) larval instar, called a puparium (Fraenkel and Bhaskaran 1973). Adults emerge from mid May and early June through July, with *D. radicum* typically emerging earlier than *D. floralis* but later than *D. platura* (Griffiths 1986a, 1986b; Broatch et al. 2006). Adult flies have a clustered distribution pattern in canola, which Griffiths (1986a) attributed to varying crop densities and plant developmental stages attracting adult *Delia* more to some parts of the field than to others. Most root damage is done in July by third-instar larvae, which then pupariate in late July or early August (Griffiths 1986a, 1986b).

Most females become gravid in mid-June when canola is beginning to bolt (Griffiths 1986b). Eggs are deposited either at the base of a host plant or in nearby soil (Mukerji and Harcourt 1970; Griffiths 1986b), either singly or in small clusters (Dosdall et al. 1994). Female oviposition preference for plants with larger stem diameters has been observed or inferred by several authors (Griffiths 1986b; McDonald and Sears 1992; Dosdall et al. 1996, 1998).

Although the exact mechanisms of longer-range host finding by root maggots are not clearly known and have not been studied for oilseed crucifers, it is generally agreed that a combination of attractive compounds and visual stimuli attract adult flies to suitable host plants (Finch and Skinner 1982; Tukahirwa and Coaker 1982). At closer distances, *D. radicum* females responded positively to both green paper and vegetation (Kostal and Finch 1994), indicating that visual colour cues are important in short-range host-finding. Both *D. radicum* and *D. floralis* employ specific behaviours, including flights and landings, to determine acceptable sites for oviposition (Kostal and Finch 1994; Hopkins et al. 1996, 1999).

1.5.2. Biological control

1.5.2.1. Pathogens, predators, and parasitoids of *Delia* in western Canada

Pathogenic organisms may have a role in controlling *Delia* populations. Mukerji (1971) found that third-instar *D. radicum* larvae were killed by an unidentified disease. Two fungal pathogens, *Entomophthora muscae* (Cohn) Fresenius and *Strongwellsea castrans* Batko & Weiser, can induce female fly sterility and mortality (Griffiths 1986a; Klingen et al. 2000); in Europe, infections of adult *D. radicum* and *D. floralis* by these pathogens have been observed in excess of 50% of field-collected flies (Klingen et al. 2000).

Predators and parasitoids of root maggots, especially of *D. radicum*, are known to cause significant juvenile mortality and are therefore critical to the control of outbreaks and the maintenance of root maggot population stability (Mukerji 1971).

Predators of *Delia* eggs can cause substantial reductions in root maggot populations (Wishart et al. 1956), with various ground beetles and rove beetles being the principal egg predators. Wishart et al. (1956) found the widely distributed *Bembidion quadrimaculatum* (L.) (Coleoptera: Carabidae) to be the most important and abundant predator, and several additional carabid species served as lesser predators of immature *Delia* (Wishart et al. 1956; Coaker and Williams 1963). Staphylinids, including the predator-parasitoid *Aleochara bilineata* Gyllenhal, also preyed upon root maggot eggs (Wishart et al. 1956). The highest egg mortality due to predation was observed among eggs that were either exposed or laid in batches, and both Wishart et al. (1956) and Coaker and

Williams (1963) hypothesized that randomly searching predators more easily encountered exposed eggs, and that predators would typically consume an entire batch before continuing their search for food. Carabids and staphylinids also prey upon root maggot larvae and pupae (Colhoun 1953; Read 1962; Coaker and Williams 1963; Mukerji 1971), although larvae are preferred over pupae (Colhoun 1953). When the density of puparia in an area increased, such as under conditions of increased crop density, predator efficiency also increased due to reduced time between encounters with prey (Finch and Skinner 1976). Some studies have predicted average predation rates of cabbage maggots by carabids and staphylinids (Colhoun 1953; Read 1962; Coaker and Williams 1963).

Parasitoids have been accorded considerable attention because of their potential for use in biological control programs. Parasitoids are often host-specific, and hosts can be collected and evaluated to determine parasitism status and other aspects of the parasitoid biology (Wishart et al. 1956). *Delia* pupal mortality, in large part due to parasitism, can serve as a major factor stabilizing root maggot populations (Mukerji 1971). The staphylinid *A. bilineata* serves as the most important parasitoid of *Delia* pupae in Canada and accounts for the bulk of mortality in this stage (Wishart et al. 1956; Wishart 1957; Mukerji 1971). *Trybliographa rapae* (Westwood) (Hymenoptera: Figitidae) is also an important parasitoid of *Delia* in Europe and Canada (Hemachandra et al. 2007a, 2007b). Additional parasitoid species, including *Aleochara verna* Say and several hymenopterans, have usually low rates of parasitism in *Delia* puparia in western Canada (Wishart 1957; Hemachandra et al. 2007a). *Aleochara bipustulata* (L.), a puparial parasitoid of *Delia* in Europe, is currently under investigation in Canada for possible release as an additional biological control agent (Hemachandra et al. 2007a).

Trybliographa rapae is a larval parasitoid of *D. radicum* and other crucifer-infesting *Delia*, parasitizing all three instars of the cabbage maggot (Wishart and Monteith 1954; Neveu et al. 2000). Low rates of parasitism by *T. rapae* have usually been reported in Alberta (Wishart 1957; Hemachandra et al. 2007a). Female *T. rapae* utilize host-damage induced plant volatile chemicals to locate their hosts (Neveu et al. 2002). Host patch-finding by *T. rapae* is density dependent (Jones et al. 1993; Björkman 2007; Hemachandra et al. 2007b), but within-patch parasitism is often limited and therefore overall parasitism of *D. radicum* larvae tends to be density independent (Bonsall et al. 2004; Hemachandra et al. 2007b). Larval *T. rapae* live as endoparasites within host larvae until the host has formed a puparium and fully pupated, after which the parasitoids emerge from the host pupae and feed as ectoparasites (Wishart and Monteith 1954). Pupal *T. rapae* overwinter within host puparia (Wishart and Monteith 1954).

1.5.2.2. *Aleochara bilineata*

Aleochara Gravenhorst (Coleoptera: Staphylinidae) is a worldwide genus of rove beetles that are, as larvae, predominantly fly pupal parasitoids (Moore and Legner 1971; Maus et al. 1998). The adult beetles are predators, feeding most commonly on the juvenile stages of various Diptera of the Cyclorrhapha (Klimaszewski 1984). There are over 400 species worldwide (Maus et al. 1998), with about 53 occurring in the Nearctic region (Ashe 2001).

Among the species in this genus, *A. bilineata* is globally the most important biological control agent (Maus et al. 1998). Larvae of *A. bilineata* predominantly parasitize *Delia* pupae, but under laboratory conditions they also successfully developed in the puparia of several other cyclorrhapheous dipteran species (Maus et al. 1998). *Aleochara bilineata*, like *D. radicum* (Biron et al. 2000), is an introduced species in North America, having invaded from Europe some time before 1870 (Moore and Legner 1971; Klimaszewski 1984).

Female *A. bilineata* can lay a lifetime average of 700 eggs on host puparia or in nearby soil (Colhoun 1953; Read 1962). Highly active triungulin, campodeid larvae emerge after five days and seek out a suitable host (Colhoun 1953). Larvae locate the most favourable site on the puparium, usually the mid-dorsal region where surface ridges are reduced (Fuldner 1960; Royer et al. 1998). Their search is limited to a small area of soil because of their need to find and enter a host puparium before nourishment can be procured. Immediately upon entering, the parasitoid pierces the cuticle of the fly pupa, and the resulting flow of haemolymph seals the entry hole (Colhoun 1953). *Aleochara bilineata* larvae feed on the haemolymph of their host. After overwintering, larvae enter a less active eruciform, parasitic state for two final instars, continuing to feed on the pupae until all that remains of their host is the cuticle (Colhoun 1953). The parasitoids pupate within the host puparia and emerge as adults after about two weeks. When hosts are scarce, superparasitism by *A. bilineata* larvae may occur, but only one larva reaches maturity (Colhoun 1953; Read 1962; Royer et al. 1999). Larvae seek out non-parasitized hosts if such are available, but if not, *A. bilineata* larvae preferentially parasitize puparia already parasitized by other species, such as *A. bipustulata* (Royer et al. 1999), and discriminate between kin and unrelated conspecifics (Lizé et al. 2006). Larvae of *A. bilineata* are also capable of parasitizing puparia already serving as hosts to *T. rapae* larvae in the endoparasitic stage, killing the competing parasitoid in the process (Reader and Jones 1990).

Host finding by *A. bilineata* is a joint effort of adult females and larvae (Langer 1996). In a study designed to investigate *A. bilineata* adult prey location, Royer and Boivin (1999) found that chemical volatiles (infochemicals) were used by the adult female parasitoid to locate prey. The authors hypothesized that the beetle likely uses a series of progressively more accurate but less widely dispersed chemical stimuli, originating from the habitat of the host, host frass, and the host larval integument, to locate *D. radicum* larvae. Parasitism by *A. bilineata* appears to be density dependent such that puparia around more heavily infested host plants have greater rates of parasitism (Tomlin et al. 1992; Jones et al. 1993; Langer 1996). *Aleochara bilineata* females may be able to preferentially locate dense host populations, or random oviposition within areas having host volatiles will result in heavier parasitism of dense host patches because of the greater chance of encountering a suitable host in such patches (Langer 1996).

Read (1962) determined that the average mortality that one pair of *A. bilineata* adults could inflict, through direct predation or parasitism by their progeny, was in excess of 1500 individual *Delia* juveniles. In Canada, parasitism of *Delia* spp. (largely of *D. radicum*) puparia by *A. bilineata* can range from 0 to 94% (Wishart 1957; Read 1962; Turnock et al. 1995; Hemachandra et al. 2005). Turnock et al. (1995) suggested that variability of weather conditions at locations in Canada inhibited the formation of an equilibrium between *D. radicum* and its major parasitoids (*A. bilineata* and *T. rapae*), resulting often in reduced parasitism rates compared to those in England, where weather conditions show a greater degree of stability. On Prince Edward Island, where *D. radicum* is multivoltine, Read (1962) found that because *A. bilineata* develops more slowly than non-parasitized *Delia* at temperatures in spring and early summer, it emerged too late to effectively control first generation root maggot larvae before they caused considerable crop damage. Once emerged, beetles helped control root maggot populations and restricted the number of overwintering puparia (Read 1962). Langer (1996) and Broatch et al. (2008a) noted that the emergence of the parasitoid coincides well with the juvenile stages of root maggots in the field. *Aleochara bilineata* therefore appears well adapted as a *Delia* parasitoid, but perhaps less so as a predator of the fly eggs or larvae.

Early attempts to enhance the effectiveness of *A. bilineata* focussed mainly on mass rearing for inundative or augmentative release (Whistlecraft et al. 1985; Tomlin at al. 1992). More recently, studies have explored using the biology of the parasitoid and its interactions with the environment to enhance root maggot biological control. Royer and Boivin (1999) suggested that the in-field use of synthetic infochemicals, like those produced by *D. radicum*, could decrease the patch-leaving tendency of the adult beetles and increase predation and parasitism of *Delia* larvae and puparia. Langer (1996) determined that intercrops of cabbage and clover reduced parasitism of *D. radicum* by *A. bilineata*, which could have long-term implications for *Delia* population limitation through egg predation and parasitism by this staphylinid in intercropping systems.

1.5.3. Host plant resistance and root maggot control

Although Griffiths (1991b) achieved significant canola yield improvements through the insecticidal exclusion of *Delia* larvae, no insecticides are currently registered in Canada for root maggot control in canola (Soroka et al. 2004). Hill (1987) mentioned a seed treatment for root maggot control in brassicaceous vegetables that was commonly used in Britain but noted that insecticides must be used judiciously to avoid excessive damage to beneficial insect populations. Studies have demonstrated that insecticide treatments to control root maggots also result in the mortality of both predators and parasitoids (Finlayson et al. 1980; Shelton et al. 1983). Even chemicals reportedly almost non-toxic to natural enemies were, in appropriate formulations, lethal to beneficial insects in doses within product label recommended rates (Cisneros et al. 2002). Insecticide use in field situations did not always affect populations of either root maggots or *A. bilineata* (Turnock et al. 1995). Neonicotinoids represent relatively new seed treatment chemistries that may be useful for root maggot control. For example, thiamethoxam and clothianidin seed treatments reduced infestations of *D. platura* and *Delia antiqua* (Meigen) in snap bean (*Phaseolus vulgaris* L.) and onion, respectively (Nault and Taylor 2004; Nault et al. 2006).

Canola species and cultivars vary with respect to their susceptibilities to root maggot attack. For example, *B. napus* is more resistant than *B. rapa* (Griffiths 1991b; Dosdall et al. 1994). Recent investigations of resistance to *Delia* attack in other Brassicaceae have led to the development of hybrid lines that carry a measure of resistance, such as *Sinapis alba* L. × *B. napus* hybrids developed by Dosdall et al. (2000).

Cultural control measures can be effective for limiting root maggot damage to canola. Brassicaceous weeds, such as mustard (*Brassica nigra* L. Koch), can harbour root maggot populations especially early in the season before canola plants are readily available, and controlling brassicaceous weeds has been suggested as a means of limiting *Delia* populations (Doane and Chapman 1962). Brassicaceous weeds along field margins or in fields between canola years in a rotation can also serve as bridges for subsequent infestations. Limitation of these bridging weed infestations should enhance root maggot control. In central Alberta, a delay in canola seeding date until late May (rather than early or mid May) reduced root maggot damage to canola, but Dosdall et al. (1996) also found that late-seeded crops missed the benefits of early season soil moisture and did not yield better despite less insect damage. An increase in canola plant density to 200 plants/m² decreased damage by *Delia* larvae; increases in row spacing (resulting in more plants per row, thus less space between plants in each row) had the same effect, both results being attributed to *Delia* oviposition preference for thicker stemmed plants and the fact that plants tend to develop thinner stems in denser stands (Dosdall et al. 1996, 1998). Despite findings that a zero-till system increased maggot attack on canola because of a cooler, moister soil surface environment, Dosdall et al. (1998) recommended the use of zero-tillage because of increased yield. Soil fertility plays a role in canola response to attack by root maggots: well fertilized plants are better able to compensate for root maggot damage than canola grown under low fertility (Griffiths 1991b; Dosdall et al. 2004).

1.5.4. Intercropping effects

Mixtures involving species of Brassicaceae have been investigated extensively for effects on insect pest populations (Altieri and Gliessman 1983). The crucifer-feeding species of *Delia* have been among the insect pests studied in intercropping systems.

In studies from Europe, Dempster and Coaker (1974), Ryan et al. (1980), and Tukahirwa and Coaker (1982) found that total numbers of *D. radicum* eggs laid in intercropped crucifers were often significantly less than numbers laid into single plantings. Greater density of plant cover in the intercrop further reduced egg deposition. Tukahirwa and Coaker (1982) attributed these results to the dilution or disruption of volatile host plant chemicals which serve as attractants to the root flies. In Canada, cauliflower and rutabaga experienced lower *D. radicum* egg populations per plant in intercrops with *Delia* non-hosts compared to when they were grown in monoculture (Dixon et al. 2004; Parsons et al. 2007).

One of the principal mechanisms reducing oviposition by female *D. radicum* in intercrops is a behavioural disruption caused by interactions with non-host plants (Kostal and Finch 1994, Finch and Collier 2000). Female *D. radicum* have a standard pattern of landings that is performed prior to egg deposition. After the fly initially lands on an acceptable Brassicaceae host, an average of four spiral flights follow, during which the fly circles the host plant, lands, circles again, lands, and so on. After observing oviposition near the base of the host plant's stem following an uninterrupted landing cycle by the fly, Kostal and Finch (1994) hypothesized that sufficient positive stimuli must be accumulated through contact with suitable plants before the fly will oviposit. An "inappropriate landing" on a non-host (Finch & Collier 2000) and the resulting loss of the host stimulus caused flies to move between nearby vertical objects in search of the host (Kostal and Finch 1994). After an inappropriate landing, female *D. radicum* were forced to restart the flight pattern and had a higher likelihood of leaving the immediate vicinity of that host plant (Kostal & Finch 1994). The effect may even be triggered by physical barriers other than living plants, such as plant residues (Kostal and Finch 1994; Milbrath et al. 1995). *Delia floralis* females also demonstrate landing behaviours (Hopkins et al. 1996, 1999) that can be disrupted by intercropping with non-host plants (Björkman et al. 2007). Females of both *D. radicum* and *D. floralis* were observed to spend greater lengths of time motionless on non-host plants compared to hosts, an effect that could reduce oviposition on host plants in mixed plantings with non-hosts (Finch et al. 2003; Morley et al. 2005; Hopkins et al. 1999). Given no choice, flies eventually oviposited on crucifers in mixed host/non-host populations, as would be expected in the mixed plant stands of natural vegetation, and the use of monoculture trap crop strips within intercrops was therefore suggested as a method of enhancing intercrop control of root maggots (Kostal and Finch 1994; Björkman et al. 2007).

The two major parasitoids of *Delia* puparia, *A. bilineata* and *T. rapae*, demonstrate different responses to intercropping brassicaceous crops with non-hosts. *Aleochara bilineata* responds similarly to intercropping as does *D. radicum*, its adult populations and rates of parasitism reduced under diversified cropping regimes compared to crop monocultures (Ryan and Ryan 1980; Helqvist 1996; Langer 1996, Dixon et al. 2004). This may be due to the density-dependence of this parasitoid to populations of its host (Jones et al. 1993).

Conversely, *T. rapae* does not demonstrate host density dependence (Hemachandra et al. 2007b) and therefore rates of parasitism by this species are not usually affected by intercropping (Langer 1996).

No studies have examined intercropping effects on root maggots in western Canadian canola production. Studies of weed removal timing and herbicide rates determined that the presence of non-brassicaceous weeds in the field reduced root maggot oviposition and damage from levels experienced in weed-free conditions (Dosdall et al. 2003; Broatch et al. 2008b). Citing evidence from O'Donovan (1992) that late emerging weeds reduced crop yield by very little and produced minimal quantities of weed seed, Dosdall et al. (2003) suggested that late-emerging weeds could prove useful in root maggot control primarily by interrupting the female's pre-oviposition behaviour. Similar results could occur when canola is intercropped with a non-host crop, such as wheat.

1.6. Flea beetles

Flea beetles (Coleoptera: Alticini) are small jumping insects of the leaf beetle family, Chrysomelidae. Many flea beetle species are of economic importance due to attack of agricultural or ornamental plants (Riley et al. 2002). In western Canada, flea beetles annually cause tens of millions of dollars of damage to canola, representing about 10% of total canola production (Lamb and Turnock 1982).

1.6.1. Impact and biology in western Canadian canola

Burgess (1977) identified five flea beetle species attacking rape crops on the Canadian prairies. *Phyllotreta cruciferae* was the most common species and caused the most significant damage (Westdal and Romanow 1972; Burgess 1977). Other noteworthy flea beetle pests of canola were *Phyllotreta striolata* (F.), *Phyllotreta albionica* (LeConte), *Phyllotreta robusta* LeConte, and *Psylliodes punctata* Melsh. Both *P. albionica* and *P. robusta* are of minimal importance and cause no significant damage to canola (Burgess 1977). Populations of *P. punctata* in western Canadian canola are also too small to be of importance (Westdal and Romanow 1972; Lamb and Turnock 1982). Several other flea beetles, in particular *Disonycha triangularis* (Say) and species of *Crepidodera* and *Chaetocnema*, can sometimes be found in canola fields but are not pests of canola (Burgess 1977).

The crucifer flea beetle, *P. cruciferae*, is present throughout the eastern hemisphere and now in parts of the western hemisphere as well. It was introduced from Europe to the west coast of North America in the early 1920's, and in 1923 was first collected from British Columbia and called *P. columbiana* Chittendon (Milliron 1953). Westal and Romanow (1972) reported a specimen taken from Winnipeg, Manitoba in 1936 and suggested that the brassicaceous crop damage by flea beetles on the Canadian prairies in the 1930's and 1940's was likely due to *P. cruciferae*. It was also collected on the U.S. east coast in the early 1940's, suggesting a possible second introduction, and it spread from there into Ontario, Québec, and the Maritimes in the early 1950's (Westdal and Romanow 1972).

P. striolata, the striped flea beetle, was introduced from Eurasia before 1801 and is a considerable pest of brassicaceous crops throughout the Holarctic (Smith and Peterson 1950; Burgess 1977). Westdal and Romanow (1972) found that *P. striolata* populations were quite low in Manitoba. Populations have increased in the cooler parkland regions of the Canadian prairies (Lamb and Turnock 1982), but the pest is virtually non-existent in the open prairie region of southern Alberta near Lethbridge (Burgess 1977).

Burgess (1977) reported two patterns of flea beetle invasion into canola fields. The first involves a creeping advance into the field from volunteer canola or other suitable weedy hosts, this being the primary means of invasion when air temperatures are too low for flight. When air temperatures exceed 15°C, adult flea beetles also take flight and whole fields of canola seedlings can be rapidly and uniformly attacked (Burgess 1977).

Certain crucivores, including flea beetles, are drawn to the presence of volatile attractants, particularly glucosinolate compounds, in their hosts (Tahvanainen and Root 1972; Putnam 1977; Altieri and Gliessman 1983; Altieri and Schmidt 1986). Peng and Weiss (1992) and Milbrath et al. (1995) found that neither *B. napus* nor *B. rapa* were chemically attractive to flea beetles because they lack the glucosinolate compound allyl-isothiocyanate which is a strong flea beetle attractant. Instead, flea beetles may randomly encounter acceptable canola hosts and then proceed to attack them (Milbrath et al. 1995). Flea beetles produce an aggregation pheromone, released upon host selection or in frass after feeding, which draws other flea beetles to that host or area (Peng and Weiss 1992).

Both *P. cruciferae* and *P. striolata* are univoltine on the Canadian prairies, overwintering as adults and emerging in the spring, usually in April or early May (Westdal and Romanow 1972; Burgess 1977). Overwintering occurs in windbreaks, amidst stubble and straw in the field, or in other sheltered environments; some flea beetles overwinter in soil near their host plants (Burgess 1977, 1981; Ulmer and Dosdall 2006). After mating in spring, female flea beetles lay their eggs in the soil at the base of brassicaceous host plants, where larvae feed on roots from June to early August (Burgess 1977). Although larvae primarily feed externally on roots, Westdal and Romanow (1972) reported some tunnelling. The effects of the larvae feeding on canola roots have not been determined (Westdal and Romanow 1972; Lamb and Turnock 1982), though Smith and Peterson (1950) stated that *P. striolata* "larvae and adults produced extensive damage." *Phyllotreta* juveniles pupate in the soil and emerge from late July into August (Burgess 1977), sometimes in considerable numbers (Westdal and Romanow 1972). Burgess (1977) reported that these late summer or fall populations sometimes attacked canola leaves and pods, especially those of isolated plants. Brassicaceous weeds and volunteer canola provide early season hosts for the beetles until canola seedlings begin to emerge in fields.

Primary flea beetle damage occurs from late May through mid June to seedling canola plants (Westdal and Romanow 1972; Burgess 1977). Attack diminished after the seedling stage mainly because of a decline in adult flea beetle populations in late June (Burgess 1977). Adult beetles feed on cotyledon and leaf surfaces, consuming small, circular patches of epidermis but rarely chewing completely through the leaf. Damaged areas dry out and give the leaf a shot-hole appearance (Westdal and Romanow 1972). When significant flea beetle feeding occurs, large sections of leaves, or entire leaves, may be destroyed. In some cases, flea beetles will consume the apical meristem of the canola seedling. Leaf damage reduces plant photosynthetic ability and can cause seedlings to wilt or die (Dosdall et al. 1999). Plants that survive the damage experience decreased growth, delayed ripening, and decreased yield and seed quality (Putnam 1977; Lamb 1984). Lamb (1984) also observed that crops suffering severe flea beetle infestations ripened unevenly, potentially increasing harvest losses due to the shatter of over-ripe pods or the presence of green seed. If fall infestations are sufficiently great, flea beetle damage to the epidermis of pods may encourage pod shatter and yield loss (Lamb 1980), though high levels of fall damage do not usually occur (Lamb and Turnock 1982). Plants cannot compensate for flea beetle damage to apical meristems (Gavloski and Lamb 2000a), but plants sustaining up to 25% damage to cotyledons and early true leaves usually compensate completely for damage sustained (Gavloski and Lamb 2000b). Some evidence exists that even seedling defoliation of up to 50% has negligible effects on crop yield (Nowatzki and Weiss 1997; Cárcamo and Blackshaw 2007).

Damage to canola seedlings is usually assessed to determine the need for or effectiveness of control measures against flea beetles. Palaniswamy and Lamb (1992) pointed out the inefficiency of quantitative assessments, and Palaniswamy et al. (1992) developed a standardized qualitative scale by which seedling damage could be assessed more rapidly.

1.6.2. Biological control

Predation on adult flea beetles is not known (Tahvanainen and Root 1972). Smith and Peterson (1950) reported parasitic activity against *P. striolata* by a nematode and a mite.

Perhaps the most important parasitoid of adult *Phyllotreta* spp. in North America is the endemic *Microctonus vittatae* Muesebeck (Hymenoptera: Braconidae) (Tahvanainen and Root 1972). *Microctonus vittatae* adapted from native host *Phyllotreta* spp. to parasitize both the introduced *P. striolata* and *P. cruciferae* (Smith and Peterson 1950; Loan 1967), although *P. striolata* appeared to be preferred over *P. cruciferae* (Wylie 1984). The parasitoid is found wherever *P. striolata* exists east of the Rocky Mountains, but it is uncommon in the southern U.S (Smith and Peterson 1950). *Microctonus vittatae* is univoltine throughout its range (Loan 1967).

Female *M. vittatae* oviposit in the thorax of flea beetles. Amniotic cells in the egg absorb the beetle's body fat, causing the egg to grow to hundreds of times its original size before hatching (Smith and Peterson 1950). Larvae feed on adipose tissues of the flea beetle and on the amniotic cells from the egg, and feeding results in host sterility (Smith and Peterson 1950). Only one larva of *M. vittatae* typically survives within each host, though multiple eggs may be laid (Smith and Peterson 1950); other larvae are cannibalized or killed by secretions from the initial parasite. Larvae complete five instars before emerging (Loan 1967), an act which kills the host (Smith and Peterson 1950). Early studies showed high rates of parasitism (46%) on *P. striolata* (Smith and Peterson 1950; Loan 1967), but lower rates (10%) on *P. cruciferae* (Loan 1967; Tahvanainen and Root 1972).

Populations of *M. vittatae* and their effectiveness against *Phyllotreta* spp. are limited by the hyperparasite *Mesochorus phyllotretae* Jourdheuil (Hymenoptera: Ichneumonidae), which is a larval parasitoid of *Phyllotreta*-parasitizing *Microctonus* spp. in both North America and Europe (Loan 1967).

1.6.3. Host plant resistance and flea beetle control

The resistance of canola to flea beetles has been investigated since the 1980's (Lamb et al. 1993). Different species of Brassicaceae, different cultivars of the same species, and even plants within a cultivar demonstrate different levels of flea beetle resistance (Putnam 1977; Lamb 1980, 1984; Palaniswamy et al. 1992; Lamb et al. 1993). Lamb (1980) determined that the hairy pods of *S. alba* reduced adult flea beetle feeding on pods in the fall, but chemical or physical mechanisms of resistance in crucifer seedlings were not known (Lamb 1984). Antixenosis (host non-preference) plays a minor role in the resistance of some new canola genotypes to flea beetles (Lamb et al. 1993). On the other hand, tolerance—the ability of a host plant to better recover from and accommodate pest feeding—was the most significant reason for observed improvements in resistance to flea beetles (Bodnaryk and Lamb 1991; Lamb et al. 1993).

The principal method by which *Phyllotreta* spp. are controlled in western Canada is by insecticides, which cost producers millions of dollars annually (Lamb and Turnock 1982; Madder and Stemeroff 1988). There are a number of insecticides currently registered in Alberta for use against flea beetles in canola (Ali 2004). Two methods of application are used. Seed treatments are applied to the seed prior to planting and often also include a fungicide to reduce the incidence of seedling diseases. The insecticide is absorbed and becomes systemic for a period of time, causing mortality or antixenosis responses in flea beetles that feed during that period. Tansey et al. (2008) demonstrated that the efficacy of neonicotinoid seed treatments is greater against *P. cruciferae* than *P. striolata*. Foliar insecticides, applied when needed based upon flea beetle feeding damage, can provide further control.

Cultural control strategies for flea beetles may provide producers with alternatives to insecticidal flea beetle management. Appropriate crop rotations can limit the build-up of flea beetle populations over multiple years by disrupting the cycle of host availability (Tahvanainen and Root 1972). Optimal seeding dates for minimizing flea beetle damage to canola appear to vary by region, with early seeding (mid-April) recommended in southern Alberta (Cárcamo and Blackshaw 2007) and later seeding recommended in North Dakota (Milbrath et al. 1995); Ulmer and Dosdall (2006) reported no seeding date effect on populations of fall-emerging flea beetles. Early seeding dates allow canola seedlings to utilize early-season moisture and to develop beyond the very susceptible cotyledon and early true-leaf stages before flea beetle emergence, but late seeding dates allow flea beetles to aggregate in earlier-seeded fields, possibly due in part to flea beetle aggregation pheromones. Dosdall and Stevenson (2005) suggested fall seeding of canola as a means of avoiding spring damage and reducing insecticide use. Milbrath et al. (1995) found that no-till systems contained smaller flea beetle populations than conventional-till fields and hypothesized that exposed wheat stubble in the no-till systems restricted or confounded flea beetle movement and host finding similarly to the response of *D. radicum* females observed by Kostal and Finch (1994). Dosdall et al. (1999) also determined that zero-till canola sustained less flea beetle attack than in conventional tillage systems and attributed this to flea beetle preference for the warmer, drier conditions that occur under conventional tillage regimes. Increased plant density (canola densities of 180 to 240 plants/m^2) and wider row spacings reduced damage to canola seedlings by flea beetles (Dosdall et al. 1999). Decreased flea beetle damage in wider row spacings may be the result of having individual plants situated closer together in the row, reducing the visual stimulus for flying beetles of a plant standing out against its soil background (Dosdall et al. 1999).

1.6.4. Intercropping effects

Flea beetles, primarily *P. cruciferae*, have been studied extensively in brassicaceous intercropping systems. Pimentel (1961) and Tahvanainen and Root (1972) demonstrated that flea beetles reached outbreak densities in monocropped Brassicaceae but were maintained at low populations in plantings into pasture and meadow vegetation. Chemical and physical interference of flea beetle host finding and the presence of fewer acceptable microhabitats have been determined as likely causes of reduced flea beetle populations in intercrops (Tahvanainen and Root 1972; Altieri and Gliessman 1983; Altieri and Schmidt 1986). Following the failure of a field pea-canola intercrop to reduce populations of *P. cruciferae*, Weiss et al. (1994) suggested that in the first two weeks after seedling emergence the small pea plants failed to sufficiently camouflage rape seedlings, and the peas did not sufficiently disrupt flea beetle aggregation pheromones. When zero tillage reduced flea beetle populations compared to conventionally tilled plots, Milbrath et al. (1995) and Dosdall et al. (1999) pointed out that cultivation, like sole cropping, causes habitat simplicity which may result in increased pest outbreaks. In an intercrop of canola, therefore, the presence of non-host material may act as a physical barrier to flea beetle host finding, as did the stubble in no-till systems.

The incidence of flea beetles parasitized by *M. vittatae* was low in both a collard monoculture and a mixture, but the parasitoid was more numerous in the monoculture (Tahvanainen and Root 1972), possibly due to the greater abundance of host beetles in the monoculture.

Although studies have examined the effects of an intercrop on flea beetles in the Midwest U.S.A., no similar investigations have been made in canola produced in western Canada.

1.7. Carabid beetles

The carabid beetles (Coleoptera: Carabidae) make up a large, worldwide family, with more than 2600 species in 189 genera in North America (Ball and Bousquet 2001). These North American species are largely ground-inhabiting (Lindroth 1961-1969). Many ground beetles have come to be associated with habitats either developed (farmland) or managed/modified (forestry land) by human activity (Ball and Bousquet 2001). Due to their responsiveness to anthropogenic effects, ground beetles are often used as indicators of change in ecosystems (Kromp 1999; Rainio and Niemelä 2003).

The Carabidae are often grouped to distinguish patterns of life history or habitat preference among the many species. Two main groups of ground beetles exist with respect to breeding and seasonality: those with larvae in summer and those with larvae in winter (Kromp 1999). Ground beetles have often also been grouped as those that breed in spring and those breeding in fall (Luff 1987; Kromp 1999). Carabids may also be grouped based upon habitat preferences (Ball and Bousquet 2001). Hygrophilous species are found closely associated with water, such as along the margins of lakes or in marshlands. Mesophiles live in wet environments but lack the association of hygrophilous species with surface water, and xerophiles live in dry environments.

Although ground beetles have often been considered as predators, they are, as a group, primarily polyphagous (Kromp 1999). The adults of some genera are active predators, such as the *Calosoma* and *Cicindela*. Others, although their diets consist largely or exclusively of animal food, may just as easily be scavengers as predators; such beetles are among the *Agonum*, *Bembidion*, *Calathus*, *Carabus*, *Notiophilus*, and *Pterostichus*. Still other genera consist of plant-eaters, including species of *Amara* and *Harpalus* (Lindroth 1961-1969). Carabid larvae are primarily predatory, although larvae of the genera *Brachinus* and *Lebia* are ectoparasitic on beetle pupae (Lindroth 1961-1969). Few ground beetles are occasional pests, such as the seedcorn beetle, *Stenolophus lecontei* (Chaudoir), and the slender seedcorn beetle, *Clivina impressifrons* LeConte, which feed on germinating seeds (Larson et al. 2008).

In research, pitfall trapping is the most common passive sampling method used for the collection and assessment of ground beetle populations (Spence and Niemelä 1994). Pitfall traps measure activity density, that is, a combination of the population density (abundance) of a species in an area and the activity and trappability of that species (Luff 1987; Kromp 1999). This method may disproportionately collect large species rather than small or medium-sized species, and carabid collections using such passive sampling methods must be carefully interpreted as a result. Other collection methods that are better measures of actual carabid densities have been developed, but these methods often lack some of the convenience of simple pitfall traps. Pitfall trapping may also not entirely accurately assess predator populations because of varying activity levels of different species under different crop cover conditions (Coaker and Williams 1963; Dempster and Coaker 1974).

1.7.1. Ground beetles as biocontrol agents

Lindroth (1961-1969) stated that the benefit carabids produce within anthropogenic environments is exaggerated, although larvae are likely more generally beneficial because of their predatory feeding habits. Despite their generalist predatory behaviour, carabids have been identified as important naturally occurring biocontrol agents in agroecosystems (Luff 1987; Kromp 1999).

Carabid beetles feed on juvenile *Delia* spp. (Wright et al. 1960; Grafius and Warner 1990; Finch 1996), although Kromp (1999) indicated in his review that the role the beetles play in root maggot mortality is exaggerated in the literature. Carabids can prey upon aphids, though often on those individuals that fall or are washed off their host plants (Kromp 1999). Some coleopteran agricultural pests, including the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Chrysomelidae), the cereal leaf beetle, *Oulema melanopus* (L.) (Chrysomelidae), and corn rootworm beetles, *Diabrotica* spp. (Chrysomelidae), may be preyed upon by carabids (Kromp 1999). Floate et al. (1990) found that carabids can prey on wheat midge *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae), and several authors have reported predation of pest Lepidoptera, including cutworm (Lepidoptera: Noctuidae) (Frank 1971; Kromp 1999).

Some species of ground beetles in the genera *Amara* and *Harpalus* serve as weed seed predators. Studies have demonstrated high seed predation rates by vertebrates or invertebrates (Harrison et al. 2003; Westerman et al. 2003; Menalled et al. 2007). Carabids comprise a considerable portion of the seed-feeding fauna in agricultural systems and are therefore important for seed removal from the soil (Luff 1987; Lövei and Sunderland 1996; Menalled et al. 2007). Weed seeds from numerous plant species and families can be consumed by carabid seed predators, including the seeds of several weed species common in western Canada (Honek et al. 2007).

Difficulties in considering ground beetles as effective biocontrol agents arise first in their assessment as such. The activity of predators is often difficult to assess or observe (Wishart et al. 1956), and many of the studies linking various carabid species to insect pest control have been performed under laboratory conditions rather than in the field (Kromp 1999). Carabids, as is the case with other predators, are typically general in their prey selection and often have somewhat irregular searching and feeding patterns (Wishart et al. 1956). Furthermore, certain species within the predator guild, such as *Pterostichus melanarius* Illiger (Coleoptera: Carabidae), may predate others in the same guild, limiting the effectiveness of the guild against pest insects (Prasad and Snyder

2004). Some species, particularly the larvae, are even cannibalistic (Lindroth 1961-1969).

1.7.2. Effects of agricultural practices

Carabid beetles are responsive to agricultural practices, particularly to the intensity of agricultural disturbances (Kromp 1999). Effects of cultivation can vary by ground beetle species, crop, and region (Cárcamo 1995), but both the diversity and abundance of ground beetles are often greater in no- or reduced-till systems compared to conventionally tilled systems (Weiss et al. 1990; Stinner and House 1990; Cárcamo 1995; Andersen 2003; Brose 2003). Carabid abundance is affected by tillage because of direct mortality (Fadl et al. 1996) and because of effects on weeds in the agricultural system (Andersen 2003), whereas carabid diversity is affected because of potentially greater vegetational diversity and increased heterogeneity of microhabitats within the cropping system (Stinner and House 1990). Time of cultivation also affects ground beetles; for example, survival of the larval-overwintering *P. melanarius* can be reduced with spring cultivation (Fadl et al. 1996).

Sustainable agricultural practices, including the use of cover crops, appropriate crop rotations, fertilization with manure, and reduced pesticide inputs tend to increase carabid activity densities compared to when these practices are not employed (Luff 1987; Ellsbury et al. 1998; Kromp 1999; Andersen and Eltun 2000; Bourassa et al. 2008). Similarly to the effects of cultivation, species differ in their responses to the sustainable practices mentioned. For example, although the use of sustainable practices (reduced tillage, manure application) promoted some ground beetle species, others, such as *B. quadrimaculatum*, were not favoured because of the increased weed density in sustainable plots (Bourassa et al. 2008). The production of transgenic, insect-resistant crops, specificially crops genetically modified to control lepidopteran larvae by expressing the gene for production of the *Bacillus thuringensis* S-endotoxin, does not affect non-target arthropods, including carabid beetles (Floate et al. 2007).

Agricultural landscape features such as hedgerows and grassy field margins can serve to enhance ground beetle abundance and diversity in fields (Carmona and Landis 1999; Fournier and Loreau 1999; Lee et al. 2001). Such perennially undisturbed areas provide important overwintering habitats for many arthropods, including ground beetles (Pywell et al. 2005). Beetles within or near these habitats also have improved physiological condition, which could lead to greater carabid population increases (Östman et al. 2001).

1.7.2.1. Intercropping effects

Carabid beetle diversity and population densities have been demonstrated to respond favourably to agroecosystem diversification in many studies (Speight and Lawton 1976; Tukahirwa and Coaker 1982; Powell et al. 1985; Brust et al. 1986; Cárcamo and Spence 1994; Armstrong and McKinlay 1997; Kromp 1999; Hummel et al. 2002; Landis et al. 2005; Haggenstaller et al. 2006). However, other studies have found no generalized effect of diversification on ground beetles (Purvis and Curry 1984; Tonhasca 1993; Cárcamo et al. 1995; Butts et al. 2003; Melnychuk et al. 2003; Björkman 2007). Observed responses of ground beetles to agroecosystem diversification are often variable among and within species, and therefore some studies warn against making generalized assumptions of carabid response (Powell et al. 1985; Tonhasca 1993; Björkman 2007). For example, Dempster and Coaker (1974), Dixon et al. (2004), and Björkman (2007) found more *Bembidion* spp. in plots free of a clover cover than in those with clover, but individual species responses to a cover of clover were variable, and effects on species diversity were negligible (Ryan et al. 1980; Björkman 2007). Twice as many carabids were captured in intercrops in another study (Tukuhirwa and Coaker 1982), but they did not appear to significantly affect root maggot populations.

Ground beetle responses to intercropping may result from the effects intercropping has on other conditions in the field environment. Therefore, crop conditions such as the degree of ground cover and the humidity and temperature within the crop canopy influence individual carabid species responses to the intercrops themselves (Cárcamo and Spence 1994; Armstrong and McKinlay 1997; Kromp 1999; Hummel et al. 2002).

The responses of carabid beetles to intercropping of field crop species common in western Canada have been investigated (Cárcamo and Spence 1994; Cárcamo et al. 1995; Butts et al. 2003), but not in combination with investigations of crop pests and agronomic parameter responses to intercropping.

1.8. Objectives

Canola and wheat are the two most commonly grown field crops in Canada, with 10,047 and 6,556 thousand seeded hectares, respectively, in 2009 (Anonymous 2009). Both of these crops are grown in monoculture in western Canada, but intercropping these two species can be an advantageous agronomic practice with regard to crop yield, value, and nitrogen-use efficiency (O'Donovan et al. 1989; Szumigalski and Van Acker 2005, 2006). The objective of this study is to investigate multiple diverse parameters related to intercrops of these two species to determine whether such intercropping systems could be useful for producers seeking more sustainable crop production options. In chapter two, agronomic parameters, principally crop grain and biomass yields, are investigated as a first step in determining if canola-wheat intercrops could be competitive with traditional canola or wheat monocultures. The study is also designed specifically to investigate responses of flea beetles to the intercropping regimes. An intercropping system that could limit flea beetle pressure to canola seedlings while still achieving an acceptable relative crop yield could represent a viable and valuable cropping option for producers. I test the hypotheses that intercrops of canola and wheat can produce grain and biomass yields equivalent to, or better than, yields of constituent monocultures and can provide the additional benefit of reducing flea beetle infestations through interference by wheat plants in the intercrops.

No previous studies have examined responses of root maggots in western Canadian canola production to intercropping. Chapter three presents the first such investigation, involving effects on adult *D. radicum* and *D. platura*, *Delia* spp.

egg populations, and root maggot damage to canola taproots. I hypothesize that, since the mechanism of female fly disruption by non-host plants ought to be the same between brassicaceous vegetable and field crops, root maggot populations and damage will be reduced by intercropping canola with wheat.

In chapter four, I investigate responses of carabid beetle assemblages to canola and wheat intercropping regimes. Specific parameters investigated are species diversity (including richness and evenness), individual species activity densities, and the structure of carabid communities. I test the hypothesis that carabid assemblages will respond to the intercropping of canola and wheat, although individual species responses may be variable.

Chapter five details responses by parasitoids, principally *A. bilineata*, to canola-wheat intercropping regimes. Adult collections of both *A. bilineata* and *A. verna* are investigated, as are rates of *Delia* puparium parasitism and superparasitism by *Aleochara* larvae. I hypothesize that the parasitoids investigated will respond similarly to their hosts with respect to intercrops, that is, parasitism rates will be reduced in intercrops compared to monocultures of canola and wheat.

In chapter six, I provide a general discussion and synthesis of observed results for the many, diverse parameters investigated in this study and their importance in the context of intercropping research. I also present considerations for the economic assessment of a canola-wheat intercrop produced with the methods used in this study and an assessment of this intercropping system for crop production in Alberta, including production under low input or organic approaches.

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2. Chapter 2 – Intercrops of canola and wheat for improved agronomic performance and integrated pest management

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2.1. Introduction

Intercropping has recently drawn increasing interest as an alternative agronomic practice for increasing crop diversity and yields, and for controlling pests. Intercrops have the potential to exceed the yields possible in monocultures of their component species (Andrews and Kassam 1976; Willey 1979; Liebman 1988), because plants in well designed intercrop systems make more effective use of available light, water, and soil nutrient resources through different plant requirements in space and time (Trenbath 1976; Willey 1979; Liebman 1988). More efficient use of resources may also make intercrops more competitive against weeds (Szumigalski and Van Acker 2005), providing cropping options to farmers practicing low-input or organic agriculture. Further agronomic benefits of intercrops can include improved crop quality, enhanced structural support of lodging-prone crops, and greater harvesting ease of one or more of the component crop species (Trenbath 1976; Vandermeer 1989; Weiss et al. 1994; Gooding et al. 2007).

Improved yields can be explained, in part, because insect and disease infestations and damage are often reduced in intercropped systems to below economically significant levels (Vandermeer 1989; Altieri 1994; Hauggaard-Nielsen et al. 2008). Concentrated plant resources in monocultures enable insect herbivores to locate their host plants more easily than in diverse plant stands (Root 1973), and plant pathogens can often more readily exploit large populations of the same crop species (Garrett and Mundt 1999). The presence of non-host plants in intercrops creates physical, chemical, and behavioural barriers to invasion and colonization of the crop by pests (Altieri and Letourneau 1982; Kostal and Finch 1994). Both canola (*B. napus* and *Brassica rapa* L.) and wheat are routinely grown in monocultures throughout western Canada; however, intercrops of the two species offer the potential benefits of improved yield and enhanced integrated pest management.

In western Canada, the crucifer flea beetle, *Phyllotreta cruciferae* (Goeze), and striped flea beetle, *Phyllotreta striolata* (Fabricius) (Coleoptera: Chrysomelidae), cause yield losses to canola estimated at tens of millions of dollars (CAD) annually, representing about 10% of total canola production (Lamb and Turnock 1982; Madder and Stemeroff 1988). Overwintered flea beetle adults attack canola seedlings in the cotyledon and early true-leaf stages, usually in late May through mid June (Westdal and Romanow 1972; Burgess 1977). Adult beetles feed on cotyledons, leaves, and stems (Westdal and Romanow 1972), reducing the photosynthetic ability of the plant. Flea beetles can also kill seedlings by consuming the apical meristems. Plants that survive flea beetle damage often experience decreased growth, delayed ripening, and decreased yield and seed quality (Putnam 1977; Lamb 1984). Studies have shown reduced flea beetle populations when brassicaceous vegetables were intercropped with non-host flora compared to vegetables grown in monoculture (Pimentel 1961; Tahvanainen and Root 1972; Altieri and Schmidt 1986), an observation that suggests a potential benefit for intercropping canola with non-host species.

Foliar diseases are major constraints to wheat production on the Canadian prairies. For example, annual yield losses due to leaf spot diseases may be as great as 20% (Wiese 1987; Gilbert and Tekauz 1993). Leaf spot diseases are caused by various pathogens, including the septoria leaf spot complex consisting of *Septoria tritici* Roberge in Desmaz. and *Stagnospora nodorum* (Berk.) Castellani & E. G. Germano, which cause septoria and stagnospora blotch, respectively, and *Pyrenophora tritici-repentis* (Died.) Drechs., which causes tan spot (Wiese 1987; Gilbert and Woods 2001; Menzies and Gilbert 2003). Although such pathogens are primary causative agents of foliar diseases, other pathogenic and saprophytic organisms, such as *Alternaria* and *Epicoccum* spp., which are widespread and common, may also be found on infected leaf tissue (Domsch et al. 1980; Zillinsky 1983).

Soil microorganisms contribute to key soil processes such as nutrient recycling, degradation of pollutants, and control of pests. Diverse soil microbial communities are more resilient in changing soil environments and are therefore important to the maintenance of soil function in agricultural systems (van Bruggen and Semenov 2000; Lupwayi et al. 2001). Because of their sensitivity to land management practices, particularly agricultural intensification, soil microbial communities are often used as indicators of soil health (Doran and Zeiss 2000).

Field intercrops in which crop species mature simultaneously, as would canola and wheat, present seed separation costs to producers that are not incurred in monocropping systems. Such added costs might be acceptable if an intercrop produced substantially greater yields than the component monocultures. Even with intercrop yields approximating those of monocultures, potential benefits such as enhanced crop quality or reduced pesticide use may be sufficient to offset additional costs incurred through seed separation.

In this study, canola-wheat intercrops were investigated to test the hypotheses that such intercrops could yield equivalently to, or overyield, monocultures of either species, and that they could provide agronomic benefits through improved harvested seed quality. I also hypothesized that the presence of wheat could provide barriers to flea beetles and plant pathogens in the intercrops, reducing damage to canola, and that increased microbial diversity and activity would be found in the more vegetationally diverse intercrops.

2.2. Materials and methods

2.2.1. Site description and experimental design

The study was conducted at Lacombe (52° 28′ N, 113° 44′ W), Ellerslie (53° 34′ N, 113° 31′ W), and Fort Vermilion, Alberta (58° 22′ N, 116° 00′ W) in 2005 and 2006. Study sites represented differing climatic and soil conditions: Lacombe and Ellerslie are in the Aspen Parkland Ecoregion, and Fort Vermilion lies in the Peace Lowland Ecoregion. Soil type was Typic Haplustol clay loam (43% sand, 21% silt, and 36% clay) with pH 5.9 and 8.2% organic matter at Lacombe. At Ellerslie, soil type was Typic Cryoboroll silty clay loam (6% sand, 56% silt, and 38% clay) with pH 6.0 and 6.1% organic matter. Fort Vermilion had Mollic Cryoboralf soil (54% sand, 37% silt, 9% clay) with pH 6.3 and 3.7% organic matter. For the period 1971-2000, mean annual precipitation, July daily mean temperature, and mean number of degree days above 5°C at Lacombe were 446.0 mm, 15.4 ± 1°C, and 1318.5, respectively. For the same period, Ellerslie experienced a mean annual precipitation of 459.6 mm, a mean daily July temperature of 16.0 ± 0.9°C, and 1373.1 degree days above 5°C. Mean annual precipitation, daily mean temperature in July, and degree days at Fort Vermilion were 394.1 mm, 16.2 ± 1.2°C, and 1225.7, respectively (Anonymous 2009).

The experiment was a randomized complete block design with four replications. Treatments were a factorial combination of insecticidal seed treatment (with or without the neonicotinoid insecticide, thiamethoxam) and canola monoculture or intercrop. A monoculture of imidazolinone-tolerant wheat (*T. aestivum* cv. Imagine), seeded at a target density of 250 plants/m², was also included to facilitate analyses of yield data and investigation of cereal leaf diseases. The monoculture of imidazolinone-tolerant canola (*B. napus* cv. 45H72) was seeded at a target density of 200 plants/m², and intercrops were seeded for target canola:wheat populations of 180:20, 160:40, 140:60, and 120:80 plants/m². Target plant densities of 200 and 250 plants/m² were selected for the canola and wheat monocultures, respectively, because of enhanced competition at these densities against tartary buckwheat (*Fagopyrum tataricum* L.) and volunteer cereals (O'Donovan et al. 1988, 1989; O'Donovan 1994), and for optimal control of some insect pests (Dosdall et al. 1996, 1999). Helix® (containing 10.3% thiamethoxam, 1.24% difenoconazole, 0.39% metalaxyl-M, and 0.135% fludioxonil) is registered to systemically reduce herbivory by *Phyllotreta* spp. and was included in the design to assess whether or not intercropping alone could reduce flea beetle feeding on canola to levels achieved when the insecticidal seed treatment was included in the monocultures, or whether the insecticial seed treatment would still be necessary in intercropped plots. Treatment plots measured 7.3 by 15.2 m, with 30-cm row spacings in Lacombe and Ellerslie and 23-cm row spacings in Fort Vermilion.

Plots were seeded in mid to late May using an air drill equipped with 1-cm knife openers. Wheat had been grown at all sites in the preceding year. Study sites were adjacent to grassed trails at Lacombe in 2005 and both Ellerslie and Fort Vermilion in 2005 and 2006. At all sites, there was a mowed grass/weed buffer between the experimental plots and the surrounding crop vegetation, which was canola at Lacombe and Ellerslie and barley at Fort Vermilion. The studies were fertilized according to soil test recommendations for canola production; fertilizer was cross-banded immediately before seeding. The two crop species were seeded simultaneously, with wheat seed replacing the granular fertilizer in the drill and side-banded with the canola. Imidazolinone tolerance in both the canola and wheat cultivars allowed the use of a single herbicide for the control of weeds in the intercrops and monocultures. A commercial herbicide formulation containing 35% imazomox and 35% imazethapyr was applied at 30 g AI/ha at the two-leaf stage of canola development. Cultivars used in the study were selected because of similar times to maturity, which is a requirement for intercrop harvest efficiency (Andrews and Kassam 1976; Carr et al. 1995). Plant counts to determine crop density were made for both canola and wheat in all plots from four randomly selected 1-m lengths of crop row at the cotyledon to 1-leaf stage of canola development.

2.2.2. Yield and other agronomic parameters

Lodging was assessed at all sites approximately one week before harvest. Crop canopy height and the maximum potential height of one canola and one wheat plant were measured at four randomly selected locations in each plot. Lodging was then calculated as the mean percentage difference between canopy and maximum plant height.

Canola and wheat above-ground biomass values were estimated from four 0.5 by 0.5-m quadrats per plot at Lacombe, Ellerslie, and Fort Vermilion in 2005, and at Lacombe and Ellerslie in 2006. Biomass data were not collected at Fort

Vermilion in 2006. Shortly before harvest, plants were clipped 1 cm above the soil surface, sorted, and dried at 25°C for 10 days; dried biomass samples were then weighed.

All plots were harvested at maturity, with yield data collected at Lacombe, Ellerslie, and Fort Vermilion in 2005 and at Lacombe and Ellerslie in 2006. Yield data were not collected at Fort Vermilion in 2006. At Lacombe and Fort Vermilion, plots were swathed before maturity and combined several days later; at Ellerslie a plot combine was used to direct-cut and harvest the plots. Samples of the harvested seed were assessed for proportions of canola and wheat and for percent dockage.

Subsamples of each crop species were assessed for seed quality characteristics, including 1000-kernel weight (TKW), percent protein, and percent oil for canola. Oil and protein (converted from percent nitrogen) content of canola were determined using near-infrared reflectance spectrophotometry (NIRS). Canola test samples were dried, ground, and sieved through a 1-mm screen before assessment. Subsamples of ground material were placed in a test sample cup (0.75-1.75 g) and reflectance measurements were taken. Percent protein in wheat was determined by obtaining nitrogen content measurements using a combustion nitrometer. Following combustion of wheat subsamples, freed nitrogen was measured in the nitrometer. Calibration and analysis for canola oil and canola and wheat protein contents were based on harvest samples from the previous seven years.

2.2.3. Soil microbial assessments

Soil microbiological properties were determined at Lacombe and Fort Vermilion in 2005 and 2006. Soil samples were collected at the flag-leaf stage of wheat development. Plants were excavated from four randomly selected 0.5-m lengths of row from each plot; canola and wheat plants were not separated. Loose soil was shaken off the roots, and the soil that adhered strongly to the roots was carefully brushed and kept as rhizosphere soil. Non-rhizosphere (bulk) soil (0-7.5 cm depth) was sampled from the middle of two adjacent crop rows near each of the four locations per plot. The four bulk or rhizosphere samples from each plot were combined, sieved through a 2-mm screen, and stored at 4 ºC until required for analysis.

Soil microbial biomass carbon content was measured using the substrate-induced respiration (SIR) method, in which 300 mg of glucose was dissolved in enough water to bring a 50-g soil sample to 50% water-holding capacity. The soil was incubated in 1-L jars for 3 h at 22 ºC, and the amount of CO_2 that accumulated in the head space was measured by gas chromatography.

The functional diversity of soil bacteria was evaluated by the Biolog™ method, which tests the ability of a microbial community to utilize different carbon substrates contained in a microplate. The procedure was adapted by colorimetrically standardizing inoculum densities in 1-g subsamples of all soil samples to about 10^3 cells mL^{-1}. Aliquots of 150 µL of the soil suspension were added to Biolog Ecoplates™ containing 31 substrates and a water control. The plates were incubated at 28 ºC without shaking. Optical densities in the wells, which indicate the levels of bacterial activity on the substrates, were read with an enzyme-linked immunosorbent assay (ELISA) plate reader (at 590 nm) after 48 h of incubation. Optical density readings were corrected for the water controls in subsequent analyses. Negative readings after the correction were adjusted to zero.

2.2.4. Flea beetle feeding and wheat leaf disease assessments

Flea beetle feeding damage to canola plants was assessed weekly in 2005 and 2006 beginning at the cotyledon stage of canola development, for three consecutive weeks at Lacombe and Ellerslie and for two weeks at Fort Vermilion. For each assessment, 25 randomly selected canola seedlings per plot were rated according to the amount of feeding damage sustained, based on the scale of Palaniswamy et al. (1992), where 0 represented no damage and 10 represented damage of either 100% of the leaf area or severance of the seedling apical meristem by flea beetles. Growth stage (Harper and Berkenkamp 1975) was also recorded for each canola plant evaluated.

At the late milk stage of wheat development, 20 randomly selected wheat flag leaves were collected from each plot, dried at room temperature, and later rated for percentage leaf area diseased. Representative leaf samples were also placed in a moist chamber, consisting of a 9 cm plastic petri dish containing one filter paper moistened with reverse osmosis water. Petri dishes were incubated at 20 to 22°C for 72 to 96 hrs and were exposed to 12 h of light per day, consisting of one long wave ultraviolet light and three fluorescent cool white lights placed about 30 cm above the plates. Cultures were then examined under a dissecting microscope for generic identification of the causal agents of the septoria leaf spot complex and tan spot, based on the presence of fungal fruiting structures.

2.2.5. Data analysis

Prior to testing for statistical significance, crop yield and dry biomass data were converted to land equivalency ratios (LER) to allow comparison between the monocultures and intercrops. The LER for an intercrop indicates the relative land area required for a monoculture to achieve the yield or biomass of that intercrop when growing conditions are the same for both. Land equivalency was calculated using the following equation (after Vandermeer 1989):

$$\mathrm{LER} = I_a/M_a + I_b/M_b$$

where I is the yield of the intercrop, M is the yield of the monoculture, and a and b represent the component species in the intercrop. Monocultures were assigned the relative value of 1, and an intercrop was considered to have greater land use efficiency than the monocultures when the LER value was greater than 1. Land equivalency ratios were calculated separately for each experimental plot. Mean monoculture grain or biomass yields across all replicate plots at a site were used as the denominators in the above equation, a method that produces conservative estimates of the LER value of intercrops (Vandermeer 1989).

On the basis of the patterns of substrate utilization by bacteria in the soil suspensions, soil microbial diversity was evaluated by calculating the Shannon-Wiener diversity index (H'):

$$H' = -\Sigma\,(p_i \times \ln(p_i))$$

where p_i is the ratio of activity (optical density reading) on the i^{th} substrate to the sum of activities on all substrates. H' is a composite measure of substrate richness and evenness, which are equivalent to bacterial species richness and evenness in the soil.

Agronomic, flea beetle, plant disease, and soil microbial data were subjected to analysis of variance (ANOVA) using the PROC MIXED procedure of SAS (SAS Institute 2004) to investigate treatment effects, with the proportion of total crop plant population comprised of canola included as a covariable. Block was included as a random effect for all analyses; for flea beetle damage data, crop stage was also included as a random effect. Because actual plant populations did not always correspond well with target plant proportions in the intercrops, regression analysis was more appropriate than the distinct intercropping treatments described above. The proportion of canola in the intercrops was therefore included as a covariable, allowing the combined analysis of intercropping proportions and the discrete variables of seed treatment, block, site-year, and crop stage, where appropriate. Planned contrasts were performed in some analyses to determine differences between canola monocultures, wheat monocultures, and intercrops, and between plots with and without the seed treatment. Analyses were also performed on data pooled over sites and years, with site (combination of site and year) and block as random effects. Treatment effects and contrasts were considered significant at $P \leq 0.05$.

2.3. Results

2.3.1. Yield and other agronomic parameters

Crop grain yield LERs for intercrops were not different compared to monocultures (LER = 1) for any site by year combination (Table 2.1), and a significant response to the proportion of canola comprising the total crop plant population was observed for only one of five site-years: at Fort Vermilion in 2005, where LER values decreased as the proportion of canola increased (regression slope coefficient = -0.003; $P = 0.0322$). The LER values of Helix®-treated plots were significantly lower compared to untreated plots at Lacombe in

2005 (mean LER, treated = 0.949 ± 0.019 SE, untreated = 1.067 ± 0.020 SE; $P <$ 0.0001). Contrary to that outcome, LER values for Helix®-treated plots were significantly higher than those for untreated plots at Lacombe in 2006 (treated = 1.042 ± 0.012 SE, untreated = 0.984 ± 0.013 SE; $P = 0.0018$). In the combined data set no differences were observed between plots in which treated seed was used and plots without the seed treatment. Similarly, intercropping did not produce LERs different from 1 in the combined data set.

Crop biomass LER for monocultures (LER = 1) were significantly greater than for intercrops for only one site-year, Ellerslie in 2005 ($P = 0.0489$) (Table 2.1), and proportion of canola in the intercrops had no effect on biomass LER in any site by year combination (data not shown). Biomass LERs were greater in plots without a seed treatment at Ellerslie (treated = 0.947 ± 0.011 SE, untreated = 0.986 ± 0.015 SE; $P = 0.0147$) and Lacombe in 2005 (treated = 0.967 ± 0.020 SE, untreated = 1.033 ± 0.021 SE; $P = 0.0262$), but were greater in Helix®-treated plots at Lacombe in 2006 (treated = 1.026 ± 0.015 SE, untreated = 0.954 ± 0.021 SE; $P = 0.0047$). Treatment effects were not significant for biomass LERs combined over all sites and years of the study.

Analyses of canola TKW showed no significant response to treatments for any of the individual site-years or the combined data. Wheat TKW was significantly affected by the proportion of canola comprising total crop plant populations at Lacombe in 2005 (regression slope coefficient = -0.113; $P =$ 0.0226), such that as the proportion of canola increased, kernel weights for wheat decreased. In general, wheat TKW was the same in monocultures and intercrops except at Lacombe in 2006, where the monoculture TKW was greater (mean TKW, monoculture = 31.440g ± 0.713 SE, intercrop = 23.021g ± 0.384 SE; $P =$ 0.0113).

Canola oil and canola and wheat protein contents were affected by intercropping canola with wheat for some site-years (Table 2.2). At Ellerslie in 2005 there was a significant negative response of canola oil content to increasing proportions of canola in the intercrops ($P = 0.0463$). Oil content was also greater in intercrops compared to canola monocultures at Lacombe in 2006 ($P = 0.0315$).

Canola protein content was greater in the monocultures at Lacombe in 2006 (*P* = 0.0397). Neither canola oil nor protein content responded to intercropping when data were combined over sites and years. Protein content of wheat increased significantly with increases in the proportion of canola at Lacombe in 2005 (*P* = 0.0219) and for data combined over sites and years (*P* = 0.0388), and was higher in intercrops compared to monocultures at Lacombe in 2006 (*P* = 0.0199).

At Lacombe in 2006, crop lodging significantly increased as the proportion of canola comprising total crop plant population increased (*P* = 0.0273), but lodging in other site-years and in the combined data showed no effect of treatments. Dockage was not affected by treatments except at Fort Vermilion in 2005 (*P* = 0.0052), where dockage in the wheat monocultures (0.4700% ± S.E. 0.5564) was significantly lower than that in either the canola monocultures (3.2813% ± 0.3935) (*P* = 0.0045) or the intercrops (3.2391% ± 0.1967) (*P* = 0.0019).

2.3.2. Soil microorganisms

Soil microbial biomass was not affected by treatments in this study. There was a significant response of bacterial diversity in bulk soil to the proportion of canola in intercrops at only Lacombe in 2005 (regression slope coefficient = -0.007; *P* = 0.0497), such that bacterial diversity decreased as the proportion of canola increased (Fig. 2.1). No significant differences in soil microbial biomass or bacterial diversity were observed at either site or in either year between plots with or without a seed treatment of Helix®. Analyses of data combined over sites and years showed no significant treatment effects on soil microbial biomass or diversity in bulk or rhizosphere soil.

2.3.3. Flea beetles

Greater flea beetle damage occurred in 2006 (mean damage rating per plant = 1.07 ± 0.021 SE) than in 2005 (0.88 ± 0.025 SE) when data were combined across sites. Mean canola seedling damage ratings over all years of this study were greatest at Fort Vermilion (1.23 ± 0.034 SE), followed by Lacombe (0.92 ± 0.028 SE) and Ellerslie (0.78 ± 0.021 SE).

When data were combined over sites and years, canola seedlings experienced the greatest flea beetle feeding damage at the first true-leaf stage (Harper and Berkenkamp (1975) crop stage 2.1) (mean damage rating per plant = 1.22 ± 0.046 SE; n = 942) (Fig. 2.2). Damage was comparable between the cotyledon (crop stage 1) (0.96 ± 0.031 SE; n = 2652) and second true-leaf stages (crop stage 2.2) (0.99 ± 0.025 SE; n = 2479), and canola seedlings displayed declining damage levels as plants developed beyond the first true-leaf stage. Emerging canola seedlings (crop stage 0) also experienced low levels of flea beetle feeding (0.46 ± 0.121 SE; n = 61).

Intercropping with wheat usually did not affect flea beetle damage to canola seedlings. Mean flea beetle damage ratings between monocultures and intercrops at Fort Vermilion in 2006 ($P = 0.0293$), the only site-year for which significant differences were detected, were not meaningfully different on the rating scale used in this study (Table 2.3). Increases in the proportion of canola in intercrops caused significant increases in flea beetle damage to canola seedlings at only Lacombe ($P = 0.0183$) and Fort Vermilion ($P = 0.0004$) in 2006. The opposite trend occurred at Ellerslie in 2006 ($P = 0.0179$). Seed treatment with Helix® significantly reduced flea beetle herbivory to canola seedlings in five of six site-years, with the combined data set showing a similar trend, although not significantly ($P = 0.0502$) (Table 2.3).

2.3.4. Wheat leaf diseases

Organisms identified from diseased wheat leaf tissues varied from site to site and year to year. At Ellerslie in 2005, the causal agents of the septoria leaf spot complex and *P. tritici-repentis* (tan spot) were present, with the septoria leaf spot complex being predominant, while at Lacombe in 2005 and both sites in 2006 only the causal agents of the septoria leaf spot complex were observed. In both years other mainly saprophytic fungi were observed, including *Alternaria* spp., *Cladosporium* spp., and *Epicoccum* spp.

Wheat leaf disease infection responded to intercropping and proportions of canola in intercrops for two of four site-years. Percent leaf area infected decreased significantly with increases in the proportion of canola comprising total crop plant populations at Lacombe (regression slope coefficient = -0.119; P = 0.0002) and Ellerslie (regression slope coefficient = -0.127; P = 0.0274) in 2005; however, at Lacombe in 2005 wheat monocultures had significantly lower percent leaf area infected compared to intercrops (mean percent wheat leaf area infected, monoculture = 7.888 ± 0.538 SE, intercrop = 10.700 ± 0.305 SE; $P < 0.0001$). Wheat leaf infection was also greater in the intercrops at Lacombe in 2006 (monoculture = 11.088 ± 0.866 SE, intercrop = 28.273 ± 0.799 SE; $P < 0.0001$). Differences were also detected between wheat monocultures and intercrops at Ellerslie in 2005, but means were not different in a practical sense (monoculture = 17.788 ± 1.632 SE, intercrop = 17.636 ± 0.615 SE; $P = 0.0425$).

2.4. Discussion

Intercrop yields that approximate or exceed those of monocultures of the component crop species are necessary for producer acceptance of any intercropping regime. In my study, grain yields of intercrops of canola and wheat were similar on a land equivalency basis to those of monocultures of the two species in all site-years and when data were combined over sites and years. Above-ground biomass LERs were different between monocultures and intercrops in only one site-by-year combination, indicating that in general biomass yields were also similar between the two systems. Szumigalski and Van Acker (2005) also found that intercrops of canola and wheat yielded comparably to monocultures of the two species in southern Manitoba. O'Donovan et al. (1988, 1989) determined that harvesting volunteer cereals in a canola crop could partially to completely alleviate the costs of reduced canola yields that resulted from competition with cereals. The lack of correspondence between grain yield and biomass LERs may be indicative of different crop resource allocation patterns, as suggested by Szumigalski and Van Acker (2005). Nevertheless, on the basis of grain yield and biomass alone, my results have not provided a compelling argument in favour of widespread adoption of this intercropping strategy for canola or wheat production.

Crop quality characteristics had variable responses to treatment factors, although in most sites and years effects were not significant. Wheat protein levels were greater in some intercrops than monocultures and increased as the proportion of canola increased. Canola oil content was also greater in some intercrops and increased with increasing proportions of wheat in the intercrops. Although quality of non-legume crops often increases in intercrops with a legume component because of N-fixation by the legume (Vandermeer 1989; Gooding et al. 2007), few studies have investigated crop quality responses in other intercropping systems, and these studies have not demonstrated quality advantages through intercropping (e.g., Santalla et al. 1995). However, if an intercrop created conditions favourable to the enhancement of a particular quality characteristic, this increased quality could be an important benefit of that intercrop. For example, drought-stressed wheat often produces lower kernel weights but greater protein that is desirable for bread-making (Souza et al. 2004); in some site-years of my study, the highly competitive canola (Tahir et al. 2003) may have sequestered more of the available water and created a moisture deficit for the wheat, resulting in the observed increase in wheat protein content. Conversely, canola oil content is improved under appropriate moisture conditions (Kirkland and Johnson 2000), and the higher competitive ability of canola than wheat may have increased the moisture available to canola plants in the intercrops relative to plants in the higher-density canola stand of the monoculture.

Soil microbial community biomass and diversity were little affected by treatment factors in this study; however, the significant positive response of microbial diversity to increasing proportions of wheat in the intercrops in one site-year may be due to an increased diversity of substrates from the two crops growing together. An increase in bacterial diversity may be important in biological control of canola pests or diseases (van Bruggen and Semenov 2000).

Flea beetle damage to canola seedlings varied from site to site and year to year, a result likely due to differing conditions among site-years and different proportions of *P. cruciferae* and *P. striolata* at the three sites in this study. The Peace River region of northern Alberta, within which Fort Vermilion is located, generally has a greater proportion of *P. striolata* than more southerly parts of the province (Burgess 1977), and such differences in species dominance may have contributed to differences in site to site responses in this study. Variable responses to environmental and agronomic conditions are also true among other congeneric pest species, such as among root maggots (*Delia* spp., Diptera: Anthomyiidae) (Soroka et al. 2004).

Flea beetle attack on canola crops is most damaging early in the growing season when plants are in the cotyledon to early true-leaf stages (Westdal and Romanow 1972; Burgess 1977; Lamb 1984); however, the crop stage experiencing greatest damage has not been determined previously. My results indicate that the first true-leaf stage of canola has the highest levels of damage (Fig. 2.2), perhaps because by this stage flea beetles have located and colonized the plant stand in sufficient numbers to cause considerable damage, whereas plants at later developmental stages rapidly outgrow damage they sustain.

My study incorporated canola seeded with and without the insecticide thiamethoxam to test the hypothesis that flea beetle damage would be reduced in an intercropped system involving non-host plants (wheat), perhaps eliminating the need for this routine insecticidal application. Although the neonicotinoid seed treatment reduced flea beetle herbivory to canola compared to levels in untreated plots, it had little effect on crop grain and biomass LER values, suggesting that flea beetle damage was insufficient to cause significant yield losses to the canola. Gavloski and Lamb (2000) found that canola plants sustaining flea beetle feeding to 20% or less of their leaf tissue can readily compensate for the damage. In only one of six site-years in this study plants sustained mean flea beetle damage to greater than 20% of their leaf tissue in monoculture plots without Helix®, suggesting that the insecticidal seed treatment was generally not necessary. It is evident, therefore, that further research is needed in this system to evaluate intercrop effects on flea beetle feeding damage under higher population densities of this herbivore. Nevertheless, this study provides additional evidence that prophylactic insecticidal seed treatment applications, practiced commonly throughout areas of canola production in the northern Great Plains, are often unnecessary, as noted previously by Dosdall et al. (1999) and Dosdall and Stevenson (2005).

Heterogeneity in agricultural systems, through intercropping or by other means, can reduce populations and damage by some insect pests, including flea beetles (Tahvanainen and Root 1972; Altieri and Schmidt 1986; Milbrath et al. 1995; Dosdall et al. 1999); however, my study did not consistently demonstrate a benefit of intercropping canola with wheat through reduced flea beetle pressure on canola seedlings. Wheat seedlings may not have provided a sufficient barrier to reduce flea beetle immigration and host-finding in intercropped plots, although wheat stubble has been suggested as providing that effect (Milbrath et al. 1995). Similarly to my results, Weiss et al. (1994) did not find that seedling peas intercropped with canola reduced flea beetle herbivory during the critical first two weeks after canola seedling emergence.

Intercropping has the potential to decrease disease incidence and severity in the component crops (Garrett and Mundt 1999; Hauggaard-Nielsen et al. 2008) by interfering with the movement of disease inocula into and throughout the mixed canopy (Vandermeer 1989) and by altering the physical structure of the crop canopy, making conditions less favourable to disease development (Weiss et al. 1994). My results suggest that canola-wheat intercrop canopies, which enclosed the inter-rows and maintained higher humidity, may have exacerbated wheat leaf disease infestations compared to those in monocultures where inter-rows were not enclosed. At the same time, in two site-years disease severity decreased with increasing canola in the intercrops, suggesting interference of the canola on the infection of wheat plants. Therefore, it appears that canola-wheat intercrops provide conditions more favourable to wheat leaf diseases than do wheat monocultures, but that canola may present a barrier to the movement of some disease inocula in the intercropped canopy.

My study reinforces the complexity of interactions among crop plants, their environment, and pests in intercropping systems. Intercrops of canola and wheat yielded similarly to monocultures of the two species and seemed to have advantages in certain crop quality characteristics. However, intercrops did not perform as well with regard to other characteristics, such as wheat leaf disease severity, and had variable effects on flea beetle feeding damage. These results emphasize that determination of the success of an intercropping regime must not be based on a single pest to be controlled, or on some other single characteristic of the system, but instead on the cropping system as a whole (Altieri and Letourneau 1982). Intercrops of canola and wheat appear to be comparable to monocultures of the two species and could be valuable to low input or organic producers when used in conjunction with other cultural methods of controlling pests. Further research into other aspects of these intercrops, such as other pests and beneficial organisms, is needed to gain a more complete understanding of this complex cropping system and its potential applicability in western Canadian agriculture.

Table 2.1. Mean and SE for grain yield and crop biomass, and land equivalency ratios (LER) for intercrops of canola and wheat.

Site-year	Canola monoculture		Intercrop				Wheat monoculture		Intercrop LER	
			Canola		Wheat					
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
					Grain yield (kg/ha)					
Lacombe										
2005	2983.120	110.412	2666.616	66.022	561.744	60.678	5079.834	157.040	1.010	0.021
2006	2949.907	79.600	2943.560	38.075	66.640	13.360	3699.098	155.379	1.017	0.012
Ellerslie										
2005	2300.569	69.568	2070.966	38.736	95.859	14.882	3139.350	108.854	0.931	0.015
2006	1651.654	95.686	1379.595	94.525	470.234	44.409	2927.795	270.689	0.997	0.049
Fort Vermilion										
2005	2597.908	233.205	2656.813	52.249	72.169	14.160	3355.215	89.500	1.044	0.020
Combined	2496.632	96.428	2343.510	52.055	253.329	23.217	3640.258	187.544	1.000	0.014
					Crop biomass (kg/ha)					
Lacombe										
2005	8620.393	284.042	7487.542	192.611	916.301	101.459	7097.534	626.057	1.002	0.019
2006	10162.965	300.719	9848.949	186.125	125.888	27.046	7289.308	717.842	0.987	0.018
Ellerslie										
2005	8801.337	290.915	8150.326	84.215	213.869	32.822	6675.283	278.193	0.958†	0.012
2006	4503.451	217.393	4089.270	177.087	574.078	65.421	4294.131	349.456	1.042	0.032
Fort Vermilion										
2005	10666.517	367.449	9688.168	203.376	207.677	37.617	6937.818	281.494	0.938	0.018
Combined	8550.933	369.269	7857.475	184.150	401.123	34.812	6458.815	318.183	0.985	0.011

† Land equivalency ratio (LER) means are significantly different ($P \leq 0.05$) from the relative value of the monoculture (1.000), as determined by ANOVA.

Table 2.2. Mean and SE for canola grain oil and canola and wheat grain protein contents in canola and wheat monocultures and intercrops, and significant slope coefficients ($P \leq 0.05$) for regressions of oil or protein content by proportion that canola comprised of the total intercrop plant community, as a covariate, at Lacombe, Ellerslie, and Fort Vermilion, AB, in 2005 and 2006.

	Monoculture		**Intercrop**		**Slope coefficient**
Site-year	**Mean**	**SE**	**Mean**	**SE**	
			Canola oil (%)		
Lacombe					
2005	47.245	0.259	47.731	0.149	—
2006	44.925 b†	0.183	45.371 a	0.126	—
Ellerslie					
2005	48.331	0.345	48.915	0.157	-0.016
2006	47.815	0.239	47.818	0.231	—
Fort Vermilion					
2005	47.703	0.276	48.333	0.145	—
Combined	47.204	0.222	47.634	0.121	—
			Canola protein (%)		
Lacombe					
2005	21.834	0.263	21.179	0.127	—
2006	24.791 a	0.272	24.211 b	0.146	—
Ellerslie					
2005	22.405	0.338	21.699	0.167	—
2006	22.858	0.206	22.728	0.289	—
Fort Vermilion					
2005	20.695	0.467	20.061	0.281	—
Combined	22.516	0.255	21.976	0.145	—
			Wheat protein (%)		
Lacombe					
2005	13.878	0.114	14.113	0.213	0.025
2006	15.468 b	0.231	18.998 a	0.229	—
Ellerslie					
2005	16.352	0.244	17.230	0.208	—
2006	13.960	0.996	14.997	0.277	—
Fort Vermilion					
2005	12.442	0.593	14.707	0.100	—
Combined	14.420	0.380	16.051	0.171	0.019

†Letters indicate significant differences ($P \leq 0.05$) between means for monocultures and intercrops.

Table 2.3. Mean and SE for per plant flea beetle feeding damage to canola seedlings in canola monocultures and intercrops with wheat, and significant slope coefficients ($P \leq 0.05$) for regressions of flea beetle damage by proportion that canola comprised of the total intercrop plant community, as a covariate, at Lacombe, Ellerslie, and Fort Vermilion, AB, in 2005 and 2006.

	Canola monoculture		**Intercrop**		**Slope**	**Seed Treated**		**Untreated**	
Site-year	**Mean**	**SE**	**Mean**	**SE**	**coefficient**	**Mean**	**SE**	**Mean**	**SE**
Lacombe									
2005	0.521	0.065	0.601	0.044	—	0.360 b†	0.048	0.810 a	0.056
2006	1.221	0.092	1.260	0.045	0.007	1.015 b	0.050	1.490 a	0.062
Ellerslie									
2005	0.492	0.049	0.456	0.027	—	0.237 b	0.024	0.690 a	0.039
2006	1.113	0.064	1.102	0.036	-0.006	1.070	0.036	1.138	0.052
Fort Vermilion									
2005	1.917	0.140	1.510	0.058	—	0.610 b	0.054	2.573 a	0.075
2006	0.867 a	0.072	0.865 b	0.042	0.013	0.432 b	0.033	1.298 a	0.060
Combined	1.022	0.037	0.966	0.018	—	0.621	0.018	1.333	0.026

†Letters indicate significant differences ($P \leq 0.05$) between means for monocultures and intercrops or treated and untreated plots.

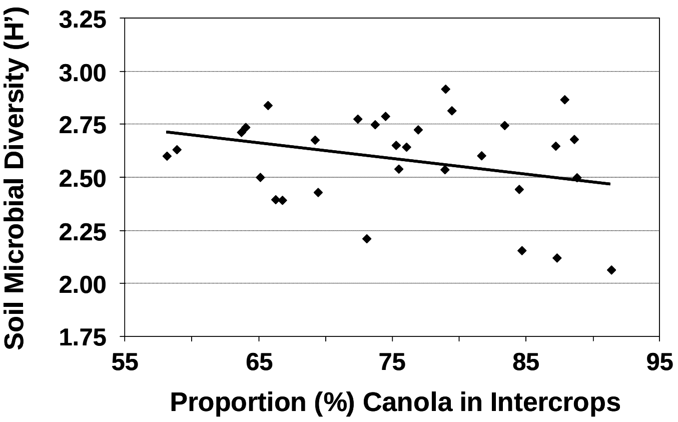

Figure 2.1. Regression of microbial diversity (H') by proportion of canola comprising total crop plant community in bulk soil in intercrops of canola and wheat at Lacombe in 2005.

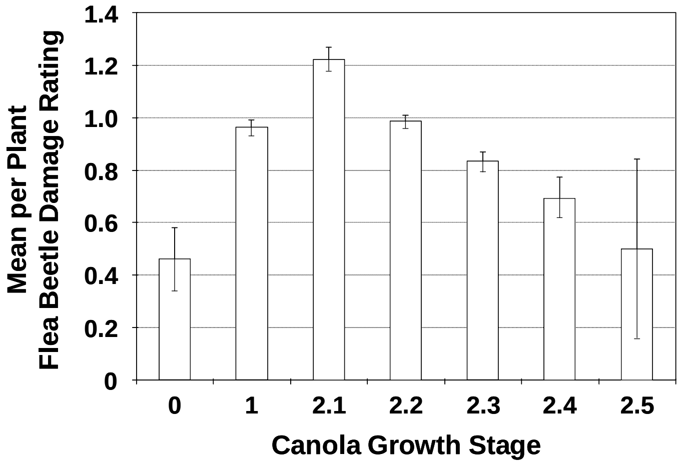

Figure 2.2. Effect of crop stage (Harper and Berkenkamp 1975) on mean and SE for flea beetle feeding damage to canola seedlings. Crop growth stage 0 represents emerging canola seedlings, 1 represents cotyledon-stage seedlings, and stages 2.1, 2.2, 2.3, 2.4, and 2.5, respectively, represent the first, second, third, fourth, and fifth true-leaf stages of canola development.

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3. Chapter 3 – Effects of canola-wheat intercrops on *Delia* spp. (Diptera: Anthomyiidae) oviposition, larval feeding damage, and adult abundance

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3.1. Introduction

In canola production systems in western Canada, root maggots (*Delia* spp.) (Diptera: Anthomyiidae) can inflict annual yield losses of up to 20 and 50% in *Brassica napus* L. and *Brassica rapa* L., respectively (Griffiths 1991a), resulting in millions of dollars in lost revenues to producers (Soroka et al. 2004). *Delia radicum* (L.), *Delia floralis* (Fallén), and *Delia platura* (Meigen) are the principal root maggot species infesting canola (Griffiths 1986b, 1991a; Broatch et al. 2006). *Delia radicum* and *D. floralis* are oligophagous on Brassicaceae and attack uninjured plants, but *D. platura* is polyphagous and typically feeds on damaged and decaying root tissue of plants in a wide variety of botanical familes. In canola, it typically infests roots alread invaded by other root maggots (Brooks 1951; Griffiths 1991b).

Root maggots overwinter as puparia in the soil and emerge as adults from mid May through July, with peak adult emergence in central Alberta during mid June (Griffiths 1986a, b; Broatch et al. 2006). After emergence, mating, and the initial location of a potential host plant, *D. radicum* females perform a series of spiral flights and landings (Kostal and Finch 1994). A fly can oviposit at the base of a brassicaceous host plant after completing an average of four consecutive flights and landings on a suitable host (Finch and Collier 2000). Contact with a non-host plant during the process (an "inappropriate landing") induces the female to restart the behavioural sequence (Kostal and Finch 1994; Finch and Collier 2000). *Delia floralis* must also complete a complex pre-oviposition behaviour before sufficient stimuli are accumulated to oviposit on a host plant (Hopkins et al. 1996, 1999), but the precise pre-ovipositin behaviour of *D. platura* is not known. Similarly, *Delia antiqua* (Meigen), which specializes on various *Allium* spp., follows pre-oviposition behaviours to locate its host plants (Dindonis and Miller 1980). In central Alberta, *D. radicum* oviposition on canola begins in mid June (Griffiths 1986b). Root maggot larvae feed on canola taproots, often forming tunnels that can facilitate invasion by root rot fungi (Griffiths 1986a). As a result, water and nutrient uptake by the plant may be severely impeded, causing smaller plant size, reduced seed set, and even plant mortality (Griffiths 1991a; McDonald and Sears 1992).

In western Canada, intercropping has drawn increasing interest as a possible agronomic practice for increasing crop yields and controlling pests. Intercrops have the potential to overyield monocultures of their component species (Andrews & Kassam 1976; Willey 1979). Even in Alberta, where intercrops are not common, barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) yields could partially to completely offset lost canola yields when either cereal was grown together with canola (O'Donovan et al. 1988, 1989).

Improved yields in intercropped systems can be explained, in part, because insect pest infestations and damage are often reduced in intercrops to below economically significant levels (Vandermeer 1989; Altieri 1994). Several hypotheses have been postulated to account for these reductions, principally the resource concentration and natural enemies hypotheses (Root 1973). According to the resource concentration hypothesis, monocultures are often favoured by insect pests over more diverse habitats because insects tend to more easily locate concentrations of their host plants. Monocultures increase "plant apparency" to host-seeking insect herbivores, while intercrops provide physical, chemical, and even behavioural barriers to colonization by pest insects (Altieri and Letourneau 1982; Kostal and Finch 1994; Milbrath et al. 1995). According to the natural enemies hypothesis, the greater diversity of herbivorous arthropods in intercrops provides natural enemies with alternate prey species when their principal prey is not locally abundant (Root 1973). In addition, more diverse and fractured microclimates within the mixed crop canopy provide refuges for herbivores, ensuring that predators and parasitoids do not completely eliminate herbivore populations, depriving themselves of prey or hosts (Altieri and Letourneau 1982).

Both canola and wheat are routinely grown in monocultures throughout western Canada; however, intercrops of the two species offer the potential benefits of improved yield and enhanced integrated management of root maggots, particularly for organic or low input producers seeking alternatives to conventional pesticides for insect control. Growing the two species together should enable wheat plants to act as non-hosts for disrupting the spiral flight pattern and subsequent oviposition of host-seeking *D. radicum* females. In this study, canola-wheat intercrops were investigated to test the hypothesis that wheat plants could disrupt *D. radicum* host-finding in the intercrops, causing reductions in overall root maggot oviposition and less damage to canola taproots than occurs in canola monocultures. Collections of adult flies were undertaken in different intercrops to determine how the abundance levels and distribution patterns of *Delia* species vary among different intercropping regimes.

3.2. Materials and methods

3.2.1. Site description and experimental design

Field studies were conducted in 2005 and 2006 at Lacombe (52° 28′ N, 113° 44′ W), Ellerslie (53° 34′ N, 113° 31′ W), and Fort Vermilion, AB (58° 22′ N, 116° 00′ W). Sites were selected to represent a range of agricultural regions with differing climates and soil types in Alberta. Soil type at Lacombe was Typic Haplustol clay loam (43% sand, 21% silt, and 36% clay) with pH 5.9 and 8.2% organic matter. Soil type at Ellerslie was Typic Cryoboroll silty clay loam (6% sand, 56% silt, and 38% clay) with pH 6.0 and 6.1% organic matter. Soil type at Fort Vermilion was Mollic Cryoboralf (54% sand, 37% silt, 9% clay) with pH 6.3 and 3.7% organic matter.

The experiment was a randomized complete block design with four replications and 11 treatments: a monoculture of canola (*B. napus* cv. 45H72) seeded at a target density of 200 plants/m², a monoculture of wheat (*T. aestivum* cv. Imagine) seeded at a target density of 250 plants/m², and intercrops seeded to produce canola:wheat populations of 180:20, 160:40, 140:60, and 120:80 plants/m². Each of the intercrop and the canola monoculture treatments was duplicated to include plots with and without a seed treatment of Helix® (containing 10.3% thiamethoxam, 1.24% difenoconazole, 0.39% metalaxyl-M, and 0.135% fludioxonil), a neonicotinoid insecticide designed to systemically reduce herbivory to seedlings by flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae). Target plant densities of the canola and wheat monocultures of 200 and 250 plants/m², respectively, were selected because these densities compete well against weeds such as tartary buckwheat (*Fagopyrum tataricum* L. J. Gaertn) and volunteer cereals (O'Donovan et al. 1988, 1989; O'Donovan 1994) and are optimal for limiting infestations of root maggots and flea beetles (Dosdall et al. 1996, 1999). Treatment plots were 7.3 by 15.2 m, with 30-cm row spacings in Lacombe and Ellerslie and 23-cm row spacings in Fort Vermilion.

Plots were seeded into wheat stubble in mid to late May using a Conserva Pak® drill. Fertilization followed soil test recommendations for canola production. The fertilizer was cross-banded prior to seeding (same day), so both crop species could be seeded simultaneously, with wheat seed replacing the granular fertilizer in the drill and side banded immediately next to the canola seed rows.

Both the canola and the wheat were Clearfield® varieties, tolerant of the herbicide imidazolinone. This allowed for the application of a commercial formulation of imazomox+imazethapyr herbicide (Odyssey®) at 30 g AI/ha to both species in the intercrop for control of dicotyledonous weeds at the two-leaf stage of canola.

3.2.2. Root maggot adult collections and infestation assessments

Delia spp. adults were collected in 2005 and 2006 at Lacombe and Ellerslie using elevated yellow bowl traps (15-cm diameter, 7-cm depth), as described by Dosdall et al. (2006), half-filled with a 1:1 mixture of water and propylene glycol. The bowls were attached to metal posts by metal brackets. As the crop grew, the brackets were raised to keep the bowl traps approximately 10 cm above the height of the crop canopy. Bowl traps were set up at the four-leaf stage of canola development, and sampling was continued until the end of flowering. Insects were removed from the traps weekly and stored in 90% ethanol.

In 2005 and 2006, root maggot oviposition data were collected at Lacombe and Ellerslie. Visual examinations were made of 25 randomly selected canola plants, and the numbers of *Delia* spp. eggs laid at the base of these plants and in the soil in a 1-cm radius and to a 1-cm depth around the plants were recorded using the method of Dosdall et al. (1994). Examinations for eggs were made weekly beginning at the three-leaf stage of the canola, for three consecutive weeks in 2005 and two weeks at Lacombe and a single week at Ellerslie in 2006.

Canola taproots were collected from all sites following harvest. A minimum sample of 25 roots was collected randomly from each plot; the outer 2 m of the plots were not sampled to limit possible edge effects. Roots were washed in the laboratory and scored as to the degree of root maggot feeding damage. The ratings were made using the method of Dosdall et al. (1994), where 0 represented no damage, 1 represented superficial damage of up to 10% of the root surface, 2 represented damage of between 11 and 25% of the root surface with minor tunnelling, 3 represented 26-50% surface damage with tunnelling, 4 represented 51-75% damage to the root surface and extensive tunnelling, and 5 represented complete severance of the root and 76-100% surface damage.

3.2.3. Species identifications and voucher collections

Delia spp. adults collected from the bowl traps were identified using Griffiths (1991b) and representative specimen identifications were validated by J.S. Broatch (Alberta Agriculture and Food, Lacombe, AB). Voucher specimens from the study have been deposited in the Strickland Museum of Entomology, University of Alberta, Edmonton, AB, and at the Agriculture and Agri-Food Canada Research Centre in Lacombe, AB.

3.2.4. Data analysis

Treatment effects for *Delia* spp. adult collections, egg count data, and canola taproot damage data were determined by ANOVA using the PROC MIXED procedure of SAS (SAS Institute Inc. 2004), with the proportion of canola comprising total crop plant population included as a covariable. Site (combination of site and year) and block were included as random effects. For *Delia* spp. adult collections, sampling date was also included as a random effect. Because actual plant populations did not always correspond well with target plant proportions, regression analysis was more appropriate for the intercropping factor than the distinct treatments described in the Methods. Therefore, the proportion of canola in the intercrops was included as a covariable, allowing investigation of this continuous variable along with the discrete variables of seed treatment, block, site-year, and sampling date, where appropriate. The basic model used to fit the data in each site-year was:

$$Y_{ij} = \mu + F_i + B_j + \beta(X_{ij} - X\ldots) + \varepsilon_{ij}$$

where Y_{ij} is the ijth observation for adult collections, egg count data, and taproot damage ratings, μ is the overall mean, F_i is the effect of the ith seed treatment (i = treated or untreated), B_j is the effect of the jth bock (j = 1, …, 4), $\beta(X_{ij} - X\ldots)$ is the regression component representing the slope (β) and the effect of the continuous variable (X_{ij}), and ε_{ij} is the experimental error.

Analyses were also performed on adult abundance, oviposition, and root damage data pooled over sites and years. Treatment effects were considered significant at $P \leq 0.05$.

3.3. Results

3.3.1. Environmental Conditions and Plant development

Environment Canada data (Anonymous 2009) indicated that mean monthly temperatures and precipitation during the growing seasons of this study (May - August inclusive, 2005-2006) were approximate to long-term averages for Lacombe, Ellerslie, and Fort Vermilion with a few exceptions (Table 3.1). Precipitation at all three sites was lower in 2005 than the long-term average, and remained so at Ellerslie into 2006. Mean monthly temperatures (May - August) were generally higher in 2006 than those of the long-term average.

Early-season counts of crop plant densities indicated that mean populations of canola and wheat in the intercrops were often, but not always, similar to those targeted for the given treatments (Table 3.2), and as a result actual proportions of the two crop species also deviated from intended proportions. Proportions of canola and wheat in intercrop plots deviated by greater than 5% in more than 25% of plots in any site-year, and by greater than 10% in more than 5% of plots.

3.3.2. Adult Delia species composition and treatment effects

Collections of adult *Delia* spp. over the entire sampling period totaled 1,330 specimens from Ellerslie and 155 from Lacombe in 2005; in 2006, Ellerslie collections totaled 190 specimens, and 822 specimens were collected from Lacombe. *Delia radicum* and *D. platura* were the most abundant anthomyiid species collected at both sites, comprising 97 and 91% of total collections in 2005 and 2006, respectively. However, their relative proportions varied considerably between sites. In 2005, the Lacombe collection was comprised of 52% *D. radicum* and 45% *D. platura*, but at Ellerslie *D. radicum* and *D. platura* made up 80 and 17% of collections, respectively. In 2006, *D. radicum* and *D. platura* comprised 80 and 13%, respectively, of the collection at Lacombe, and 72 and 16% of specimens at Ellerslie. Other anthomyiids collected in the bowl traps were *D. floralis*, *Delia florilega* (Zetterstedt), and *Delia planipalpus* (Stein).

Male *D. radicum* were captured in bowl traps more frequently than females in both Lacombe (69 ♂ : 31 ♀) and Ellerslie (79 ♂ : 21 ♀) in 2005, but in 2006 females were more frequently collected at Ellerslie (14 ♂ : 86 ♀) and were collected in equal numbers to males at Lacombe (50 ♂ : 50 ♀). Frequencies of male and female *D. platura* were more consistent than those of *D. radicum*. In 2005, 43% of *D. platura* collected at Lacombe were female, and 54% at Ellerslie were female. In 2006, females accounted for 49 and 37% of *D. platura* collections at Lacombe and Ellerslie, respectively.

Adults of *D. radicum* were usually common in trap collections when sampling was initiated each year. With the exception of Lacombe in 2005, *D. radicum* populations decreased dramatically in late June to early July from peak numbers found in early-season sampling in both years of the study, and in all site-years there was an increase of *D. radicum* adults between late July and early August (Figures 3.1, 3.4). A temporal shift in abundance of male and female *D. radicum* occurred at Lacombe in 2005 and 2006, with females collected in greater numbers than males in the earlier part of the trapping period (Figures 3.2, 3.5). At both Lacombe and Ellerslie in 2005 and at Lacombe in 2006, males were responsible for increases in *D. radicum* collections late in the trapping period.

Populations of *D. platura* remained low throughout the collection periods, except at Lacombe in 2005 when two population peaks were evident: one in early July and a second in early August (Figures 3.1, 3.4). The early peak was due to both males and females, while the later was caused almost exclusively by males. At Ellerslie, however, both male and female *D. platura* were most abundant in bowl trap collections in late June, declining steadily following this period (Figure 3.3). In 2006, female *D. platura* were again most abundant in late June and declined following this at both Lacombe and Ellerslie. Males at both sites in 2006 peaked in late July, and this resulted in a temporal shift in abundance of males and females (Figure 3.6).

The presence of wheat in the intercrops had a significant negative effect on *D. radicum* male collections at Ellerslie in 2005 (F = 5.74; df = 1, 252; P = 0.0173) and Lacombe in 2006 (F = 12.58; df = 1, 254; P = 0.0005); a similar effect was observed for *D. platura* males (F = 4.66; df = 1, 254; P = 0.0318) and the combined collection of *D. platura* males and females at Lacombe in 2006 (F = 8.34; df = 1, 254; P = 0.0042) (Table 3.3). The presence of wheat had a significant positive effect on collections of *D. radicum* females at Lacombe in 2006 (F = 4.12; df = 1, 254; P = 0.0434). However, when adult collections of *D. radicum*, *D. platura*, and all *Delia* spp. were combined over sites and years, there was no response in root maggot adult abundance to the canola proportion of the total crop plant population ($P > 0.05$) (Table 3.3).

3.3.3. Root maggot oviposition

Root maggot egg populations were greater at Ellerslie (mean eggs per plant = 0.21 ± 0.011 SE) than Lacombe (0.09 ± 0.006 SE), and greater in 2006 (0.29 ± 0.015 SE) than in 2005 (0.07 ± 0.004 SE). Egg populations were significantly affected by intercropping at Ellerslie in 2006 ($F = 6.07$; df = 1, 993; $P = 0.0139$) (Table 3.4), such that as the proportion of canola comprising total crop plant populations increased, root maggot oviposition decreased. A seed treatment with Helix® did not affect root maggot oviposition in any individual site-year ($P > 0.05$). Neither intercropping ($F = 1.84$; df = 1, 3; $P = 0.2685$) nor seed treatment ($F = 2.98$; df = 1, 3; $P = 0.1830$) had significant effects on per plant egg populations in analyses of the combined data (Table 3.4).

3.3.4. Canola root damage

Mean root maggot damage ratings to canola taproots over all years of this study were highest in Ellerslie (mean damage rating per plant = 2.52 ± 0.021 SE), followed by Lacombe (2.39 ± 0.023 SE) and Fort Vermilion (2.24 ± 0.020 SE). Mean damage rating across all sites and treatments were greater in 2006 (2.88 ± 0.013 SE) than in 2005 (1.72 ± 0.016 SE).

When plots were grouped according to agreement between actual and targeted plant populations, approximating proportions of canola of 100, 90, 80, 70, and 60% ± 5%, mean root maggot damage often declined with a decrease in canola proportion (Table 3.5). Feeding damage to canola taproots by *Delia* spp. larvae increased significantly with an increase in the proportion of canola comprising total crop plant populations in 2005 at both Ellerslie ($F = 4.40$; df = 1, 993; $P = 0.0362$) and Fort Vermilion ($F = 4.07$; df = 1, 992; $P = 0.0440$) (Table 3.6). When damage ratings for all sites and years were combined, canola root damage increased with increasing proportions of canola in the crop plant populations ($F = 8.39$; df = 1, 5; $P = 0.0339$) (Table 3.6).

At Lacombe in 2005, damage to canola taproots was significantly greater in those intercrops and canola monocultures where a seed treatment of Helix® was used ($F = 11.48$; df = 1, 993; $P = 0.0007$) (Table 3.6). The interaction between proportion canola and seed treatment was also significant (*F* = 9.35; df = 1, 993; *P* = 0.0023), indicating that root maggot feeding damage response to intercropping differed when the seed treatment was used from when it was excluded. Significant differences were not observed in either Ellerslie or Fort Vermilion in 2005 and 2006 between root damage in Helix®-treated plots and those without the seed treatment ($P > 0.05$). Data pooled over sites and years showed no significant effect of a Helix® seed treatment on root maggot damage to canola plants ($P > 0.05$) (Table 3.6).

3.4. Discussion

My study investigating intercropping of canola and wheat builds upon the principals of *Delia* spp. behavioural interference in the presence of non-host plants. Kostal and Finch (1994) and Finch and Collier (2000) observed that the spiral flight pattern preceding oviposition in gravid *D. radicum* females was interrupted by encounters with non-host plants when hosts and non-hosts were grown together, resulting in reduced egg deposition as opposed to when host plants were grown in monoculture. Finch et al. (2003) and Morley et al. (2005) found that, instead of being induced to leave non-host plants in the minutes after landing, female *D. radicum* movements were arrested on non-hosts, and host-plant stimuli received previously were lost during this prolonged period of non-host contact. *Delia* spp. per plant oviposition at Ellerslie in 2006 was greater in intercrops than monocultures (Table 3.4), which may have reflected the dispersion of egg load over lower densities of canola in the intercrops. In the other three of four site-years and the combined data of my study, *Delia* spp. oviposition was not affected on a per plant basis by the wheat as a non-host intercropped with canola. The reasons for this are unclear, but could reflect the stronger competitive ability of canola plants relative to wheat (Harker et al. 2007), resulting in wheat populations with insufficient aboveground biomass to interrupt the flight sequence of root maggot females. In my study, canola was more competitive than wheat, resulting in greater canola than wheat biomass at harvest for all treatment plots except the wheat monoculture (Hummel, unpublished data). Egg data may also have been confounded by populations of *D. platura*, which would likely have had differing behavioural responses to the presence of wheat intercropped with canola than did female *D. radicum*, as Parsons et al. (2007) suggested for a relay cropping system of cauliflower, *Brassica oleracea* L. variety *botrytis* (Brassicaceae), and lettuce, *Lactuca sativa* L. (Asteraceae). *Delia radicum* and *D. platura* eggs were not differentiated during in-field egg population assessments in my study.

Intercrop design in this study followed a replacement series (Vandermeer 1989), where wheat replaced canola plants in the intercrops. The number of canola plants/m^2 decreased with increasing proportions of wheat in the intercrops, yet I observed that similar root maggot egg numbers were deposited per plant in canola monocultures and intercrops, resulting in lower egg densities on a land area basis in intercrops than monocultures. Given that collections of adult female *Delia* were usually similar in intercrops and monocultures (Table 3.2), my results suggest that an equivalent number of female flies laid a lower total number of eggs in the intercrops compared to the monocultures. In studies intercropping brassicaceous vegetables with non-host plants, where monocultures and intercrops had equal densities of host plants, researchers also found reduced *Delia* spp. egg densities in the intercrops (Tukahirwa and Coaker 1982; Finch et al. 2003; Dixon et al. 2004; Björkman et al. 2007). Similarly, reduced root maggot egg populations per plant were observed by Dosdall et al. (2003) in weedy compared to weed-free canola with equivalent canola plant densities in the weedy and weed-free situations. My results suggest that, similar to the findings of other researchers, root maggot egg populations were reduced on a land area basis in diverse plantings with host and non-host plants, an observation that further validates the importance of non-host plants for reducing infestations by these pests.

Collections of adult *D. radicum* and *D. platura* were usually similar in canola monocultures and intercrops of canola and wheat, although significant effects were observed in some sites and years (Table 3.3). Attraction of herbivores to their host plants is influenced by plant volatile compounds (Visser

1986), so it might be predicted that numbers of adult *Delia* spp. would be greater in monocultures than intercrops. However, Finch and Skinner (1982) found that the direction of long-range movements of *D. radicum* females was little mediated by host-plant odours but substantially influenced by wind direction. Rather than indicating the direction of host plants, volatile host plant chemicals signal passing crucivores like *D. radicum* that suitable host plants are nearby (Finch and Collier 2000). Further, Tukahirwa and Coaker (1982) found that flies arrived at monoculture and intercropped brassicaceous crops in similar frequencies and suggested that initial location of suitable host plants was not disrupted by the presence of non-hosts. Studies have also shown that non-host plants do not repel *D. radicum* through release of volatile chemicals (Finch et al. 2003; Morley et al. 2005). My results suggest that the numbers of *Delia* spp. adults initially locating canola monocultures or intercrops with wheat were similar, as Björkman et al. (2007) also concluded for *D. floralis*. In agreement with my results, Dixon et al. (2004) usually found non-significant differences in *D. radicum* trapped in rutabaga (*Brassica napus* L. subsp. *rapifera* Metzg.) undersown with clover as opposed to rutabaga monocultures.

Combined data over all sites and years of my study determined that damage to canola taproots declined when the proportion of wheat in the intercrops increased (Table 3.6). The mechanism for this response is not readily apparent, because root maggot egg populations per canola plant were similar among the intercrops and monocultures. The activities of natural enemies or other mortality factors of pre-imaginal root maggots may have affected infestation levels and subsequent root damage. Natural enemies of the juvenile stages of root maggots, particularly the predator-parasitoid *Aleochara bilineata* Gyllenhal (Coleoptera: Staphylinidae), the parasitic wasp *Trybliographa rapae* Westwood (Hymenoptera: Figitidae), and various carabid beetles (Coleoptera: Carabidae), are important biocontrol agents of *D. radicum* and some other *Delia* species (Wishart et al. 1956; Wishart 1957; Coaker and Williams 1963; Mukerji 1971) and are known to occur in central Alberta (Hemachandra et al. 2007; Broatch et al. 2008b). Intercrops or weedy crops often harbour a greater abundance than monocultures of predators, parasites, and pathogens, particularly carabid and staphylinid beetles (Horn 1981, 1987; Tukahirwa and Coaker 1982; Purvis and Curry 1984; Kromp 1999). However, some parasitoids of *Delia* spp., such as *A. bilineata* and *T. rapae*, are not favoured in intercrops of cruciferous vegetables with non-host ground cover (Langer 1996; Dixon et al. 2004). Langer (1996) suggested that host-specific parasitoids are better able to locate their hosts in the more homogenous conditions of a monoculture than in an intercrop. Relationships of the various natural enemy species to the range of environmental conditions created in different canola-wheat intercrops warrants further investigation.

Crop stand results in my study stress the importance of measuring actual versus targeted plant populations in intercropping research to enable the most appropriate interpretation of results. Agreement between targeted and actual proportions of canola and wheat in intercropped plots often did not occur (Table 3.2), but the reasons for this are unclear. Lack of such concurrence could have resulted from a number of abiotic or biotic factors (e.g., damage to germinating seedlings by phytopathogens, inadequate soil moisture, etc.), alone or in combination. Intercropping effects in this study were therefore more appropriately determined by regression than analysis of variance. A similar situation was encountered by Broatch et al. (2008a) who varied weed populations in canola with herbicide to study interactions of weeds and root maggots, but difficulties in matching targeted with actual weed populations indicated that regression analysis was the most robust analytical approach.

Neonicotinoids like thiamethoxam and clothianidin represent relatively new seed treatment chemistries for insect control and function as nicotinic acetylcholine receptor ‘super’ agonists (Brown et al. 2006). Evidence exists that some neonicotinoids may be useful for root maggot control. For example, thiamethoxam and clothianidin delivered as seed treatments reduced infestations of *D. platura* in snap bean (*Phaseolus vulgaris* L.) (Nault and Taylor 2004), and seed treatment with clothianidin provided good control of the onion maggot, *Delia antiqua* (Meigen) (Nault et al. 2006). However, Griffiths (1991a) showed that although a number of different insecticidal seed treatments slowed the progress of *Delia* spp. infestation of canola roots, by mid-July all treatments had similar levels of root damage, and a delayed release insecticide was suggested for root maggot control. My study indicated that thiamethoxam (Helix$^{®}$) did not provide sufficient residual activity to control root maggots in canola, as in most sites and years the seed treatment had no effect on root maggot oviposition or on larval feeding damage to canola taproots.

Griffiths (1986b) determined that greater root maggot infestations corresponded to higher soil moisture content. Low moisture conditions may have reduced root maggot populations at the three sites in this study in 2005, an effect that continued into 2006 at Ellerslie. These low moisture levels and resultant root maggot populations may also have affected the abundance of their dominant parastoid, *A. bilineata*.

Adult *Delia* spp. differed in abundance levels in Lacombe and Ellerslie in 2005 and 2006. *D. radicum* was substantially more abundant than *D. platura* at Ellerslie in 2005 and at both Lacombe and Ellerslie in 2006, but the two species were approximately of equal abundance at Lacombe in 2005. This concurs with observations of Griffiths (1986b) who reported *D. radicum* as the most abundant root maggot species infesting canola in central Alberta, and Broatch et al. (2006) who found that *D. platura* was approximately as abundant or more abundant than *D. radicum* in Lacombe in 2002, 2003, and 2004. Such differences in the dominance of *Delia* spp. among sites and years may contribute to the variation in observed damage levels. Different species exhibit different seasonal abundances and phenologies, as well as different host-plant preferences, potentially causing differences in resulting damage levels (Griffiths 1986b).

Trap collections of *D. radicum* adults suggest that only in some years the partial, incomplete second generation of this species, reported by Griffiths (1986a), occurs in Lacombe, although two population peaks are indicated for Ellerslie: one in mid to late June through early July and one in early August. This second generation would likely not oviposit on canola (Griffiths 1986b).

Seasonal abundance patterns for *D. platura* at Lacombe in 2005 were similar to those found in 2002, 2003, and 2004 by Broatch et al. (2006) who proposed the existence of two distinct generations. However, the increase in *D. platura* male collections in mid-July at Lacombe in 2006 does not necessarily demonstrate a second generation. Declining collections of *D. platura* from late June through early August at Ellerslie in 2005 suggest a population peak around early to mid June; therefore a second generation of *D. platura* in this site-year is likely. The limited collection period at Ellerslie in 2006 prevented the determination of the number of *D. platura* generations, though the results suggest at least one peak of both males and females in early to mid June. The phenology of *D. platura* in central Alberta, therefore, requires further investigation.

My studies on the phenologies of *D. radicum* and *D. platura* largely support the findings of Griffiths (1986a, b) and Broatch et al. (2006) but emphasize that both the phenology and abundance of these species in central Alberta are variable from site to site and from year to year. Both *D. radicum* and *D. platura* are hosts of *A. bilineata* (Klimaszewski 1984), and the presence of a second generation of *D. platura* in Lacombe would provide additional hosts for the beetle, increasing its overwintering populations and affecting the population dynamics of the flies in subsequent years (Broatch et al. 2006). The lack of a second generation of *D. platura* in Ellerslie, as my data seem to suggest, would greatly influence not only the dynamics of *D. radicum* and *D. platura* populations, but also those of the parasitoid.

Relative abundances of male and female root maggot adults may have been influenced by trapping method. Griffiths (1986a) and Broatch and Vernon (1997) found that males and females responded differently to distinct trap types, and that gender responses varied over time (Broatch and Vernon 1997). I found that males of both *D. radicum* and *D. platura* were typically collected in greater numbers than females in bowl traps. Similarly, greater numbers of males than females of the two species were collected using sticky traps (Griffiths 1986a; Broatch and Vernon 1997; Broatch et al. 2006), and Broatch et al. (2006) concluded that males of *D. radicum* and *D. platura* are either more attracted to these traps than females or are more active than females and so more readily collected.

In tropical regions where intercropping is more prevalent, this practice provides the diverse food supplies and yield stability that farmers require, and intercropping is efficient for making use of available labour and plant nutrients (Altieri 1991). However, in the large-scale farming systems that dominate North American grain production, farmers are unlikely to adopt intercropping without clearly demonstrated evidence of its potential advantages over monocropping because of the increased complexity involved in managing intercrops. This study provides evidence that intercrops of canola and wheat have the potential advantage of enhancing root maggot control. No insecticides are currently registered for reducing crop damage from these pests in canola, yet root maggots are annually responsible for serious yield losses and reduced economic returns (Griffiths 1991a; Soroka et al. 2004). Intercropping canola and wheat appears to provide an opportunity for reducing these losses without compromising environmental sustainability.

Table 3.1. Mean monthly temperature (°C) and precipitation (millimetres) received during the growing season (May - August inclusive) at Lacombe, Ellersle, and Fort Vermilion, Alberta, in 2005 and 2006, and long-term normal temperatures and precipitation levels.

	2005		**2006**		**Long-term average**	
	Temp.	**Precip.**	**Temp.**	**Precip.**	**Temp.**	**Precip.**
Lacombe	12.9	63.8	14.7	71.2	13.5	72.9
Ellerslie	13.6	61.9	14.9	58.9	14.1	70.0
Fort Vermilion	14.3	42.8	15.7	60.8	13.6	52.7

Table 3.2. Mean target and actual canola (C) and wheat (W) densities (plants/m²) in intercropping plots at Lacombe, Ellerslie, and Fort Vermilion, Alberta, in 2005 and 2006.

Target Densities		**Actual Densities**											
		2005						**2006**					
		Lacombe		**Ellerslie**		**Fort Vermilion**		**Lacombe**		**Ellerslie**		**Fort Vermilion**	
C	**W**	**C**	**W**	**C**	**W**	**C**	**W**	**C**	**W**	**C**	**W**	**C**	**W**
180	20	192	18	189	26	165	28	87	17	175	31	107	9
		166	30	226	32	155	17	65	15	153	45	207	12
		160	21	196	28	165	17	86	12	161	32	116	14
		162	24	213	24	177	35	88	16	143	32	112	19
		145	26	167	19	142	33	127	12	208	15	133	13
		214	31	208	11	217	30	134	21	179	33	115	10
		189	24	208	35	182	22	125	15	188	32	119	24
		197	27	191	38	152	25	120	15	169	46	115	7
160	40	156	20	212	41	214	39	87	20	138	25	115	26
		169	45	189	33	130	49	93	17	145	34	133	11
		174	64	204	22	165	30	54	21	130	56	148	24
		157	31	169	29	147	39	97	39	140	42	125	32
		183	41	184	30	142	39	105	17	140	59	132	28
		141	75	189	37	151	43	84	16	163	43	150	17
		155	51	165	40	150	38	59	84	148	57	90	24
		175	45	180	62	172	34	62	45	148	35	108	17
140	60	172	54	153	49	130	52	75	39	112	64	118	43
		155	68	165	71	142	56	89	24	145	53	130	31
		161	55	168	67	129	49	71	52	155	65	94	27
		151	40	156	75	145	90	58	44	132	78	124	48
		125	62	138	43	116	55	98	21	139	63	94	46
		157	51	148	43	131	31	103	39	155	68	118	35
		139	71	167	48	150	51	83	43	139	57	86	22
		153	46	162	48	156	90	80	44	139	52	93	34
120	80	134	51	133	75	85	58	67	38	129	69	101	70
		133	93	154	61	118	66	80	45	116	83	127	55
		166	59	152	94	150	69	46	56	118	70	52	34
		148	84	143	80	130	90	55	70	129	80	125	52
		125	56	109	80	110	56	60	49	105	84	81	62
		99	71	126	64	116	83	66	51	125	80	113	43
		114	64	140	59	131	51	76	68	98	84	84	38
		135	71	123	79	144	78	85	52	103	94	85	62

Table 3.3. Analysis of variance for *Delia* spp. adult collections investigating effect of intercropping (proportion canola comprised of total intercrop plant community, as a covariate; numerator df = 1) on root maggot infestations.

Site-year	**Species, Sex**	***P* value**	***F* value**	**Denominator df**	**Slope coefficient**
Lacombe					
2005	All *Delia* spp.	0.1466	2.12	253	0.000527
	D. radicum male + female	0.0942	2.82	253	0.000419
	male	0.0832	3.02	253	0.000378
	female	0.7152	0.13	253	0.000041
	D. platura male + female	0.3459	0.89	253	0.000188
	male	0.3171	1.00	253	0.000135
	female	0.7077	0.14	253	0.000050
2006	All *Delia* spp.	0.0996	2.73	254	0.001425
	D. radicum male + female	0.2125	1.56	254	0.000979
	male	**0.0005**	12.58	254	0.001972
	female	**0.0434**	4.12	254	-0.00098
	D. platura male + female	**0.0042**	8.34	254	0.000576
	male	**0.0318**	4.66	254	0.000310
	female	0.0646	3.45	254	0.000261
Ellerslie					
2005	All *Delia* spp.	0.0584	3.61	252	0.004906
	D. radicum male + female	0.0590	3.60	252	0.003931
	male	**0.0173**	5.74	252	0.003974
	female	0.9517	0.00	252	-0.00004
	D. platura male + female	0.2240	1.49	252	0.000802
	male	0.3525	0.87	252	0.000288
	female	0.2457	1.35	252	0.000514
2006	All *Delia* spp.	0.4555	0.56	168	-0.00038
	D. radicum male + female	0.4462	0.58	168	-0.00033
	male	0.0918	2.88	168	-0.00021
	female	0.7704	0.09	168	-0.00012
	D. platura male + female	0.5341	0.39	168	-0.00011
	male	0.5089	0.44	168	-0.00009
	female	0.9001	0.02	168	-0.00001
Combined	All *Delia* spp.	0.2911	1.63	3	0.001669
	D. radicum male + female	0.3144	1.45	3	0.001279
	male	0.2288	2.27	3	0.001555
	female	0.2974	1.58	3	-0.00031
	D. platura male + female	0.1831	2.97	3	0.000404
	male	0.1706	3.22	3	0.000188
	female	0.2371	2.17	3	0.000224

Separate analyses were performed for each site-year combination. Statistically significant values ($P \leq 0.05$) are in bold font .

Table 3.4. Analysis of variance for per plant root maggot egg populations from field experiments investigating the effect of intercropping (proportion that canola comprised of the total intercrop plant community, as a covariate; numerator df = 1) and seed treatment on root maggot infestations.

Site-year	**Effect**	***P* value**	***F* value**	**Denominator df**	**Slope coefficient**
Lacombe					
2005	Proportion canola (C)	0.7340	0.12	993	-0.00064
	Seed treatment (T)	0.2675	1.23	993	
	C × T	0.3634	0.83	993	
		0.2221	1.49		-
	T	0.1295	2.30	993	
	C × T	0.1345	2.24	993	
Ellerslie					
2005	C	0.2724	1.21	993	-0.00085
	T	0.1301	2.30	993	
	C × T	0.0882	2.91	993	
2006	C	**0.0139**	6.07	993	-0.00600
	T	0.8189	0.05	993	
	C × T	0.9572	0.00	993	
Combined	C	0.4256	0.85	3	-0.00046
	T	0.6319	0.28	3	
	C × T	0.6864	0.20	3	

Separate analyses were performed for each site-year combination. Statistically significant values ($P \leq 0.05$) are in bold font.

Table 3.5. Mean and SE canola taproot damage ratings in canola monocultures and intercrops of canola and wheat. Treatments are based on actual crop plant count data and include experimental plots with ± 5% deviation in proportion canola comprising total crop plant populations.

Site-year	**Treatments (proportion canola in intercrops)**									
	100%		**90%**		**80%**		**70%**		**60%**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Lacombe										
2005	1.57	0.06	1.50	0.06	1.51	0.05	1.57	0.05	1.56	0.08
2006	3.12	0.05	3.11	0.04	3.14	0.04	2.90	0.06	3.13	0.04
Ellerslie										
2005	1.76	0.07	1.78	0.06	1.89	0.07	1.71	0.07	1.54	0.08
2006	3.07	0.05	3.09	0.06	2.97	0.04	2.95	0.04	2.97	0.04
Fort Vermilion										
2005	1.92	0.06	1.98	0.06	1.87	0.05	1.78	0.05	1.83	0.07
2006	2.51	0.06	2.63	0.05	2.50	0.06	2.51	0.06	2.49	0.08

Table 3.6. Analysis of variance for canola taproot damage data from field experiments investigating the effect of intercropping (proportion that canola comprised of total intercrop plant community, as a covariate; numerator df = 1) and seed treatment on root maggot infestations.

Site-year	**Effect**	***P* value**	***F* value**	**Denominator df**	**Slope coefficient**
Lacombe					
2005	Proportion canola (C)	0.6412	0.22	993	0.006945
	Seed treatment (T)	**0.0007**	11.48	993	
	C × T	**0.0023**	9.35	993	
2006	Proportion canola (C)	0.6109	0.26	1192	-0.00102
	Seed treatment (T)	0.0892	2.89	1192	
	C × T	0.1338	2.06	1192	
Ellerslie					
2005	Proportion canola (C)	**0.0362**	4.40	993	0.004725
	Seed treatment (T)	0.6886	0.16	993	
	C × T	0.8243	0.05	993	
2006	Proportion canola (C)	0.0534	3.74	1590	0.004613
	Seed treatment (T)	0.0750	3.17	1590	
	C × T	0.1632	1.95	1590	
Fort Vermilion					
2005	Proportion canola (C)	**0.0440**	4.07	992	0.006415
	Seed treatment (T)	0.5351	0.39	992	
	C × T	0.3107	1.03	992	
2006	Proportion canola (C)	0.5861	0.30	1240	0.000013
	Seed treatment (T)	0.9340	0.01	1240	
	C × T	0.5850	0.30	1240	
Combined	Proportion canola (C)	**0.0339**	8.39	5	0.002882
	Seed treatment (T)	0.2721	1.52	5	
	C × T	0.3161	1.24	5	

Separate analyses were performed for each siet-year combination. Statistically significant values ($P \leq 0.05$) are in bold font.

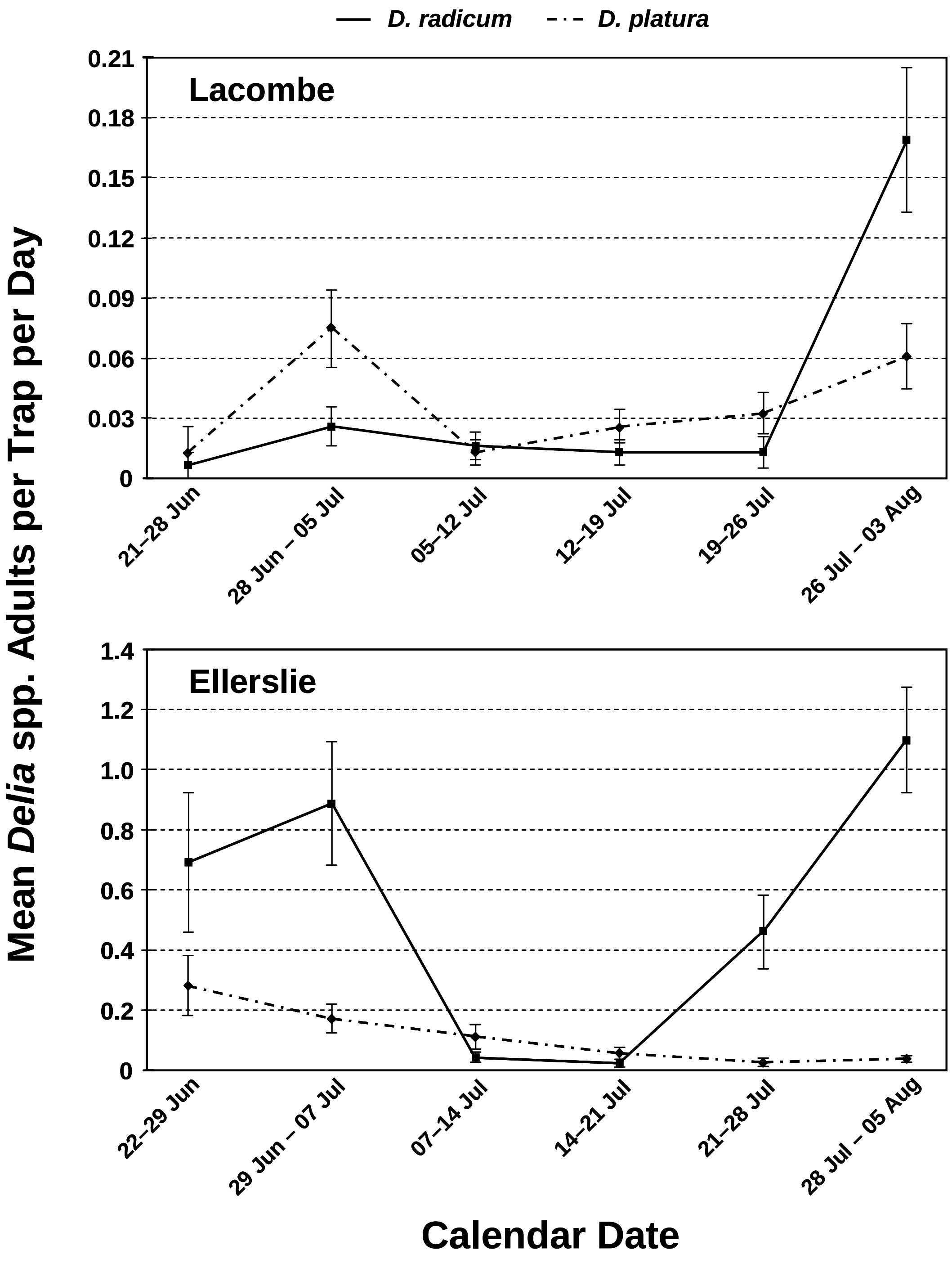

Figure 3.1. Mean and SE adult collections of *Delia radicum* and *Delia platura* per bowl trap per day at Lacombe and Ellerslie, Alberta, in 2005.

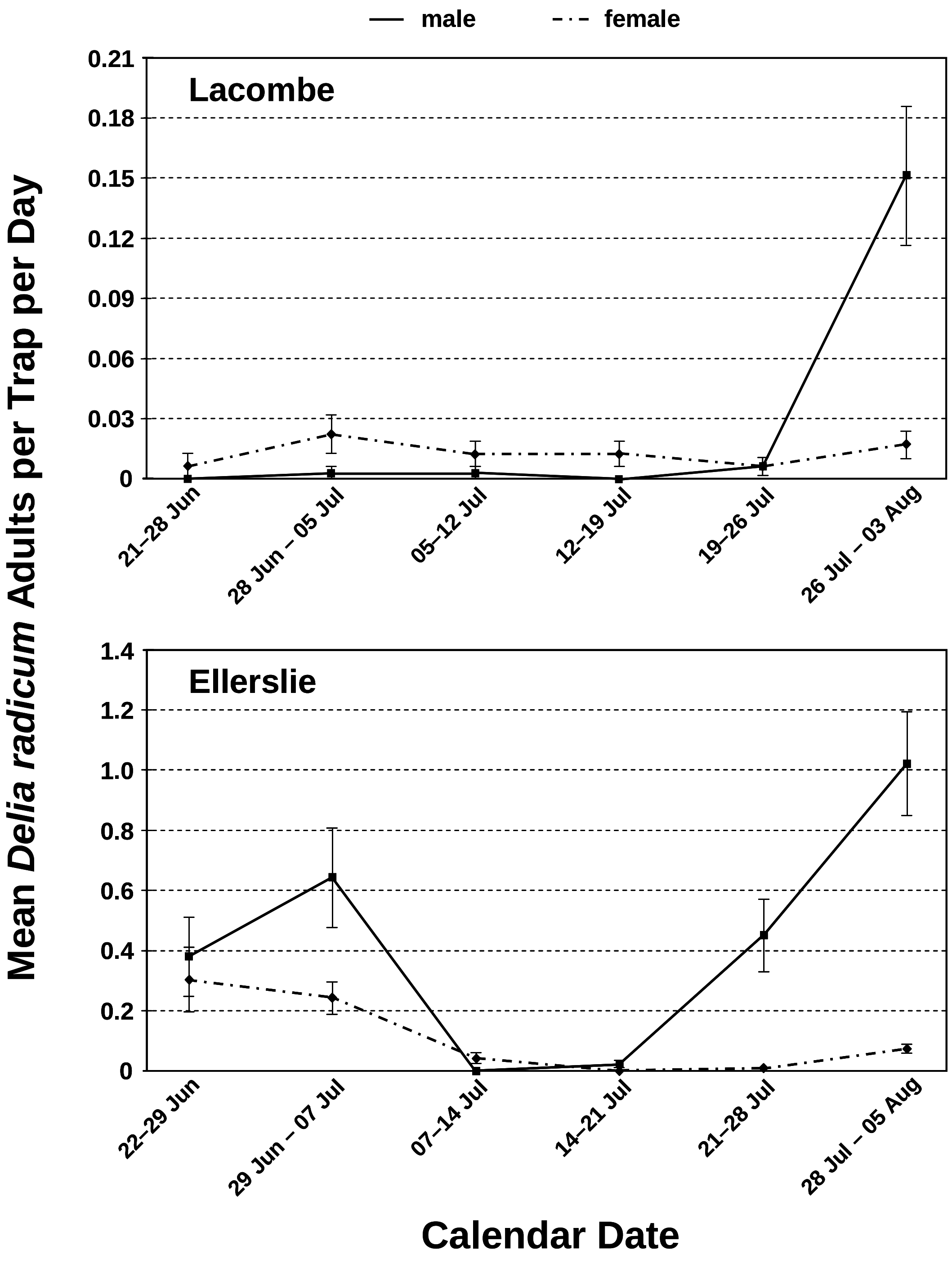

Figure 3.2. Mean and SE adult collections of male and female *Delia radicum* per bowl trap per day at Lacombe and Ellerslie, Alberta, in 2005.

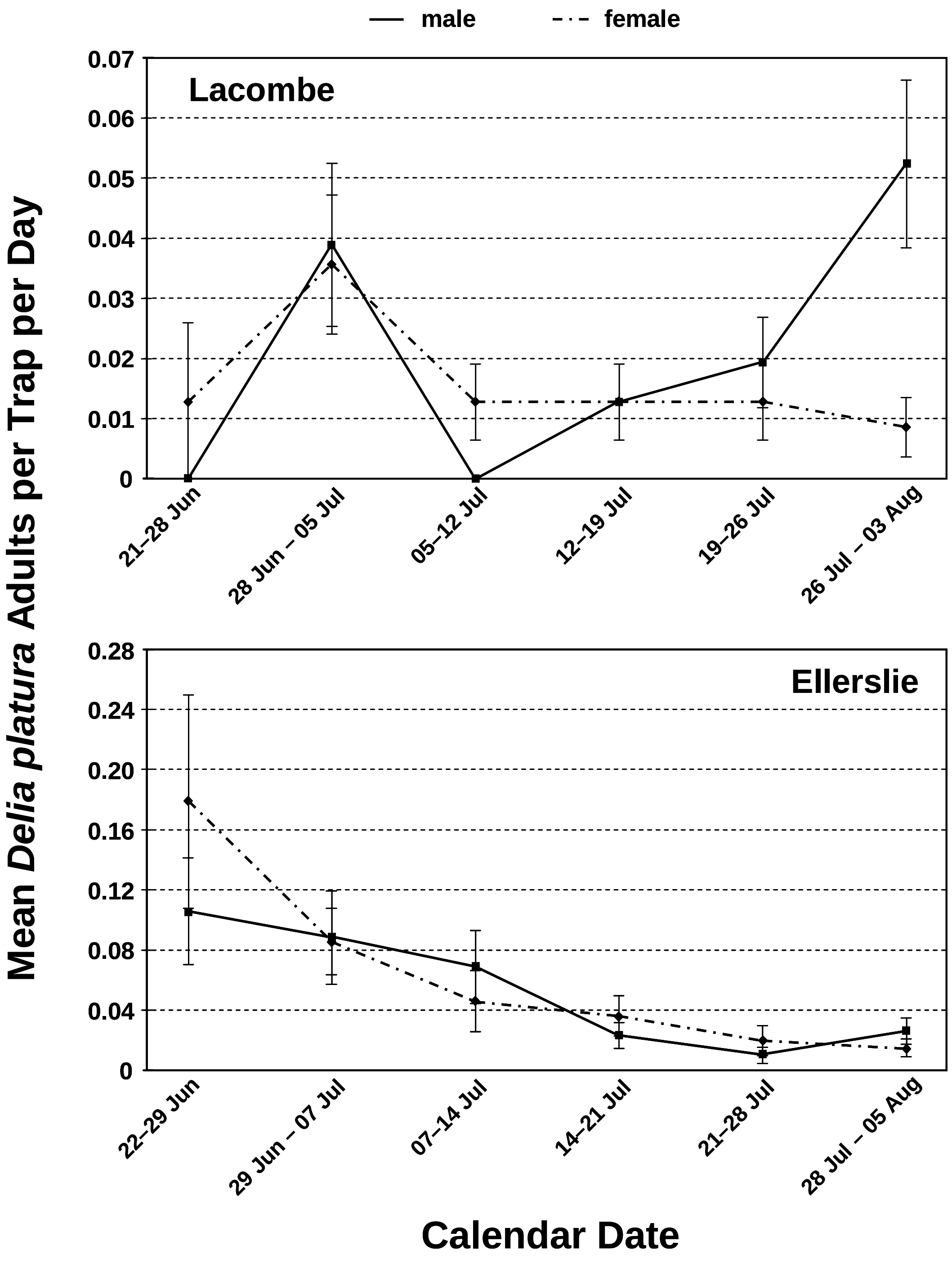

Figure 3.3. Mean and SE adult collections of male and female *Delia platura* per bowl trap per day at Lacombe and Ellerslie, Alberta, in 2005.

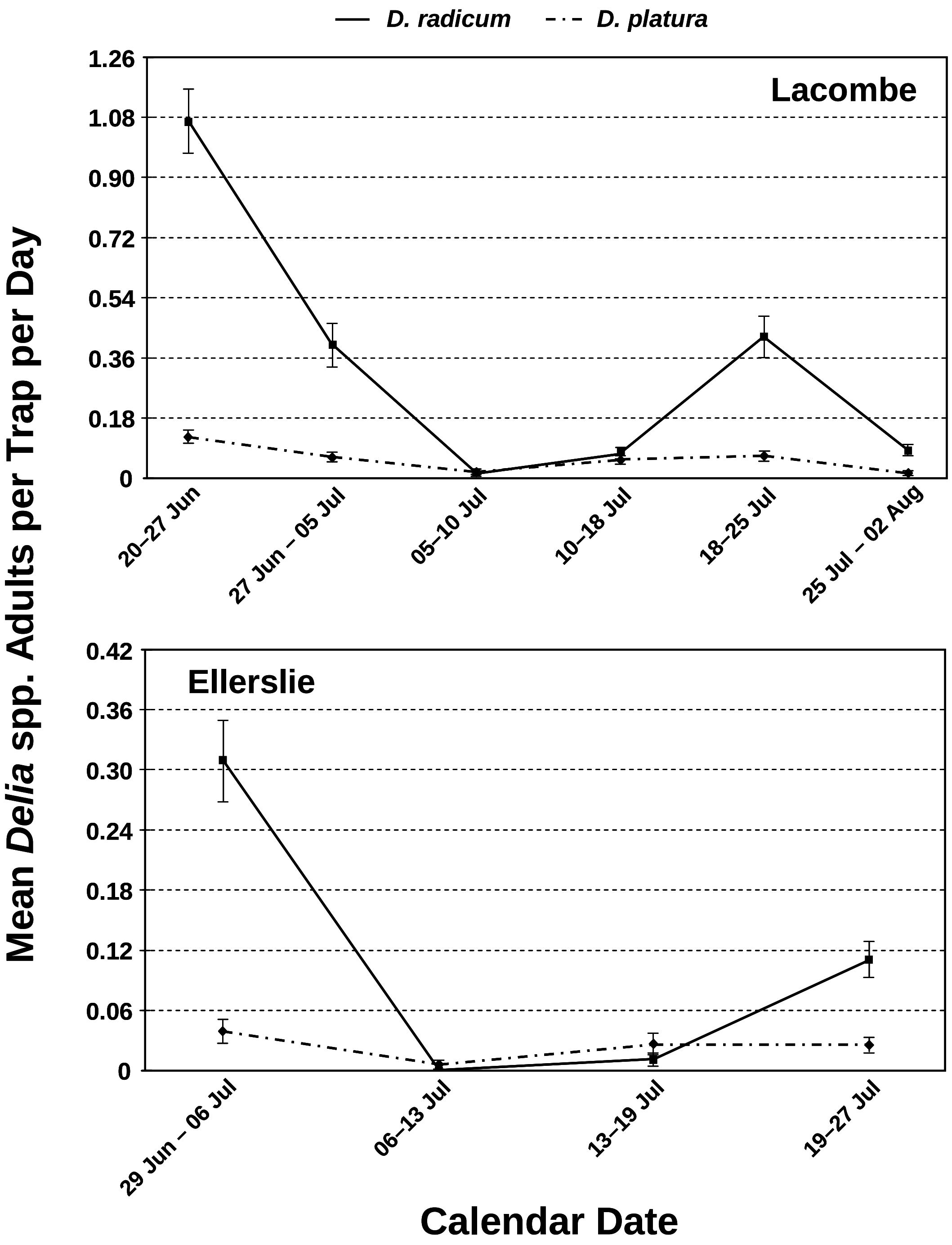

Figure 3.4. Mean and SE adult collections of *Delia radicum* and *Delia platura* per bowl trap per day at Lacombe and Ellerslie, Alberta, in 2006.

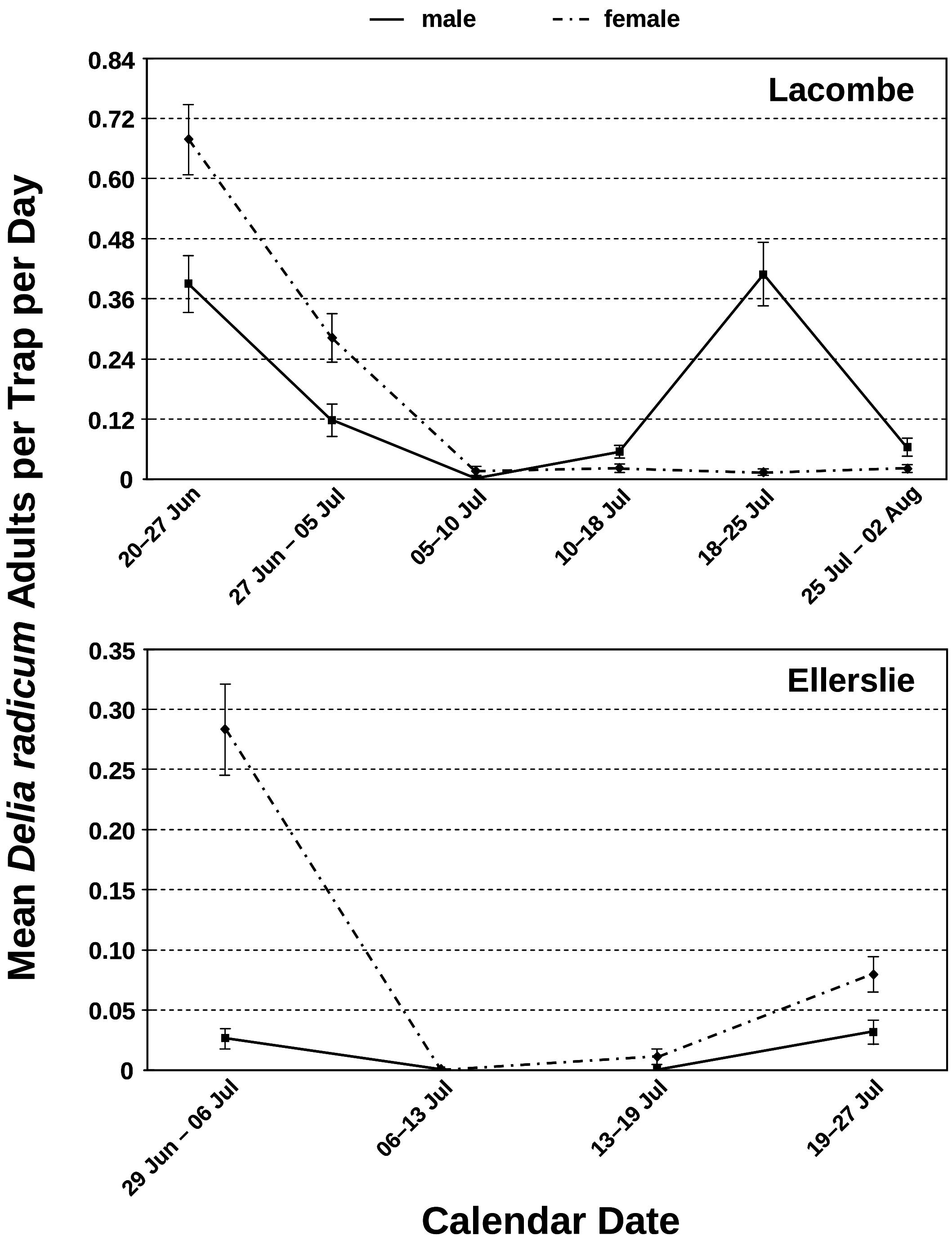

Figure 3.5. Mean and SE adult collections of male and female *Delia radicum* per bowl trap per day at Lacombe and Ellerslie, Alberta, in 2006.

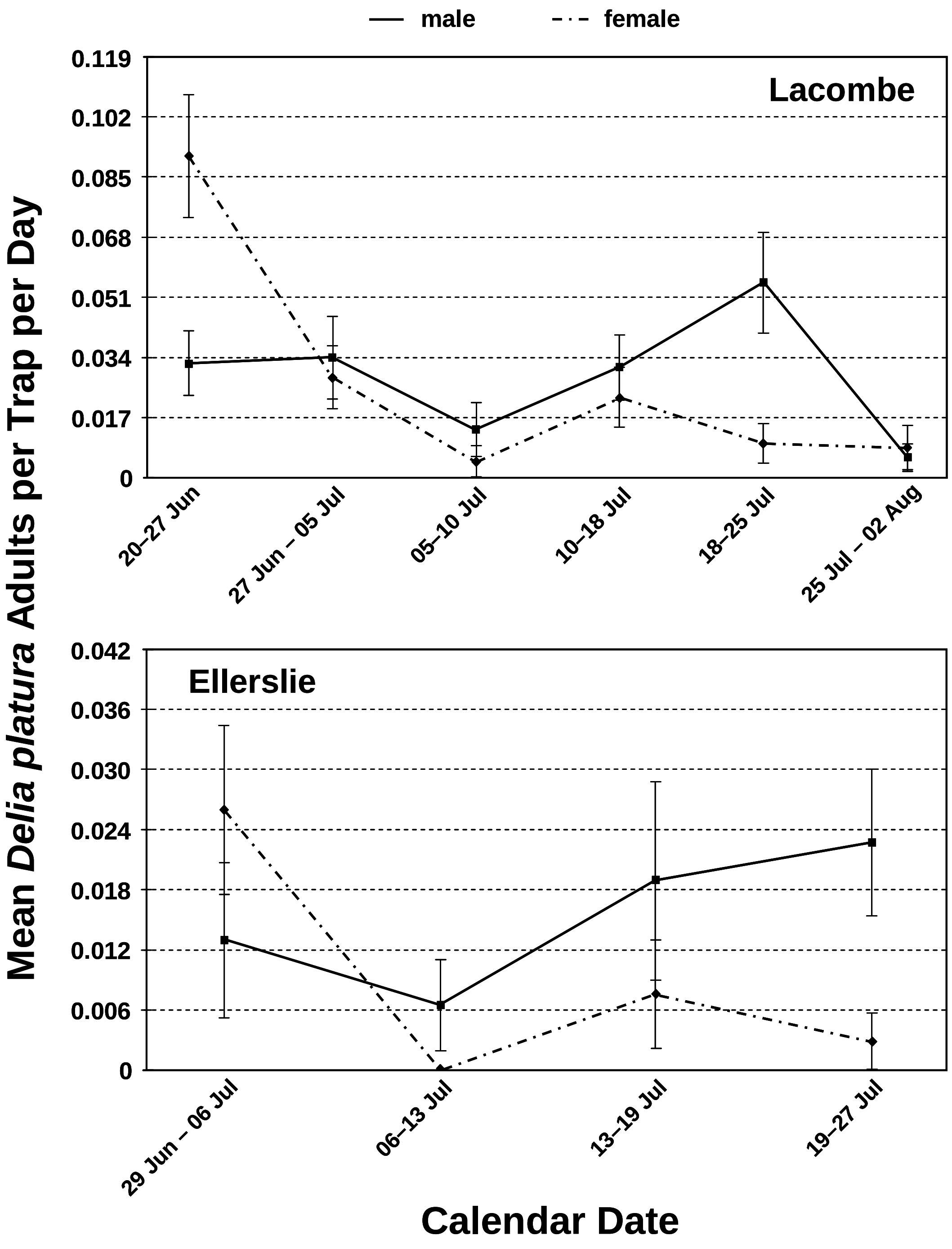

Figure 3.6. Mean and SE adult collections of male and female *Delia platura* per bowl trap per day at Lacombe and Ellerslie, Alberta, in 2006.

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4. Chapter 4 – Ground beetle (Coleoptera: Carabidae) diversity, activity density, and community structure in a diversified agroecosystem

4.1. Introduction

Intercropping is a common practice in small-scale farming in tropical regions (Altieri 1991), and it has gained interest in the larger-scale agricultural production systems of the Northern Great Plains of North America because of the enhanced plant biodiversity of intercrops and their capacity to produce increased yields (Andrews and Kassam 1976; Willey 1979; Fukai and Trenbath 1993) and improved pest limitation (Vandermeer 1989; Altieri 1994) compared to monocultures. Canola (*Brassica napus* L.) and wheat (*Triticum aestivum* L.) are commonly grown in large-scale monocultures in North America; intercrops of the two species have been demonstrated to produce crop yields comparable to those of monocultures (Szumigalski and Van Acker 2005; Hummel et al. 2009a). Intercrops of the two species also limit canola infestation by root maggots (*Delia* spp.) (Diptera: Anthomyiidae) (Hummel et al. 2009b), which are responsible for substantial reductions of canola yield and revenue in western Canada (Griffiths 1991; Soroka et al. 2004).

Carabidae is a species-rich family and is abundant and well-represented in agroecosystems in North America (Goulet 2003). Because of the responsiveness of many carabid species to anthropogenic changes in their environments, they have been promoted as bioindicators (Kromp 1999; Rainio and Niemelä 2003). The biology of many species is relatively well known, and many Canadian species are easily identified using the extensive taxonomic work available (Lindroth 1961-1969), further increasing their indicator value.

Carabids are generally considered to be of benefit in agroecosystems, with many species opportunistic predators on potential agricultural pests (Lindroth 1961-1969; Kromp 1999). Carabids have been shown to feed on juvenile root maggots (Wright et al. 1960; Grafius and Warner 1989; Finch 1996), making them potentially valuable in the control of this canola pest. For example, when carabids were excluded from portions of fields, *Delia radicum* (L.) egg populations were 50% greater than when carabids were not excluded (Wright et al. 1960). In western Canadian crop production, ground beetles have also been demonstrated to prey upon wheat midge, *Sitodiplosis mosellana* (Géhin) (Diptera: Cecidomyiidae) (Floate et al. 1990), and cutworm (Lepidoptera: Noctuidae) (Frank 1971). Although the efficacy of carabids against crop pests has been questioned (Kromp 1999), studies determining that augmented beetle populations result in increased prey removal (Menalled et al. 1999) demonstrate the potential value of carabids for pest control.

Intercrop systems may benefit from increased carabid populations. Studies have generally demonstrated that carabid populations are enhanced in intercrops compared to monocultures (Tukahirwa and Coaker 1982; Kromp 1999), due to increased immigration rates, longer tenures, and decreased emigration from intercropped plots (Perfecto et al. 1986; Cárcamo and Spence 1994). Other studies have demonstrated varied responses by different carabid species to intercrops, with some species being more abundant in intercrops than monocultures (Tonhasca 1993; Armstrong and McKinlay 1997; Dixon et al. 2004). Dixon et al. (2004) suggested that carabid beetles were in part responsible for differential reductions in root maggot juvenile populations between the egg and puparial stages in intercrops versus monocultures of rutabaga, *Brassica napus* L. subsp. *rapifera* Metzg. (Brassicaceae), and white clover, *Trifolium repens* L. (Leguminosae).

In this study, intercropping systems of canola and wheat were investigated to determine effects on the carabid beetle communities found therein and to assess whether differences among carabid communities could be attributable to differences in intercropping regime. Carabid species diversity and individual species activity densities were also investigated to test the hypothesis that carabid beetle diversity and abundance would be enhanced in intercrops compared to monocultures of these two crop species.

4.2. Materials and methods

4.2.1. Site description and experimental design

Field studies were conducted in 2005 and 2006 at Lacombe (52° 28′ N, 113° 44′ W) and Ellerslie, AB (53° 34′ N, 113° 31′ W). Sites were selected to represent agricultural regions in Alberta with differing climates and soil types. At Lacombe, soil was a Typic Haplustol clay loam (43% sand, 21% silt, and 36% clay) with pH 5.9 and 8.2% organic matter. Soil type at Ellerslie was Typic Cryoboroll silty clay loam (6% sand, 56% silt, and 38% clay) with pH 6.0 and 6.1% organic matter.

The experiment was a randomized complete block design with four replications and 11 treatments. Treatments consisted of a monoculture of canola (*B. napus* cv. 45H72) seeded at a target density of 200 plants/m², a monoculture of wheat (*T. aestivum* cv. Imagine) seeded at a target density of 250 plants/m², and intercrops seeded to produce canola:wheat populations of 180:20, 160:40, 140:60, and 120:80 plants/m². Duplicates of the canola monoculture and each of the intercrop treatments were established to include plots with and without a seed treatment of Helix® (containing 10.3% thiamethoxam, 1.24% difenoconazole, 0.39% metalaxyl-M, and 0.135% fludioxonil), a neonicotinoid insecticide designed to systemically reduce herbivory to canola seedlings by flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae). Target plant densities of 200 and 250 plants/m² for canola and wheat monocultures, respectively, were selected because these densities compete well against weeds such as tartary buckwheat (*Fagopyrum tataricum* L. J. Gaertn.) and volunteer cereals (O'Donovan et al. 1988, 1989; O'Donovan 1994) and are optimal for limiting infestations of some insect pests (Dosdall et al. 1996, 1999). Treatment plots measured 7.3 by 15.2 m, with 30-cm row spacings.

In each site-year, plots were seeded into wheat stubble in mid to late May using a Conserva Pak® drill. Sites were fertilized following soil test recommendations for canola production, with fertilizer cross-banded prior to seeding (same day). This allowed both crop species to be seeded simultaneously, with wheat side-banded immediately next to canola seed rows. Crop plant counts were taken from four randomly selected 1-m lengths of crop row per plot at the cotyledon to 1-leaf stage of canola development to determine actual crop density.

The canola and wheat cultivars were Clearfield® varieties, tolerant to imidazolinone herbicides. This allowed for equivalent control of most weeds in both crops. A commercial formulation of imazomox+imazethapyr herbicide at 30 g AI/ha was applied at the two-leaf stage of canola in all plots.

4.2.2. Carabid collections

Adult carabid beetles were collected in pitfall traps at Lacombe and Ellerslie in 2005 and 2006. Two traps were established per plot and sampled weekly from late June, when the canola was between the 4-leaf and rosette stages of development, to harvest. Collected material was stored in 90% ethanol. Each trap consisted of a sleeve (a 0.5-L plastic cup dug into the ground below the soil surface) and a collection cup (a 0.5-L cup placed into the first so that it was level with the soil surface). The collection cup was half-filled with propylene glycol, and the preservative was changed during sampling. A cover over each trap, consisting of a plastic plate elevated above the soil, reduced evaporation of the preservative, prevented leaves or other debris from entering the trap, and deterred scavenging by birds.

Carabid beetles were sorted from pitfall trap samples and determined to species using Lindroth (1961-1969). Species that could not be reliably identified morphologically were placed into groups for analyses: the *Amara carinata* (LeConte) group also included *Amara lacustris* LeConte and *Amara torrida* (Panzer), and the *Harpalus funerarius* Mannerheim group also included *Harpalus fraternus* LeConte. Representative specimen identifications were validated by D. Shpeley (University of Alberta, Edmonton, AB). Voucher specimens from the study have been deposited in the Strickland Museum of Entomology, University of Alberta, Edmonton, AB, and at the Agriculture and Agri-Food Canada Research Centre in Lacombe, AB.

4.2.3. Data analysis

Prior to statistical analyses of carabid beetle trap capture data, collections for each species from the two traps per plot on each sampling date were standardized for trapping effort by dividing the number of specimens captured for each species by the number of days each trap was active during the sampling period. Total per trap per day collection rates over the entire season were then determined by pooling the catch rates per plot for each sampling period and dividing by the number of sampling periods in the season. This standardization corrected raw collection numbers for the occasional flooded or debris-filled trap that was not sampled during a particular sampling period.

Carabid diversity in replicate plots was determined by calculating the Shannon-Weiner diversity index (H') (Krebs 1989), which is a composite measure of species richness and evenness. Species richness indicates the number of species collected from a replicate plot. Species evenness (J') indicates the equitability of collections of the various species in a replicate plot. The Shannon-Weiner index and species evenness were calculated using:

$$H' = -\Sigma (p_i \times \ln(p_i))$$

where p_i is the proportion of the carabid collection comprised by the i^{th} species, and

$$J' = H' / \ln(N)$$

Treatment effects for carabid diversity were determined by analysis of variance (ANOVA) using the MIXED procedure of SAS (SAS Institute 2004). The proportion of canola comprising total crop plant populations was included as a covariable because actual plant populations did not always correspond well with target plant proportions. Regression analysis was therefore more appropriate for determining the effects of the different intercropping regimes than were the distinct intercropping treatments described above, and therefore the inclusion of the proportion canola covariable allowed the investigation of this continuous variable along with the discrete variables of crop type (canola monoculture vs. wheat monoculture vs. intercrop), seed treatment, block, and site-year, where appropriate. Block was included as a random effect. Analyses were also performed on diversity data pooled over sites and years, with site-year (combination of site and year) as a random effect.

Treatment effects for individual species activity densities were determined by ANOVA using the MIXED procedure of SAS (SAS Institute 2004). Activity density is commonly used to assess carabid populations because it considers both the density of a carabid population and the activity or trappablity of that species (Luff 1987; Kromp 1999). The numerically dominant species comprising 90% of the total collection at Lacombe in 2005 and 2006 and Ellerslie in 2005 were used in the analyses of data from those site-years. Numerically dominant species comprising 95% of the collection were used for Ellersie, 2006, because *Pterostichus melanarius* (Illiger) comprised a high proportion of the total collection in that site-year. Fixed and random factors investigated followed those used in analyses of carabid diversity, described above. Individual differences among activity density means for canola and wheat monocultures and intercrops were determined using Tukey-adjusted LSMEANS. Effects were considered significant at $P \leq 0.05$.

Analyses of carabid communities were conducted using multi-response permutation procedures (MRPP) in PC-ORD (McCune and Mefford 2006). MRPP, a non-parametric equivalent of MANOVA, was used to determine whether replicate plots within a treatment were homogenous with regard to carabid communities collected therein (A value), and whether treatments differed from one another (T value). A-values more closely approaching 1.0 indicate greater homogeneity within groups (treatments), and a more negative T-value indicates greater separation between treatments with regard to beetle community (McCune and Grace 2002). Individual differences between treatments were investigated using pair-wise comparisons in the MRPP procedure. Results of MRPP analyses were considered significant at $P \leq 0.05$. Treatments used in carabid community data analyses consisted of replicate plots grouped on the basis of real plant density data collected in this study rather than on the prescribed intercropping treatments described above. Treatment groups consisted of plots with real plant populations approximating proportions of canola of 100, 90, 80, 70, 60, and at Lacombe in 2006, 50 ± 5%.

Carabid communities were also analyzed with the non-metric multidimensional scaling (NMDS) analysis of PC-ORD (McCune and Mefford 2006), using Sorensen (Bray-Curtis) distances. NMDS provides a graphical representation of the dissimilarities between carabid communities in different replicate plots and is well suited to ecological data, which may not meet the assumptions of normality (McCune and Grace 2002). A greater distance between two points on the NMDS graph indicates a greater dissimilarity between the carabid communities collected in those plots. A step-down approach was used to determine the appropriate number of dimensions for the final ordination, which was selected when the stress did not decrease by greater than 5 and a Monte Carlo probability test indicated significance at $P \leq 0.05$, that is, when ordination stress differed from random. Stress in NMDS indicates the distortion of the graphical representation from the positions of real data points, with low stress indicative of a more accurate representation of the dissimilarities among species compositions in the replicate plots.

4.3. Results

4.3.1. Carabid fauna

At Lacombe in 2005, 3859 specimens were collected between 5 July and 22 August, representing 37 species in 14 genera (Table 4.1). In 2006, 11,432 specimens were collected from Lacombe between 13 June and 15 August, representing 49 species in 14 genera. At Ellerslie in 2005, 6235 specimens from 41 species in 15 genera were collected between 1 July and 26 August, and in 2006, 19,579 specimens representing 33 species in 13 genera were collected between 22 June and 18 August. In all site-years, *P. melanarius* was the most abundant species collected, comprising 45.5 and 59.2 % of the total collection at Lacombe in 2005 and 2006, and 41.4 and 86.3 % at Ellerslie in 2005 and 2006, respectively. At Lacombe, other species commonly collected were *Agonum placidum* (Say), members of the *A. carinata* group, *Amara quenseli* (Schönherr), and *Bembidion rupicola* (Kirby). At Ellerslie, other commonly collected species included *A. placidum*, *Bembidion quadrimaculatum* (L.), *B. rupicola*, and *Poecilus lucublandus* (Say).

4.3.2. Carabid beetle diversity

Ground beetle species diversity was generally not affected by intercropping of canola and wheat. However, increased species evenness at Ellerslie in 2005 in intercrops with greater proportions of wheat ($F = 12.04$; df = 1, 78; $P = 0.0009$) resulted in a similar response by overall species diversity (H') ($F = 9.03$; df = 1, 78; $P = 0.0036$) (Fig. 4.1). Species richness was not affected by intercropping in any site-by-year combination ($P > 0.05$). Differences among means for canola monocultures, wheat monocultures, or intercrops were observed for diversity measures at Ellerslie in 2005 (Fig. 4.1), but not in other site-years. Carabid species diversity (H'), richness, and evenness did not respond to the canola seed treatment factor ($P > 0.05$), with means for treated and untreated plots similar. In the combined data, diversity was not affected by treatment factors ($P > 0.05$).

4.3.3. Species activity densities

Although carabid species activity density responses were often detected between pairs of means for the different crop types investigated in this study (canola monoculture, n=16; wheat monoculture, n=8; intercrop, n=64) (Table 4.2), the overall effect of cropping treatment was often not significant. Significant effects of crop type were observed for the *A. carinata* group at Lacombe in 2005 ($F = 4.17$; df = 1, 78; $P = 0.0446$) and for *A. quenseli* at Lacombe in 2006 ($F = 4.74$; df = 1, 78; $P = 0.0326$). Crop type also significantly affected activity densities of *A. placidum* ($F = 9.44$; df = 1, 78; $P = 0.0029$) and *C. fossor* ($F = 7.27$; df = 1, 78; $P = 0.0086$) at Lacombe in 2005, but pairwise comparisons did not identify additional significant differences between means of different treatments for these species. Significant interactions between crop type and seed treatment were detected for the activity densities of several species at Lacombe in 2005 (*P. melanarius*: $F = 4.61$, df = 1, 78, $P = 0.0349$; *A. placidum*: $F = 4.12$, df = 1, 78, $P = 0.0459$; *C. fossor*: $F = 8.69$, df = 1, 78, $P = 0.0042$; total carabid collection: $F = 8.15$, df = 1, 78, $P = 0.0055$) and 2006 (*A. quenseli*: $F = 4.79$; df = 1, 78; $P = 0.0316$). Among pairwise comparisons of crop type, individual species responses sometimes varied among site-years (Table 4.2).

The proportion of the total crop plant population comprised of canola affected activity densities for some species, but significant effects were not consistent among site-years (Table 4.2). For example, *A. placidum* activity density increased with increasing proportions of canola at Lacombe in 2005 (F = 5.12; df = 1, 78; P = 0.0264) but decreased at Lacombe in 2006 (F = 5.14; df = 1, 78; P = 0.0262). Activity densities of *P. melanarius* and the total carabid collection at Ellerslie in 2005 also increased with increasing proportions of canola (F = 9.27, df = 1, 78, P = 0.0032; F = 6.96, df = 1, 78, P = 0.0100, respectively). By contrast, activity density of *C. fossor* at Lacombe in 2005 decreased with increasing proportions of canola comprising total crop plant populations (F = 5.42; df = 1, 78; P = 0.0225), and a marginally non-significant negative effect of increasing canola in intercrops was detected for *B. quadrimaculatum* at Ellerslie in 2005 (F = 3.63; df = 1, 78; P = 0.0606). Canola proportions interacted with canola seed treatment for *C. fossor* (F = 11.42; df = 1, 78; P = 0.0011) and the total carabid collection (F = 4.23; df = 1, 78; P = 0.0431) at Lacombe in 2005 and for *A. placidum* (F = 4.72; df = 1, 78; P = 0.0431) at Lacombe in 2006.

Inclusion of an insecticidal seed treatment did not significantly affect the activity densities of the numerically dominant carabid species or total carabid activity density in any site-year in comparisons of means of treated and untreated plots (P > 0.05).

4.3.4. Carabid community structure

Cropping treatment significantly influenced carabid community composition only at Ellerslie in 2005. Results of MRPP (A = 0.0407; T = -1.8298; P = 0.0490) indicated high heterogeneity within groups but a significant separation between groups. Pair-wise comparisons revealed that carabid communities in wheat monocultures were significantly different from those of canola monocultures (A = 0.0846; T = -2.2365; P = 0.0369) and intercrops having canola crop plant proportions approximating 90 (A = 0.1310; T = -4.5457; P = 0.0015) and 80% (A = 0.0912; T = -2.4483; P = 0.0277). The carabid communities of intercrops comprised of approximately 90% canola also differed significantly from those with 60% canola (A = 0.0765; T = -3.0059; *P* = 0.0117). When carabid community structure was represented graphically using NMDS ordination (Fig. 4.2; Table 4.3), there appeared to be a shift in the carabid communities of the intercropping treatments to become more similar to those of wheat monocultures as the proportion of wheat in the intercrops increased.

Although differences among treatments were not observed in analyses of community data in the other site-years (MRPP, *P* > 0.05), some pair-wise comparisons between treatments at Lacombe in 2005 and Ellerslie in 2006 did indicate significant differences between individual treatments. At Lacombe in 2005, 60, 70, and 80% canola intercrops differed from the wheat monocultures (A = 0.1565, T = -3.3632, *P* = 0.0071; A = 0.0652, T = -2.6037, *P* = 0.0175; A = 0.0555, T = -2.2744, *P* = 0.0291, respectively). Carabid species composition of 80% canola intercrops also differed from that of wheat monocultures at Ellerslie in 2006 (A = 0.1436; T = -2.9204; *P* = 0.0167).

4.4. Discussion

Agroecosystem diversification has been promoted as a means of enhancing ground beetle diversity, activity density, and insect pest reduction due to increased predation. Methods of diversification that may increase carabid populations or enhance their beneficial effects include the establishment of refuge habitats such as hedgerows or grassy strips around or within fields (Carmona and Landis 1999; Fournier and Loreau 1999; Lee et al. 2001; Menalled et al. 2001) and plant diversification through limited weed retention, the use of cover crops, or the establishment of intercropping systems (Speight and Lawton 1976; Tukahirwa and Coaker 1982; Brust et al. 1986; Kromp 1999; Haggenstaller et al. 2006). In only one site-year carabid species diversity increased as intercrops became more diverse. Ground beetle responses to crop diversification are mediated not only by the richness and evenness of plant diversity in a crop but also by the structure and extent of the canopy (Letourneau 1990; Booij and Noorlander 1992; Cárcamo and Spence 1994) and by soil conditions and other biotic and abiotic factors not investigated in this study (Thiele 1977; Kromp 1999). These factors may have had greater effects on species diversity than did enhanced vegetational diversity through intercropping.

Responses of beetle activity densities to crop type and crop plant proportions in intercrops varied among species and site-years but were often reflective of the preferences of different carabid species for type or extent of ground cover. Ground cover influences soil moisture, temperature, light penetration through the canopy, and other microhabitat conditions (Honek 1997; Kromp 1999) to which carabids respond. For example, *B. quadrimaculatum* is typically abundant in open places with sparse ground cover (Lindroth 1961-1969). In my study, *B. quadrimaculatum* tended to favor wheat monocultures and some high-wheat intercrops, the canopies of which are usually more open than canola canopies. Members of the *A. carinata* group (*A. carinata*, *A. lacustris*, and *A. torrida*), *A. placidum*, and *P. lucublandus* generally also prefer open ground (Lindroth 1961-1969), and these preferences were demonstrated in the observed activity densities of these species in my study. When significant differences between crop types were observed for *P. melanarius*, this species was collected in greater numbers under the more closed canopies of canola monocultures and intercrops with a high proportion of canola. Studies have found that *P. melanarius* is either unresponsive to cropping factors (Clark et al. 1997) or is captured more frequently under largely enclosed, shady canopies (Cárcamo and Spence 1994; Armstrong and McKinlay 1997; Dixon et al. 2004).

Pterostichus melanarius was the most abundant species collected in all site-years of my study. Prasad and Snyder (2004) demonstrated that the generalist predatory behaviour of this species allowed it to prey even upon other carabid beetles, including species in the genera *Amara* and *Bembidion*. Increased abundance of *P. melanarius* was also observed to reduce the activity densities of smaller beetles by causing them to forage less when the larger predator was present (Prasad and Snyder 2004, 2006a). Similarly, activity density responses of other carabid species to treatment factors in my study may also have been influenced by the greater abundance of *P. melanarius* in some plots than others.

Many carabid species are often abundant on agricultural land, and some of these prey, at least in part, upon crop pests. For example, *B. quadrimaculatum* and some other Carabidae can serve as predators of the eggs of root maggots (Wishart et al. 1956; Wright et al. 1960; Coaker and Williams 1963; Grafius and Warner 1989; Finch 1996). Egg predation constitutes only part of the effect ground beetles may have on root maggot juvenile populations, and studies have demonstrated enhanced larval or puparial removal and decreased crop damage in the presence of greater carabid populations (Wright et al. 1960; Menalled et al. 1999). Some Carabidae that are ineffective predators of *Delia* eggs, including large species such as *P. melanarius* (Finch 1996; Prasad and Snyder 2004), may predate root maggot larvae or puparia.

Using the same experimental plots investigated in this study, Hummel et al. (2009b) found that although per plant *Delia* egg populations were the same regardless of the proportion of canola, taproot damage was reduced when proportions of wheat increased. The authors suggested that this discrepancy was likely due to differential juvenile root maggot mortality between the canola monocultures and intercrops of canola and wheat (Hummel et al. 2009b). Such differential mortality could result from abiotic factors or from biotic factors such as differences in predator abundance and predation rates among canola-wheat combinations. My study demonstrates that some small to medium-sized carabid beetles, including *B. quadrimaculatum*, tended to have higher activity densities in wheat monocultures and intercrops with higher proportions of wheat. Because prey removal was not investigated in this study, the interaction between increased predator activity densities and reduced canola taproot damage by *Delia* in the more diverse intercrops cannot be determined. However, my results and those of Hummel et al. (2009b) suggest a possible differential effect by predators on the survival of juvenile *Delia* spp. depending on the composition of the crop. Dixon et al. (2004) determined that potential egg predators of *Delia* were more abundant in rutabaga monocultures than in rutabaga plots undersown with white clover, and that the open-canopy monocultures experienced greater reductions in *Delia* juvenile populations between the egg and puparium stages than did the undersown plots with more dense ground cover, in which *P. melanarius* was more abundant.

Neonicotinoid canola seed treatments have the potential for effects on some non-target soil organisms including ground beetles, particularly those that might feed upon treated canola seed or seedlings, such as *Amara* and *Harpalus* spp. that are predominantly seed-feeding herbivores (Lindroth 1961-1969). Interactions between seed treatment and crop type indicated that the activity densities of some carabid species were reduced in canola monocultures compared to intercrops in treated versus untreated plots (data not shown), but the reasons are not readily apparent. It is possible that the seed treatment influenced the abundance of potential prey for the affected carabid species, with prey less abundant in canola monocultures than intercrops because of the greater proportion of the total crop plant population comprised by treated plants. However, seed treatment with thiamethoxam did not reduce mean activity densities of any of the numerically dominant species, nor did seed treatment influence carabid beetle diversity in my study.

In only one site-year, carabid community data demonstrated a shift along the intercrop plant proportion gradient, such that as intercrop proportions of wheat increased, carabid assemblages became increasingly similar to those found in wheat monocultures. This general lack of a response in my study is somewhat surprising. At Ellerslie in 2006, the considerable dominance of *P. melanarius* in pitfall trap collections appeared to mask the response of the rest of the carabid community. *Pterostichus melanarius* did not respond to intercropping in that site-year but instead appeared to immigrate in large numbers from surrounding farmland, causing much higher numbers to be collected from peripheral replicate plots and blocks than those in the centre of the study area (Hummel, unpublished data). This dominant influence of *P. melanarius* resulted in an NMDS ordination for Ellerslie 2006 mainly aligned along a single axis (Table 4.3) and demonstrating no response to the intercrop treatments.

My study of carabid activity density and community data demonstrates that, although responses by individual species and species assemblages were sometimes observed, the canola-wheat intercropping regimes investigated did not generally affect carabid beetle populations. One potential benefit of intercropping is enhanced pest control through the presence of greater populations of natural enemies (Root 1973; Trenbath 1993), but this seems unlikely in canola-wheat intercrops with respect to predation by polyphagous ground beetles given my results. Although predator searching, which was not investigated in this study, may be affected by the intercrops, it is encouraging that activity densities of most carabids, including some known predators of canola pests, were not reduced in intercrops, and therefore potential predation compared to monocultures may also be similar between the two systems. Also, my study provides evidence that the diversity of Carabidae can sometimes be enhanced by intercropping canola with wheat compared to canola monocropping. These results are already of value to organic or low-input producers seeking enhanced on-farm diversity and alternative methods of pest control; however, further investigation of other parameters is needed to determine whether intercrops of canola and wheat can provide a management option that allows conventional producers in western Canada to produce acceptable canola crops while maximizing environmental sustainability.

Table 4.1. Carabid species count (C) and frequency (F) (percent of total carabid capture per site-year) from pitfall trap collections at Lacombe and Ellerslie, Alberta in 2005 and 2006.

	Lacombe				**Ellerslie**			
	2005		**2006**		**2005**		**2006**	
Carabid Species	**C**	**F**	**C**	**F**	**C**	**F**	**C**	**F**
Pterostichus melanarius (Illiger)	1755	45.48	6772	59.24	2584	41.44	16901	86.32
Agonum placidum (Say)	305	7.90	2014	17.62	2023	32.45	433	2.21
Amara torrida (Panzer)	401	10.39	335	2.93	248	3.98	121	0.62
Bembidion quadrimaculatum (L.)	12	0.31	19	0.17	522	8.37	263	1.34
Bembidion rupicola (Kirby)	118	3.06	261	2.28	151	2.42	262	1.34
Carabus granulatus L.	38	0.98	382	3.34	40	0.64	209	1.07
Agonum cupreum Dejean	254	6.58	86	0.75	176	2.82	68	0.35
Poecilus lucublandus (Say)	6	0.16	7	0.06	141	2.26	421	2.15
Clivina fossor (L.)	254	6.58	179	1.57	17	0.27	109	0.56
Amara quenseli (Schönherr)	152	3.94	277	2.42	16	0.26	41	0.21
Amara spp.	68	1.76	288	2.52	6	0.10	117	0.60
Amara littoralis Mannerheim	53	1.37	196	1.71	15	0.24	40	0.20
Pterostichus adstrictus Eschscholtz	17	0.44	74	0.65	20	0.32	172	0.88
Notiophilus aquaticus (L.)	22	0.57	38	0.33	44	0.71	138	0.70
Harpalus spp.	60	1.56	76	0.66	8	0.13	66	0.34
Bembidion bimaculatum (Kirby)	31	0.80	115	1.01	4	0.06	40	0.20
Amara lacustris LeConte	115	2.98	49	0.43	6	0.10	9	0.05
Amara obesa (Say)	23	0.60	5	0.04	67	1.07	25	0.13
Amara latior (Kirby)	57	1.48	18	0.16	17	0.27	19	0.10
Amara apricaria (Paykull)	23	0.60	25	0.22	11	0.18	11	0.06
Calosoma calidum (Fabricius)	3	0.08	8	0.07	26	0.42	22	0.11
Amara carinata (LeConte)	32	0.83	16	0.14	6	0.10	4	0.02
Amara avida Say	9	0.23	17	0.15	1	0.02	22	0.11
Amara farcta LeConte	—	—	40	0.35	—	—	—	—
Harpalus amputatus Say	—	—	28	0.24	2	0.03	8	0.04
Unidentified Carabidae	6	0.16	5	0.04	—	—	17	0.09
Harpalus affinis (Schrank)	1	0.03	22	0.19	—	—	—	—
Agonum spp.	7	0.18	5	0.04	5	0.08	6	0.03
Calathus ingratus Dejean	7	0.18	8	0.07	4	0.06	2	0.01
Agonum corvus (LeConte)	2	0.05	8	0.07	8	0.13	1	0.01
Carabus serratus Say	—	—	1	0.01	8	0.13	10	0.05
Bembidion mutatum Gem. & Harold	—	—	1	0.01	14	0.22	1	0.01
Cymindus cribricollis Dejean	8	0.21	—	—	6	0.10	2	0.01
Dyschirius globulosus (Say)	—	—	—	—	15	0.24	—	—
Harpalus funerarius Mannerheim	1	0.03	15	0.13	1	0.02	—	—
Bembidion spp.	1	0.03	2	0.02	1	0.02	9	0.05
Harpalus pleuriticus Kirby	2	0.05	4	0.03	3	0.05	—	—
Harpalus fuscipalpus Sturm	—	—	3	0.03	3	0.05	—	—
Harpalus opacipennis (Haldeman)	2	0.05	3	0.03	1	0.02	—	—
Poecilus corvus (LeConte)	—	—	1	0.01	—	—	5	0.03
Calathus advena (LeConte)	2	0.05	2	0.02	1	0.02	—	—
Harpalus paratus Casey	2	0.05	3	0.03	—	—	—	—
Patrobus lecontei Chaudoir	3	0.08	—	—	—	—	2	0.01
Agonum sordens Kirby	1	0.03	2	0.02	—	—	1	0.01
Harpalus carbonatus LeConte	—	—	4	0.03	—	—	—	—
Loricera pilicornis (Fabricius)	—	—	4	0.04	—	—	—	—
Cymindus borealis LeConte	1	0.03	—	—	2	0.03	—	—
Agonum gratiosum (Mannerheim)	—	—	—	—	2	0.03	—	—

Amara cupreolata Putzeys	—	—	—	—	1	0.02	1	0.01
Bembidion nitidum (Kirby)	—	—	1	0.01	1	0.02	—	—
Bembidion sordidum (Kirby)	1	0.03	1	0.01	—	—	—	—
Carabus taedatus Fabricius	—	—	—	—	2	0.03	—	—
Harpalus fraternus LeConte	—	—	2	0.02	—	—	—	—
Patrobus septentrionis Dejean	2	0.05	—	—	—	—	—	—
Pterostichus riparius (Dejean)	1	0.03	1	0.01	—	—	—	—
Amara ellipsis (Casey)	—	—	—	—	—	—	1	0.01
Agonum ferruginosum (Dejean)	—	—	1	0.01	—	—	—	—
Amara confusa LeConte	—	—	1	0.01	—	—	—	—
Amara familiaris (Duftschmid)	—	—	1	0.01	—	—	—	—
Amara patruelis Dejean	—	—	1	0.01	—	—	—	—
Bembidion coloradense Hayward	—	—	1	0.01	—	—	—	—
Carabus maeander Fischer	—	—	1	0.01	—	—	—	—
Chlaenius alternatus Horn	—	—	1	0.01	—	—	—	—
Chlaenius sericeus (Forster)	1	0.03	—	—	—	—	—	—
Cymindus planipennis LeConte	—	—	—	—	1	0.02	—	—
Dicheirotrichus cognatus (Gyllenhal)	—	—	—	—	1	0.02	—	—
Diplocheila striatopunctata (LeConte)	—	—	1	0.01	—	—	—	—
Harpalus desertus LeConte	—	—	1	0.01	—	—	—	—
Harpalus somnulentus Dejean	—	—	—	—	1	0.02	—	—
Platynus decentis (Say)	—	—	—	—	1	0.02	—	—
Total	3859		11431		6235		19579	

Two pitfall traps were established in each of 44 experimental plots at each site; plots measured 7.3 by 15.2 m. Traps were sampled weekly at Lacombe from 5 July to 22 August in 2005 and 13 June to 15 August in 2006, and at Ellerslie from 1 July to 26 August in 2005 and 22 June to 18 August in 2006.

Table 4.2. Mean and SE activity densities (specimens/trap/day) and slope coefficients (proportion canola comprising total crop plant population) for the most abundant carabid species in monoculture and intercropping treatments at Lacombe and Ellerslie, AB, in 2005 and 2006.

	Cropping treatment			
Site-year **Carabid Species**	**Canola monoculture**	**Wheat monoculture**	**Intercrop**	**Slope coefficient**
Lacombe, 2005				
P. melanarius	0.481 ± 0.064 a	0.259 ± 0.047 b	0.427 ± 0.025 a	-0.00337
A. carinata group	0.090 ± 0.023 a	0.082 ± 0.028 ab	0.161 ± 0.015 b	-0.00143
A. placidum	0.050 ± 0.013	0.049 ± 0.011	0.079 ± 0.007	**0.00047**
A. cupreum	0.054 ± 0.017 ab	0.008 ± 0.004 a	0.067 ± 0.008 b	-0.00005
C. fossor	0.043 ± 0.015	0.082 ± 0.021	0.062 ± 0.009	**-0.00085**
A. quenseli	0.045 ± 0.012	0.025 ± 0.013	0.036 ± 0.004	-0.00033
B. rupicola	0.062 ± 0.028 a	0.012 ± 0.005 ab	0.022 ± 0.004 b	0.00008
A. littoralis	0.012 ± 0.005	—	0.014 ± 0.002	0.00024
Total carabids	0.958 ± 0.094 a	0.600 ± 0.081 b	0.973 ± 0.038 a	-0.00691
Lacombe, 2006				
P. melanarius	1.138 ± 0.205	1.433 ± 0.253	1.291 ± 0.069	0.00387
A. placidum	0.274 ± 0.032 a	0.393 ± 0.051 ab	0.394 ± 0.021 b	**-0.00587**
C. granulatus	0.076 ± 0.016	0.053 ± 0.010	0.070 ± 0.005	0.00057
A. carinata group	0.041 ± 0.008 a	0.213 ± 0.047 b	0.059 ± 0.005 a	0.00003
A. quenseli	0.078 ± 0.012 a	0.060 ± 0.017 ab	0.042 ± 0.003 b	0.00031
A. littoralis	0.040 ± 0.009	0.019 ± 0.006	0.039 ± 0.004	0.00003
B. rupicola	0.041 ± 0.008	0.019 ± 0.008	0.051 ± 0.005	-0.00076
Total carabids	1.869 ± 0.193	2.395 ± 0.309	2.161 ± 0.070	-0.00410
Ellerslie 2005				
P. melanarius	0.662 ± 0.159 a	0.264 ± 0.054 b	0.520 ± 0.042 ab	**0.01402**
A. placidum	0.459 ± 0.051	0.310 ± 0.056	0.430 ± 0.024	0.00633
B. quadrimaculatum	0.092 ± 0.024 a	0.236 ± 0.040 b	0.094 ± 0.011 a	-0.00065
A. carinata group	0.043 ± 0.009 a	0.101 ± 0.022 b	0.051 ± 0.005 a	-0.00069
A. cupreum	0.046 ± 0.013	0.015 ± 0.007	0.037 ± 0.004	-0.00041
B. rupicola	0.016 ± 0.005	0.049 ± 0.021	0.030 ± 0.005	0.00025
P. lucublandus	0.019 ± 0.005 a	0.067 ± 0.017 b	0.026 ± 0.003 a	-7.37E-7
Total carabids	1.401 ± 0.162	1.182 ± 0.106	1.262 ± 0.050	**0.01851**
Ellerslie, 2006				
P. melanarius	2.629 ± 0.392	1.858 ± 0.186	3.758 ± 0.395	0.07230
A. placidum	0.052 ± 0.011 a	0.149 ± 0.033 b	0.089 ± 0.010 a	9.37E-6
P. lucublandus	0.064 ± 0.017 a	0.138 ± 0.023 b	0.084 ± 0.008 ab	0.00018
B. rupicola	0.070 ± 0.009 a	0.082 ± 0.018 a	0.044 ± 0.005 b	0.00075
B. quadrimaculatum	0.047 ± 0.010	0.062 ± 0.020	0.051 ± 0.005	-0.00036
C. granulatus	0.021 ± 0.006	0.021 ± 0.005	0.048 ± 0.007	-0.00049
Total carabids	3.097 ± 0.377	2.563 ± 0.209	4.287 ± 0.393	0.07373

Species analyzed represent approximately 90% of total carabid collection for a particular site-year except Ellerslie, 2006, where species analyzed represent 95% of specimens collected.

Letters indicate significant results of Tukey-adjusted pairwise LSMEANS comparisons ($P \leq 0.05$).

Significant slope coefficients for the regression of species activity density by proportion canola in the intercrops ($P \leq 0.05$) are shown in bold.

Table 4.3. Non-metric multidimensional scaling (NMDS) ordination results for carabid communities at Lacombe and Ellerslie, AB, in 2005 and 2006.

Site-year	Iteration	Stress	Monte Carlo *P*	Axis 1 R^2	Axis 2 R^2	Axis 3 R^2	R^2 cumulative
Lacombe †							
2005	84	10.412	0.0040	0.134	0.467	0.312	0.913
Ellerslie							
2005	71	11.085	0.0040	0.529	0.395	—	0.924
2006	332	3.251	0.0080	0.973	0.001	—	0.974

† A useful ordination for the Lacombe 2006 community data could not be found (Monte Carlo $P > 0.05$ for ordinations on all dimensions).

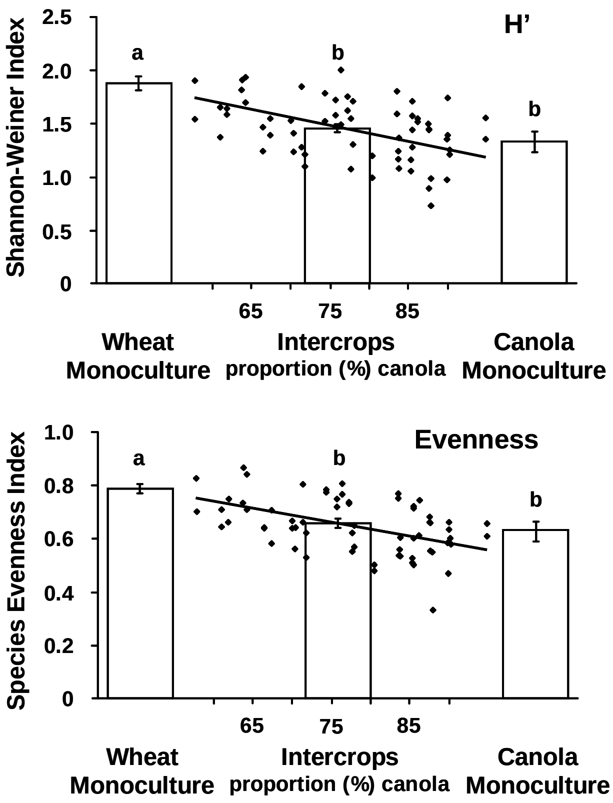

Figure 4.1. Mean (± SE) Shannon-Weiner Diversity (H’) and species evenness for intercrops and monocultures of wheat and canola, and regression of per trap diversity measures by proportion canola (%) comprising crop plant populations in intercrops at Ellerslie in 2005. Letters indicate significant results of Tukey-adjusted pairwise LSMEANS comparisons ($P \leq 0.05$).

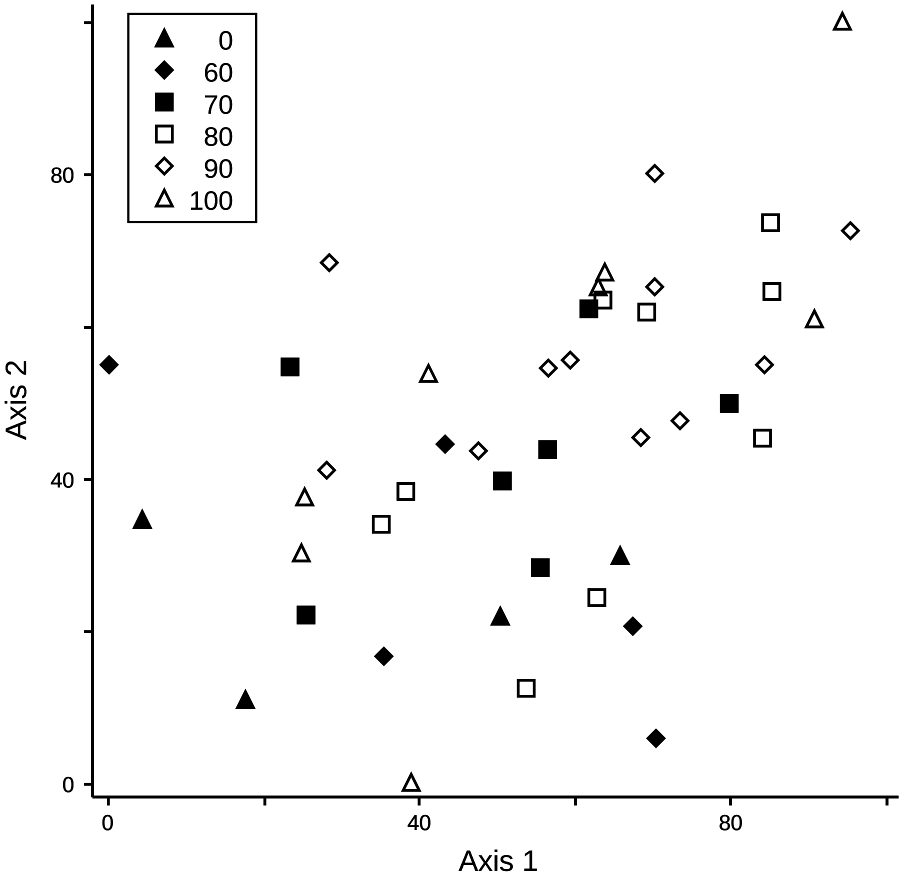

Figure 4.2. Nonmetric multidimensional scaling (NMDS) ordination of carabid community structure at Ellerslie in 2005. Distances between points represent relative differences in carabid species composition among experimental plots. Symbols represent various proportions of canola comprising the canola-wheat intercrop ranging from 0 (for a wheat monoculture) to 100% (for a canola monoculture). Experimental plots were assigned to treatments on the basis of mean canola proportion ± 5% SE.

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5. Chapter 5 – Responses of a specialist predator-parasitoid, *Aleochara bilineata* (Coleoptera: Staphylinidae), to the vegetational diversity of intercrops

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Hummel, J. D., L. M. Dosdall, G. W. Clayton, K. N. Harker, and J. T. O'Donovan. Responses of a specialist predator-parasitoid, *Aleochara bilineata* (Coleoptera: Staphylinidae), to the vegetational diversity of intercrops. Biol. Control.

5.1. Introduction

Canola production in western Canada can be severely constrained by infestations of root maggots (*Delia* spp.) (Diptera: Anthomyiidae), which inflict annual yield losses to *Brassica napus* L. and *Brassica rapa* L. of up to 20 and 50%, respectively (Griffiths 1991). Such damage results in millions of dollars in lost canola revenues (Soroka et al. 2004). The principal root maggot species infesting canola in this region are *Delia radicum* (L.), *Delia floralis* (Fallén), and *Delia platura* (Meigen) (Griffiths 1986, 1991; Broatch et al. 2006). Insecticidal control of root maggots is not feasible in canola production systems (Soroka et al. 2004), and although cultural practices like altering cultivar selections, plant densities, and row spacings can be effective (Dosdall et al. 1994, 1996), damage from these pests is still substantial. Strategies for increasing the effectiveness of biological control agents have not been investigated previously in canola cropping systems, but such measures could enhance the integrated management of these pests.

Several biological control agents of root maggots are known from western Canadian canola fields, including the puparial parasitoids *Aleochara bilineata* Gyllenhal and *Aleochara verna* Say (Coleoptera: Staphylinidae), the larval parasitoid *Trybliographa rapae* Westwood (Hymenoptera: Figitidae), and several other hymenopteran larval parasitoids (Hemachandra et al. 2005, 2007a). Globally, *A. bilineata* is the most economically important species of *Aleochara* (Maus et al. 1998), and in Canada it is often the principal natural enemy attacking root maggot pests of brassicaceous vegetables and canola, particularly *D. radicum* (Turnock et al. 1995; Dixon et al. 2004; Hemachandra et al. 2005, 2007a). Adult *A. bilineata* prey upon root maggot eggs and larvae (Colhoun 1953; Fuldner 1960; Read 1962); approximately 1,210 eggs and 128 larvae may be consumed over the lifetime of a single pair. First-instar *A. bilineata* larvae enter host puparia, feeding initially on haemolymph and then consuming the host pupa (Colhoun 1953). Larvae of *A. bilineata* pupate within the host puparium. The effectiveness of *A. bilineata* for biological control of *Delia* spp. in different cropping systems is dependent upon phenological synchronization of the host and parasitoid. When adults of *A. bilineata* emerge later in spring than their hosts, control of first-generation *Delia* eggs and larvae can be limited (Read 1962). However, in canola in western Canada, synchronization of *A. bilineata* with *D. radicum* makes it an effective biological control agent against this species (Broatch et al. 2008a), capable of achieving parasitism rates of up to 95% of *Delia* puparia in field situations (Read 1962; Turnock et al. 1995; Hemachandra et al. 2007a). Agricultural practices that enhance the abundance or parasitism of *Delia* spp. by this beetle would benefit canola producers by potentially reducing chronic yield losses due to root maggots.

Intercropping systems have been gaining interest in western North America as possible alternatives to conventional methods of crop production and pest management. Intercrops of canola (*B. napus*) and wheat (*Triticum aestivum* L.), two crop species commonly grown in monoculture in western Canada, can produce yields comparable to monocultures of the two species (Szumigalski and Van Acker 2005; Hummel et al. 2009a), and can suppress populations and damage of insect pests, including root maggots attacking canola (Hummel et al. 2009b). Non-host plants of *D. radicum* and *D. floralis* present barriers to the female flies, disrupting their normal pre-oviposition behaviour (Kostal and Finch 1994; Hopkins et al. 1999; Finch and Collier 2000). As a result, flies are less able to locate suitable oviposition sites in intercrops of host and non-host plants, fewer eggs are deposited (Tukahirwa and Coaker 1982; Dixon et al. 2004; Björkman et al. 2007; Parsons et al. 2007), and damage to the roots of brassicaceous crops can be reduced (Hummel et al. 2009b). In vegetable production systems, *A. bilineata* appears to respond to intercrops similarly to its root maggot hosts, with parasitism of *D. radicum* puparia reduced when brassicaceous vegetables are intercropped with *Delia* non-host plants compared to parasitism rates in monocultures (Ryan and Ryan 1980; Hellqvist 1996; Langer 1996; Dixon et al. 2004).

In this study, field intercrops of canola and wheat were investigated to determine effects on the parasitism of *D. radicum* puparia by *A. bilineata*. Activity densities of *A. bilineata* and *A. verna* adults were also assessed to investigate responses of the parasitoids to mono- and intercropped host and non-host habitats, and to explore the temporal responses of *A. bilineata* to mixed plant stands.

5.2. Materials and methods

5.2.1. Site description and experimental design

In 2005 and 2006, field studies were conducted at Lacombe (52° 28′ N, 113° 44′ W) and Ellerslie, AB (53° 34′ N, 113° 31′ W). Soil at Lacombe was a Typic Haplustol clay loam (43% sand, 21% silt, and 36% clay) with pH 5.9 and 8.2% organic matter. Soil type at Ellerslie was a Typic Cryoboroll silty clay loam (6% sand, 56% silt, and 38% clay) with pH 6.0 and 6.1% organic matter.

The experiment was established with four replications in a randomized complete block design. The 11 treatments consisted of monocultures of canola (*B. napus* cv. 45H72) and wheat (*T. aestivum* cv. Imagine) seeded at target densities of 200 and 250 plants/m², respectively, and intercrops seeded for target canola:wheat densities of 180:20, 160:40, 140:60, and 120:80 plants/m². Intercrop and canola monoculture treatments were duplicated to include plots with and without the neonicotinoid insecticide seed treatment Helix® (containing 10.3% thiamethoxam, 1.24% difenoconazole, 0.39% metalaxyl-M, and 0.135% fludioxonil). Helix® functions systemically in canola seedlings to reduce herbivory by flea beetles (*Phyllotreta* spp.) (Coleoptera: Chrysomelidae). Target canola and wheat monoculture plant densities were selected because they achieve effective competition against weeds such as tartary buckwheat (*Fagopyrum* *tataricum* L. J. Gaertn) and volunteer cereals (O'Donovan et al. 1988, 1989; O'Donovan 1994), and because these crop densities optimally limit the infestations of some insect pests (Dosdall et al. 1996, 1999). Treatment plots measured 7.3 by 15.2 m.

Plots were seeded into wheat stubble in mid to late May using a Conserva Pak® drill, with crop rows spaced 30 cm apart. Plots were fertilized before seeding (same day) based on soil test recommendations for canola production. The two crop species were seeded simultaneously, with the wheat seed side-banded immediately next to the canola seed rows. At the cotyledon to 1-leaf stage of canola development, crop plant emergence counts were taken from four randomly selected 1-m lengths of crop row per plot to determine actual canola and wheat densities.

Canola and wheat cultivars used in this study were Clearfield® varieties, tolerant to imidazolinone herbicides. As a result, a commercial formulation of imazomox+imazethapyr herbicide at 30 g ai/ha to both species in the intercrop was available for the control of weeds and was applied at the two-leaf stage of canola.

5.2.2. Aleochara adult collections and parasitism assessments

Adult *A. bilineata* were collected in pitfall traps at Lacombe and Ellerslie in 2005 and 2006. Each trap consisted of two 0.5-L plastic cups, the first dug into the ground below the soil surface to serve as a sleeve, and the second half-filled with propylene glycol and placed in the first so that it was level with the soil surface. A plastic plate was placed over each trap, elevated above the soil, to prevent leaves or other debris from entering the trap, to reduce evaporation, and to deter scavenging by birds. Two traps were established per plot in mid-June when canola was between the 4-leaf and rosette stages of development, and sampling was conducted weekly until harvest. Insects were removed from the traps using a fine-mesh aquarium net and specimens were stored in 90% ethanol. Fresh propylene glycol was used each week.

Specimens of adult *Aleochara* were separated from other insects collected in the pitfall traps. *Aleochara* specimens were identified to species and sex through examinations of external characteristics and dissections of adult genitalia, based on Klimazewski (1984). Representative species identifications were confirmed by Dr. J. S. Broatch (personal communication). Representative voucher specimens have been deposited in the Strickland Museum of Entomology, University of Alberta, Edmonton, AB, and at the Agriculture and Agri-Food Canada Research Centre in Lacombe, AB.

In late March through April of 2006 and 2007, *D. radicum* puparia were collected at Lacombe and Ellerslie from the treatment plots of the previous year. Only plots without the Helix® seed treatment were sampled. A minimum sample of 20 puparia was collected from each plot, except at Lacombe in 2005, when very low puparium densities resulted in collections of approximately 15 per plot. To collect puparia, soil from crop rows was excavated and visually examined for puparia; excavations measured between 10 and 15 cm wide and 10 cm deep. Puparia were identified as *D. radicum* or *D. platura* based on size and the appearance of the posterior tubercles, which distinguish the larvae of different *Delia* spp. (Brooks 1951) and are retained on the puparium. Puparia collected at Lacombe and Ellerslie in 2006 (puparia from the 2005 field season), were stored in 90% ethanol until processed. At both sites in 2007 (puparia from the 2006 field season), collected puparia were placed singly in glass vials half-filled with vermiculite and stored at 5°C. Puparia collected in 2007 were then reared out at room temperature. All puparia collected in 2006 and those from 2007 from which an insect did not emerge were examined for the characteristic entry hole of an *Aleochara* larva (Colhoun 1953; Fuldner 1960; Read 1962; Royer et al. 1998), and all puparia lacking a clearly visible entry hole were dissected to determine parasitism status. Numbers of puparia from which hymenopteran parasitoids emerged or were dissected were also recorded.

5.2.3. Data analysis

Prior to statistical analysis of *Aleochara* adult activity density, collections from the two traps per plot on each sampling date were standardized for trapping effort by dividing the number of *Aleochara* specimens collected by the number of days each trap was active during the sampling period. This allowed *Aleochara* collections to be corrected for the occasional flooded or debris-filled trap. Capture rates per trap for each sampling period were then pooled and divided by the number of sampling periods in the season to obtain a total per trap per day catch rate over the entire season.

Treatment effects for *Aleochara* spp. adult collections and *Delia* puparium parasitism rates were determined by ANOVA using the PROC MIXED procedure of SAS (SAS Institute Inc. 2004), with the proportion that canola comprised of the total crop plant population included as a covariable. Proportion of canola in the intercrops was included as a covariable because actual plant populations and target plant proportions did not always correspond well. Covariate analysis allowed investigation of both the continuous variable (proportion canola) and the discrete variables of seed treatment, block, and site-year, where appropriate. Analyses of data pooled over sites and years were also performed, with site (combination of site and year) and block included as random effects. Treatment effects were considered significant at $P \leq 0.05$.

5.3. Results

5.3.1. Parasitoid activity densities

Adults of both *A. bilineata* and *A. verna* were collected in pitfall traps at Ellerslie and Lacombe in 2005 and 2006, although specimens of *A. verna* were infrequent. Collections of *A. bilineata* from Lacombe totaled 434 specimens in 2005 and 2879 specimens in 2006; males and females respectively comprised 53 and 46% in 2005 and 52 and 46% of the population in 2006. At Ellerslie, 958 *A. bilineata* were collected in 2005, and 8862 specimens were collected in 2006. Collections at Ellerslie in 2005 were 55% male and 43% female; 2% of specimens were damaged such that sex could not be determined. In 2006, specimens of *A. bilineata* were 53 and 46% male and female, respectively, with 1%

indeterminable. Both male and female *A. verna* were also collected in all site-years (Lacombe 2005, 6 ♂ : 25 ♀; Lacombe 2006, 11 ♂ : 26 ♀; Ellerslie 2005, 5 ♂ : 11 ♀; Ellerslie 2006, 19 ♂ : 29 ♀). Other Staphylinidae not identified beyond the family level were also collected in the pitfall traps, totaling 3125 and 5886 specimens at Lacombe and 7258 and 8000 specimens at Ellerslie in 2005 and 2006, respectively.

Aleochara bilineata adult collections in pitfall traps tended to be greater in canola monocultures and intercrops with high proportions of canola than in wheat monocultures. At Lacombe in 2005, male, female, and total collections of *A. bilineata* increased with increasing proportions of canola in crop plant populations (regression slope coefficients, male = 0.003, $P < 0.0001$; female = 0.001, $P = 0.0094$; total = 0.004, $P = 0.0002$). Similarly, *A. bilineata* collections at Ellerslie in 2006 increased with increasing proportions of canola (regression slope coefficients, male = 0.014, $P < 0.0001$; female = 0.015, $P < 0.0001$; total = 0.029, $P < 0.0001$) (Fig. 5.1). Effects were not significant for data combined over sites and years ($P > 0.05$). When adult collection data were separated on the basis of sampling date (Figs. 5.2, 5.3, 5.4, 5.5), trends toward a mid-season shift in beetle habitat preference were suggested for Lacombe and Ellerslie in 2005 and Lacombe in 2006. Mean *A. bilineata* numbers were similar in early to mid July between canola monocultures and intercrops, but mid to late August collection numbers, particularly of females, tended to be greater in the canola monocultures. Adult numbers in wheat monocultures were generally lowest among the three habitat types throughout the collection period

In some site-years, *A. verna* specimens were also collected in greater numbers in plots with greater proportions of canola, although this species tended not to respond to intercropping canola with wheat. At Lacombe in 2005, female and total *A. verna* collections increased with increasing proportions of canola comprising crop plant populations ($P = 0.0376$, $P = 0.0161$, respectively). The same result was observed for *A. verna* males at Lacombe in 2006 ($P = 0.0160$). Significant effects were not observed for data combined over sites and years ($P > 0.05$).

Inclusion of an insecticidal canola seed treatment did not affect collections of *A. bilineata*, *A. verna*, or the combined collection of other rove beetles in any site-year or in the combined data ($P > 0.05$).

5.3.2. Parasitism of Delia puparia

Parasitism rates of *D. radicum* puparia by *A. bilineata* varied among sites and years. Very few *D. platura* puparia were collected, and only in some site-years. Mean rates of parasitism for treatment plots at Ellerslie were 46.70% ± 3.43 SE and 81.69% ± 3.21 SE in 2005 and 2006, respectively. Parasitism rates at Lacombe were lower than at Ellerslie in both 2005 (7.27% ± 2.79 SE) and 2006 (50.80% ± 3.89 SE). Adult insects, whether *D. radicum*, *Aleochara*, or parasitic Hymenoptera, emerged from 52.86 and 10.60% of puparia reared in the laboratory from Lacombe and Ellerslie, respectively. Of the 65 *Aleochara* adults that emerged from field-collected puparia reared in the laboratory, all were *A. bilineata*. Superparasitism by *A. bilineata*, as indicated by multiple entry holes and/or the presence of desiccated *Aleochara* larvae in addition to the surviving parasitoid, was observed at all sites except Lacombe in 2005 and was associated with greater parasitism rates: 37.54% ± 4.95 SE of *Aleochara*-parasitized *Delia* puparia at Ellerslie in 2006 were superparasitized, followed by Lacombe in 2006 (19.14% ± 5.04 SE) and Ellerslie in 2005 (18.45% ± 2.79 SE). Parasitism of *Delia* puparia by hymenopteran parasitoids (principally *T. rapae*) was highest at Lacombe in 2005 (14.17% ± 2.98 SE). Parasitism by Hymenoptera was lower in the other site-years, with rates of 6.17% ± 1.23 SE at Lacombe in 2006, 2.18% ± 0.71 SE at Ellerslie in 2005, and 2.17% ± 1.14 SE at Ellerslie in 2006.

Mean parasitism rates of *D. radicum* puparia by *A. bilineata* tended to be depressed slightly in intercrops relative to those of canola monocultures (Table 5.1). A significant response to intercropping was observed at Ellerslie in 2005, where parasitism increased as the proportion that canola comprising crop plant populations increased ($P = 0.0087$) (Fig. 5.6). Significant effects were not observed in the other site-years ($P > 0.05$). The effect of intercropping on parasitism in the combined data set indicated an overall trend toward reduced parasitism rates in intercrops with greater proportions of wheat but was not significant (*P* = 0.0714).

5.4. Discussion

Aleochara bilineata adults are attracted to olfactory stimuli arising both from infested host plants of *Delia* and from juvenile *Delia* (Royer and Boivin 1999) and respond in a density-dependent manner to host puparia (Jones et al. 1993). Greater root damage and densities of root maggots are found in monocropped or weed-free Brassicaceae (Langer 1996; Dosdall et al. 2003; Dixon et al. 2004; Broatch et al. 2008b), and greater population densities and parasitism rates by *A. bilineata* have also been observed in monocultures compared to intercrops (Langer 1996; Dixon et al. 2004). Observations by Hummel et al. (2009b) that canola root damage in the experimental plots in this study was greater in plots with higher proportions of canola suggest that *Delia* larval populations and puparia increased as canola plant densities increased. The density-dependent relationship between *A. bilineata* and its root maggot hosts could then explain the greater pitfall trap captures of the predator-parasitoid in canola-wheat intercrops with higher proportions of canola in two of six site-years in my study. Wheat monocultures, which would be expected to provide no attraction to *A. bilineata*, yielded the lowest collection numbers. The inclusion of these monocultures in regressions of *A. bilineata* collections by intercrop plant populations may have influenced the observed regression results. Such responses of the parasitoid differ from those of its host, *D. radicum*, the adults of which occur in similar numbers in monocultures and intercrops (Tukahirwa and Coaker 1982; Hummel et al. 2009b). A similar response was observed in a potato intercropping system, where *Lebia grandis* (Herntz) (Coleoptera: Carabidae), a predator-parasitoid of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), was more abundant in tilled plots compared to those with a rye cover crop mulch, but predation of *L. decemlineata* juveniles in field cages was not influenced by habitat manipulation regime (Szendrei and Weber 2009).

Based on individual sampling date collections, populations of *A. bilineata* were similar in intercrops and monocultures of canola until approximately the time *Delia* puparia could be expected to occur in soil around canola roots (Griffiths 1986). Such a temporal shift suggests that early in the season, when puparia are not available to be parasitized, *A. bilineata* adults may be density independent with respect to their larval hosts. Instead, they may forage more generally in areas with evidence of the presence of larval hosts. Host density independence with respect to host-feeding is displayed in some hymenopteran parasitoids (Heimpel and Collier 1996). Later in the season, when the success of female *A. bilineata* and their offspring relies on the ability of the females to select quality oviposition sites (Fournet et al. 2001), the distribution of *A. bilineata* appears to become more density-dependent with respect to expected puparium populations. My results therefore support the observation that *A. bilineata* adults respond in a density-dependent manner to their hosts, but dissections to determine sex ratios in trap captures determined that this response most affects adult female distributions when females are actively seeking oviposition sites later in the season. Parasitoid responses to host/prey can be affected by both host density (Lauzière et al. 1999; Szendrei and Weber 2009) and parasitoid maturity (Heimpel and Collier 1996). Puparia acceptable for parasitism would not have been present around canola roots during the earliest pitfall sampling dates, but as juvenile *Delia* developed on canola roots and then pupariated some time during mid summer, density of acceptable puparia would have increased. Ovary development or egg load in female *A. bilineata* was not determined. Read (1962) determined that *A. bilineata* females oviposit primarily between five and 50 days after emergence; therefore it is unlikely that this parasitoid has a protracted period of ovary development during which its responses to host species densities are variable.

Field crop and vegetable intercrops differ dramatically in the structures of their crop canopies and the nature of ground cover in each system. Langer (1996) discussed the effect of ground cover on *A. bilineata* adults and suggested that dense cover in intercrops with clover compared to cabbage monocultures may have impeded the movement of adult beetles through the crop. Intercrops of canola and wheat were little different from canola monocultures with regard to ground cover, indicating that, in my study, the response of *A. bilineata* adult collections was not due to the physical density of the intercrop and any resulting impairment of beetle movement.

Given the response of *A. bilineata* adults to intercropping regimes and to the density of host puparia, it is not surprising that puparial parasitism in my study was greatest in canola monocultures and often decreased with increasing proportions of wheat in the intercrops. Ryan and Ryan (1980), Langer (1996), and Dixon et al. (2004) reported similar results in intercrops of brassicaceous vegetables with *Delia* non-hosts. Although the trend was consistent over the entire study, three site-years did not demonstrate significant results, possibly due to the low puparium collection numbers throughout the study.

Parasitism rates of *D. Radicum* puparia by *A. bilineata* observed in this study were within The range previously observed in western Canada (Turnock et al. 1995; Hemachandra et al. 2007a). The increase in parasitoid collections and parasitism rates at both sites in 2006 from levels□in 2005 probably reflects the resovery of root maggot populations following a period of below-average annual precipitation between 2000 and 2004 (Anon. 2009), which Broatch et al. (2006, 2008a) reported to have reduced the populations of both the pest and, as a result, the parasitoid.

Superparasitism of *Delia* spp. puparia by *A. bilineata* has been associated with heavily parasitized populations (Morris 1960; Finch and Collier 1984; Turnock et al. 1995), as were observed in this study. From a biocontrol standpoint, neither superparasitism nor multiparasitism may be desirable, as they can significantly reduce survival of the parasitoids (Reader and Jones 1990; Fournet et al. 1999), a result suggested by the lower rates of emergence of live insects from the Ellerslie 2007 puparium collection, which had high rates of both parasitism and superparasitism by *A. bilineata*. Parasitism by Hymenoptera, principally *T. rapae*, was greater when parasitism by *A. bilineata* was low. This observation may be influenced by different population sizes of the hymenopteran at different sites and in different years, but it is likely also a result of the greater competitive ability of *A. bilineata* compared to *T. rapae*, such that *A. bilineata* is capable of parasitizing puparia already parasitized by *T. rapae* (Reader and Jones 1990). *Trybliographa rapae* is generally host density independent (Jones et al. 1993; Bonsall et al. 2004; Hemachandra et al. 2007b), and as a result, parasitism of *Delia* larvae by *T. rapae* is not affected adversely by intercropping (Langer 1996). Intercrops of canola and wheat, which appear to reduce parasitism by *A. bilineata*, may instead favor parasitism by *T. rapae* or other hymenopteran parasitoids by reducing parasitoid loss through multiparasitism; however, puparium collections and parasitism rates by these Hymenoptera were too low in the current study to investigate statistically the effects of intercropping on hymenopteran parasitoids.

No *A. verna* emerged from field-collected puparia reared in the laboratory, and adult numbers in pitfall traps were low in all site-years. *Aleochara verna* sometimes parasitizes canola-feeding *Delia* spp. (Hemachandra et al. 2005, 2007a), but *A. verna* is also commonly associated with decaying plant and animal material (Klimaszewski 1984). Reasons for the reduced activity densities of *A. verna* relative to *A. bilineata* in this study are unclear but it is unlikely that *A. verna* utilizes the same host-finding cues as does *A. bilineata*. Even *A. bilineata* and *A. bipustulata* (L.), both of which primarily parasitize Brassicaceae-feeding *Delia* puparia, do not use the same host and host-plant cues (Riley et al. 2007); it is likely that host-finding cues used by *A. verna* adults are associated with decaying material and not specifically with brassicaceous plants or the root maggots that attack them.

Vegetationally diverse agroecosystems are known to impart diverse benefits to farmers in various parts of the world (Altieri 1991), and although intercrops currently do not comprise a substantial component of canola production systems in North America, they are often promoted among low-input and organic producers as means of controlling pests and enhancing natural enemies. Potential reductions in populations and parasitism of *A. bilineata* need to be considered when determining the applicability of canola-wheat intercrops for agricultural production in western North America. Although canola-wheat intercrops provide advantages over monocultures for some agronomic parameters and the limitation of root damage by *Delia* larvae (Szumigalski and Van Acker 2005; Hummel et al. 2009a, b), intercropping canola with wheat does not appear to be a useful strategy for maximizing the beneficial effects of *A. bilineata*. Nevertheless, the density and activity of other predators in this system, such as carabid beetles, should be considered, because increases in vegetational diversity through intercropping may enhance their effectiveness in achieving the biological control of these important insect pests.

Table 5.1. Mean and SE percent parasitism of field-collected *D. radicum* puparia by *A. bilineata*, in canola monocultures and intercrops with wheat at Lacombe and Ellerslie, Alberta in 2005 and 2006. Root maggot puparia from the 2005 and 2006 field seasons were collected in early spring of 2006 and 2007, respectively.

Site-year	**Canola monocultures**		**Intercrops**	
	Mean	**SE**	**Mean**	**SE**
Lacombe				
2005	7.39	3.15	7.19	3.42
2006	59.83	9.68	48.39	4.16
Ellerslie				
2005	59.75	7.11	42.62	3.42
2006	82.90	7.45	81.09	3.50

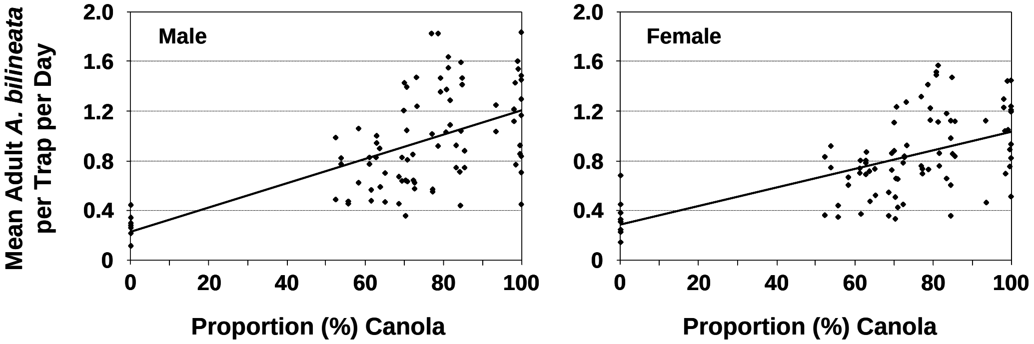

Figure 5.1. Responses of male and female *A. bilineata* to proportion of canola comprising intercrop plant populations with wheat at Ellerslie, Alberta, in 2006.

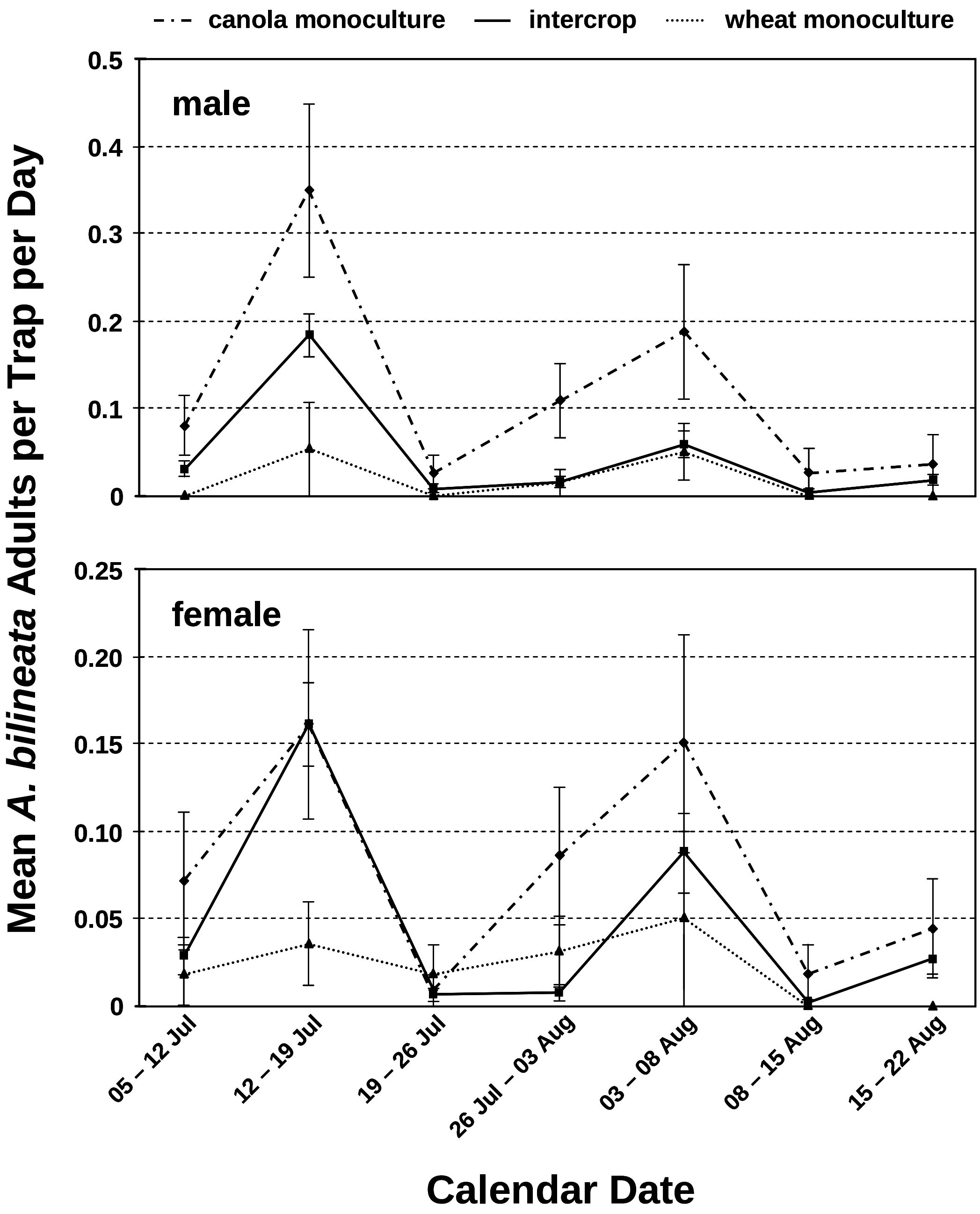

Figure 5.2. Mean and SE adult collections of male and female *A. bilineata* per pitfall trap per day in canola and wheat monocultures and intercrops of canola and wheat at Lacombe, Alberta, in 2005.

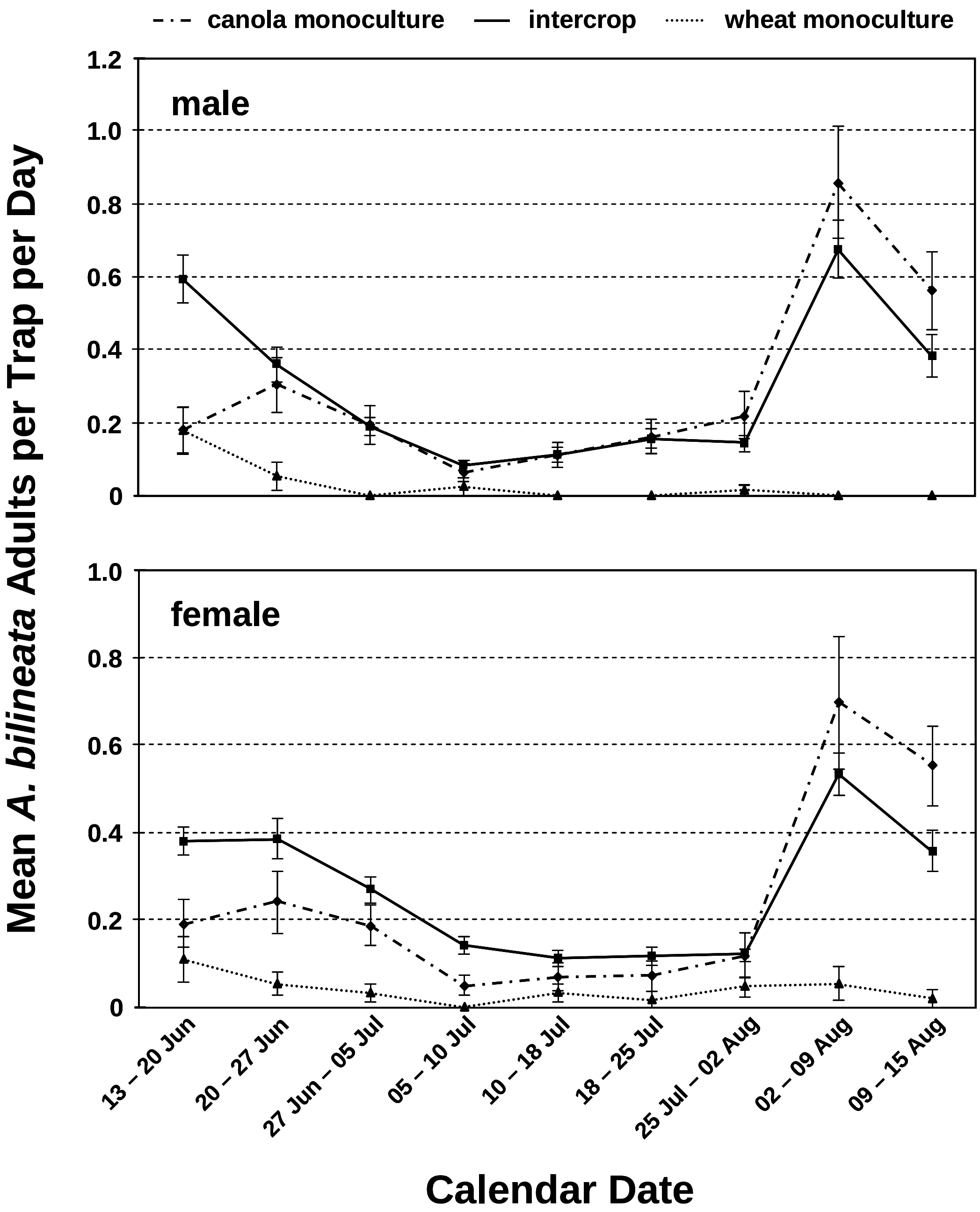

Figure 5.3. Mean and SE adult collections of male and female *A. bilineata* per pitfall trap per day in canola and wheat monocultures and intercrops of canola and wheat at Lacombe, Alberta, in 2006.

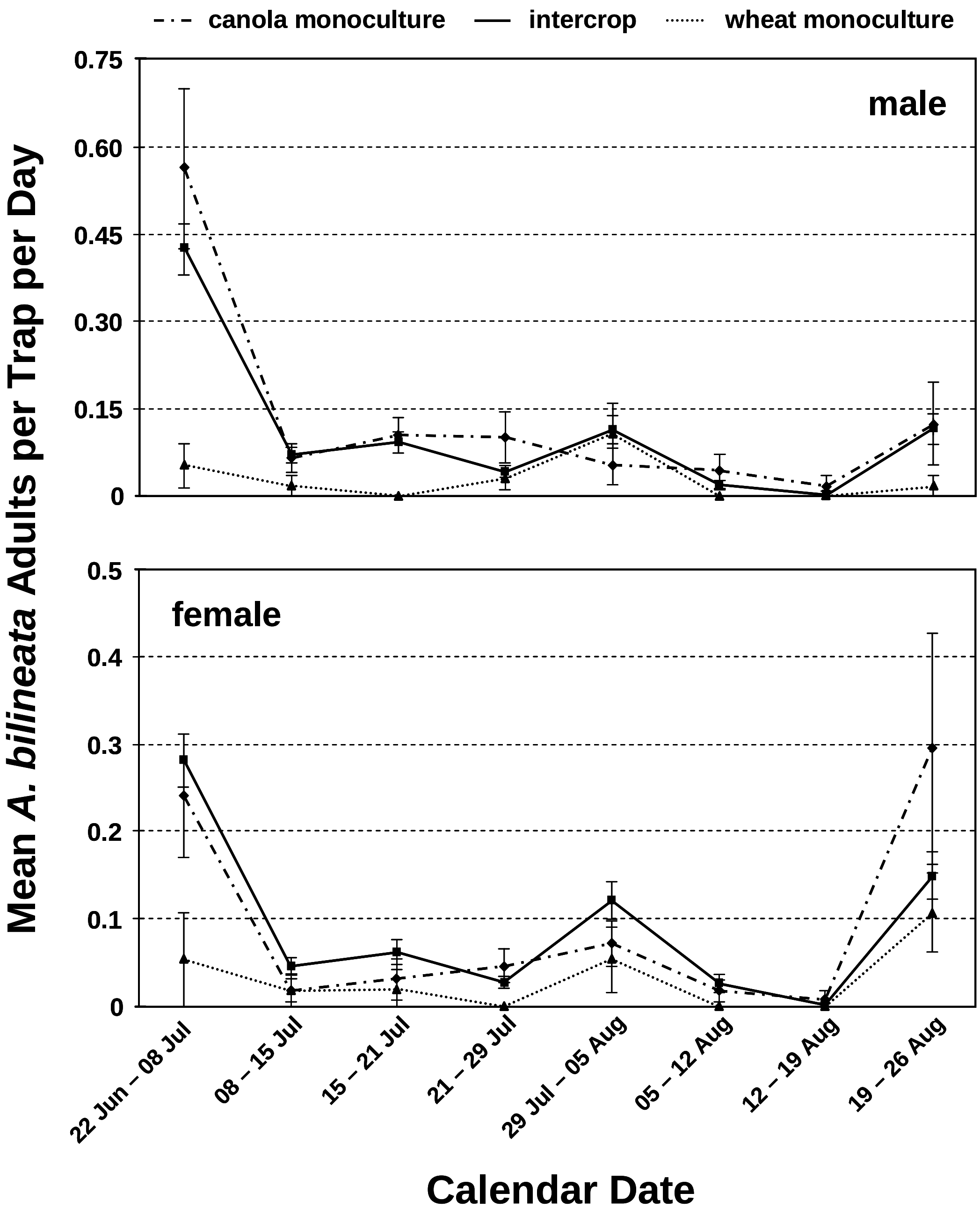

Figure 5.4. Mean and SE adult collections of male and female *A. bilineata* per pitfall trap per day in canola and wheat monocultures and intercrops of canola and wheat at Ellerslie, Alberta, in 2005.

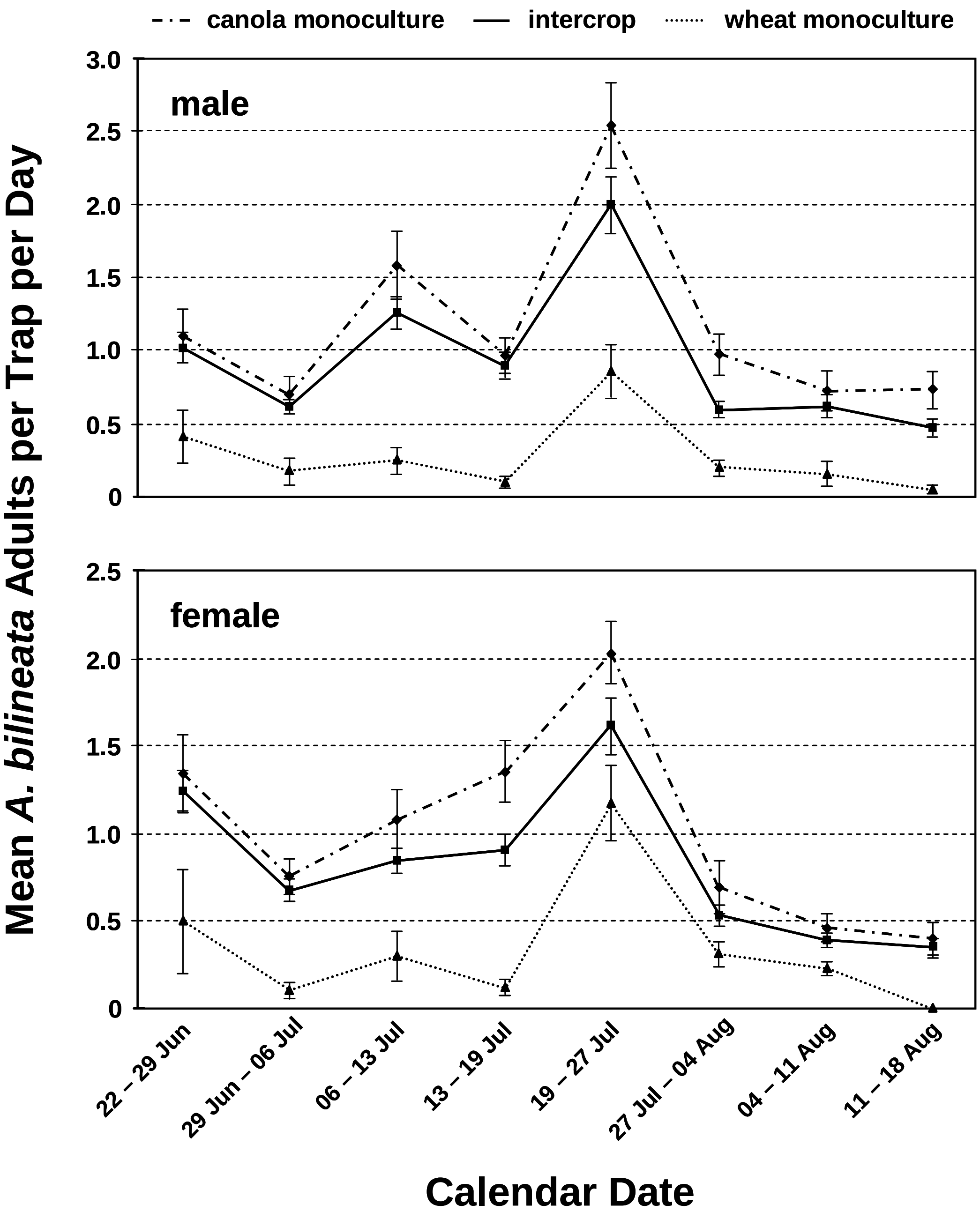

Figure 5.5. Mean and SE adult collections of male and female *A. bilineata* per pitfall trap per day in canola and wheat monocultures and intercrops of canola and wheat at Ellerslie, Alberta, in 2006.

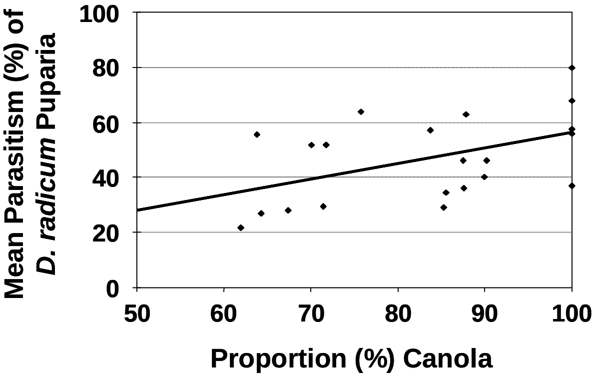

Figure 5.6. Response of parasitism of *Delia* spp. puparia by *A. bilineata* to proportion of canola comprising intercrop plant populations with wheat at Ellerslie, Alberta, in 2005.

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6. Chapter 6 – General Discussion

6.1. Summary

This thesis details my investigation of canola-wheat intercropping systems for crop production in western Canada. My study is one of the most comprehensive investigations of field intercrops in western Canada carried out to date and emphasizes that the complexity of intercropping systems, even those consisting of only two crop species, necessitates the investigation of many varied parameters to provide an assessment of the value of the system as a whole.

Chapter two investigated primarily the effect of intercropping regimes on agronomic parameters, particularly crop yields and crop quality. On a land equivalency basis, yields of both crop grain and dry crop plant biomass were similar between intercrops and monocultures. Quality characteristics of harvested canola and wheat seed had variable responses to intercropping, although both canola oil content and wheat protein content were greater in intercrops than canola or wheat monocultures in one of four site-years. Crop lodging was largely unaffected by intercropping. Other studies have also demonstrated that canola and wheat can be intercropped to produce equivalent or greater yields than achieved by monocultures (Szumigalski and Van Acker 2005), but my study is unique in the wide extent of agronomic and pest management factors encompassed in the study. I also investigated soil microbial communities, flea beetle damage, and wheat leaf diseases in response to intercrops of canola and wheat, all of which responded variably to intercropping but rarely showed significant responses.

In chapter three I investigated responses of root maggots to intercropping regimes. Adult *Delia* were collected in similar numbers in canola monocultures and intercrops with wheat. Tukahirwa and Coaker (1982) also found that monocultures of a brassicaceous crop and intercrops with a *Delia* non-host did not differ with regard to the numbers of adult flies collected. Contrary to the findings of Tukahirwa and Coaker (1982), Finch et al. (2003), Dixon et al. (2004), and

Björkman et al. (2007), per plant *Delia* spp. egg populations were not greater in monocultures than intercrops. Canola taproot damage by root maggots consistently declined as proportions of wheat in the intercrops increased.

In chapter four I assessed effects of canola-wheat intercrops on carabid beetles. Three parameters—carabid diversity, community structure, and species activity densities—were investigated. Few significant responses were observed, and trends were sometimes inconsistent among site-years. Some small to medium-sized carabid beetles, such as *B. quadrimaculatum* and *A. placidum*, were collected in greater numbers in wheat monocultures and some high-proportion wheat intercrops than in canola monocultures. This could be a positive result in terms of the biological control of root maggots. In one site-year, ground beetle community structure shifted as the proportion of wheat in the intercrops increased, more closely approximating carabid communities associated with wheat monocultures. Such a shift in community composition could be useful if the intent is to promote the abundance of certain species within the Carabidae, such as those preferring more open canopies as would occur in wheat monocultures.

Chapter five summarized my investigations of responses of *A. bilineata* to canola-wheat intercrops. Although adult *A. bilineata* numbers collected in pitfall traps increased with increasing proportions of canola comprising crop plant populations in two of four site-years, the trend toward greater numbers in canola monocultures than intercrops was mainly true in mid to late summer collections, corresponding approximately to the time when *Delia* spp. larvae pupariate (Griffiths 1986). Numbers of *A. bilineata* were fairly similar earlier in the collection period. Puparial parasitism rates tended to be greater in canola monocultures and intercrops with high proportions of canola than in intercrops with increasing proportions of wheat, suggesting a possible interference of intercrops on *A. bilineata* host-finding and an effect of the greater *A. bilineata* numbers collected in canola monocultures. These results are similar to those of Langer (1996) and Dixon et al. (2004), who found greater parasitism rates by *A. bilineata* in brassicaceous monocultures compared to intercrops with non-hosts.

The minor predator-parasitoid *A. verna* was generally unaffected by the intercropping treatments.

6.2. Importance of understanding intercrop design

In most field intercrops, such as were established for this study, a replacement design is used in which the density of the principal crop in the intercrop is reduced from monoculture densities and replaced by a secondary crop (Izaurralde et al. 1990; Szumigalski and VanAcker 2005; Hauggaard-Nielsen et al. 2006; Hauggaard-Nielsen et al. 2008; Pridham and Entz 2008). In vegetable and some field intercrops, the density of the principal crop is kept the same in the intercrops as in the monocultures (Carr et al. 1993, 1995; Tukahirwa and Coaker 1982; Finch et al. 2003; Dixon et al. 2004; Hauggaard-Nielsen et al. 2006; Björkman et al. 2007). These studies follow an additive design (Vandermeer 1989): the secondary crop is added in excess of monoculture densities of the principal crop. Differences between additive and replacement intercropping designs complicated the interpretation of results for three parameters in this study.

The response of root maggot egg populations to canola-wheat intercropping differed from responses observed in vegetable intercrops and weedy field crops. As discussed in chapter three, this study and studies reported by Tukahirwa and Coaker (1982), Dosdall et al. (2003), Finch et al. (2003), Dixon et al. (2004), and Björkman et al. (2007) measured root maggot egg populations as "eggs per plant". In these studies involving interactions of multiple plant species, the number of *Delia* spp. host plants per unit land area was the same in monocultures and intercrops, but in my study more canola plants were present per unit land area in canola monocultures than in intercrops, and canola densities varied among intercrops. As a result, "eggs per plant" in my replacement design intercrops was not actually the same measure as in the additive design of vegetable intercrops and weedy field crops; instead, eggs per unit land area would have been a more comparable measure between the differently designed studies and demonstrated a similar response to vegetational diversification.

A second example of complications arising from different intercrop designs among studies occurred in chapter four regarding carabid beetle activity densities. Dixon et al. (2004) found that certain carabid beetles preferred the open canopies of vegetable monocultures; however, in my study wheat monocultures had canopies open to light penetration, and canola monocultures had closed canopies. The intercrop canopy was mainly closed as well, but generally less so than the canola monoculture. Carabid community structures and species abundances seemed more closely associated with the structure of the crop canopy than whether the system was a monoculture or intercrop, as also suggested by Butts et al. (2003). This emphasizes the importance of understanding habitat preference and behaviour, such as responses to ground cover, when assessing the effects of intercropping on arthropods.

Finally, in chapter five I discussed how crop density was unlikely to have influenced pitfall trap collection numbers of *A. bilineata*, since total plant densities were often similar among the various intercropping regimes investigated. In contrast, the additive design of a cabbage-clover intercrop resulted in much greater plant densities in intercrops than monocultures, and led to the suggestion by Langer (1996) that the movement of *A. bilineata* may have been impeded by the high-density clover in the intercrops.

These three examples from investigations in this study emphasize the importance of appropriate interpretation of results, based on the design of the intercropping system, and an understanding of the parameters assessed in view of the underlying intercrop design employed. They also demonstrate the danger of making generalized deductions of insect biology in intercrops based on one design type alone.

6.3. Crop production and insect biology in canola-wheat intercrops

Despite the four data chapters of my thesis representing four diverse topics, they remain part of the same picture of crop production and insect biology in intercrops, and interactions among the parameters investigated likely occurred that were not expressly investigated in my research. In chapter two I investigated the agronomic effects of intercropping and determined that flea beetle damage was too low to have a significant yield effect on yield in canola monocultures or intercrops with wheat. Although canola taproot damage by root maggots was sometimes reduced by intercropping (in the Ellerslie and Fort Vermilion, 2005, site-years), LERs that similarly improved with increasing proportions of wheat in the intercrops occurred only at Fort Vermilion in 2005. The correspondence of these two parameter responses in this site-year may suggest an interaction, but it is also noteworthy that the improved canola taproot damage ratings at Ellerslie in 2005 did not correspond to a LER yield improvement. Intercropping canola and wheat, therefore, while affording a reduction in root maggot damage to canola, likely does not always result in a corresponding yield enhancement with regard to LER. This may be due to reduced canola plant densities and competition between canola and wheat in the intercrops.

Oil content of harvested canola grain tended to be greater in intercrops than monocultures, and greater in intercrops with higher proportions of wheat than those with fewer wheat plants. Canola plants in intercrops, which were more competitive than wheat, may have been able to sequester more of the available water than plants in the higher-density canola monocultures and therefore had higher oil contents in the harvested seed. McDonald and Sears (1992) determined that root maggot feeding to canola taproots reduced water uptake by canola plants. Limitation of water resources limits the oil content of canola seed (Kirkland and Johnson 2000). As shown in chapter three, canola taproot damage by *Delia* larvae was greatest in canola monocultures and intercrops with high proportions of canola. It is possible, therefore, that reduced canola taproot damage in intercrops was also involved in the enhanced oil contents observed in intercrops compared to canola monocultures. Further research to determine whether harvested canola seed characteristics are affected by root maggot feeding would be useful for resolving this aspect. However, my results suggest that root damage by *Delia* larvae may have measurable implications not only for canola yields, as demonstrated by Griffiths (1991a), but also for crop quality.

Given the effects of intercropping on various canola and wheat seed characteristics, responses of the viability of harvested seed could be an interesting characteristic to investigate further. Seed viability responses to intercropping could affect future seeding rates and, as a result, the profitability for producers of using seed produced on-farm. As with canola quality characteristics already discussed, canola seed viability may be affected by root maggot damage to canola taproots independently of an intercropping effect.

The results of *Delia* larval feeding damage to canola taproots, detailed in chapter three, and of parasitism of *D. radicum* puparia, in chapter five, suggest a correspondence between these two parameters. This is not surprising, as greater maggot damage is intuitively indicative of greater root maggot populations, and *A. bilineata* respond in a density-dependent manner to their host puparia (Jones et al. 1993). These corresponding responses of host (*Delia*) and parasitoid (*A. bilineata*) demonstrate the synchronization of the biology of these two organisms in vegetationally diverse systems. As suggested by Langer (1996), however, these two parameters appear to negate each other with regard to the benefit provided by the intercropping system. Canola yields respond to taproot damage by *Delia* (Griffiths 1991a). Negative effects of intercropping on the principal parasitoid of *D. radicum* could increase canola taproot damage in intercrops vs. monocultures and as a result decrease the yield of the canola portion of the intercrop and perhaps the relative yield of the entire intercrop; this was not observed in my study. Although reduced damage in intercrops may have influenced the higher canola oil contents observed in chapter two, similarly reduced parasitism rates would result in lower ratios of *A. bilineata* to *Delia* in subsequent seasons compared to ratios resulting from the higher parasitism rates in canola monocultures. Such between-year effects could possibly impacting future biological control of root maggots in the cropping system.

Long-term depressions in *A. bilineata* : *Delia* population ratios could be mitigated by other good agricultural management practices. For example, rotation of canola with other crops is recommended in place of continuous canola production, and rotation would continue to be important for producers employing canola-wheat intercrops. Crop rotation would force emigration of both the pests and parasitoids to fields with suitable host crops and could be instrumental in balancing the host:parasitoid ratio over subsequent years.

A temporal shift in the response of *A. bilineata* to intercrops and neighbouring monocultures, as my results in chapter five suggest, may have implications for predation of juvenile root maggots by this predator-parasitoid. Similarly abundant *A. bilineata* in intercrops and monocultures would exert greater potential predation on root maggot eggs and larvae in monocultures because of the greater abundance of root maggot prey, as Langer (1996) also suggested as a possible explanation for enhanced parasitism in monocultures. However, assuming a greater abundance of *A. bilineata* in monocultures early in the season might suggest a greater disparity between root maggot egg and larval predation in intercropping compared to monoculture systems than is likely to be the case. Further studies should be conducted to investigate specifically whether the behaviour of *A. bilineata* with respect to larval host densities changes over the season in correspondence with the developmental period of its hosts, and whether such a temporal change impacts root maggot predation by the beetle.

Delia platura comprised as much as 45% of the collection of Anthomyiidae in the site-years encompassed by this study, making it a significant member of the root maggot complex in this cropping system, particularly at Lacombe. The species can serve as a host of *A. bilineata* (Maus et al. 1998). Broatch et al. (2006) discussed how *D. platura* could influence the dynamic between *D. radicum* and *A. bilineata*. *Delia platura* puparia are distinguishable from puparia of *D. radicum* (Griffiths 1991b), and although they were present in very low numbers in some of the study sites, puparia of *D. platura* were not assessed for parasitism in this study. An investigation of the parasitism status of field-collected *D. platura* puparia could shed light on the role this species has in the interplay between *A. bilineata* and *D. radicum* in Alberta. Densities of *D. radicum* or *D. platura* puparia in monoculture or intercrop plots were not determined in this study, but such an investigation would further illuminate responses by these species to the treatment factors investigated.

Between-year variations and prolonged periodic depressions or increases in insect abundance, due to droughts or other natural phenomena, are unavoidable during field research in entomology. This study followed several years of below-average annual precipitation (Anonymous 2009) that were the most likely cause of reduced populations both of root maggots and their parasitoids, particularly *A. bilineata*. Low populations particularly affected my investigation of *D. radicum* puparium parasitism, in which low sample numbers may have inhibited the detection of some treatment effects. It would be informative to investigate parasitism in the context of canola-wheat intercrops under conditions favourable to greater populations of the pest and parasitoid.

Stability in ecosystems is a complex relationship between disturbance events, diversity, and resistance and resilience of organisms in the community. Enhanced diversity has been increasingly suggested as resulting in an overall enhancement of ecosystem stability (Ives and Carpenter 2007). The establishment and maintenance of stability is also a long-term process, one often disrupted by field operations in agroecosystems. As a result, my two-year study may have been insufficient to detect all of the responses of insect diversity and, especially, carabid beetle abundances that would result from long-term incorporation of canola-wheat intercrops into the agricultural landscape.

The numbers and frequencies of the different carabid species collected (Table 4.1) suggest that other factors not determined in this study dramatically influenced ground beetle populations and may have accounted to a greater extent for some of the variable species responses between years than did treatment factors investigated.

Kromp (1999) reported that pitfall trapping tends to underestimate populations of small carabid species and overestimate populations of large species. Considering that the potential predators of *Delia* eggs tend to be small to medium-sized beetles, such as the 3-mm-long *B. quadrimaculatum* (Lindroth 1961-1969), pitfall trapping may have underestimated populations of these potential predators. An overestimation or underestimation of any species may have influenced the determined responses of that species and overall carabid diversity to treatment factors investigated in this study.

Criticism has arisen regarding the optimism with which some carabids, including *B. quadrimaculatum*, are promoted as biological control agents against root maggots (Kromp 1999). This is because many of the investigations of this effect have been made in the laboratory rather than under field conditions (Grafius and Warner 1989; Finch 1996; Kromp 1999), although some recent field studies have investigated predation of root maggot eggs and puparia by carabid beetles (Menalled et al. 1999; Prasad and Snyder 2004, 2006a). Studies into the predation of *Delia* eggs, larvae, or puparia by various Carabidae and the predator-parasitoid *A. bilineata*, done in simulated field environments in a greenhouse, could clarify the importance of predatory beetles for the control of this pest.

Differences in the abundance and/or behaviour of various carabid species under the crop canopies of canola and wheat monocultures and the various canola-wheat intercrops would affect not only the carabid fauna in the system. Large Carabidae, such as *P. melanarius*, are often antagonistic to smaller predators in the system, such as *B. quadrimaculatum* and *A. bilineata* (Prasad and Snyder 2004, 2006a, b). Even small predators could be antagonistic to each other if they compete for the same resource, such as the generalist *B. quadrimaculatum* and the specialist *A. bilineata* both feeding on *Delia* spp. eggs. Greater rates of predation on juvenile *Delia*, whether on eggs or larvae, would decrease root maggot populations, reduce taproot damage to canola, and potentially increase yields. Similarly, decreased rates of egg or larval predation could have negative effects on crop yields or some quality characteristics, such as canola oil content. The general lack of response of the most abundant carabid species to the intercropping treatments used in this study and the diversity of responses between and within single species makes determination of effects of ground beetle activity densities on crop agronomic parameters difficult to pinpoint.

6.4. Economic considerations

Although this study was an extensive investigation of intercrops of canola and wheat, the issue of economic value of intercrops versus monocultures was not addressed. This would be a useful addition to our knowledge about this intercropping system as it would contribute to assessing the applicability of the system for western Canadian agriculture. An economic assessment could also promote producer acceptance if the system was demonstrated to have benefits that outweighed its downfalls.

Regarding an economic assessment, several factors would be of particular interest. First, there would likely be additional costs associated with the intercrop. Following the methods used in this study, an additional equipment pass was needed to lay down the fertilizer immediately prior to seeding. Over a large land area, this could amount to a considerable expense in fuel, labour, and equipment costs. Other additional costs would arise at harvest. Because of the mixed nature of the harvested product and the harvesting techniques involved in retaining two very different types of crop seed, seed separation and cleaning costs could be considerable. These costs would be influenced by the volume of harvested material and the amount of weed seed and other material needing to be separated from the crop. Due to the difficulty of synchronizing maturity of two crops, even when the cultivars selected have similar times to maturity, seed from one of the component crops may be harvested too early, and drying costs may result. Alternatively, a component crop such as canola harvested too late could result in increased yield losses through pod shattering. These increased costs could potentially make the intercrop unprofitable if relative yields are not in excess of those of the monocultures.

Even when relative yields in an intercrop exceed those of the component monocultures, the combined yield of the intercrop may not be as valuable as the single yield of a high-priced monoculture. Commodity prices for canola and wheat are variable over time, and the basic LER equation does not account for this variation or for differences between the prices of canola and wheat. Vandermeer (1989) presented methods for determining value equivalents for intercrops, which would accommodate volatile commodity prices and differently priced crops.

Despite the possibility that yields of the primary, higher-valued crop could be depressed by the secondary crop, an intercrop of canola and wheat could provide a measure of insurance to a producer by spreading out risk; should prices of the higher-valued crop suddenly plummet or some other unforeseen factor affect marketability, the producer could benefit from the harvest and sale of the secondary crop.

This study demonstrated that the quality of harvested canola and wheat seed can be manipulated through intercropping. Sufficiently great quality improvements in the harvested seed could provide a benefit to a producer by increasing the value of the crop (Gooding et al. 2007). However, the greater canola oil and wheat protein levels in harvested seed from intercrops in this study was not such that it would influence the price a producer received for the product.

Results of this study did not demonstrate a potential economic advantage to intercropping canola and wheat with regard to the insect pests investigated. Flea beetle feeding pressure on canola seedlings was little affected by intercropping. My results demonstrated that low flea beetle pressure itself, not the intercropping regimes, made the thiamethoxam canola seed treatment generally unnecessary. Investigation of intercropping regimes under flea beetle outbreak conditions would be valuable to determine if flea beetle pressure was insufficient to determine an effect of intercropping.

6.5. Conclusions/recommendations

Certain parameters investigated in this study demonstrated a benefit of intercropping canola and wheat. For example, canola oil and wheat protein contents were sometimes enhanced in the intercrops compared to monocultures, canola taproot damage by *Delia* larvae decreased with increasing proportions of wheat in intercropped plots, and some Carabidae were collected in greater numbers in intercrops than either the canola or wheat monocultures. Nevertheless, other parameters did not demonstrate an advantage of intercropping. Some of these parameters included crop yields, flea beetle damage to canola seedlings, wheat leaf diseases, and *Delia* puparium parasitism rates by *A. bilineata*. Intercropping regimes of canola and wheat, as investigated in this study, would therefore not be an attractive option for widespread adoption by producers in western Canada. To offset likely additional costs related to the intercrops, benefits that are more clearly demonstrable would need to be evident.

In the chapter discussions, I have suggested that canola-wheat intercropping systems could be useful for organic or low-input producers seeking to sustainably produce canola or wheat crops. Although this remains the case, an additional consideration needs to be made regarding canola-wheat intercrops under organic management. This study used imidazolinone-tolerant (Clearfield®) cultivars of canola and wheat to allow an herbicide application for weed control at the two-leaf stage of canola development. Organic producers would have to rely on alternate methods of weed control or accept an increased level of weed pressure and the resulting yield reductions. Some studies have determined that intercrops produced under organic or herbicide-free conditions did not provide productivity benefits over monocultures (Szumigalski and VanAcker 2005; Pridham and Entz 2008). Further research is clearly necessary to investigate weed competition in order to determine management strategies that could make canola-wheat intercrops more productive both for conventional and organic crop production.

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