The Role of Ground Beetles in Biological Control of Weeds

by

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Abstract

Ground beetles (Coleoptera: Carabidae) are important components of temperate agroecosystems, and contribute many ecological services including weed seed predation. Although their role as arthropod predators is well known, their contributions to weed biological control through seed predation and management of weed seedbanks is not fully understood. The goal of this dissertation was to develop insights into aspects of carabid weed seed predation in canola agroecosystems of western Canada, and to investigate factors influencing weed seed predation in those agroecosystems. I investigated carabid weed seed preferences, role of olfactory cues involved in weed seed detection, effects of weed seed burial in seed predation, and field dynamics and the spatial distribution patterns of seed predatory carabids under field conditions.

My studies to investigate adult carabid preferences for three brassicaceous weed species (*Brassica napus* L., considered weedy as volunteers; wild mustard, *Sinapis arvensis* L.; and field pennycress, *Thlaspi arvense* L.) in canola revealed that carabids exhibited specific, distinct preferences for weed seeds. Seed consumption among carabids was influenced by several factors, including weed species, the physiological state of seeds, and carabid activity–density. All carabid species preferred seeds of volunteer canola the most and those of field pennycress the least and showed intermediate preference for wild mustard seeds. Beetles highly preferred imbibed seeds of all three weed species. Activity–density of carabids and mean weed seed removal were highly correlated in field plots of canola, with activity–density accounting for 67% of the observed variation in seed removal.

I further investigated behavioural responses of carabids to olfactory cues, and whether such responses translated into seed preferences. Results of olfactometer-based bioassays suggested that imbibed volunteer canola seeds were preferred over other weed species by two of the three carabid species tested. Only *A. littoralis* responded significantly to odours from unimbibed seeds of *B. napus*. Sensitivity to olfactory cues appeared to be highly specific as all carabid species discriminated between the olfactory cues of imbibed brassicaceous weed seeds, but did not discriminate between weed seeds that were unimbibed. Overall, data suggested that depending on seed physiological state, odours can play an important role in the ability of carabids to find and recognize seeds of particular weed species.

Seed burial depth influenced seed consumption rates as demonstrated by a significant interaction between seed burial depth, carabid species, and gender of the carabid species tested. We observed higher seed consumption by females of all species, and greater consumption of seeds scattered on the soil surface compared with seeds buried at any depth. However, there was evidence of seed consumption at all depths and seed burial did not eliminate weed seed predation.

My studies to investigate spatial relationship between carabid beetles, weeds, and weed seeds in canola (*Brassica napus* L) under field conditions using Spatial Analysis by Distance Indices (SADIE) revealed that carabids and weed populations were highly clustered. Moreover, there was significant spatial overlap between activity-density of carabids and patches of high weed density, with an association index, X, ranging between 0.40 and 0.71. Our results suggest that the presence of weedy patches of vegetation in cropped areas may contribute to biodiversity by conserving populations of carabids, which can also increase rates of weed seed predation.

Preface

This thesis is an original work conducted by Sharavari Kulkarni. Mrs. Kulkarni conducted all experiments and wrote the first draft of all chapters. The chapters were then examined by Mrs. Kulkarni's supervisors, Dr. Christian Willenborg and Dr. John Spence. Drs. Willenborg and Spence provided editorial revisions and suggestions for each chapter, which were then incorporated by Ms. Kulkarni.

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In all publications, Mrs. Kulkarni was responsible for the research concept formation, experimental layout, data collections and data analysis as well as the manuscript composition. For Chapter 1, (Late) Dr. Lloyd Dosdall and Dr. Christian Willenborg were supervisory author and were involved with research concept formation, and editorial revision of the manuscripts.

In all other publications Drs. Willenborg and Spence were supervisory authors and were involved in developing research concepts and editorial revisions.

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List of Abbreviations

m	meter
cm	centimeter
mm	Millimeter
km	kilometer
ha	hectare
mg	milligram
d	day(s)
h	hour(s)
SADIE	Spatial Analysis by Distance Indices
δ/D	SADIE index of distance to regularity
X	SADIE association Patch index
Vi	Gap index
Vj	
°C	degree Celsius
USD	United States Dollar
IWM	Integrated Weed Management
IIA	Insect Inlet Adapter

Chapter 1. Introduction

A version of this chapter has been published:

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Among all agricultural practices, the management of weeds has historically been the most resource demanding practice performed by growers, requiring considerable time and monetary resources (Holm and Johnson 2009). For example, total weed control costs in the United States alone have been estimated to be approximately 27 billion USD/year (Pimentel et al. 2005). In Canada and elsewhere, weed management creates challenges in various agroecosystems besides the costs incurred in weed management operations. For instance, a single species such as Canada thistle, *Cirsium arvense* (L.), can cause up to 60% yield reduction in canola (*Brassica napus* L. and *Brassica rapa* L.) (Canola Council of Canada 2014). Similarly, the cost of controlling wild oat (*Avena fatua* L.) across the Prairie Provinces of Canada has been estimated at $500 million annually (Leeson et al. 2005).

In North America, herbicide-based weed management has been the major strategy for weed control in agroecosystems (Ghersa et al. 2000). In fact, 20 to 30% of the cost of producing a crop can be attributed to herbicide application (Derksen et al. 2002). Excessive dependence on herbicides has resulted in problems such as herbicide-resistant weeds (Holm and Johnson 2009), nontarget spray drift, persistent chemical residues, and environmental pollution (Boyetchko et al. 2009). Further, high application rates of herbicides and other agrochemicals for pest management negatively affect crop microhabitats, thereby influencing beneficial arthropod species and affecting biodiversity (Navntoft et al. 2006). Hence, a weed management approach relying on the application of chemical herbicides alone has several negative consequences, and the integration of several small ‘‘hammers’’ of weed management in an integrated system can help to overcome these negative consequences (Liebman and Gallandt 1997; Swanton and Murphy 1996).

Integrated weed management (IWM) has been defined as the ‘‘application of numerous alternative weed control measures, which may include cultural, genetic, mechanical, biological, and chemical means of weed control’’ (Swanton and Murphy 1996). Among these, biological control of weeds using arthropods provides a potential supplement to herbicide applications, and also serves as a sustainable method of long-term weed management (Boyetchko et al. 2009). Biological control also can be combined harmoniously with other weed management practices such as cultural and physical weed control. Postdispersal seed consumption reduces addition of seeds in the weed seed banks (Crawley 2000; Harper 1977), and serves as a critical factor determining the population dynamics of weeds in agroecosystems (Crawley 2000; Lundgren 2009). In agroecosystem both vertebrates (e.g., rodents, birds) and invertebrates (mainly insects) contribute to the postdispersal consumption of weed seeds (Heggenstaller et al. 2006; Honek et al. 2009, Inouye 1980, Westerman et al. 2003a; Ward et al. 2011). In temperate agroecosystems, carabid beetles (Coleoptera: Carabidae) are key members of epigaeic invertebrate assemblages, with the potential to provide valuable ecological services (Thiele 1977; Zhang et al. 1997; Tooley and Brust, 2002). Carabids consume substantial numbers of seeds produced by numerous weedy species, and in so doing, can reduce weed populations through both direct effects on seed mortality (Honek et al. 2003, 2005; Westerman et al. 2003a; Saska et al. 2008; Trichard et al. 2014) and by reducing seed addition in the weed seedbank (Crawley 2000; Lundgren 2009; Bohan et al. 2011). However, the magnitude of contributions to weed seed predation is site and region-specific (Brust and House 1988; Ward et al. 2011; Davis et al. 2013).

1.1 Carabid beetles and granivory

1.1.1. Biology of Carabidae

Most carabids spend all of their life stages on or in the soil rhizosphere. Carabid eggs are white in color, oval and elongated in shape, and are laid either in the soil, leaf litter, or in rotting wood. The oviposition site is chosen carefully by the female, depending upon microclimatic factors such as shadow, relative humidity, and the availability of prey (Brandmayr and Zetto-Brandmayr 1979; Trefas and van Lenteren 2008). Oviposition ranges from 30 to 600 eggs in a female beetle's total life span, with fecundity largely influenced by adult diet (Fawki and Toft 2005; Jørgensen and Toft 1997; Wallin et al. 1992) and body size (Juliano 1985).

A typical larva is a free-moving campodeiform (elongated, flattened, and active) with long thoracic legs. It has mandibles, antennae, and bears fixed urgomorphi (paired horn-like structures at posterior tip of abdomen of larvae and pupae) (Crowson 1981). Larvae usually undergo three larval instars, except in a few genera such as species of *Amara* and *Harpalus*, which only undergo two instars (Lovei and Sunderland 1996). Pupation occurs in a specially constructed pupal chamber in the soil. Adult carabids have a wedge-shaped body that allows movement under cracks and crevices and beneath litter (Evans 1977, 1986; Evans and Forsythe 1985; Forsythe 1981, 1983, 1991). A carabid head has prominent mandibles, palps, and filliform antennae. The antennal cleaning organ on the protibia facilitates chemosensory reception among carabids (Evans 1994). Striated elytra provide protection to the wings and abdomen, preventing water loss from the body (Hammond1979). Further, carabids possess long slender legs that help them in running, digging, burrowing, climbing, and swimming (Evans 1977, 1986; Lindroth

1961–1969; Thiele 1977). In general, temperate ground beetles are univoltine. However, under harsh conditions some species can survive up to 4 years (Lovei and Sunderland 1996).

1.1.2. Ground beetles and seed diets

Carabids are generally polyphagous and habits vary from carnivory to omnivory to granivory (Hurka and Jarosik 2001). Forbes (1883) first reported the granivorous behavior of carabid beetles, and based on gut dissections, Zhavoronkova (1969) classified carabids into three categories: strict predators (obligate zoophages), predominant zoophages, and predominant phytophages, with members of the latter two categories being the highest consumers of seed material. Larochelle (1990) published the food range of 1,054 carabid and cicindelid species: 74% species were exclusively carnivorous, 8% were phytophagous, and 20% were omnivorous. However, many of these studies were laboratory-based and overestimated the predatory habits of carabid species (Lovei and Sunderland 1996). Within plant-feeding carabids, two groups are mainly distinguished: the first utilizes green plant parts and fruits for supplementing beetle water requirements whereas the second group, called ‘‘spermophagus,’’ prefers to feed on seeds (Zetto- Brandmayr 1990). The two tribes with the most granivorous members include the Harpalini (Goldschmidt and Toft 1997; Lundgren 2009; Saska2005; Thiele 1977;), and Zabrini (Lundgren 2009; Saska 2005; Thiele 1977; Tooley and Brust 2002). Species of *Amara*, *Anisodactylus*, *Harpalus*, *Ophonus*, *Poecilus*, *Pterostichus*, and *Stelophonus* have demonstrated mainly granivorous habits (Lundgren 2009).

However, seed feeding is not limited to the granivorous species. Many species that are generally considered highly carnivorous, including *Bembidion quadrimaculatum*(L.), *Cyclotrachelus alternans* (Casey), *Elaphropus* sp., *Poecilus lucublandus* (Say), *Poecilus* *versicolor* (Sturm), and *Pterostichus permundus* (Say), have been documented in recent molecular studies to feed on weed seeds (Lundgren et al. 2013). Evidently the diet requirements of many carabid species have not been fully understood and the potential role of several such species in weed seed feeding is perhaps underestimated. Further, most studies have reported weed seed consumption by adult carabids only. Larvae can also contribute substantially to weed seed removal, which is not well documented (Saska 2005), except for a few species such as *Amara similata* (Gylenhall) (Fawki and Toft 2005; Jørgensen and Toft 1997). Understanding larval feeding habits is complicated by their subterranean habits, and the complexities associated with laboratory rearing (Lovei and Sunderland 1996).

1.2. Potential of granivorous carabid species in the biological control of weeds

Weed seed banks are major contributors to the widespread development of weed communities in agricultural fields (Fox et al. 2013), and weed management strategies need to focus on controlling seeds entering the soil seed bank (Fox et al. 2013). In this context, weed seed consumption by invertebrates plays an important role. There have been some indications that interception of seeds entering the weed seed bank can be more affected by the activity of ground beetles than other causes such as natural aging of seeds or seed decay (Westerman et al. 2003; Bohan et al. 2011).

In general, levels of weed seed predation in the field can vary (Table 1), and specific weed seed consumption rates are difficult to quantify as species of the same genus can differ in terms of consumption. In some cases, predation rates can be low as 4% per day (Brust and House 1988). In other studies, carabids can consume the majority of seeds in a system, sometimes consuming 70% per year (Harrison et al. 2003). Such variations can be attributed to agricultural management activities (Brust and House 1988; Hatten et al. 2007; Menalled et al. 2007), seasonal population fluctuations of beetles (Honek et al. 2006), phenological changes in the carabid life cycle (e.g. overwintering stages, breeding season, dispersal etc.), biotic factors such as high level trophic interactions (Davis and Raghu 2010), the presence of alternative food sources (Frank et al. 2010; Frank et al. 2011), abiotic factors such as temperature (Saska et al. 2010), seed distribution patterns on the soil surface (Noroozi et al. 2012) and method of seed exposure in the field (Shuler et al. 2008; Saska et al. 2014), and landscape characteristics (Trichard et al. 2014) .

Under greenhouse conditions, reduction in seeds of *C. album* L. and *A. retroflexus* L. by 56% and 63%, respectively, have been reported for eight carabids species belonging to *Amara*, *Anisodactylus, Harpalus* and *Stenolophus* (Brust 1994). Likewise, carabid species such as *Harpalus affinis* Schrank and *Pseudoophonus rufipes* (DeGeer) have been shown to feed on as many as 120 seeds of the economically-important species, *C. arvense* (L.), in a 5 day period (Martinkova et al. 2006). Similarly, *Harpalus* spp. have been reported as the dominant weed seed consumers in several field experiments (Brust and House 1988).

1.3. Factors affecting weed seed consumption under field conditions

Several factors influence carabid weed seed consumers and their seed consumption activity either directly or indirectly. An understanding of these factors is important to conserve seed consumer fauna and increase seed consumption activity in order to enhance weed management. Below, I present an account of the major factors that affect weed seed consumption under field conditions.

1.3.1 Agricultural Management Practices.

Because of their epigeal habit, carabid activity in agroecosystems is affected by agricultural management practices such as crop species, tillage intensity, and crop diversification. Factors such as species habitat preference (Thomas et al. 1997), soil tillage pattern (Cárcamo et al. 1995; Holliday and Hagley 1984; Tyler and Ellis 1979), cropping system (Blubaugh et al. 2011; Booij and Noorlander 1992; Cárcamo et al. 1995; Carmona and Landis 1999; Dritschilo and Wanner 1980; Kromp 1989, 1990), and the use of pesticides (Lee et al. 2001; Marko and Kadar 2005) can influence carabid activity. Agricultural management practices influence the characteristics of the habitats for different carabid species by altering soil physical properties. For example, soil microclimate, sod layer, and crop stand characteristics influence carabid life history parameters such as overwintering.

1.3.1.2. Tillage

Tillage influences carabid abundance because of the direct mortality it causes to carabid populations (Fadl et al. 1996). It also indirectly influences microclimate and habitat structure (Stinner and House 1990). Tillage operations influence both the distribution of weed seeds and the depth to which they are buried (Swanton 2000). Also, changes caused to vegetation bring about differences in microhabitat conditions by altering factors such as humidity and vegetation cover (Shearin et al. 2007). In general, seed-feeding species tend to prefer undisturbed fields (Hatten et al. 2007; Menalled et al. 2007; Trichard et al. 2013). However, the effects of tillage on carabid populations depend on timing of tillage (Cárcamo 1995; Fadl 1996; Hatten et al. 2007; Lalonde et al. 2012; Shearin et al. 2007), species habitat preferences and habits (Briggs 1965; Speight and Lawton 1976), and the equipment used for tillage operations (Shearin et al. 2007). Prior studies indicated that seed-feeding carabid species thrive in undisturbed habitats. Based on these observations, one might assume that seed consumption rates could be higher under no tillage conditions. However, earlier studies determined that the impact of disturbance on seed distribution and subsequent seed consumption can be ambiguous (Cromar et al. 1999; Menalled et al. 2007; Trichard et al. 2013). For example, no tillage regimes create undisturbed conditions, which sustain high arthropod diversity (House and Parmelee 1985). This also ensures higher prey availability, therefore, alternate prey resources for invertebrate predators, including ground beetles. This ultimately influences the seed consumption behavior of seed predators (Cardina et al. 1996). Due to availability of alternate prey sources, variable weed seed consumption rates can be observed.

Given the above observations, the interrelations among tillage, carabid population dynamics, and weed seed consumption are obviously complex (Shearin et al. 2007).

1.3.1.2. Cropping diversity

The diversity of carabid beetles under different cropping systems has been studied extensively. Studies have usually demonstrated that carabid populations increase under diversified cropping systems (Armstrong and McKinlay 1997; Kromp 1999; Tukarhiwa and Coaker 1982) because of increased immigration rates, longer residence times in patches, and decreased emigration from intercropped plots (Ca´rcamo and Spence 1994; Perfecto et al. 1986). However, the impact of these strategies in promoting thriving granivorous carabid taxa depends largely on the crop type (Shearin et al. 2008, Bourassa et al 2010), crop phenology (Heggenstaller et al. 2006; Westerman et al. 2011) and the habitat requirement of the granivorous taxa present in that field (Hummel et al. 2012). A recent study by Blubaugh et al. (2016) shows that increasing vegetative cover facilitates weed seed predation rate by increasing weed seed foraging behaviour.

1.3.1.3. Landscape characteristics

Very few studies have investigated the role of landscape characteristics on granivorous and omnivorous carabid communities. Local agricultural management practices substantially influence landscape characteristics, which in turn influence carabid activity (Trichard et al. 2013). Factors such as surrounding landscapes and the proportion of vegetation cover surrounding cropped areas are known to positively influence the activity of granivorous carabids (Trichard et al. 2013). Habitats surrounding agricultural fields largely determine insect biodiversity and the associated agriculture environmental services (AES) these species provide, although such effects are mainly measured on rather large spatial scales (Flohre et al. 2011). Complex habitats (< 20% arable land) are a source of shelter and food resources and are attractive to many arthropod species. As a result, higher immigration rates to such habitats from surrounding seminatural or simple landscapes are observed (Ricketts et al. 2008; Tscharntke et al. 2005). Habitat complexity can thus compensate for the impacts of local management practices on biodiversity and allied environmental services through species immigration from surrounding areas. The impact of habitat complexity on carabid diversity can also vary with food guilds. Carnivorous and granivorous species are more sensitive to landscape simplification processes than are omnivorous species (Purtauf et al. 2005), and this can result from a decrease in perennial non-crop habitats surrounding field areas and the resulting shortage of specific food resources for strictly carnivorous or granivorous species.

1.3.1.4. Other factors

In general, the use of insecticides and fungicides has been considered to negatively affect carabid activity (Fielding et al. 2013; Trichard et al. 2013). Estimation of direct and indirect effects of insecticidal applications on carabid groups and their biological control services can be complicated by the scale of study, species dispersal patterns, and immigration of untreated individuals from surrounding areas (Holland and Luff 2000). Studies investigating insecticides effect indicate that insecticidal applications negatively affect carabid populations (Brown et al. 1983; Floate et al. 1989). Some studies indicate that the effects of insecticides applications can be short-lived, and populations can recover in time (Holland 1998; Holland and Luff 2000). The major sources of natural mortality in carabids are natural enemies and environmental abiotic factors (Lovei and Sunderland 1996). Among major predatory species feeding on carabids, the important groups include farm birds (Green 1984; Poulsen et al. 1998), and birds with nocturnal habits such as owls, bats, amphibians (including frogs and toads), lizards, and rodents (Brandmayr et al. 2009). Among invertebrate natural enemies are ants (Formicidae) that can prey on carabids and compete for habitat, robber flies (Asilidae), and some species of rove beetles (Staphylinidae) (Brandmayr et al. 2009). The levels and extent of natural predation have not been reported, and effects on seed predation services have not been quantified.

Variations in population dynamics and rates of carabid seed consumption in relation to seasonal climatic changes are known, and factors such as temperature, relative humidity, precipitation, and wind speed can affect carabid population dynamics and activity (Davis and Raghu 2010; Saska et al. 2010).

1.3. Rationale of the study

Despite recent attention to the role of ground beetles in postdispersal weed seed predation, very few studies have focused on this important ecological service in western Canada. Contributions of ground beetles as arthropod predators have been well documented over many years (Crawley 2000; Lundgren 2009; Bohan et al. 2011; Brust and House 1988; Ward et al. 2011; Davis et al. 2013). However, several aspects of ground beetle bioecology and field dynamics have not been studied in detail in the context of their role as weed seed predators. In western Canada, studies on carabids have mainly focused on aspects of ground beetle responses to agricultural practices (Cárcamo and Spence 1994; Cárcamo et al. 1994; Floate et al. 2007) or vegetation diversity (Butts et al. 2003; Bourassa et al. 2008, 2010; Hummel et al. 2012). Consequently, there are knowledge gaps associated with the main carabid species contributing to weed seed predation of common brassicaceous weed species in important agroecosystems like canola in the study area. The mechanisms involved in foraging and detecting weed seeds on the soil surface are not known. Carabid species such as *Pterostichus melanarius* use olfactory cues in habitat (Kielty et al. 1996; Trefas et al. 2001) and prey selection (Kielty et al. 1996). However, the extent to which such cues are used in the foraging of seeds remains unexplored. Elucidating the cues used in seed predation can help to understand the determinants of seed detection, and the probability of species consuming various weed seeds in different environments. Earlier research has shown that carabid species are able to detect weed seeds that are buried in soil (White et al. 2007; Harrison and Gallandt 2012), which suggests that adult beetles may use mechanisms other than visual or tactile cues to detect buried seeds. Preferences for imbibed seeds have also been documented (Cardina et al. 1996; Harrison et al. 2003; Kulkarni et al.

2015c), and these may be due to release of organic compounds during germination, which can act as olfactory cues (Linton and Wright 1993; Law and Gallagher 2015).

The role of carabids in detecting and consuming seeds that are buried at different soil depths has been investigated to a limited extent (Harrison and Gallandt 2012; White et al. 2007), and needs to be investigated further. Field dynamics of seed predatory carabids on a spatial scale is not particularly well-documented, and underlying determinants need to be identified. Conservation biological control can be implemented efficiently if the relationship between seed predatory carabids and weed species is well understood. My thesis attempts to contribute to the body of knowledge on carabid weed seed predation, and understand biological and ecological aspects of weed seed predation in canola agroecosystems.

The goal of this dissertation was to develop insights into aspects of carabid weed seed predation in canola agroecosystems of western Canada and to investigate factors influencing weed seed predation in those agroecosystems. My investigation focused on four major research themes and their interrelation in the context of weed seed predation, including: a) understanding carabid weed seed preferences under laboratory and field conditions, b) understanding the role of olfactory cues involved in weed seed detection, c) understanding the effect of weed seed burial in seed predation, d) understanding field dynamics and the spatial distribution patterns of seed predatory carabid under field conditions. Figure 1 provides a detailed summary of the major research themes investigated in this project, and underscores the interlinking among the themes.

As depicted in Figure 1.1, the first important component was to identify important weed seed predatory species in the canola agroecosystems in western Canada, and to investigate their weed seed preferences. The results of my investigation on carabid seed preferences are described in Chapter 2. I evaluated carabid weed seed feeding and preferences among brassicaceous weed seeds under laboratory and field conditions. Earlier studies have shown that carabid beetles exhibit weed seed preferences that might be related to seed size (Honek et al. 2003; 2007; 2011), seed coat hardness (Lundgren and Rosentrater 2007) and other governing factors. I hypothesized that carabid species will exhibit specific preferences for weed species both under laboratory and field conditions. My investigation also included two distinct states in which seeds may be encountered by predatory carabids, imbibed seeds and unimbibed seeds.

Preferences for seeds and the capacity to detect weed seeds may be influenced by factors such as seed burial, and the cues involved in weed seed detection. Thus, Chapters 3 and 4 investigated role of sensory cues and effects of seed burial in weed seed detection, respectively. In Chapter 3, I investigated the role of sensory cues, particularly olfactory cues associated with weed seeds, in seed detection by omnivorous carabid beetle species. I investigated whether carabids use olfactory cues to detect and discriminate among both unimbibed and imbibed seeds of three common brassicaceous weed seeds. Seeds are known to release volatile compounds upon imbibition (Lee et al. 2001; Paulsen et al. 2015) and insects use these as cues to detect seed (Law and Gallagher 2015). Previous studies have reported the use of olfactory cues in prey (Kielty et al. 1996) and seed detection (Law and Gallagher 2015) by carabid beetles. However, very little is known about whether carabid beetles can discriminate among different weed species by olfaction. Hence, a four choice olfactory bioassay was carried out on three common ground beetle species by giving them the choice of three brassicaceous weed seeds. I hypothesized that carabid beetles would be able to discriminate among the seeds of different weed species.

Weed seeds are available at the soil surface, but may also be buried at varying depths under field conditions as a result of agronomic practices and natural processes including soil movement, erosion, and the development of soil cracks (Martinkova et al. 2006). Such burial may affect postdispersal seed consumption, but little is known about this possibility (Harrison and Gallandt 2012; White et al. 2007). Hence, in Chapter 4, the effect of seed burial depth on seed predation was evaluated under greenhouse conditions. I hypothesized that seed burial will influence seed detection, and with higher burial depths the rates of seed predation will decrease. I also hypothesized that carabid species will respond differently to seed burial in terms of their capacity to detect buried seeds.

In Chapter 5, I determined if the spatial distribution of seed predatory carabid beetles in canola (*Brassica napus* L.) agroecosystems and to determine if spatial patterns of weed density and seed availability in the seedbank influenced local activity-density of beetle density. I also aimed to determine if activity-density and spatial dynamics were influenced by crop development. To accomplish this, I employed spatial analysis by distance indices (SADIE), a powerful tool for spatial analysis (Thomas et al. 2001), to model the distribution dynamics of carabid assemblages using data derived pitfall traps at four sites in central Alberta, Canada.

In Chapter 6, I discussed the results in context of their broader implications for weed management. Through this investigation, I have attempted to improve our understanding of important seed consuming carabid species, with a focus on their seed preferences and feeding potential, the effects of seed burial on seed predation, the use of olfactory cues in seed detection, and spatial dynamics under field conditions.

Table.

Table 1.1. An overview of studies focusing on weed seed consumption by different granivorous taxa under field conditions

Seed consumer	**Weed species**	**Removal rate**	**Crop**	**Study duration**	**References**
Ground beetles, ants and crickets	*Ambrosia artemisiifolia* L. *Amaranthus retroflexus* L. *Cassia obtusifolia* L. *Datura stramonium* L.	4.2-4.8 % day^{-1}	Soybean-corn	5 weeks	Brust and House 1988
Vertebrate exclusion	*Alopecurus myosuroides* Huds. *Bromus sterilis* L. *Avena fatua* L.	1.43-7.2% day^{-1}	Grassy margins of cereal fields	1 month	Povey et al. 1993
Carabids, crickets	*Abutilon theophrasti* Medik.	11% day^{-1}	Corn	4 years	Cardina et al. 1996
Inverterbrates	*Echinochloa crus-galli* (L.) *Chenopodium album* L.	28-31% day^{-1}	Corn; soybean and wheat	2 years	Cromar et al. 1999
Invertebrate	*Digitaria sanguinalis* L.	11% day^{-1}	corn	2 weeks	Menalled et

	Setaria faberi Herrm. *Amaranthus retroflexus* L. *Abutilon theophrasti* Medik.				al. 2000
Mainly cricket, ground beetles also captured	*S. faberi*	58% day^{-1}	Wheat w/ red clover cover crop	3 months	Davis and Liebman 2003
Harpalus pensylvanicus	*Ambrosia trifida* L.	57–70% year^{-1}	No-till corn	12 months	Harrison et al. 2003
Carabids	*Capsella bursa-pastoris* (L.) Medik., *Cirsium arvense* (L.) Scop., *Descurainia sophia* L., *Lepidium ruderale* L. , *Sisymbrium loeselii* L., *Taraxacum officinale* F.H.Wigg	0.71-3.8 seeds day^{-1}	Wheat, oilseed rape, soybean, millet and corn	3 months in summer 1999 6 months in summer 2000	Honek et al. 2003

Carabids and mice	*C. album* L., *S. media* and *A. fatua*	38 -74% year $^{-1}$	Organic cereal field	4 months for two years	Westerman et al. 2003
Carabids	*C. album* L.; *Sinapis arvensis* L.; *Stellaria media* L. and *Polygonum aviculare* L.	35% week^{-1}	Spring barley	2 weeks	Mauchline et al. 2005
Crickets, carabid beetles, prairie deer mice	*A. theophrasti*	17% day^{-1} 32%/day^{-1}	Corn-soybean Corn-soybean-Triticale+alfalfa-alfalfa	2 year 4 year	Westerman et al. 2005
Invertebrates	*S. faberi and A. theophrasti*	16-30% day^{-1}	Different crop rotations of cereals and legumes	4 months for 2 years	Heggenstaller et al. 2006
Carabids	*C. album* L., *Panicum dichotomiflorum* Michx.	10-90% day^{-5}	Corn (organic; no-till and conventional)	4 Aug.- 7 Sept. 2000	Menalled et al. 2007

Invertebrates	*Poa annua* L., *S. media* L., *C. bursa-pastoris*, *Lamium amplexicaule* L.	14.1 -16.8% week^{-1}	Winter wheat	March-July 2004	Saska et al. 2008
Carabids and Isopoda	*T. officinale*	34-40% year^{-1}	Grassland	2 years	Honek et al. 2009
Carabids	*S. faberi*, *A. trifida*, *Ab. theophrasti and A. retroflexus*	11% day^{-1}	Potato fields	4 weeks	Gaines and Gratton 2010
		5% day^{-1}	Surrounding non-crop habitat	4 months	
Inveterbrates (*Harpalus pensylvanicus*)	*S. faberi*	55% over the season	Corn fields	July-September	Ward et al. 2011
Vertebrates and invertebrates	*Avena ludoviciana* (Durieu), *Hordeum spontaneum* L., *S. arvensis*, *Rumex obtusifolius* L., *Rapistrum rugosum* (L.)	30 - 60% week^{-1}	Barley fields	June-August (6 weeks)	Noroozi et al. 2012

	All.				
Carabids	*Viola arvensis*, *S. media*, *C. bursa-pastoris*	16.5 % day^{-1}	Organic; conventional farm over 1 km radius; mainly studied landscape factors	2 weeks	Jonason et al. 2013
Carabids	*V. arvensis*, *S. media*, *C. bursa-pastoris*, *Alopecurus myosuroides* Huds.	30% week^{-1}	28 winter cereal fields	5 weeks	Trichard et al.2013
Vertebrates and invertebrates	*S. faberi*, *A. trifida*, *A. theophrasti*	31.1-51.6% year^{-1}	corn–soybean soybean–wheat wheat/red clover–corn	3 years	Davis et al. 2013

Figures

Conceptual framework

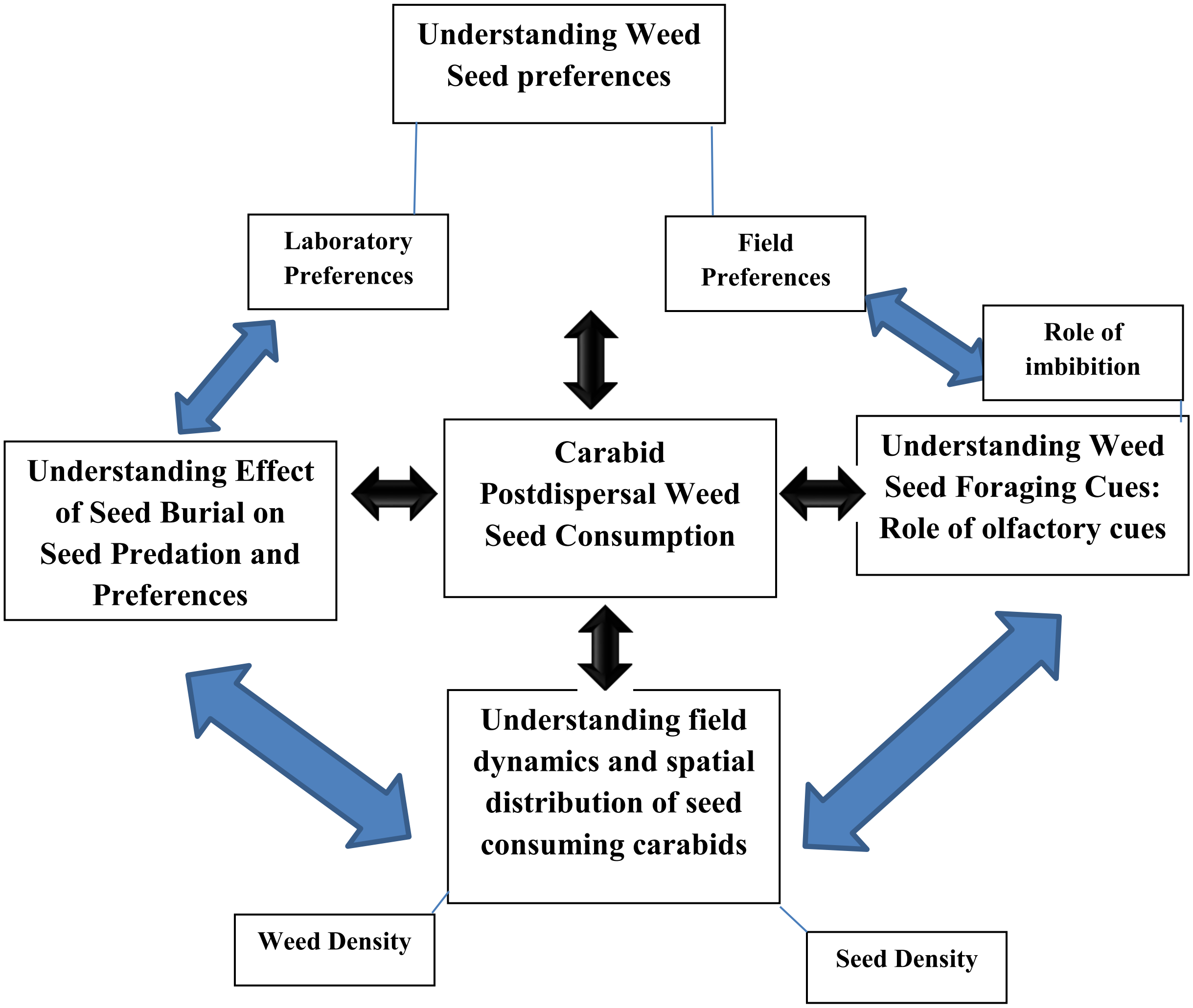

Fig 1.1 Conceptual framework of research activities undertaken in this thesis

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Chapter 2. Brassicaceous weed seed predation by ground beetles (Coleoptera: Carabidae)

This chapter has been published:

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2.1. Introduction

Weed management in agroecosystems is limited by time and monetary constraints (Holm and Johnson 2009). In North America, herbicide use is the major strategy for weed control (Ghersa et al. 2000), and herbicide application comprises 20 to 30% of the cost of crop production (Derksen et al. 2002). In Canada, herbicides represent the major weed management cost, comprising approximately 80% of total annual pesticide sales (Holm and Johnson 2009). In recent years, however, dependence on herbicides has created issues, including selection for herbicide-resistant weeds (Beckie et al. 2006; Egan et al. 2011), off-target spray drift (Grover et al. 1976; Taylor et al. 2004), chemical residues, environmental pollution, and public discontent (Boyetchko et al. 2009; Ruegg et al. 2007).

An integrated approach to weed management that incorporates many “little hammers” or multiple weed-management tactics could be used to manage weed populations more sustainably (Swanton and Murphy 1996). Focusing on management of seedbanks is beneficial because dispersal of weed seeds is central to both weed population dynamics (Davis et al. 2004) and development of weed communities in agricultural fields (Fox et al. 2013). Thus, limiting the number of seeds entering the soil seedbank is critical (Bagavathiannan and Norsworthy 2012; Fox et al. 2013), and, in this regard, the role of natural seed mortality is usefully considered (Petit et al. 2014). Upon dispersal, weed seeds are subjected to a variety of losses, and the ecosystem service of seed predation accounts for a significant proportion of those losses (Heggenstaller et al. 2006). In fact, weed seeds dispersed on the ground are a diverse, spatially heterogeneous, resource-rich food source for seed predators (Hulme 1998) and are associated with diverse assemblages of seed predators in agroecosystems (Lundgren 2009).

Carabid beetles (Coleoptera: Carabidae) are important invertebrate consumers of seeds in temperate agroecosystems (Lundgren 2009; Zhang et al. 1997). Postdispersal seed consumption by carabids can limit seedling recruitment (Crawley 2000; Harper 1977). Some species remove weed seeds buried in the soil because of agricultural operations, in addition to those dispersed on the ground (White et al. 2007). In fact, predation by carabids can be critical to population dynamics of weeds in agroecosystems (Crawley 2000; Lundgren 2009), causing substantial reductions in seedbank numbers (Honek et al. 2003; Martinkova et al. 2006; Tooley and Brust 2002). For example, Jonason et al. (2013) documented weed seed consumption rates of up to 74% in agricultural habitats for field violet (*Viola arvensis*Murr.), common chickweed [*Stellaria media* (L.) Vill.], and shepherd's-purse [*Capsella bursa-pastoris* (L.) Medik.]. Such rates are highly significant, given that annual weed seed losses of 25 to 30% can be sufficient to reduce weed population growth (Firbank and Watkinson 1986). Thus, adjusting agricultural activities to enhance seed predation by carabids has considerable potential for sustainable weed management.

Understanding seed preferences of carabid beetles is an important step toward facilitating natural suppression of weed populations. The relative abundance of granivorous and omnivorous species partially determines the efficacy of the ground beetle assemblage in weed seed consumption. It is, therefore, important to identify the species that can contribute to weed seed removal and to understand their seed feeding preferences. In Canada, more than 900 carabid species are known (Lindroth 1961–1969), and in agroecosystems, 15 to 20% of the soil macrofauna consists of carabids (Goulet 2003); however, their role in weed-seed predation is unclear for many agroecosystems. I focus here on the potential of several common carabid beetle species to act as seed predators of important brassicaceous weeds associated with canola production in western Canada by investigating the seed-feeding preferences of the beetles. Our objective was to identify the important seed-consuming carabid species in canola, the second most widely and frequently grown crop in Canada. In addition to providing data about their feeding preferences, I also determined weed-seed removal rates under field conditions and estimated the relationship between the activity–density of omnivorous carabids and weed-seed removal.

2.2. Materials and methods

2.2.1. Carabid species

Seed preferences of adults of four omnivorous carabid species (*Amara littoralis* Mannerheim [average length: 7.1 mm], *Harpalus affinis* Schrank [average length: 9.4 mm], *Poecilus lucublandus* Say [average length: 9.2 mm] and *Pterostichus melanarius* Illiger [average size: 1.62 cm]) were investigated using laboratory and field studies. Carabids were collected in weedy patches and canola field margins using dry pitfall traps (12 cm in diameter by 14 cm in depth) at the South Campus (53.50°N, 113.52°W) and Ellerslie (53.25°N, 113.33°W) research stations of the University of Alberta (Edmonton, AB, Canada) during the summers of 2011 and 2012. Before initiating the experiments, adult beetles were kept in plastic containers (Gladware; 14 cm by 12 cm by 10 cm; 1.89 L capacity) and starved for 48 h to standardize their hunger level (Lundgren and Rosentrater 2007).

2.2.2. Weed species

Seeds of three common brassicaceous weed species in the study area (Leeson et al. 2005) were used in the laboratory and field experiments. These weed species included volunteer canola 'Q2', as well as field-collected wild mustard and field pennycress. The density of field pennycress typically varies between 6 and 160 plants m^{-2} in canola crops across western Canada, whereas wild mustard densities vary between 2 and 38 plants m^{-2} (Leeson et al. 2005). All seeds were obtained from the South Campus Research Facility, University of Alberta. Seeds were stored at 5 C for 7 mo.

2.2.3. Laboratory choice test

I tested feeding preferences of carabid species for the seeds of the three weed species using laboratory "choice" tests. Because weed imbibition can change the physiological state of the seed (Weitbrecht et al. 2011), I also examined seed feeding preferences for both dry and imbibed seeds in separate choice tests. For choice tests involving imbibed seeds, weed seeds of each species were imbibed separately in Petri dishes (Fisherbrand, Fisher Scientific, Fair Lawn, NJ) lined for 24 h with a wet Whatman filter paper. In each replicated choice test for dry and imbibed seeds, I offered the seeds to an individual beetle of a given carabid species using seed cards (Westerman et al. 2003). For each weed species, I used seed cards (10 cm by 2 cm) made of sand paper and on which 30 seeds (either dry or imbibed) of a given weed species were glued using a double-sided sticky tape (Duck fiberglass indoor and outdoor tape, ShurTech, Avon, OH). Empty parts of the cards, as well as the spaces between seeds, were covered with a thin layer of sand.

For the choice test involving dry seeds, three seed cards, each representing one weed species, were placed at the three corners of a plastic container (Gladware, Glad, Oakland, CA) (22 cm by 22 cm; depth = 6 cm; 2.4 L capacity). An individual adult beetle that had been starved for 48 h was then introduced into the center of the container and held for 72 h. The choice test for imbibed seeds was conducted as above, but with three seed cards each containing imbibed seeds of each weed species placed at the three corners of the container. Tests were replicated 20 times for each carabid species for both dry and imbibed seeds. At the end of the test period, I removed the beetle from the container and counted the number of seeds that had been consumed for each weed species. I used each individual beetle only once. The experiment was conducted at 22 C and with a 16-h photoperiod. Seed size was determined for 50 seeds of each species using an electronic digital caliper (Fisher Scientific).

2.2.4. Field Experiments

To understand seed choice among carabid species and differences in seed consumption rates, a field-choice experiment was also performed. The experiment used a randomized complete-block design, in which weed seeds were exposed to field populations of carabids in cage trials over a 3-wk period. Fields studies were conducted in canola fields at Leduc (53.36°N, 113.58°W) and Vegreville (53.50°N 112.10°W) in 2011, and at Leduc (53.36°N 113.59°W) and St. Albert (53.70°N 113.62°W), AB, Canada, in 2012. The field-choice tests were conducted in August for a period of 3 weeks (Table 2.1) to coincide with the peak activity period of the carabid species tested (Lindroth 1961–1969). The details of the total field area and other agronomic operations are presented in Table 2.1.

Seeds of three weed species (field pennycress, wild mustard, and volunteer canola) were included in the field choice tests. To estimate seed predation among the three weed species, I used the following two different types of cages to limit the access of seed predators to the experimental arena: (1) cages with invertebrate access only (inclusion cages), and (2) exclusion (control) cages that prevented access to all types of seed consumers. The inclusion cages measured 20 cm by 20 cm by 25 cm and were constructed using a hardware mesh (mesh size = 1.1 cm). The exclusion (control) cages had the same dimensions as inclusion cages, but the mesh size was very small (< 1 mm), and the bottom of the cage was also screened to restrict access to all carabid seed consumers. I secured the bottom surface of the cages to the ground using nails, and placed a rain cover made of corrugated plastic sheets (20 cm by 20 cm) over the cages to protect them and the seeds inside from rain.

At each field, cages were constructed at 25 locations spaced 40 m apart, with each of the 25 locations having one inclusion cage and one exclusion cage. Within each type of cage, I placed three seed cards, one for each weed species. Fifty-five seeds of an individual weed species were adhered to a seed card made of a corrugated plastic sheet (8 cm by 7 cm) using double-sided sticky tape (Duck fiberglass indoor and outdoor tape). Empty parts of the cards, as well as the spaces between seeds, were covered with a thin layer of sand. Three seed cards, each containing one of the three weed species, were placed in each cage with placement of cards within the cages randomized across fields. As each of the 25 locations represented all treatment (cage type by weed species) combinations, each location was considered a replicate. Seed cards in each cage were replaced weekly with fresh seed cards. At that time, the number of intact unconsumed seeds was counted on the old seed cards. Seed removal was quantified using the following formula:

$$SR= \{[Re/Ne-Rt/Nt] / \ [Re/Ne]\}*100$$

where *SR* is the percentage of seeds removed because of invertebrate activity (per week), *R* is the number of seeds remaining on the cards in exclusion (*e*) and inclusion (*t*) cages, and *N* was the total number of seeds placed on cards in exclusion (*e*) and inclusion (*t*) cages (Abbott 1925).

To monitor activity–density of carabid species, I placed one pitfall trap half-filled with diluted propylene glycol 1 m away from each pair of inclusion and exclusion cages at each field. Pitfall traps consisted of 0.5 L plastic cups half filled with diluted propylene glycol (11 cm in diameter) dug into the ground and placed flush with the soil surface (Spence and Niemela 1994). Traps were emptied weekly, with adult specimens preserved in 70% ethanol until they could be identified using Lindroth (1961 to 1969). Omnivorous species were categorized and counted based on Larochelle (1990) (Table 2.2).

2.1.5. Statistical analyses

All analyses were conducted using SAS statistical software (version 9.2, 2010, SAS Institute, Cary, NC). The laboratory choice tests were analyzed with ANOVA using the MIXED procedure. Number of seeds consumed by individuals of each carabid species over a 72 h period was modeled as the dependant variable, with the physiological state of the seed (imbibed or dry) included as the fixed effect in the model. Each choice container was considered a block, and block was treated as a random effect. Differences in mean seed consumption among weed species were compared using Tukey's test.

Data for weed seed removal from the field experiment were also analyzed with ANOVA using PROC MIXED, with locations (replicates) treated as random effects, and seed species, sampling week, and their interaction modeled as fixed effects. After a significant result from ANOVA, percentage of seed removal was compared among weed seed species using a posthoc Tukey's test. The data from St. Albert in 2012 were arcsin-transformed to meet the assumptions of normality.

The relationship between activity–density of omnivorous carabids (pooled across species) and the percentage of weed seed removed was explored using linear correlation analysis (PROC CORR). The association between percentage of seed removal and activity–density (pooled across fields) was assessed with Pearson's linear correlation coefficient (ρ). Linear regression was used to assess the relationship between activity–density of omnivorous species and the mean seed removal rate at each field (PROC REG, SAS Institute 2010), with data pooled across species and fields over the entire sampling period. The model contained mean seed removal rate as a dependent variable and the mean activity–density as an independent variable.

2.3. Results

2.3.1. Laboratory choice test

Mean seed consumption of the three weed species differed significantly (Figure 2.1). Carabids of all species preferentially consumed the volunteer canola seeds, whereas field pennycress was least preferred. This ranking was generally consistent for both dry and imbibed seeds, except that mean seed consumption of the three weed species did not differ significantly for *A. littoralis* when seeds were imbibed, but differed when seeds were dry. In short, all other carabid species preferred volunteer canola > wild mustard > field pennycress, regardless of seed physiological state (Figure 2.1).

Each carabid species in this study showed preferences for different weed seeds based on weed species and whether the seed had been imbibed (Figure 2.1). On average, carabids of all species consumed significantly more imbibed seeds than they did dry seeds, although differences varied with weed species (Figure 2.1). For example, *P. lucublandus* adults consumed twice as many imbibed as dry seeds of field pennycress (Figure 2.1d). Likewise, adults of *H. affinis* consumed approximately 1.5-fold more volunteer canola, twofold more wild mustard, and threefold more field pennycress when seeds had been imbibed (Figure 2.1b).

2.3.2. Field Experiments

In this study, seeds of all species were consumed. The greatest weed seed removal was observed for volunteer canola, followed by wild mustard and field pennycress, which is generally in line with results from laboratory preference studies (Table 2.3). At Leduc (2011) and St. Albert (2012), the percentage of weed seed removal varied significantly among weed species ($P < 0.001$) but was not influenced by the effects of sampling week or the interaction between weed species and sampling week. At Vegreville (2011) and Leduc (2012), the percentage of weed-seed removal was significantly influenced by both weed species ($P < 0.001$) and sampling week ($P < 0.01$) but not by the interaction between weed species and sampling week. The mean seed removal rates (pooled across weed species) over the sampling period are presented in Table 2.4.

The activity–density of omnivorous carabids was high during the sampling periods at each field in both years. Carabid species captured in pitfall traps included the omnivores *P. melanarius*, *A. littoralis*, *Amara quenseli* Schönherr, *H. affinis*, and *A. obesa* (Say), among others (Table 2.2). At all fields and in both years, there were statistically significant ($P < 0.001$), positive correlations between activity–density of carabids and the percentage of seed removal. Overall, the strength of relationship between activity–density and mean seed removal rates was high ($\rho = 0.81$) across all fields and years.

I further examined the extent to which the activity–density explained variation in percentage seed removal under field conditions using regression analysis. The effect of activity-density on seed removal was highly significant ($P < 0.0001$), and a linear relationship provided a good fit to the data pooled across all study fields and years (Fig.2.2). The activity–density of omnivorous carabids explained 67% of the variation in mean seed removal rates across all fields and years.

2.4. Discussion

The results of my investigation on carabid weed seed preferences indicate that the three carabid species tested showed specific preferences in terms of weed seed consumption both under laboratory and field conditions, and these preferences were influenced by factors including weed species, physiological state of seeds, and carabid activity-density. Recent findings by Ward et al. (2014) also demonstrated that carabid beetles exhibited preferences for specific weed seeds. In their study, *Harpalus pensylvanicus* DeGeer preferred seeds of giant foxtail (*Setaria faberi* Herrm.) over those of common lamb's quarters (*Chenopodium album* L.) and velvetleaf (*Abutilon theophrasti* Medik). However, my study is, to our knowledge, the first to report preferences of carabid beetles for seeds of phylogenetically related species within a single plant family.

Carabids of all species preferentially consumed the volunteer canola seeds, whereas field pennycress was least preferred. Although the basis of these preferences remains unclear, factors such as nutritional quality and chemical composition of seeds may have contributed to results. For example, the complex effects of domestication might increase palatability of seeds (Chen et al. 2015). Secondary plant compounds can contribute to specific weed-seed preferences in seed predators (Janzen et al. 1977). Members of the Brassicaceae family contain glucosinolates, which are both bitter and toxic to generalist feeders, thus, affecting their palatability (Samuni-Blank et al. 2014). Glucosinolates can cause digestive system damage in insect species that lack specialized mechanisms to neutralize such effects. Field pennycress plants (both foliage and seeds) contain high levels of glucosinolates (Vaughn et al. 2005; Warwick et al. 2002). However, the exact role of glucosinolates in determining weed-seed preferences has not been elucidated, and further research is necessary to determine whether this is the mechanism behind the preferences observed in this study. Seeds of field pennycress also contain up to 36%

erucic acid, which could affect the palatability of seeds (Isbell et al. 2015; Warwick et al. 2002). The toxicity of secondary compounds in seeds can result in feeding deterrence or can contribute to specific weed-seed preferences in seed predators (Janzen et al. 1977). Understanding how plant composition and toxicity shapes feeding preferences of potentially beneficial organisms like carabids will be interesting. As Hulme and Benkman (2002) suggested, the relative influence of seed traits, such as secondary chemical compounds, is not similar for all seed predators but depends on interactions between the traits of consumer species and seed traits. Although well studied for foliage consumers (Berenbaum et al. 1986), potential coevolutionary interactions are less well explored for seed predators. Seed size is also an important determinant of carabid feeding preferences (Gaines and Gratton 2010; Honek et al.2007, 2011; Lundgren 2009). Carabid species belonging to the tribe Zabrini (*Amara aenea* DeGeer and *Amara similata* Gyllenhal) prefer small seeds of the Brassicaceae and Caryophyllaceae compared with, for example, more generalist medium to large Harpaline species, such as *H. affinis*, and *Harpalus signaticornis* (Duftschmid) (Honek et al. 2007). However, there was little variation in seed size among the species included in this study. The average seed sizes (mean ± SD) of volunteer canola, wild mustard, and field pennycress seeds were 3.16 mm (± 0.055), 2.12 mm (± 0.035), and 2.68 mm (± 0.032), respectively, and it is unlikely that such minor differences in seed size contributed to the observed differences in feeding preferences.

Preferences of some other carabid species for imbibed seeds have been reported earlier (Cardina et al. 1996; Harrison et al. 2003; Koprdova et al. 2012). Greater preference toward imbibed seeds may be attributable to softening of the seed coat, thereby improving seed palatability (Lundgren 2009) or to improved nutritional status of imbibed seeds because of changes in metabolic activity (Koprdova et al. 2012). Nonetheless, the nature of changes in seed chemical and nutritional properties in field pennycress upon imbibition and its subsequent effect on seed predatory species like carabids are unknown. However, greater acceptability of imbibed field pennycress seeds may indicate significant changes in nutritional properties.

Weed seed preferences observed in the field studies were in line with the laboratory studies. At all fields and in both years, I observed statistically significant, positive correlations between activity–density of carabids and the percentage of seed removal, which is in agreement with numerous previous studies (Gaines and Gratton 2010; Honek et al. 2003, 2005; Jonason et al. 2013; Menalled et al. 2007; Trichard et al. 2013). Carabid beetle species composition can also influence seed removal rates and overall seed mortality patterns (Honek et al. 2003). In my study, for example, the higher seed removal rates for volunteer canola, compared with wild mustard and field pennycress, are attributable to the local abundance of *P. melanarius*. *Pterostichus melanarius*, which is now a well-established invasive species in western Canada (Bourassa et al. 2011), was the most abundant species at Leduc and to some extent at St. Albert (Table 2.2). A recent study of the gut contents in *P. melanarius* confirms the granivorous behavior of this species under field conditions (Lundgren et al. 2013). Although *P. melanarius* avoids seeds of some species, such as common chickweed (Honek et al. 2003) and field violet (Petit et al. 2014), it does feed on seeds of volunteer canola in Europe (Koprdova et al. 2008: 2012). The results indicate that *P. melanarius* actually prefers volunteer canola seeds over those of other brassicaceous weeds. In contrast, at Vegreville, where activity–

density of *P. melanarius* was much lower, equal numbers of volunteer canola and wild mustard seeds disappeared, perhaps reflecting the fact that *A. littoralis* was numerically the dominant species.

Nevertheless, the strong positive relationship between activity–density of omnivorous carabids and seed removal rates observed in all study fields likely reflects the importance of the nutritional value of seeds. For these omnivorous species, seeds are significant alternate food resources, and their availability can influence biological parameters, such as fecundity and survivorship, while also increasing residence time in a patch (Frank et al. 2011). However, other factors besides nutritional quality can influence seed predation. These other traits include seed coat hardness, seed density, nutritional quality or other morphological traits that determine relative food quality in a habitat (Tooley and Brust 2002; Lundgren 2009).

Understanding seed removal patterns and preferences for weed seeds under field conditions can assist in developing tactics to aid in ecological management of weeds. Seedbank replenishment from seed shed contributes strongly to the establishment and maintenance of volunteer canola populations, which is an important weed in western Canada (Beckie et al. 2006; Knispel et al. 2008). For example, harvest losses of canola can be as high as 3,000 seeds/m^2 in this region (Gulden et al. 2003), and it appears that ground beetle populations can respond (Floate and Spence 2015). In this context, ground beetles may reduce seed stocks in agroecosystems that include canola in the crop rotation. All carabid species that I considered consumed greater numbers of volunteer canola seeds than the other brassicaceous species tested. My results not only quantify volunteer canola seed consumption in western Canada, they also suggest that seed consumption could contribute significantly to volunteer canola management. Reduced tillage systems and other agricultural practices that conserve ground beetle habitat and populations will likely maintain, and perhaps, even increase, weed seed predation, thus contributing to more effective integrated weed management.

Tables.

Table 2.1. Description of canola fields and major agronomic activities during study period.

Fields	**Year**	**Field size (ha)**	**Crop seeding date**	**Herbicide application**	**Study period**
Leduc	2011	35	May 24, 2011	June 18, 2011	August 3 to August 24
Vegreville	2011	21	May 19, 2011	June 21, 2011	August 4 to August 25
Leduc	2012	12	May 21, 2012	June 16, 2012	August 7 to August 26
St. Albert	2012	17	May 21, 2012	June 12, 2012	August7 to August 28

Table 2.2. Total count of omnivorous carabid beetle species (carabid beetles trapped in pitfall traps through sampling period) in the fields at Leduc, AB, and Vegreville, AB in 2011 and Saint Leduc, AB and St. Albert, AB 2012. The beetles were collected using pitfall traps during August, 2011 and 2012.

Carabid Species	Species count			
	Leduc 2011[a]	Vegreville 2011[a]	Leduc 2012[a]	Saint Albert 2012[a]
Pterostichus melanarius Illiger	5480	56	3669	490
Amara carinata LeConte	0	64	0	18
Amara littoralis Mannerheim	765	721	146	297
Amara quenseli Schönherr	43	67	96	0
Amara obesa Say	0	17	12	148
Amara torrida Panzer	32	21	24	43
Harpalus affinis Schrank	14	58	3	17
Ophonus spp.	8	0	0	40

Table 2.3. The percentage of weed seed removal per week for volunteer canola, wild mustard and field pennycress in canola fields at Leduc, AB, Canada in 2011 and 2012, Vegreville, AB in 2011and St. Albert, AB, Canada in 2012.

	Percentage of seeds removed week^{-1}		
	Volunteer Canola	Wild Mustard	Field Pennycress
Leduc 2011	69.7 ± 2.0[a]	58.9 ± 2.0[b]	28.2 ± 2.0[c]
Vegreville 2011	42.3 ±0.9[a]	41.0±0.9[a]	16.9 ± 0.9[c]
Leduc 2012	76.6 ± 1.2[a]	68.0 ± 1.2[b]	22.9 ± 1.2[c]
St. Albert 2012	65.6 ± 2.1[a]	57.1 ± 2.1[b]	25.0 ± 2.1[c]

[a] within a row, different letter represents significant differences ($P < 0.05$)

Table 2.4. The percentage weed seed removal per week in canola fields at Leduc, AB, Canada in 2011 and 2012, Vegreville, AB in 2011and St. Albert, AB, Canada in 2012.

	Percentage Seed removal		
	Week1	Week2	Week3
Leduc 2011	52.5 ± 2.1 [a]	51.8 ± 2.1 [a]	52.5 ± 2.1 [a]
Vegreville 2011	34.4 ± 0.9[a]	34.9 ± 0.9[a]	31.6 ± 0.94 [b]
Leduc 2012	56.3± 1.2 [a]	57.2 ± 1.2 [a]	53.33 ± 1.2 [b]
St. Albert 2012	49.4 ± 2.1[a]	48.9 ± 2.1 [a]	49.43± 2.1 [a]

[a] within a row, different letter represents significant differences ($P < 0.05$)

Figures.

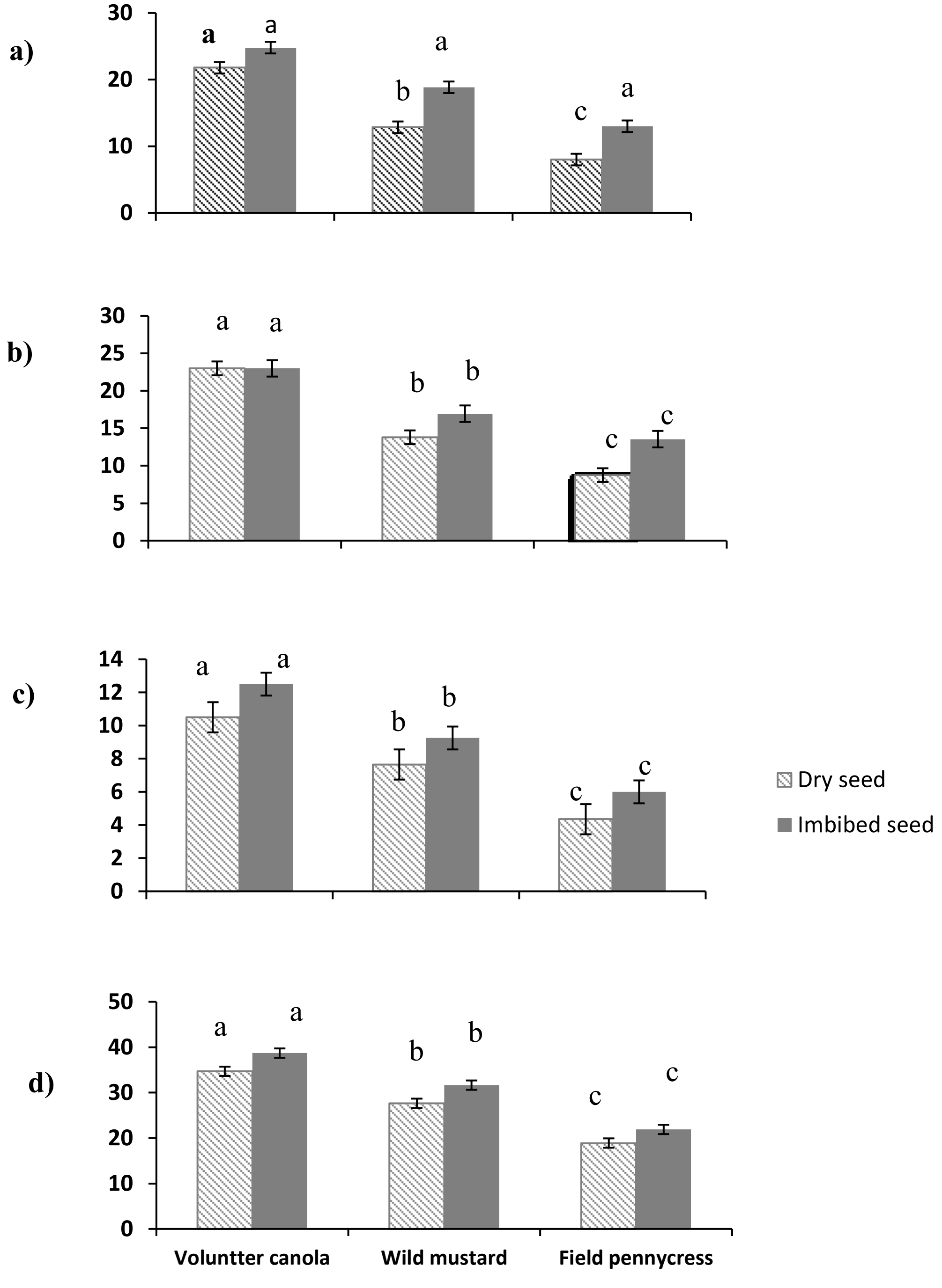

Fig. 2.1a-2.1d.The mean seed consumption by a)*A. littoralis*, b)*H. affinis*, c) *P. melanarius* and d) *P. lucublandus* on the seeds of three brassicaceous weed species over a period of 72 h. Respective bars for dry and imbibed species followed by the different

letter indicate statistically significant treatment differences. Means followed by the same letter are not significantly different at P = 0.05 by using ANOVA and Tukey’s studentized range test. Comparisons of weed seed consumption are valid only within each carabid species, weed species and physiological state

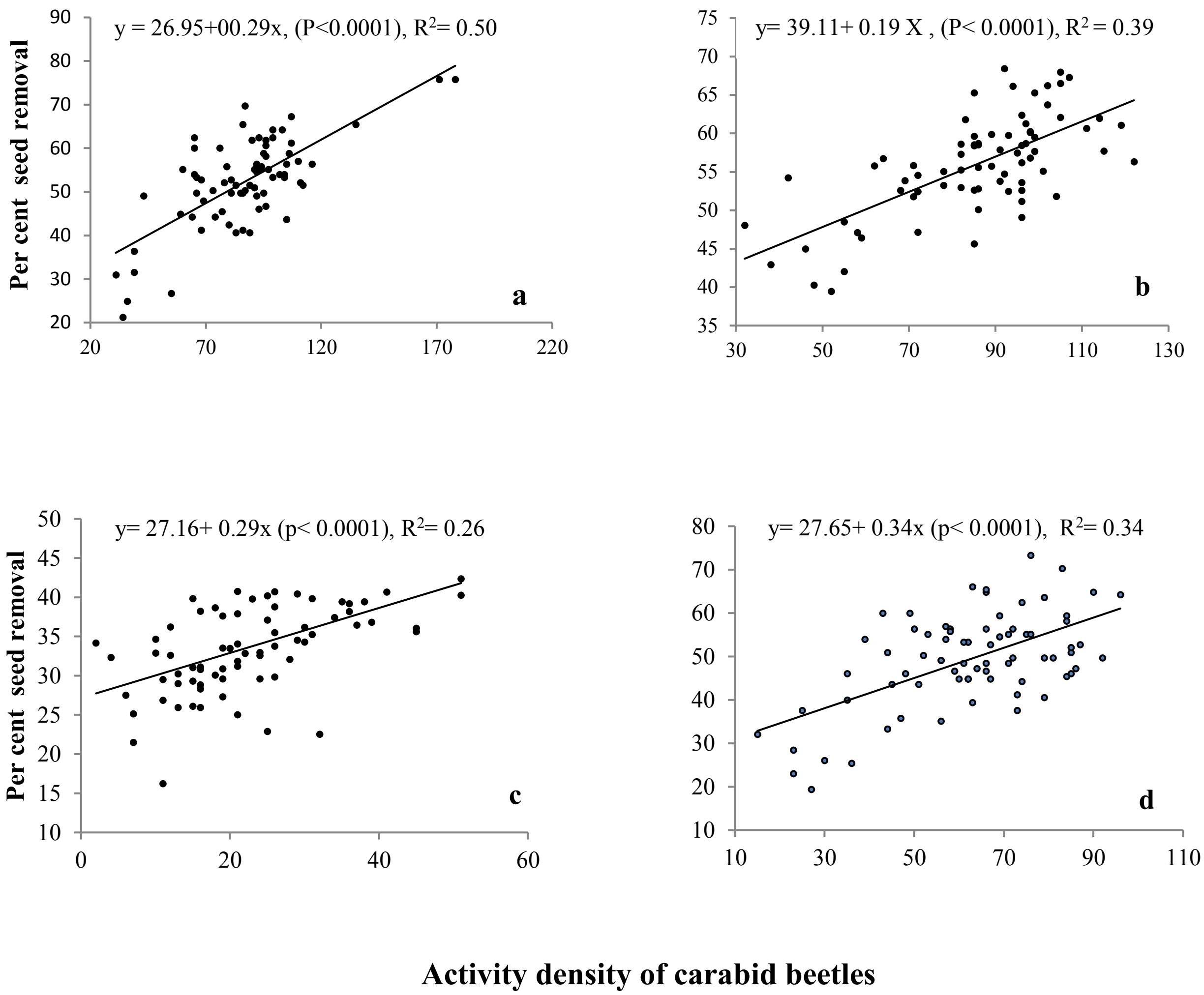

Fig.2.2a-2.2d. Relationship between per cent seed removal per week and activity-density of omnivorous carabid species at a) Leduc, AB in 2011, b) Leduc, AB in 2012, c) Vegreville, AB in 2011 and d) St. Albert, AB in 2012. The middle line represent the linear model *y= a+bx,* where *y* represents per cent seed removal per week at *x* activity-density (beetles trapped per week) of omnivorous carabid species and b is slope. The 95% Confidence intervals around the fitted line are presented in the figure.

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Chapter 3. Seed detection and discrimination by ground beetles (Coleoptera: Carabidae) are associated with olfactory cues

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3.1. Introduction

Carabid beetles (Coleoptera: Carabidae) are invertebrate predators, some of which consume weed seeds in temperate agroecosystems (Zhang et al. 1997; Bohan et al. 2011). In fact, post-dispersal seed consumption by carabids can limit population growth of weedy plants (Harper et al. 1977; Crawley 2000) and affects the population dynamics of weeds in agroecosystems (Crawley 2000; Lundgren 2009). However, the extent to which seed predation constrains weed population growth depends on the ability of predators to detect them (Lundgren 2009; Westerman et al. 2006; Baraibar et al. 2009; Cromar et al. 1999; Honek et al.2003, 2007; Ward et al. 2014), and little is known about these processes.

Most invertebrate predators use a variety of sensory cues in localizing prey or habitats in which prey may be found (Vet et al. 1983; Toft et al. 2002; Schapers et al. 2015). Ground beetles assess habitat suitability using a range of cues and it is well known that volatile chemicals associated with the habitat can be involved (Thiele 1977; Lovei and Sunderland 1996). Granivorous carabids also use tactile stimuli associated with seeds, particularly seed structural strength and physical density in seed detection (Trefas et al. 2001). Volatile compounds associated with hosts or prey items provide olfactory cues that help many invertebrates orient to food (Kielty et al. 1996; Trefas and Van Lenteren 2008), and perception of such olfactory cues also play an important role in detecting food patches or selecting sites for oviposition among ground beetles (Vet et al. 1983; Trefas and Van Lenteren 2008; Evans 1983).

Despite the probable importance of olfactory cues in organizing these behaviours, research about the possible role of olfaction in seed detection has been limited. For example, it remains uncertain whether visual cues, olfactory cues, or a combination of both guides seed detection and selection. A recent study (Law and Gallagher 2015) suggests that volatile compounds emitted by imbibed seeds influence weed seed detection in the ground beetle, *Harapalus pensylvanicus* DeGeer; however, potential differences among carabid species in response to olfactory cue recognition and in seed preferences have not been well explored.

Many dormant weed seeds linger in in the soil seedbank either partially or completely imbibed (Law and Gallagher 2015). *B. napus* seeds, for example, can remain dormant in an imbibed state for up to five years (Dalling et al. 2011). As a result, weed seed predators such as carabids are likely to be exposed to both dry and imbibed seeds during foraging. Whether seeds are imbibed is an important consideration for seed predation research because imbibition triggers chemical processes in the seed that can result in the release of volatile compounds such as ethanol and acetaldehyde (Tokumasu and Kakihara 1990; Lee et al. 2001). Release of these cues may, in turn, affect seed discovery and, ultimately, seed consumption, and thus elucidating such cues can help us to better understand the mechanisms of seed detection, and thus, the probability of species consuming various weed seeds in different environments.

Carabids are able to detect weed seeds that are buried in soil (White et al. 2007; Jorgensen 2001; Harrison and Gallandt 2001), suggesting that adult beetles use cues in addition to visual or tactile stimuli to detect seeds. However, both the mechanisms underlying weed seed detection and the potential role of olfactory cues are unknown for a significant proportion of carabid species that eat weeds. In order to better understand these relationships, I investigated whether three omnivorous carabid species used olfactory cues to detect the presence of seeds of brassicaceous weed species, and whether beetle responses to olfactory cues differed between unimbibed and imbibed seeds. I tested beetle preferences for both imbibed and unimbibed seeds in olfactory bioassays. I hypothesized that cues associated with seed odors lead to a behavioural response in adult carabids, and that such responses will differ among unimbibed and imbibed species.

3.2. Materials and methods

3.2.1. Carabid species

The carabid beetles used in the study were collected in weedy patches and canola (*Brassica napus* L.) field margins using dry pitfall traps (12 cm diameter by 14 cm depth). All collections were made during the summers of 2012 and 2013 at the South Campus (53.50° N, 113.52° W) and Ellerslie (53.25° N, 113.33° W) Research Stations of the University of Alberta, Edmonton, Canada. For the experiments described here, I used adults of three omnivorous carabid species, *Amara littoralis* Mannerheim, *Harpalus affinis* Schrank, and *Pterostichus melanarius* Illiger, all of which are common in agroecosystems of central Alberta, and known to feed on weed seeds. After capture, adult beetles were held in plastic containers (Gladware®, 14 cm x 12 cm x a cm, 1.89 L capacity) at 21°C with a 16 h photoperiod in the laboratory, and were starved for 48 h, prior to use in the bioassay experiments described below.

3.2.2. Olfactory bioassays

To investigate whether olfactory cues associated with particular seeds played a role in seed foraging, I used both multi-choice and two-choice bioassays. Seeds of three brassicaceous weed species (*Brassica napus* L. (considered weedy as volunteers), wild mustard, *Sinapis arvensis* L., and field pennycress, *Thlaspi arvense* L.) were collected from the sites mentioned above and stored at 5° C for seven months prior to use in the bioassays. All three weed species are common in local agroecosystems (Leeson et al. 2005) and their seeds are readily consumed by carabids (Kulkarni et al. 2016).

Laboratory bioassays were conducted using a four-chambered olfactometer (Analytical Research Systems, Gainesville, Florida, USA, Model #OLFM-4C-2440PE, Fig.3.1). Single carabids were introduced into the insect inlet adapter (IIA) of the olfactometer (Fig. 3.1) and given 20 minutes to orient and choose a 'preferred' odour source chamber from among four treatments. Two sets of experiments were carried out as described below.

In the first set of bioassays, the treatments were three 20mg masses of seeds of *B. napus*, *S. arvensis* and *T. arvense*, respectively, placed on a piece of filter paper in one of the chambers, and a similar blank filter paper without seeds provided as a control. All trials were replicated 40 times, using either imbibed or unimbibed seeds of all three weed species, each time with naïve beetles.

I assumed that beetles either chose insect isolation traps (IITs) at random or that their choices reflected odours emanating from different seeds held in the internal odour source (IOS). I observed the behavior of each beetle and recorded the times when it entered any IIT and exited this chamber and into the main arena. Absence of specific orientation behavior or apparently random walking movements, e.g., entry and immediate retreat from various IITs, or a lack of any movement in the olfactometer arena, were scored as lack of choice. For each insect tested, data were recorded for choice of IIT and 'residence time' (time in minutes spent in each IIT). The longest residence time was taken to be the 'choice' of each individual beetle.

Treatments were assigned randomly to the odour chambers for replicate trials, and positions of the chambers were changed every five runs to minimize bias resulting from orientation of the apparatus. Internal odour sources (IOS) and insect isolation traps IITs were rinsed with 70% ethanol and dried between runs to minimize effects of any residual odours. Olfactory bioassays were conducted under red light (Philips 23 W PAR38 Red light) to simulate nocturnal conditions in the field (Allema et al. 2012).

Given the overall preference observed among all three carabid species for seeds of *B. napus* (Kulkarni et al. 2016), I employed a second bioassay to further understand how preferences were affected by imbibition by directly comparing responses between imbibed and unimbibed seeds in a two-choice olfactometer. For these experiments, I converted the olfactometer to function as a two-chambered arena by plugging and stopping airflow to two of the odour inlets. In one of the two operational chambers, I placed 200 mg of unimbibed *B. napus* seed, while in the other I placed the same mass of imbibed seeds. As above, 40 individual beetles of each species were tested.

3.2.3. Statistical analyses

A chi-square (PROC-FREQ) test was used to analyze data from the first (four-chambered) olfactometer experiments. To identify if preferences existed among the odours emanating from imbibed and unimbibed seeds of the three weed species, residence time for each weed seed species and a control (four-choice assay) were compared with mixed-model ANOVA (PROC MIXED) (SAS 2010), using residence time as the response variable to be predicted by weed species. Analyses were carried out separately for both imbibed and unimbibed seeds for each carabid species, with weed species treated as a fixed effect.

Data about imbibed seeds did not meet the assumptions of ANOVA; therefore, I fitted generalized estimating equations (GEEs) to these data using PROC GLIMMIX with a negative binomial error distribution function (PROC GLIMMIX) (SAS 2010). Numerous possible error distribution functions were tested, including the Poisson distribution, but the negative binomial error function provided the best fit (based on the ratio of Chi-square/df ratio being close to 1). I tested models similar to those for unimbibed seeds. Differences in mean residence times among weed species were compared using Tukey's *post-hoc* test. Data from the second bioassay comparing responses to unimbibed and imbibed *B. napus* seeds were analyzed using a chi-square test (PROC FREQ) to establish if preferences existed.

Numerous possible error distribution functions, including the Poisson distribution, were tested but the negative binomial error function provided the best fit (based on the ratio of Chi-square/df ratio being close to 1). I tested similar mode to those for unimbibed seeds. Differences in mean residence times among weed species were compared using Tukey's *post-hoc* test. Data from the second bioassays comparing responses to unimbibed and imbibed *B. napus* seeds were analyzed to establish preferences using a chi-square test (PROC FREQ).

3.3. Results

More adults of all three carabid species responded to odours from unimbibed seeds of *B. napus* in the four-choice bioassays than to other weed species (Fig. 3.2a), and this was especially pronounced for *A. littoralis* adults ($\chi^2 = 45$, $P < 0.0001$). Although not statistically significant, similar trends were observed for *H. affinis* ($\chi^2 = 7.05$, $P = 0.07$) and *P. melanarius* ($\chi^2 = 5.2$, $P = 0.16$).

Residence times were significantly longer in response to unimbibed seed odour than to controls for *P. melanarius* ($F = 4.51$; df = 3, 117; $P = 0.004$), *H. affinis* ($F = 13.53$, df =3, 114; $P = 0.001$ Fig. 3.3a;) and *A. littoralis* ($F = 86.12$; df = 3, 117; $P = 0.0001$). Post-hoc tests reveal, however, that residence times differed significantly among the three weed species for only *A. littoralis*. Adults of *A. littoralis* spent approximately 10, 4, and 1 minutes in the chambers with odors of unimbibed seeds of *B. napus*, *S. arvensis* and *T. arvense*, respectively. Residence times in chambers with *B. napus* were significantly greater than in chambers with *S. arvensis, T. arvense* or controls. Interestingly, responses of *A. littoralis* did not differ between the control and field pennycress, but both treatments prompted significantly less response than did odours from *B. napus* and *S. arvensis*.

Responses to odours from imbibed seeds of the three weed species also varied among carabid species but in a different way (Fig. 3.2b). A greater percentage of both *P.*

melanarius ($\chi^2 = 15.6$, $P < 0.001$) and *H. affinis* ($\chi^2 = 17.1$, $P < 0.001$) responded to odours of *B. napus* compared with *S. arvensis* and *T. arvense*, and both species responded more strongly to *S. arvensis* than to *T. arvense* (Fig. 3. 2b). For example, 52% of *P. melanarius* adults responded to odours from *B. napus* compared with 25% from *S. arvensis* and only 16% from *T. arvense*. Interestingly, the percentage of *A. littoralis* adults responding to different odour sources from imbibed seeds did not differ significantly among weed species ($\chi^2 = 2.1$; $P = 0.34$), although the same trend was observed among the mean responses (i.e., *B. napus* > *S. arvensis* > *T. arvense*) (Fig. 3.2b).

Overall response, measured as residence times differed among odour treatments for imbibed seeds in all three species: *P. melanarius* ($F = 18.11$, df = 3, 108; $P < 0.0001$), *A. littoralis* ($F = 19.53$, df = 3, 117; $P < 0.0001$) and *H. affinis* ($F = 34.02$, df = 3,117; $P < 0.0001$) (Fig.3.3b). Although mean residence times did not differ between weed species for *A. littoralis*, responses to all weed species differed from those of the control (0 minutes). Both *P. melanarius* and *H. affinis* spent longer times in the odour chamber of *B. napus* seeds than the other two weed species and control.

To explicitly compare carabid responses to unimbibed and imbibed seeds I compared these in two-choice bioassays using seeds of *B. napus*. In these two-choice experiments adults of all three species showed a stronger response to imbibed seeds (*P. melanarius*: $\chi^2 = 8.10$, $P < 0.01$; *A. littoralis*: $\chi^2 = 14.40$, $P < 0.0001$; *H. affinis*: $\chi^2 = 6.40$, $P = 0.01$) compared to unimbibed seeds (Fig.3.4).

3.4. Discussion

Carabid beetles of three species common in prairie agroecosystems of western Canada exhibited different behavioral responses to olfactory cues associated with the seeds of weed species also common in those ecosystems. In bioassays of response to odours of both unimbibed and imbibed seeds, *B. napus* seeds were most preferred overall, followed by those of *S. arvensis* and *T. arvense*, respectively. Because these carabids also exhibited the same order of preference for consumption of these species in previous experiments (Kulkarni et al. 2016), I reason that olfactory cues are being used in seed foraging. Taken together, and assuming that response to odours should be strongest for preferred seeds, these results show that carabid species differ in their physiological abilities to detect particular odours associated strictly with seeds alone. This may not necessarily be associated with differences in ability to find seeds under field conditions, however, as ecological setting may also influence the ability of beetles to detect weed seeds (Kulkarni et al. 2015).

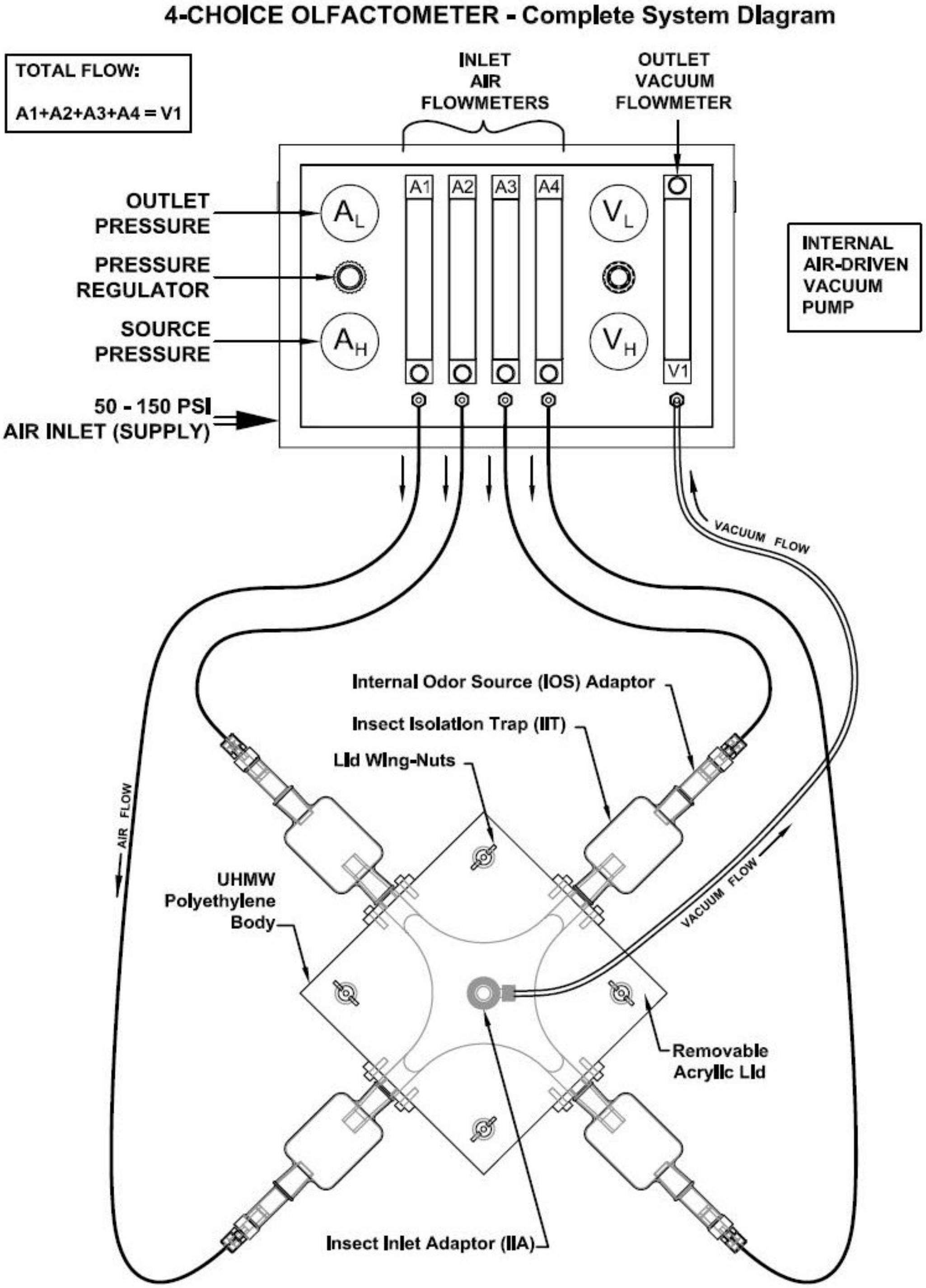
Response of all carabids to olfactory cues was much enhanced by seed imbibition. In fact, two of the three species included in my study, *P. melanarius* and *H. affinis,* responded significantly only to odours emanating from imbibed seeds. Although *A. littoralis* responded to odours emanating from both dry and imbibed seeds, the beetles of this species responded more strongly to odours associated with imbibed seeds of *B. napus* compared with unimbibed seeds. Thus, preferences for imbibed seeds of various weed species appears to vary among carabid species.

Residence time in an odour chamber has been frequently used to indicate the attractiveness of an odour to the test species (Vet et al. 1983), and longer residence times have been interpreted as arrestment caused by an odour (Trefas et al. 2001). In our study, *A. littoralis* had longer residence times in chambers with odours emanating from either unimbibed or imbibed *B. napus* seeds, while both *P. melanarius* and *H. affinis* showed greater arrestment only in response to imbibed *B. napus* seeds. This suggests that arrestment responses of carabids may be a function of both the physiological state of the seed and the carabid species tested.

Although I know that olfactory cues can be significant in carabid detection of invertebrate prey (Kielty et al. 1996; Mundy et al. 2000; Oster et al. 2014), relatively little is known about behavioural responses of carabids to potential olfactory cues emitted by weed seeds. A better understanding differential responses of beetles to seed odours has implications for understanding weed seed predation under field conditions. For example, the extent to which carabids will affect the fate of weed seeds, particularly unimbibed dormant seeds in the seedbank, will be determined by the capacity of individual species to detect weed patches. The fate of imbibed seeds, on the other hand, is more likely to be a function of weed species as opposed to composition of carabid species assemblages. Weed species such as *B. napus*, for example, appear more likely than other brassicaceous weeds to be detected by seed predators, such as *A. littoralis* and *H. affinis* that are prominent in canola fields.

My research indicates that the carabid species tested showed differential behavioral responses to weed seed odors, in isolation of other cues. In addition, I have shown that carabid responses to seeds are affected by the physiological state of seeds. In particular, seed imbibition increased the attraction to olfactory signals emanating from seeds of all weed species. Variation in the sensitivity of carabids to olfactory cues from three common brassicaceous weed species could be associated with discrimination among weed species in the field by carabid seed predators.

Figures.



Source: ARS, Gainsville, USA

Fig. 3.1. Schematic of a four-chambered olfactometer. The main choice arena of the olfactometer measured 30.48 x 30.48 x 2.54 cm, and was covered with a removable lid. It consisted of four outlet ports laterally connected to four odour source chambers, and a ventral insect inlet port to introduce the test insect. Each lateral outlet port was connected to the internal odour source (IOS) with a glass insect isolation trap (IIT). The odour source was connected to an air delivery system that pumped moist air through the odour sources to the choice arena, and a vacuum to the insect inlet chamber to centralize the airflow throughout the choice arena. The rate of air delivery was 1 L/min. The air from all the odour sources was directed to the insect inlet chamber using a vacuum suction mechanism, and this exposed the test insect to odours emanating from different chambers, allowing it to make a choice.

Image source: ARS, Gainesville, Florida

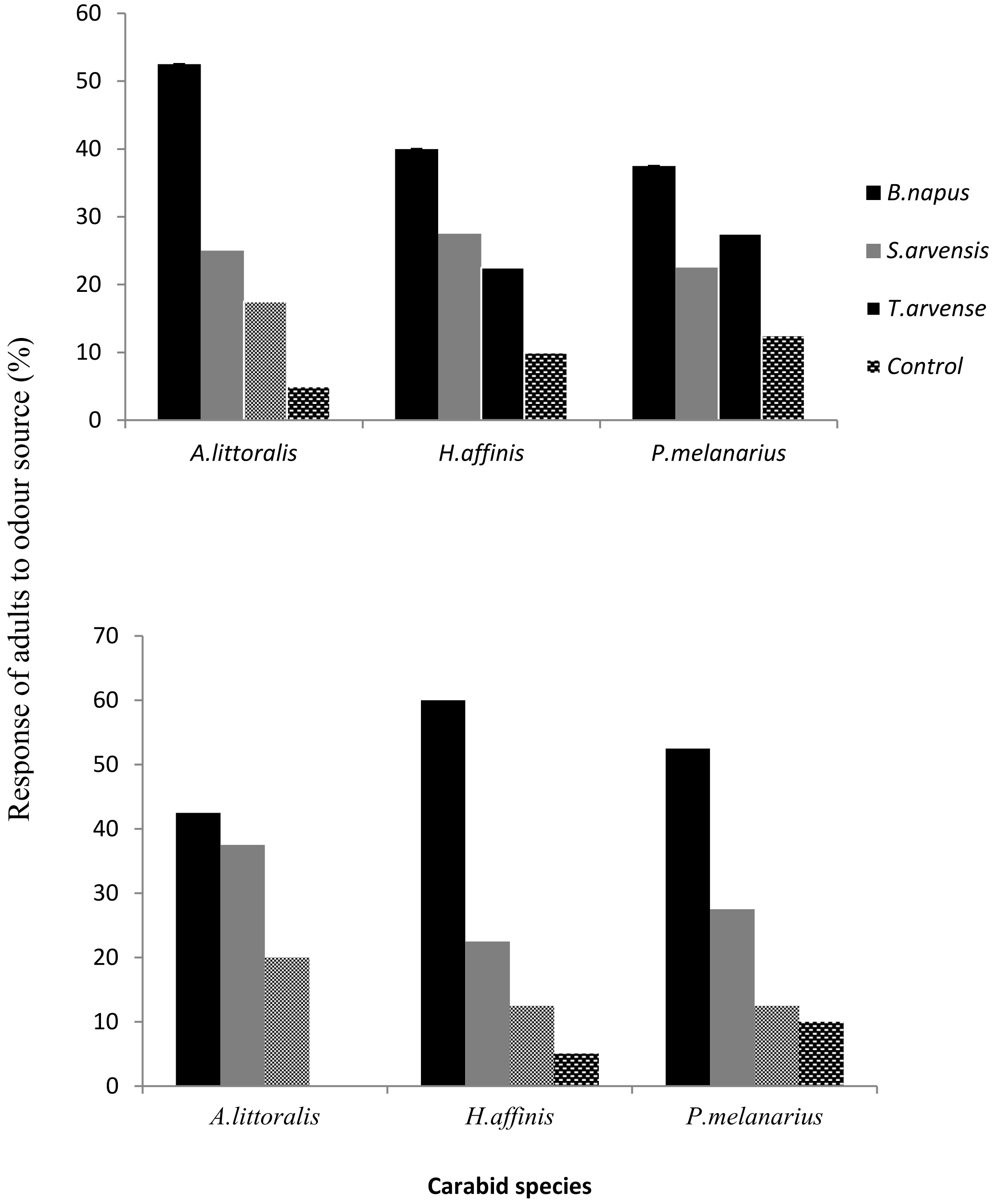
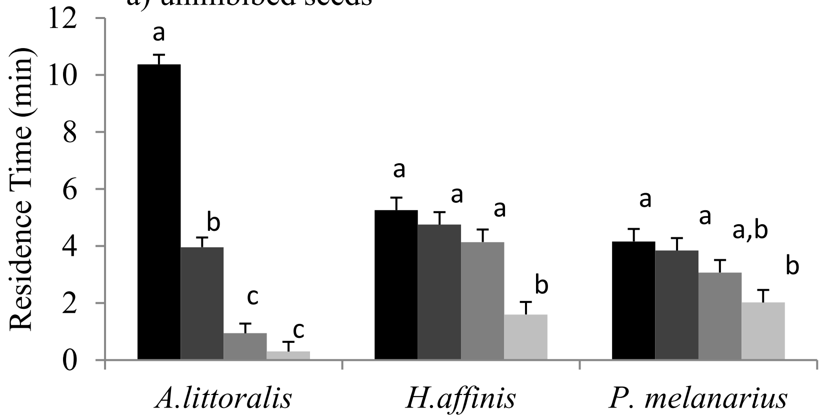


Fig. 3.2a-b. Percentage of *A. littoralis* and *H. affinis* and *P.melanarius* adults responding to odour emanating from a) unimbibed seeds and b) imbibed seeds of *B.napus, S.arvensis, T. arvense* and control chambers of a four chambered olfactometer.

a) unimbibed seeds



b) imbibed seeds

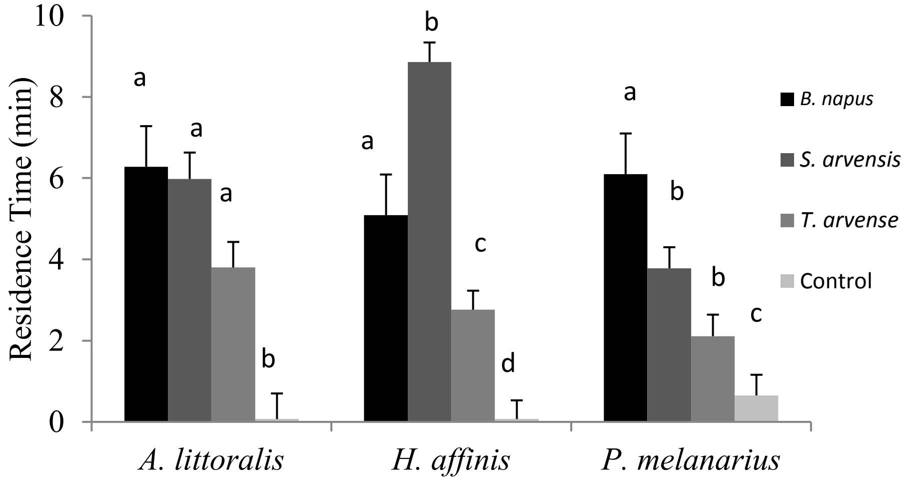


Fig. 3.3. Mean residence time, i.e., time spent by the carabid species *P. melanarius*, *A. littoralis* and *H. affinis* in the odour chambers (min ± S.E) with a) unimbibed seeds and b) imbibed seeds of *B.napus, S.arvensis, T. arvense* and control chambers of a four chambered olfactometer. The chamber with longest residence time from among four choice treatments was considered the final choice of the species. Bars with similar letters indicate no significant difference between residence times among treatments using Tukey's *post-hoc* test

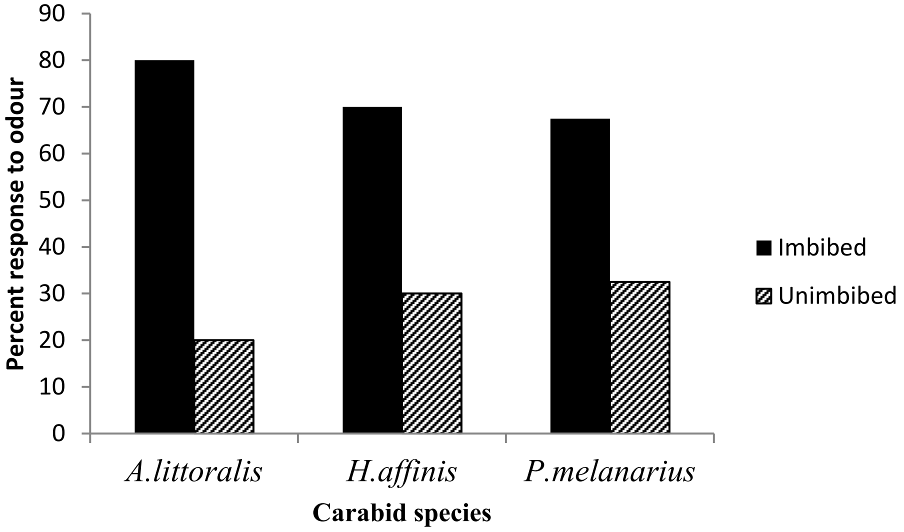


Fig. 3.4. Percentage of *P. melanarius*, *A. littoralis* and *H. affinis* adults responding to odour emanating from unimbibed and imbibed seeds of *B.napus* in a two choice bioassay

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Chapter 4. Depth of seed burial and gender influence weed seed predation by three species of ground beetle (Coleoptera: Carabidae)

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4.1. Introduction

Seedbanks contribute significantly to the assembly of weed communities in agricultural fields and, therefore, effective weed management strategies minimize the number of weed seeds entering the soil seedbank (Fox et al. 2013). The role of ecological services, such as weed seed predation provided by invertebrates, can thus be an important component in the ecological management of weed populations (Petit et al. 2014). Weed seeds are available at the soil surface, but may also be buried at varying depths under field conditions as a result of agronomic practices and natural processes including soil movement, erosion, and the development of soil cracks (Martinkova et al. 2006). Such burial may affect postdispersal seed consumption, but little is known about this possibility (Harrison and Gallandt 2012; White et al. 2007). Other factors known to influence seed predation include the impact of agricultural management activities (Brust and House 1988; Hatten et al. 2007; Menalled et al. 2007), seasonal population fluctuations of seed predators (Honek et al. 2005), phenological changes in the seed predator's life cycle (e.g., overwintering stages, breeding season, dispersal, etc.), high-level trophic interactions (Davis and Raghu 2010), presence of alternative food sources (Frank et al. 2010, 2011), air temperature (Saska et al. 2010), seed distribution patterns on the soil surface (Noroozi et al. 2012), and the method of seed exposure in the field (Saska et al. 2014; Shuler et al. 2008).

Among invertebrate seed consumers, carabid beetles (Coleoptera: Carabidae) are important seed predators in temperate agroecosystems (Kulkarni et al. 2015; Lundgren 2009). Postdispersal seed consumption by carabids can effectively limit the population growth of weedy plants (Crawley 2000; Harper 1977) and influences the population dynamics of weeds in agroecosystems (Crawley 2000; Lundgren 2009). For example, White et al. (2007) reported a reduction in the range of 4–6% and 4–13%, respectively, in the emergence of weed species such as velvetleaf (*Abutilon theophrasti*Medik) and giant foxtail (*Setaria faberi* Herrm.) under field conditions. Adults of some carabid species, such as *Harpalus pensylvanicus* DeGeer, remove weed seeds that are buried in the soil as well as those that are dispersed on the surface (White et al. 2007), and these species could prove beneficial in reducing the soil seedbank.

The large and rapid adoption of canola in western Canada (Canola Council of Canada 2014) has produced a sizeable volunteer canola population, due in part to pre- and postharvest canola seed losses (Beckie et al. 2006, Knispel et al. 2008), which can be as high as 3,000 seeds m^{-2} (approximately 5.9% of the crop seed yield) (Gulden and Shirtliffe 2009). As a result, volunteer canola has become a prominent weed in western Canada (Gulden et al. 2003, Leeson et al. 2005). Some of these seeds are buried, often at shallow depths, where they are prone to a variety of dispersal and mortality factors (Gulden et al. 2004). However, seed burial at greater depths can result in secondary dormancy and the potential for future weediness (Gulden et al. 2004). Weed seed predators, such as ground beetles, may play an important role in management of volunteer canola populations.

A better understanding of the role of weed seed predation by carabids in canola agroecosystems could potentially contribute to designing ecologically based integrated weed management tactics. However, only a few studies have addressed the effects of seed burial on seed consumption by invertebrates, including carabids (Harrison and Gallandt 2012; White et al. 2007) and field crickets (*Gryllus pennsylvanicus* DeGeer) (White et al. 2007). Although these studies did report that seed burial depth affected seed consumption, the results depended on both the species of carabid beetle and the species of weed seed (White et al. 2007). None of these studies examined interactions among seed burial depth, beetle species, and beetle gender. Therefore, the objective of this study was to determine the impact of seed burial depth and beetle gender on canola seed consumption and feeding potential of three carabid species common to western Canada.

4.2. Materials and Methods

Live adult beetles of each species (*Amara littoralis* Mannerheim, *Harpalus affinis* (Schrank), and *Pterostichus melanarius* (Illiger)) were collected using dry pitfall traps (12-cm diameter and 14-cm length) in canola fields at the South Campus Research Station (53.50° N, 113.52° W) and in weedy volunteer canola patches at the Ellerslie Research Station (53.25°N, 113.33°W) in the summer of 2013. Both of these University of Alberta research stations are near Edmonton, AB, Canada. Captured beetles were identified to species and their gender was determined using Lindroth (1961–1969). All beetles were then placed in plastic containers (Gladware®; 14 cm by 12 cm by 10 cm;

1.89 L capacity) lined with plant material and weed debris. To standardize hunger levels, beetles were separated individually in Petri dishes with moist filter paper and starved for 48 h at 5^0 C before initiation of each experiment as in Lundgren and Rosentrater (2007).

For each carabid species, consumption rates were determined for seeds on the soil surface and at four depths (0.5, 1, 2, and 4 cm) below the soil surface. For experiments with *H. affinis* and *P. melanarius*, 40 dry seeds of volunteer canola (average diameter = 3.13-cm and seed mass = 0.272 mg for 40 seeds) were included in each treatment, whereas only 20 seeds were used for *A. littoralis*. The number of seeds used in each experiment was determined on the basis of laboratory research showing that the daily consumption of volunteer canola seeds differed markedly among these carabid species (data not shown).

Experiments were conducted in plastic containers (25-cm diameter and 20-cm deep) in which seeds had been buried at different depths, with one container used for each depth treatment. The bottom of each container was covered with a mesh sieve (1 mm) to prevent beetle escape through drainage holes. The soil used for experiments was collected from the fields where beetles were initially gathered. Soil was first steam sterilized and sifted (500-µm slots) to remove organic matter and seeds, and was then placed in each container to form a 10-cm-deep layer. Soil was moistened periodically by sprinkling water using a wash bottle. Surface-available canola seeds (0 cm) were scattered on top of the soil layer, whereas the seed burial depth treatments were established by placing seeds at 0.5, 1, 2, or 4 cm depths in the soil layer. For each burial depth, 10 containers were maintained separately for either males or females of each carabid species (i.e., 10 replicates/gender per species per burial depth). A single adult beetle was released in each container for an exposure period of 72 h. All containers were held in an insect rearing cage (51.5 by 72.5 cm) on a greenhouse bench at 22 C and under a 16-h photoperiod. At the end of each trial, beetles were counted and removed and the soil was carefully sifted using a sieve (1.2 mm) to recover any intact seeds in all containers that still harbored a single beetle. There was no mortality at the end of the trial. The total number of seeds consumed was calculated for each trial as the final number of seeds exhumed subtracted from the initial number of seeds placed in each container.

Statistical analysis was conducted using SAS (SAS Institute version 9.2, Cary, NC) in a manner consistent with a completely randomized experimental design. Before analyses, I used Kolmogorov–Smirnov and Levene's tests to confirm that data met the assumptions of ANOVA. Although the data were normally distributed, the residual variances were unequal and so heterogeneous error variances were modeled using Satterthwaite's method for variance adjustments (SAS Institute 2010). This was accomplished with a REPEATED statement that adjusted for unequal variances in ANOVA by defining the interaction among species, gender, and depth with a GROUP statement in PROC MIXED (SAS Institute 2010). Carabid species, gender, and burial depth of seeds and interactions of these factors were treated as fixed effects in the model. Differences in least-square means among treatments were compared using Tukey's test (SAS Institute, 2010). Data on weed seed predation for males and females of each carabid species were fitted using appropriate linear or nonlinear models (PROC REG). The data on weed seed consumption with respect to depth for females of *A. littoralis* and *H. affinis* were fitted using a linear model. Second-order polynomial models were fitted to both males and females of *P. melanarius* and to males of *A. littoralis* and *H.*

affinis because the quadratic term significantly increased the explained variance relative to a linear model.

4.3. Results

Mean weed seed consumption was significantly influenced by the depth of seed burial ($P < 0.001$), carabid species ($P < 0.001$), gender of the beetles ($P < 0.001$), and the three-way interaction among depth, species, and gender ($P = 0.04$). Consequently, effects of seed burial depth were further analyzed within species and gender. The rate of seed consumption varied substantially at different depths, and consumption of seeds buried at specific depths differed among carabid species and gender (Table 4.1, Fig. 4.1). Higher seed consumption was observed for seeds scattered on the soil surface (0 cm) compared with buried seeds. However, the nature of the relationship between seed consumption and seed burial was not linear for all species, or even within species. For example, females of *A. littoralis* and *H. affinis* exhibited a linear decline in weed seed consumption with increasing depth, whereas a quadratic relationship was observed for males of these species (Fig. 4.1). Seed consumption for both males and females of *P. melanarius* exhibited a curvilinear response to increasing seed burial depth (Fig.4.1).

Mean weed seed consumption also differed among carabid species. *A. littoralis* consumed a lower proportion of seeds present on the soil surface (65%), whereas *H. affinis* (90%) and *P. melanarius* (91%) consumed higher proportions of seeds on the surface (Table 4.1). It is important to note that the number of seeds offered to each species in these trials was proportionate to their feeding capacity. Hence, despite the differences in seed consumption rates, the relative impact of each species in terms of weed seed consumption may differ. Factors such as species population size and field dynamics will also determine the overall impact of a species on weed seed consumption. Further, seed consumption generally decreased with seed burial depth, although results were inconsistent among carabid species. Seed consumption rates for *A. littoralis* were much less affected by seed burial depth than was seed consumption for the other two carabid species, both of which exhibited steep declines in seed consumption beyond the 2-cm depth.

Gender of adult beetles influenced the effect of seed burial depth on seed consumption rates for all three species (Table 4.1). An important finding of my study was that females of all three carabid species consumed significantly more seeds than males. Females consumed more seeds than males across all species and at all depths, except for seeds on the soil surface. Furthermore, females of all species were able to feed on seeds buried at shallow depths (0.5 cm) as efficiently as for seeds on the surface. Consumption of seeds by males, however, started to decline as depth increased to 0.5 cm, regardless of carabid species (Table 4.1). Species identity also interacted with gender, as females of *H. affinis* were more able to consume seeds at greater depths than were females of the other carabid species. At the 2-cm depth, *H. affinis* females consumed 45% of the weed seeds present compared with only 36 and 20% for *A. littoralis* and *P. melanarius*, respectively (Table 4.1).

4.4. Discussion

The results of my investigation indicate that the weed seed predation was influenced by the interaction between the depth of seed burial, carabid species, and gender. I surmise that interspecific differences in capacity to burrow may have helped the adults to access the seeds placed at different depths, and most likely this explains the higher seed consumption patterns (relative to other species) at shallow depths observed for *H. affinis* females. Previous studies (e.g. Marshall 2008; Sasakawa 2010; Saska et al. 2010) identified a similar pattern, particularly for members of Pterostichini. White et al. (2007) also reported that reductions in weed seed consumption as a result of seed burial depended on both carabid and weed species. In that study, *Amara aenea* (De Geer) consumed fewer seeds of redroot pigweed (*Amaranthus retroflexus* L.) and velvetleaf buried at 0.5 cm than seeds on the soil surface. In the current study, seed consumption by both males and females was negatively influenced by seed burial, as overall seed consumption decreased beyond a burial depth of 1 cm for all carabid species. This finding agrees with Harrison and Gallandt (2012), who reported that adults of *Harpalus rufipes* (DeGeer) consumed more seeds of *Sinapsis arvensis* L. on the soil surface compared with those that were buried. Among species, adults of *A. littoralis* consumed fewer seeds than did those of the other two species, likely due to the smaller body size and mass of this species. Such associations between carabid body size and weed seed consumption have been reported (Honek et al. 2003).

Most agricultural weeds are highly fecund and volunteer canola is no exception. Harvest losses of canola can be as high as 3,000 seeds m^{-2} (Gulden et al. 2003) and these seeds can either become buried at shallow depths, where they are prone to a variety of postdispersal mortality factors, or may be buried at greater depths, promoting secondary dormancy and the potential for long-term proliferation (Gulden et al. 2004). In this context, the role of ground beetles in weed seed predation at shallow depths could be important in reducing the number of buried seeds of volunteer canola and other weed species, as all carabid species in this study consumed volunteer canola seeds in high proportions to a depth of 2 cm. The results may, however, underestimate the true seed consumption at depth as I studied only the seed consumption of adult beetles; I did not include the potentially important effects of carabid larvae, which are likely more active in soil than adults. Larvae of granivorous carabids exhibit burrowing habits (Alcock 1976; Hartke et al. 1998) and contribute to seed feeding (Klimes and Saska 2010). However, their efficiency in consuming buried seeds has received little attention, particularly in terms of quantifying weed seed consumption patterns under field conditions.

Under field conditions, weed seeds are available both at the soil surface and buried in the soil profile as a result of agronomic practices, soil movement, and erosion (Martinkova et al. 2006). Moreover, the distribution of weed seeds varies with tillage practices (Swanton et al. 2000). The majority of weed seeds are scattered on the soil surface in no tillage systems, whereas most weed seeds are buried at depths greater than 5 cm in conventional tillage systems (Mohler 2001; Swanton et al. 2000). The results corroborate the findings of studies with other species that showed that seed consumption by carabid beetles is determined by the accessibility of seeds and the depth of seed burial (e.g. Harrison and Gallandt 2012; White et al. 2007). In general, seed consumption was greater for seeds at or near (0.5 cm below) the soil surface than for seeds buried at depths of 2–4 cm. On the basis of these results, weed seed consumption is expected to be lower in conventionally tilled fields than in those under no tillage regimes. Thus, tillage system impacts in combination with the effects of variable activity–density likely explain the lower weed seed predation rates observed in conventionally tilled fields compared with those that are not tilled (Cromar et al. 1999; Menalled et al. 2007). Further adoption of no tillage practices may increase the positive weed-management impact of seed-predating ground beetles as the dispersed seeds remain on the soil surface in this system (Ball 1992; Cardina et al. 1991) and are thus subject to greater rates of seed predation.

In summary, the results of this study show that seed predation by carabids differed markedly between surface-scattered and buried seeds, as well as among beetle species and between genders. Although seed predation was high at the soil surface and at shallow burial depths, deeper burial of seeds reduced but did not eliminate weed seed predation. My studies were conducted under controlled greenhouse conditions and thus, fieldwork is needed to validate the results of this experiment and to quantify seed predation under field conditions. Ideally, such studies would include an attempt to quantify contributions of carabid larvae to seed predation.

Tables.

Table 4.1. Mean numbers of volunteer canola seeds consumed at different depths under the soil surface by the females (F) and males (M) of three carabid species *Amara littoralis, Harpalus affinis, and Pterostichus melanarius* over a period of 72 h in a greenhouse study. Different letters indicate statistically significant differences (p<0.05) in mean seed consumption. Comparison is valid across row (within species and gender).

		Seed burial depth (cm)				
Carabid species		0cm	0.5cm	1cm	2cm	4cm
		Number of seeds consumed				
A. littoralis	F	13.44 ± 1.47a	11.26 ± 0.56a	8.67± 0.60b	7.7 ± 0.69b	2.90± 0.53c
	M	12.82 ± 0.71a	5.11 ±0.79b	3.00 ±0.77b	3.30±0.83b	0.33±0.21d
H. affinis	F	36.55±1.39a	33.67±0.87a,b	30.80±1.44b	18.10±1.44c	7.54±0.55d
	M	35.25±1.58a	26.16±1.22b	22.53±1.03c	4.41 ±1.01d	1.2 ±0.51e
P. melanarius	F	36.97±1.20a	35.00±1.32a	27.10±0.59b	8.30±2.11c	4.10±0.92d
	M	36.12±1.43a	31.27±0.95b	23.37±1.34c	3.62±0.75d	1.30±0.40e

Figures.

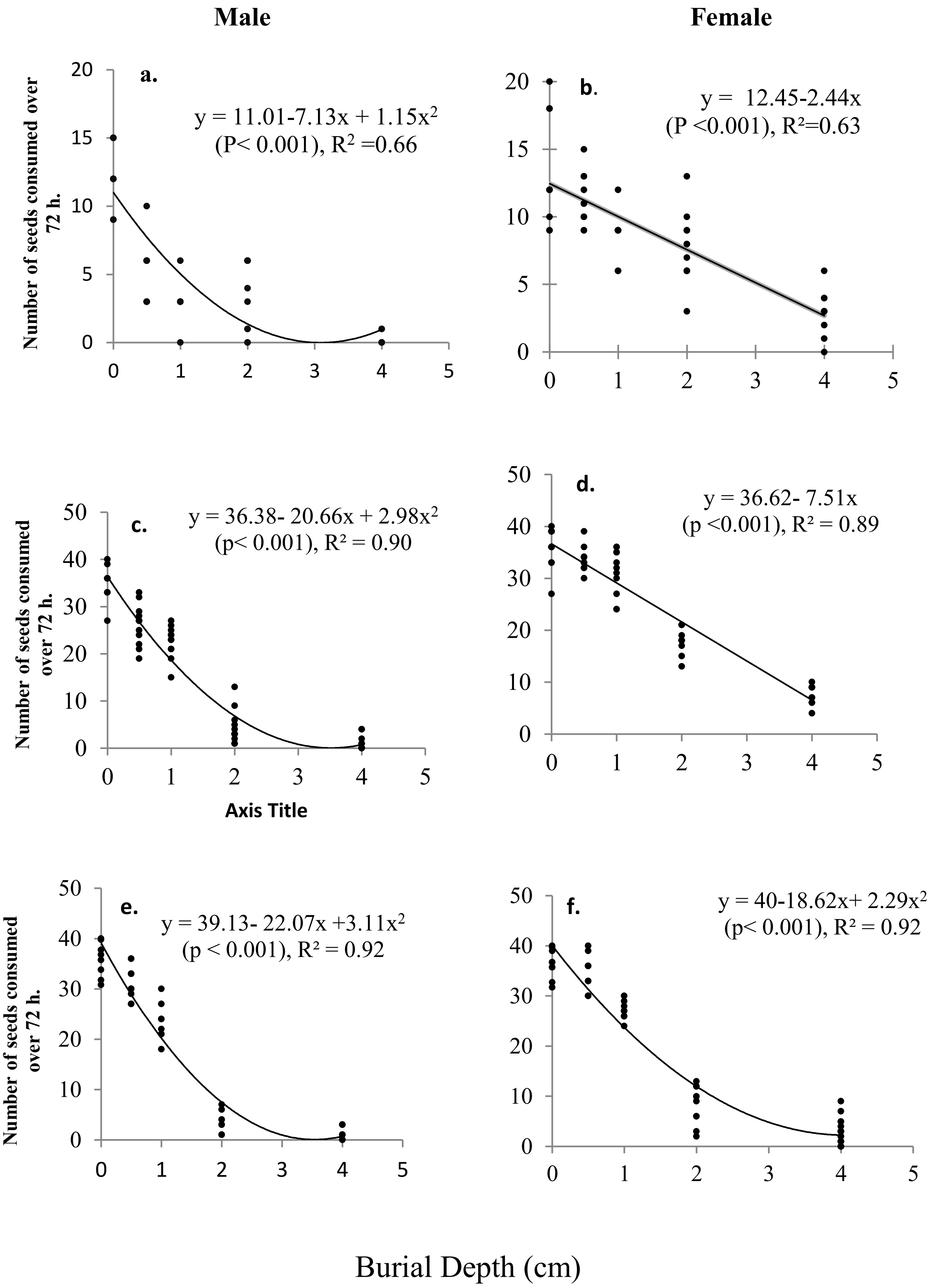
Male
Female
a.
y = 11.01-7.13x + 1.15x^2
(P< 0.001), R^2 =0.66
Number of seeds consumed over 72 h.
20
15
10
5
0
0
1
2
3
4
5
b.
y = 12.45-2.44x
(P <0.001), R^2=0.63
20
15
10
5
0
0
1
2
3
4
5
c.
y = 36.38- 20.66x + 2.98x^2
(p< 0.001), R^2 = 0.90
Number of seeds consumed over 72 h.
50
40
30
20
10
0
0
1
2
3
4
5
Axis Title
d.
y = 36.62- 7.51x
(p <0.001), R^2 = 0.89
50
40
30
20
10
0
0
1
2
3
4
5
e.
y = 39.13- 22.07x +3.11x^2
(p < 0.001), R^2 = 0.92
Number of seeds consumed over 72 h.
50
40
30
20
10
0
0
1
2
3
4
5
f.
y = 40-18.62x+ 2.29x^2
(p< 0.001), R^2 = 0.92
50
40
30
20
10
0
0
1
2
3
4
5
Burial Depth (cm)

Fig. 4.1a-4.1.f. Effect of seed burial depth on seed consumption of volunteer canola by a) *A. littoralis* male b) *A. littoralis* female c) *H. affinis* male d) *H. affinis* female e) *P. melanarius* male f) *P. melanarius* female.

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Chapter 5. Field density and distribution of weeds are associated with spatial dynamics of omnivorous ground beetles (Coleoptera: Carabidae)

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5.1. Introduction

Predatory arthropods are significant functional components of agroecosystem biodiversity, and are known to provide important beneficial effects for agriculture (Thomas et al. 2001; Snyder and Wise 2001). In temperate agroecosystems, carabid beetles (Coleoptera: Carabidae) are key members of epigaeic invertebrate assemblages, with the potential to provide valuable ecological services (Thiele 1977; Zhang et al. 1997; Tooley and Brust 2002). In addition to their significant role as predators of invertebrate pests, carabids consume substantial numbers of seeds produced by numerous weedy species, and in so doing, can reduce weed populations by reducing seed addition in the weed seedbank (Crawley 2000; Honek et al. 2005; Westerman et al. 2003; Saska et al. 2008; Lundgren 2009; Bohan et al. 2011; Trichard et al. 2014). Because weed seedbanks promote widespread development of weeds in agricultural fields, effective weed management strategies should give attention to weed seeds entering the soil seedbank (Buhler et al. 1997). To improve ecological management of weeds through enhancing weed seed predation, it is necessary to better understand the field dynamics of seed consuming carabids.

Intensification of agricultural management can lead to declines in the diversity of arthropods within agroecosystems as micro-habitats are altered for many arthropods, including carabids (Lövei and Sunderland 1996; Stoate et al. 2001). Management affects arthropod assemblages in a variety of ways (Weibull et al. 2003; Diekötter et al. 2010), including the influences of seasonality, crop type (Booij and Noorlander 1992; Cárcamo and Spence 1994; Weilbull and Ostman 2003; Eyre et al. 2013), phenological development of the crop (Martins et al. 2016), tillage (Cárcamo et al. 1995), presence of non-crop habitats, and intensity of disturbances (Gaines and Gratton 2010; Trichard et al. 2013). Abundance and distribution of non-cropped habitats (Clark et al. 1997; Trichard et al. 2013), presence of field edges, and extent and composition of other crops surrounding the cropped area (Lee and Landis 2002; Geiger et al. 2009; Frank et al. 2011) also can affect the spatial distribution of carabid species.

Weed cover in cropped areas provides both refuge and an alternate food source for omnivorous carabids (Speight and Lawton 1976; Holland et al. 1999; Lundgren 2009). Nonetheless, carabid species differ in their responses to weed cover (Speight and Lawton 1976; Kromp 1990; Pavuk et al. 1997), and the extent of spatial associations between carabid abundance and weed cover in cropped areas is not clear. In general, granivorous ground beetles appear to aggregate in response to weed seed distributions (Honek and Jarošík 2000), and carabid abundance has also been associated with above-ground seed density (Frank et al. 2011). However, it is unknown whether the extent of association varies with crop type, and there is no information on such associations in canola (*Brassica napus* L.), one of the most widely grown crops in Canada. Therefore, the main objectives of this study were to assess the spatial distribution of seed predatory carabid beetles in canola (*Brassica napus* L.) agroecosystems and to determine if spatial patterns of weed density and seed availability in the seedbank are associated with local activity-density of beetles. I hypothesized that activity-density of seed predatory carabids will spatially overlap with the weed and weed seed density. To accomplish this, I employed spatial analysis by distance indices (SADIE), a powerful tool for spatial analysis (Thomas et al. 2001), to model the distribution dynamics of carabid assemblages using data derived from pitfall traps at four sites in western Canada.

5.2. Materials and methods

5.2.1. Study sites

I established grids of pitfall traps in four commercial canola fields in the Aspen Parkland ecoregion of central Alberta, Canada. The region is characterized by short, warm summers with annual mean temperatures of 15^0C, annual precipitation of 400–500 mm, and an average frost-free season of approximately 95 days. These sites accumulate continuous snow cover (15–20 cm) throughout winter (Environment Canada, 2016). Soils in this ecoregion are fertile Black Chernozems that are generally high in organic matter. In 2011, the fields I studied had all been in wheat the previous year and were located at Leduc (53.36^0 N, 113.58^0 W) and Vegreville (53.50^0 N 112.10^0 W), while in 2012, they were at St. Albert (53.70^0N 113.62^0 W) and another field at Leduc (53.35^0 N 113.59^0 W). Thus, analyses are based on data from four different site-year combinations. The no-tillage regime and other management practices were similar for all fields.

5.2.2. Study design

Grids of pitfall traps were used to collect within-field distribution data for the most common carabid species at each site. From these data I explored possible associations between activity of carabid weed seed predators, weed density, and the weed seedbank. In the interior of each of the four fields, 200 m^2 was sub-divided to form 25 plots each measuring 40 m X 40 m and comprising a single cell of a square grid. Grids were established approximately 40 m from field edges. Activity-density of carabid species was monitored at the centre of each of the resulting 40 m X 40 m grid cells using a single pitfall trap over a sampling period of 12–13 weeks. Pitfall traps consisted of two 0.5 L plastic cups (11 cm diameter), one acting as a sleeve that was dug into the ground and kept flush with the soil surface, and the other (the actual trap) inserted into it (Spence and Niemelä 1994). Each trap cup was filled with 0.25 L of a dilute (50%) solution of propylene glycol to act as a killing agent and preservative. Traps were emptied and recharged with preservative weekly, and captured adult specimens were preserved in 70% ethanol until they could be identified using Lindroth (1961–Lindroth, 1961-1969).

I focused on omnivorous species known to consume seeds, as categorized by Larochelle (1990). The activity-density of each omnivorous species was estimated as the number of captured adults/grid cell/week and summed over weeks. Adults of *Amara carinata* (Leconte), *Amara torrida* (Panzer) and *Amara lacustris* (LeConte and Panzer) were captured, pooled for analysis, and henceforth are referred to as *Amara* spp. I first calculated the activity-density for the most abundant species in each of the fields (the species with the highest average activity density/week), and then pooled the data for the remaining species, referred to hereafter as “other omnivorous species”. Average activity-densities of all other omnivorous species were calculated on a weekly basis and summed over weeks for subsequent analyses. I also estimated the density of weeds and dispersed weed seeds in the soil seedbank for each grid cell. Weed density was estimated during the last week of June in each year by averaging weed counts in three randomly placed 1 m $^{-1}$ m quadrats within each cell. Weed seed density was estimated as the average number of seeds contained in three soil cores (5 cm diameter by 8 cm depth) taken within each cell, also during the last week of June. All samples were wet-sieved by first washing soil samples and then passing the resulting liquid through a series of sieves in the laboratory to extract seeds of different sizes (Forcella 1992). The weed seeds were identified using keys provided by Delorit (1970).

5.2.3. Data analysis

5.2.3.1. Spatial analyses

Spatial Analysis by Distance Indices (SADIE) is used to quantify spatial patterns in count data, and to test associations of spatial patterns between two data sets sampled at the same location (Perry and Dixon 2002). I used SADIE to test two hypotheses about spatial patterns in field populations of carabid species. First, I asked if the species were distributed randomly, or whether their distributions were more clustered. Second, I asked whether there was statistically significant spatial association among weed abundance, seed density and abundance of omnivorous carabids.

I studied dispersion of carabids using the SADIE approach, by calculating two indices namely, a patch index (Vi) and a gap index (Vj). These two indices define patch clusters (Vi, relatively high density of counts close to one another) or gap clusters (Vj, relatively few or zero counts close to one another) from field distributional data (Perry 1998). Thus SADIE estimates a local clustering index (Vi or Vj) for each sample point through tests of randomization in which the observed counts are permuted among the sample units across the entire grid. Sample units with counts greater than the overall mean are assigned a positive patch index, while the units with counts less than the overall mean are assigned a negative gap index. These local indices are then used to calculate the probabilities of the observed overall patch (Pi) and gap indices (Pj) for the entire grid in relation to the hypothesis of randomness (Perry et al. 1999). Significant patch and gap indices indicate that populations within the grid have non-random spatial structure.

Finally, I used the SADIE index of association, X (Perry and Dixon 2002), to estimate spatial association between carabid activity-density, weed, and weed seed density during a single time period. X is equivalent to the correlation coefficient between the clustering indices (Vi or Vj) of the two data sets and it has an associated probability value of P. If the patch or gap clusters of one data set coincide with a patch or a gap cluster for the other data set, X indicates a positive association. Similarly, if the patch clusters of one data set coincide with the gap clusters of another, spatial disassociation is indicated.

By convention, $X > 0$ indicates association, $X < 0$ indicates a disassociation, and $X = 0$ indicates lack of association or disassociation (random distribution). The appropriate degrees of freedom for the correlation were determined using the Dutilleul adjustment (Dutilleul, 1993). For a two-tailed test with $a = 0.05$, probability (P) values <0.025 indicated significant association, whereas P values >0.975 indicated significant disassociation. When probability values fall between the critical values, one concludes that the data are not strong enough to make the case for either association or disassociation. Values of the spatial association index (Xi) were interpolated using the spatial analyst extension of ArcGIS (ESRI, 2002) to create contour maps to visualize associations for each field during the peak activity periods of carabid species (rosette to maturity stages of canola).

5.3. Results

5.3.1. Activity-density and distribution patterns of carabids

Pterostichus melanarius L., *Amara littoralis* Mannerheim, *Amara spp*. (LeConte), *Amara obsesa* (Say), *Amara quenseli* (Schoenher), *Poecilius lucublandus* (Say) and *Harpalus affinis* (Schrank) were the major seed predatory carabids captured in the study (Fig. 5.1). In general, overall adult activity-densities were low during early stages of crop development and highest between weeks 6 and 12, coinciding with the rosette to ripening growth stages of canola (Fig. 5.1). Declining activity-densities at season's end suggest that periods of peak adult activity were well sampled at all four sites. Patterns of relative abundance varied across fields. At Leduc in 2011, the most common species were captured in the following order of relative abundance: *P. melanarius*, *A. littoralis*, *A. quenseli*, *Amara* spp. and *H. affinis* (Fig. 1a), and this was similar to the pattern for the other Leduc grid in 2012 (Fig. 5.1c). At Vegreville (2011), *A. littoralis* exhibited the highest activity-density, followed by *P. melanarius* (Fig. 1b), and the group of other species, which included *Amara* spp. and *H. affinis*. At St. Albert (2012), *P. melanarius* and *A. littoralis* were co-dominant, while only *P. lucublandus* and *A. obsesa* were included in the pooled group. Thus, even in this relatively constrained geographical area there was much local variation in ground-beetle assemblages and activity in similar canola agroecosystems (Fig. 25.). The SADIE (Vi) and gap (Vj) indices indicated clustering in the populations of carabid species at all sites (Table 5.1). At Leduc in 2011, activity-densities of *P. melanarius* and the other omnivorous species showed patchy distribution over the entire sampling period. Similar trends were observed at Vegreville in 2011, Leduc in 2012 and St. Albert in 2012 in terms of the distribution patterns of the most abundant species, and all other omnivorous species.

5.3.2. Distribution patterns of weed and weed seeds across grids

Substantial differences in average density of weeds and weed seeds, as well as weed species, were observed among the four sites (Tables 5.2 and 5.3). Both average weed (plants m^{-2}) and weed seed densities (seeds m^{-2}) per grid cell were highest at Leduc (2012), while the lowest densities of weeds and weed seeds were recorded in Leduc 2011 and Vegreville 2011, respectively (Table 5.2). There were notable differences among grids in weed and weed seed dispersion (Table 5.2). Both weeds and weed seeds were aggregated in both fields at Leduc, as indicated by highly significant patch (Vi) and gap (Vj) indices (Table 2). At both Vegreville and St. Albert, however, only weed populations appeared to be spatially aggregated with significant patch (Vi) and gap (Vj) indices; patterns of seed dispersion at these two sites could not be distinguished from a random distribution (Table 2).

5.3.3. Spatial associations among carabids, weeds and weed seeds

Significant positive spatial associations were observed between activity densities of carabid species and weed seedling density on all grids (Table 5. 4), although the magnitude and extent of these associations differed. However, despite these positive relationships at all sites, I found no statistically significant spatial association between carabid activity-density and seed density in the soil.

Association between carabid activity-density and weed seedling density was greatest at Leduc (2012) and Vegreville (2011) ($X = 0.73$ and 0.72, respectively, both $P < 0.001$), but was notably lower at Leduc (2011) ($X = 0.56$, $P < 0.01$) and St. Albert (2012) ($X = 0.40$, $P < 0.001$). At Leduc and St. Albert, catches of the most common species, *P. melanarius*, were strongly associated with weed seedling density (Table 4). Captures of *A. littoralis* were most common at Vegreville and St. Albert, and these too showed significant spatial association with weed seedling density (Grid 2: $X = 0.70$, $P < 0.0001$, Grid 4: $X = 0.49$, $P < 0.01$).

5.4. Discussion

The results show that field distribution patterns of omnivorous carabid species were quite variable at all four sites, but that populations of both carabids and weed seedlings were highly clustered in the grid area. In all four fields carabid populations of both the most abundant species and the pooled sample of less abundant species were significantly patchy, giving rise to local aggregations that were spatially associated with weed distributions. Trichard et al. (2014) observed similar clustering in the local distributions of several omnivorous and granivorous carabid species in winter wheat fields, although such information does not exist for canola fields.

The aggregation of carabids in cropped areas is influenced by factors such as carabid life cycle, habitat preferences, dispersal ability, and prey availability (Williams et al. 2010). Both *P. melanarius* and Amara spp. have been reported previously to aggregate in certain areas, albeit at different scales (Thomas et al. 2001). The introduced species, *P. melanarius*, has recently become very common in urban and agricultural habitats across Canada (Spence and Spence 1988; Cárcamo and Spence 1994; Cárcamo et al. 1995; Hartley et al. 2007). This phenomenon is underscored by the high activity-densities recorded for this species at study sites, especially at Leduc. Even at St. Albert, where *A. littoralis* was most common overall, its activity declined during the cropping season, as is typical for Amara species (Thomas et al. 2001). Activity-density of *P. melanarius* was much greater for the last 4–5 weeks of the frost-free season at St. Albert. Thus, I conclude that *P. melanarius* is now firmly established in agroecosystems of central Alberta after the first report of its presence in the City of Edmonton in 1956 (Madge 1959).

I did not find strong spatial association between the activity- densities of seed predatory carabids and areas of high weed seed density. Colonization and concentration of carabid activity in weedy patches may reflect both responses to availability of shelter or food, and seeds represent only one source of potential food. It is important to note that the seeds in the seedbank may not necessarily represent the above-ground weed community in the current year, and several factors such as depth of burial (White et al. 2007; Kulkarni et al. 2015a), physiological state of the seeds (Cardina et al. 1996; Law and Gallagher 2015; Kulkarni et al. 2016), and seed type (mono vs. dicotyledonous seeds) (Bohan et al. 2011) can influence spatial associations of carabids with weed seeds. Observed spatial associations with weedy patches may indicate associations with potential seed rain (Bohan et al. 2011) and availability of seeds for consumption late in the cropping season.

Further, plant canopy structure and vegetation density in cropped areas influence abiotic factors including temperature, humidity, and light conditions; these, in turn, are well known to influence carabid habitat selection and field distribution (Honek 1997; Thomas et al. 1998; Trefas and Van Lenteren 2008). Weedy patches in cropped areas may benefit a variety of arthropods, particularly those that are specialized for feeding on weeds or weed seeds (Blubaugh et al. 2011; Saska et al. 2014). Such patches provide refuge for carabids and other arthropod species, alter the microclimate and improve humidity and soil moisture status, thus providing suitable sites for invertebrate reproduction (Saska et al. 2014). In this study, high spatial association between carabids and weed density was driven largely by the dominance of a single species, *P. melanarius*. Adults of this species are frequently associated with more closed and dense plant canopies (Cárcamo and Spence 1994; Armstrong and McKinlay 1997; Dixon et al. 2004; Shearin et al. 2008; Hummel et al. 2012), and patches of weed cover may have provided attractive microhabitat for this particular species. The adults of autumn-breeding *P. melanarius* tend to oviposit in shadowed, moist soils created by structurally diverse habitats, and these conditions can be associated with weedy patches that might be judiciously promoted as refuge areas for seed predators (Trefas and Van Lenteren 2008). Strong associations between *P. melanarius* activity and weed cover should raise local predation pressure on weed seeds. Given that this species mounts strong functional responses to prey, as seen in positive responses to slug

(Bohan et al. 2000; Symondson et al. 1996) and aphid (Bryan and Wratten 1984; Thomas et al. 2001; Trichard et al. 2014) abundance, they may also respond to abundance of weed seeds.

I have demonstrated that carabid seed predators exist in clustered distributions under field conditions and their spatial patterns coincide with variation in weed density in the field. I suggest that carabid adults respond to weeds mainly for shelter and possibly oviposition sites (Trefas and van Lanteren 2008) and thus, weedy areas may be crucial for conservation of seed predatory carabids. Storkey (2006) suggested that maintaining economically acceptable populations of weed species in cropped areas as a resource for food and shelter to beneficial organisms (such as carabids) can improve biodiversity and in turn, ecosystem services provided by these bioagents. Although difficult, various approaches to provide for the ecological needs of carabids have been suggested. For example, provision of weed cover or hedge rows in or near agroecosystems can increase rates of weed seed predation in crop fields (Menalled et al. 2000). Maintenance of non-crop species on the farm, perhaps in field margins, can also help to maintain biologically diverse communities in the field to enhance multiple ecosystem services (weed biocontrol, soil health) (Storkey et al. 2015). Therefore, the identification of functional links between companion non-crop plants and their associated invertebrate communities will be the first step to promote services such as weed seed predation (Storkey and Westbury 2007; Storkey et al. 2015). It is very likely that the suggestion of maintaining weedy patches in cropped areas will raise concerns from producers. However, given the potential of carabids to manage potential crop pests and weed seeds, the advantages of maintaining economically acceptable weedy patches may outweigh the disadvantages. The feasibility of such an approach and quantification of cost and benefits associated with it need further research.

Currently, limited information is available on spatial patterns of larval activity of seed predatory carabids, and the impact of larvae on seeds. Because sampling larval populations is complex (Thomas et al. 2001), there is little information about spatial associations between larval and adult carabid populations that could address how adult clustering may reflect larval activity. Further information is needed to describe the response of carabid beetles to artificially manipulated above- and below-ground seed density to develop insights into how seed consuming carabids respond to changes in seed density patterns on a spatial scale. Nonetheless, because the impact of seed predation can be high (Honek et al. 2003, 2005; Westerman et al. 2003; Saska et al. 2008; Trichard et al. 2014; Kulkarni et al. 2015b) and natural relationships in the field dispersion of adult carabids and weeds exist, as I have shown here, development of tactics to enhance in-field populations of carabids is promising in the context of biological control strategies for weed management.

Given the design of my experiment, I could not isolate whether the observed associations were due to weed population structure or to an underlying factor driving the spatial distribution of the weed population. However, the results clearly show that there is substantial spatial aggregation of carabids in areas of high weed populations. More research is needed to fully determine the underlying causes for these associations. I suggest that a future study intentionally structure weeds in different spatial arrangements to assess whether carabid activity density changes in response to the spatial heterogeneity of weeds.

Tables.

Table 5.1. Spatial patterns of distribution of omnivorous carabid species at the grid study sites observed in canola fields in 2011 and 2012, as indicated by SADIE patch (V_i) and gap (V_j) indices. The mean activity-density of the major species (total beetles caught per week per trap) at each site, and of the other omnivorous seed predatory species combined, is presented below. Figures in the parentheses indicate probability values for SADIE indices at α = 0.05.

Site and Year	Species	Mean ± S.E.	Patch index (Vi)	Gap index (Vj)
Leduc 2011	*P. melanarius*	21.76 ± 1.87	1.43 * (0.03)	-1.33* (0.01)
	All carabids	47.04 ± 4.39	1.32 * (0.03)	-1.38* (0.02)
Vegreville 2011	*A. littoralis*	34.28 ± 4.92	1.71* (0.001)	-1.75 * (0.003)
	All Carabids	40.88 ± 4.65	1.68* (0.04)	-1.48 * (0.03)
Leduc 2012	*P.melanarius*	70.48 ± 5.77	1.94* (0.002)	-1.78* (0.002)
	All carabids	76.4 ± 5.42	1.49* (0.007)	-1.47 * (0.004)
St. Albert 2011	*P. melanarius*	37.2 ± 0.53	1.51 * (0.008)	-1.24 * (0.004)
	A.littoralis	6.12 ± 1.23	1.37* (0.00)	-1.39* (0.00)
	All carabids	40.24±3.33	1.51* (0.005)	-1.65 * (0.008)

Table 5.2 The average weed density (per m^2 per grid cell) and the weed seed density(per m^2 per grid cell), and their spatial patterns of distribution as indicated by SADIE patch ($\overline{V\iota}$) and gap ($\overline{VJ}$) indices in fields of canola in 2011-2012 near Edmonton, AB, Canada.

Grid	Parameter	Mean ± S.E.	V_i	V_j
Leduc 2011	Weed Density	25.33 ± 2.21	1.36*	-1.38*
(Grid 1)	Seed Density	144.96 ± 4.17	1.38*	-1.38*
Vegreville 2011	Weed Density	21.76 ± 4.51	1.13*	-1.17*
(Grid 2)	Seed Density	297.92 ± 28.80	1.51	-1.52
Leduc 2012	Weed Density	27.64 ± 6.76	1.51*	-1.57*
(Grid 3)	Seed Density	313.84 ± 20.80	1.13*	-1.17*
St.Albert 2012	Weed Density	22.00 ± 3.30	1.18*	-1.21*
(Grid 4)	Seed Density	303.00 ± 31.23	1.42	-1.37

Note: Values noted with asterisks indicate significant gap and patch indices as calculated by SADIE.

The indices $\overline{V\iota}$ and $\overline{VJ}$ were calculated using SADIE (see text for the details)

Table 5.3 Relationships among carabid activity-density, density of weeds and density of weed seeds as indicated by the SADIE point index of association X_k in canola fields at Leduc (Grids 1 and 3), Vegreville (Grid 2), and St. Albert (Grid 4) near Edmonton, Alberta, Canada.

Site	**Parameters**	**Index of Association X_k**	
		Weed density	**Seed density**
Leduc 2011 (Grid 1)	Omnivorous Carabid Activity density	0.56*	0.30
	Major species: *P. melanarius*	0.41*	0.25
Vegreville 2011 (Grid 2)	Omnivorous Carabid Activity density	0.72*	0.23
	Major species: *A. littoralis*	0.70*	0.32
Leduc 2012 (Grid 3)	Omnivorous Carabid Activity density	0.73*	0.42
	Major species: *P. melanarius*	0.71*	0.30
St. Albert 2012 (Grid 4)	Omnivorous Carabid Activity density	0.40*	0.27
	Major species 1: *P. melanarius* and *A. littoralis*	0.45*	0.18

*indicates significant association at $P < 0.025$

Figures.

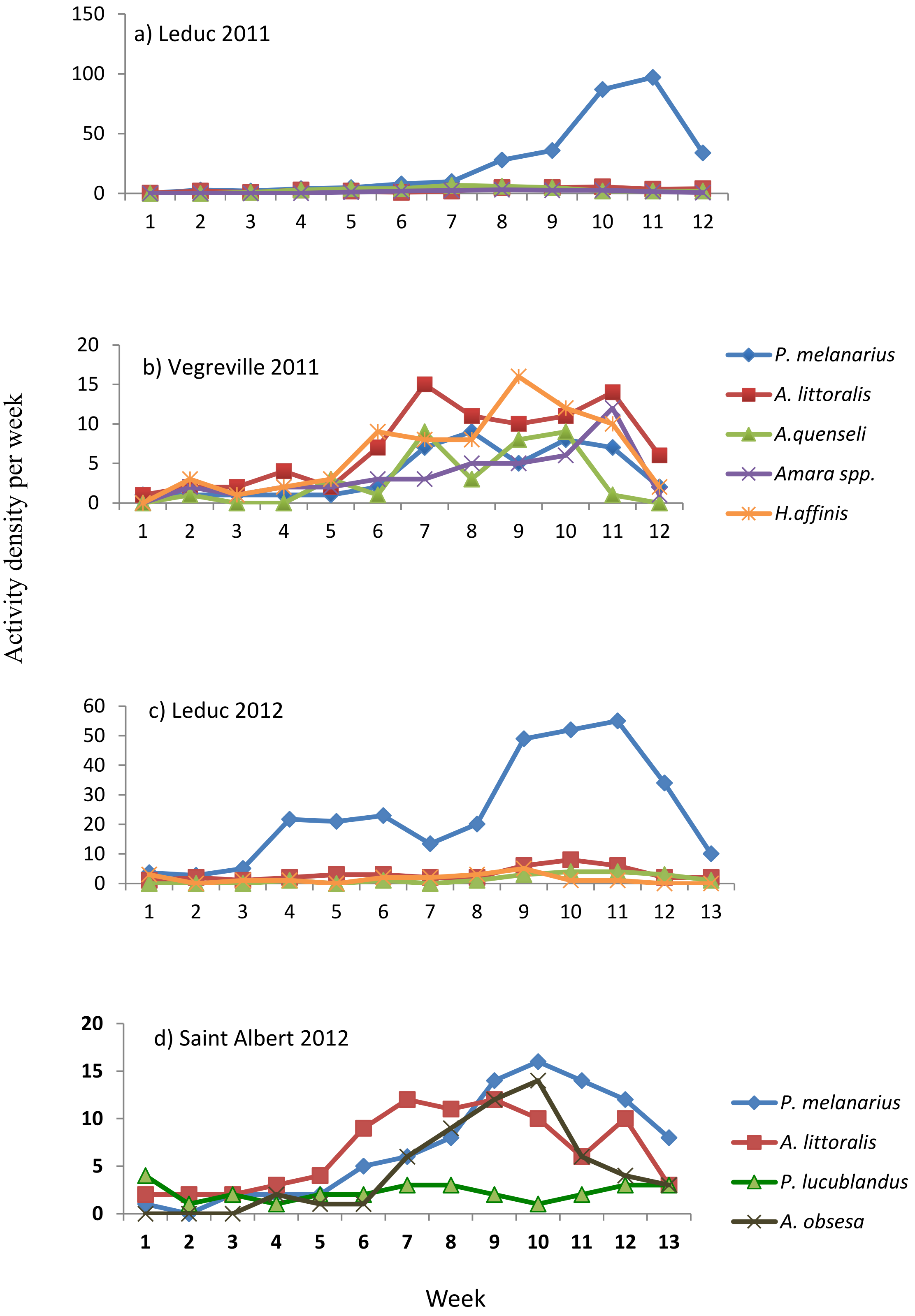
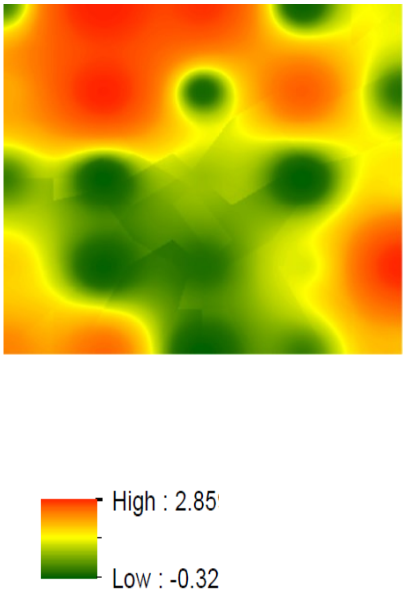
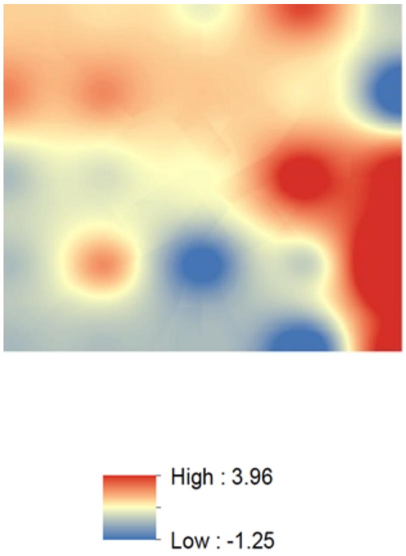

a) Leduc 2011
0
50
100
150
1 2 3 4 5 6 7 8 9 10 11 12
b) Vegreville 2011
0
5
10
15
20
1 2 3 4 5 6 7 8 9 10 11 12
P. melanarius
A. littoralis
A.quenseli
Amara spp.
H.affinis
Activity density per week
c) Leduc 2012
0
10
20
30
40
50
60
1 2 3 4 5 6 7 8 9 10 11 12 13
d) Saint Albert 2012
0
5
10
15
20
1 2 3 4 5 6 7 8 9 10 11 12 13
P. melanarius
A. littoralis
P. lucublandus
A. obsesa
Week

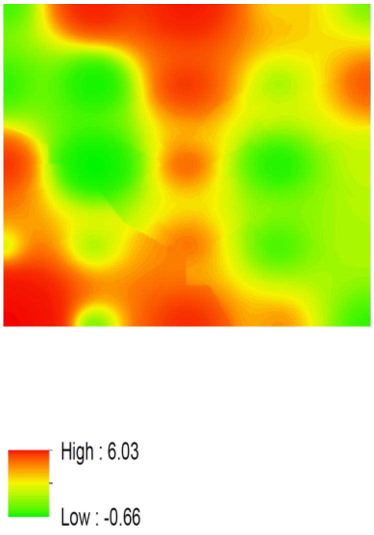
Figure 5.1.a-d Activity-density (total number of beetles captured per week per trap) and seasonal activity of major omnivorous carabid species in: a) Grid 1 (Leduc, 2011), b) Grid 2 (Vegreville, 2011), c) Grid 3 (Leduc, 2012), and d) Grid 4 (St. Albert, 2012). The activity-density was calculated using pitfall traps at each study site as the average per trap per week of numbers of omnivorous species observed in trap catches


High : 2.85
Low : -0.32

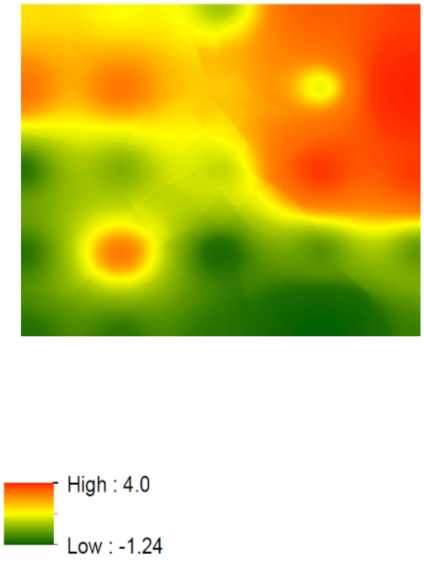
a)


High : 3.96
Low : -1.25

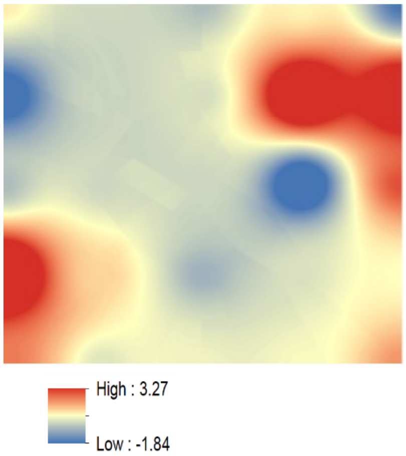
b)


High : 6.03
Low : -0.66

c)


High : 4.0
Low : -1.24

d)



e)

Fig. 5.2. Contour maps interpolated from SADIE point index of association, Xk, showing the distributions of areas of association and disassociation between activity-density of major carabid species and weed density a) Leduc 2011 b) Vegreville 2011 c) Vegreville 2011 d) Leduc 2012 e) St. Albert 2012

a) Leduc 2011 (Grid 1): Weed association with *P. melanarius* activity density

b) Vegreville2011 (Grid2): Weed association with *A. littoralis* activity density

c) Leduc 2012 (Grid3): Weed association with *P. melanarius* activity density

d) St. Albert 2012.:Weed assocoation with *P.melanarius* activity-density

e) St. Albert 2012 (Grid4): Weed association with *A. littoralis* activity density. The individual cell size was 40 m x 40m for each grid.

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roxType=custom& txtCentralLatDeg=53&txtCentralLatMin=50&txtCentralLatSec=0&txtCentralLongDeg=112&txtCentralLongMin=10&txtCentralLongSec=0&stnID=1812&dispBack=0. (Accessed 21 August 2016)

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Chapter 6. General Discussion

Omnivorous predators like ground beetles contribute to biological control of agricultural pests (Argen et al. 2012) as they can survive on a broad range of diets, overcoming seasonal disturbances and food scarcity (Eubank and Denno 1999). Seed predation has been known as a source of weed mortality for more than 100 years (Honek et al. 2003); however, the topic has received much research attention in recent years (O'Rourke et al. 2006). Carabids consume substantial numbers of seeds produced by weedy species, and in so doing, can reduce weed populations through direct effects on seed mortality (Honek et al. 2003, 2005; Westerman et al. 2003; Saska et al. 2008; Trichard et al. 2014) and reduce weed seedbank (Crawley 2000; Lundgren 2009; Bohan et al. 2011).

Given the importance of seed predation by carabids as an ecological service in reducing weed populations, it is critical to gain a better understanding of the processes involved to formulate strategies that can bolster carabid activity as a part of weed biological control efforts. Much of the research about weed seed predation has resulted from the focus on ecological approaches to weed management in crop systems (Landis et al. 2005). In western Canada, many such studies have focused mainly on ground beetle responses to agricultural practices (Cárcamo and Spence 1994; Cárcamo et al. 1995; Floate et al. 2007) or vegetation diversity (Butts et al. 2003; Bourassa et al. 2008, 2010; Hummel et al. 2012). While there have been fewer studies focusing particularly on weed seed predation, our ability to promote weed seed predation through biological control using carabids depends on being able to identify species strongly connected to this ecological service in a given agroecosystems.

My research, as presented in this dissertation, attempts to bridge the knowledge gap associated with seed preferences and field dynamics of carabids that are potential weed seed predators in the canola agroecosystem. I have developed insights into their ecology, and I believe that the data presented here is the first attempt to study the consumption of weed seeds by carabids in western Canada. My dissertation addresses the following core objectives: 1) to identify important seed predatory carabid species in the canola agroecosystem, and to identify their seed preferences, 2) to investigate the role of olfactory cues in weed seed detection and preferences, 3) to investigate the effect of seed burial on seed predation, and 4) to understand spatial dynamics of populations of carabids that are significant seed predators. I used a combination of laboratory, greenhouse and field experiments to understand carabid weed seed predation, and tested both imbibed and unimbibed seeds to also explore effects of different physiological states in seeds that may be encountered by carabids when seeds are dispersed on the soil.

Knowledge of seed preferences of the major species of particular seed predator guilds can promote understanding of variation in local weed seed predation patterns (Cardina et al. 1996; Petit et al. 2014), although the results may vary based on the composition of the seed predatory guild and the preferences of the major species (Petit et al. 2014). In Chapter 2, I identified the following potential species as contributing to weed seed predation in canola agroecosystems: *Amara littoralis, Harpalus affinis, Pterostichus melanarius*, and *Poecilus lucublandus*. Under field conditions, carabid species captured in pitfall traps also included other omnivorous species, such as *P. melanarius*, *A. littoralis*, *A. quenseli*, *H. affinis*, and *A. obesa* among others. As hypothesized, carabids exhibited specific, distinct preferences for weed seeds. Carabid species and physiological state of the seed (imbibed vs. unimbibed) were associated with these preferences. Of four weed species tested, carabids preferred seeds of volunteer canola the most and field pennycress the least; nonetheless the acceptability of field pennycress was greater when the seeds were imbibed. Seed preferences were similar under field conditions with greater preference for volunteer canola seeds.

At all sites and in both years studied, there were statistically significant positive correlations between activity-density of carabids and percentage seed removal, which is in agreement with numerous studies (Honek et al. 2003; 2005; Menalled et al. 2007; Gaines and Gratton 2010; Jonason et al. 2013; Trichard et al. 2013). I observed greater preference towards imbibed seeds that is likely attributable to softening of the seed coat, this is thought to improve seed palatability (Lundgren 2009), or nutritional status of imbibed seeds due to changes in their metabolic activity (Koprdova et al. 2012). As might be expected, I observed low preference for field pennycress seeds compared with volunteer canola and wild mustard seeds; however, I did not investigate whether this preference has nutritional correlates. Field pennycress seeds were more acceptable upon imbibition and further work could usefully focus on whether the chemical composition of seeds differs between imbibed vs. dry seeds, or whether imbibition changes biocidal activity of chemical compounds in the seeds, thereby making them more acceptable. Greater preference for imbibed field pennycress seeds may correspond with significant changes in nutritional properties. In that regard, I would speculate that processes such as imbibition can facilitate seed detection and improve seed feeding, particularly for those weed seeds that were less consumed when dry. However, further research is required to test this idea.

Seedbank replenishment resulting from seed shed contributes strongly to establishment and maintenance of populations of volunteer canola as an important weed in western Canada (Beckie et al. 2006; Knispel et al. 2008). For example, harvest losses of canola can be as high as 3000 seeds m^{-2} in the Prairie Provinces (Gulden et al. 2003), and it appears that ground-beetle populations can respond (Floate and Spence 2015). In this context my results show that carabid preference for volunteer canola seeds has potential to affect volunteer canola population dynamics. My investigation provides a basis for future studies, including quantification of weed seed predation in the field and its impact on volunteer canola populations, and estimation of rates of seed removal.

Other factors that can influence seed preferences include seed odor, and pathogens and toxic compounds associated with seeds (Ward et al. 2014), although the exact role of olfaction in seed detection and preferences is poorly understood. Omnivorous and carnivorous carabids use olfactory cues in prey detection (Evans 1983; Kielty et al. 1996), but research about the possible role of olfaction in seed detection and discrimination is largely unexplored (except Law and Gallagher, 2015). I therefore investigated behavioural responses of carabids to olfactory cues, and whether such responses translated into seed preferences (Chapter 3). My research suggests that carabid beetles exhibited different behavioral responses to olfactory cues associated with the seeds of volunteer canola, wild mustard and field pennycress. The process of seed imbibition had marked effects on carabid responses, apparent to olfactory cues associated with the change in seed physiological state. The bioassays involving both unimbibed and imbibed seeds of weed species showed that volunteer canola seeds were most preferred by all carabid species, followed by those of wild mustard and field pennycress, respectively. Because these carabids also exhibited the same order of preference for these species in a seed choice experiment (Chapter 2), I reason that olfactory cues are being used in seed foraging. Taken together, and assuming that positive response to odours should be strongest for preferred seeds, these results show that carabid species differ in their ability to detect particular olfactory stimuli associated strictly with seeds alone. Moreover, two of the three species included in study, *P. melanarius* and *H. affinis,* responded only to odours emanating from imbibed seeds. Imbibition may thus not only improve the palatability of seeds, but also increases the probability that a seed will be detected by predatory ground beetles.

Many dormant weed seeds are partially or completely imbibed in the soil seedbank (Forbes and Watson 1992), and seeds can remain in an imbibed state for long time (Dalling et al. 2010). For example, Tokumasa and Kakihara (1990) demonstrated that *B. napus* seeds can remain dormant in an imbibed state for up to five years. The process of imbibition triggers chemical changes in the seed that can result in the release of volatile compounds such as ethanol and acetaldehyde (Lee et al. 2001; Jorgensen 2001). Mammalian seed predators (rodents and hamsters) use olfactory cues associated with imbibed seeds that are buried (Jorgensen 2001; Paulsen et al. 2013), but not much is known about the responses of seed predatory carabids to seed associated olfactory cues. In this context, it can be speculated that differences in seed chemistry due to imbibition may change the nature of olfactory cues associated with seed, resulting in the observed differences in behaviour and seed preferences. Further, Ward et al. (2014) have suggested that carabids may use seed odors to detect high quality seeds based on seed volatiles, particularly in detecting fresh vs. old seeds. Behavioural responses observed in response to seed odors in my bioassays may be indicative of seed preferences as associated with seed quality, but this needs further investigation.

My olfactory bioassays tested behavioural responses and not the effects of individual odors or composite odor sources extracted from seeds. Such reductionist work to clearly describe details of the process could be interesting, but it will require extraction of specific volatiles exposed to a complex mosaic of sensory stimuli (Yakubowski et al. 2016), and clearly such stimuli can significantly influence the nature of responses of adult carabids (Law and Gallagher 2015). Nevertheless, my results indicate that olfactory stimuli are important aspects of seed foraging, at least as short-range cues about seed location. The associated behavioural responses to olfactory cues may have a connection to my findings that buried seeds are detected by adult carabids. Although my investigation did not substantiate this finding, it hints at the possible role of such cues in the detection of buried seeds because buried seeds are unlikely to be detected by visual, gustatory or other mechanical stimuli unless they are in direct contact with the adults. Imbibed seeds may be better detected by adult carabids than dry seeds, a matter that may prompt further investigation.

In continuing with seed detectability, I further investigated whether adult carabids could detect seeds buried at various depths (Chapter 4). I used seed burial depths of up to 4 cm, and my results showed that seed burial can indeed affect seed predation. Gender also played an important role in seed predation, particularly when seeds were buried at different depths. Females consumed more seeds when buried at deeper depths than males. Higher feeding among female carabids (Sasakawa 2010) particularly during breeding and egg laying season has been reported (Holland 2002; Tooley and Brust 2002), and my results may indicate probable association between diet and reproduction. Although seed predation was high at the soil surface and at shallow burial depths, deeper burial of seeds reduced, but did not eliminate, weed seed predation.

Seeds in a no-till system are more available at the surface (Mohler 2001; Swanton et al. 2000) and undisturbed habitat under no tillage fields increases the activity density of carabid beetles (Menalled et al. 2007). Based on these observations, one might assume that seed consumption rates could be higher under zero tillage conditions. However, earlier studies determined that the impact of disturbance on seed distribution and subsequent seed consumption can be ambiguous (Cromar et al. 1999; Menalled et al. 2007; Trichard et al. 2013).

Currently, no-tillage practices account for more than 50% of tillage practices on the Canadian Prairies (Statistics Canada 2011). This may have a positive impact on weed consuming ground beetle communities as the seeds remain available on the surface of the soil (Cardina et al. 1991). However, further long-term studies to quantify rates of weed seed predation under no-till systems are required to estimate the impact of carabid weed seed predation.

Having delved into aspects of seed preferences and seed detectability, I further investigated aspects of field dynamics and factors underlying spatial distribution of carabids. In the context of improving biological control of weeds, it is essential to understand how seed predatory carabids aggregate in the field, and respond to the availability of weed cover and seeds in the soil seedbanks at a local spatial scale over the cropping season. In Chapter 6, I document significant clustering in field populations of seed predatory carabids. My results showed that at all field sites, carabid populations of both the most abundant species and the pooled sample of less abundant species were patchy, giving rise to local aggregations that were spatially associated with weed density. However, I did not find strong spatial association between the activity-densities of seed predatory carabids and areas of high seed density. Thus, colonization and concentration of carabid activity in weedy patches may more strongly reflect responses to the availability of shelter, although I cannot rule out the possibility that seed populations were lower because of the activity of particular carabids. A lack of carabid response to seed availability has been documented. Several studies indicate a lack of carabid response to seed density (Marino et al. 2005; Westerman et al. 2008; Baraibar et al. 2012; but see Frank et al. 2011) or prey density (Birkhofer et al. 2007; Frank et al. 2011; Al Hassan et al. 2012). Potential associations between shelter and food availability have not been well understood, and it has been suggested that vegetative cover is the missing link that can help to quantify the response of carabids to food availability (Blubaugh et al. 2016). Vegetative cover and food resources co-occur and interact, and employing mechanistic approaches to quantify their effects on omnivorous predators in general, or their role in biological control, may be difficult (Blaubaugh et al. 2016). However, my results underline the importance of vegetation cover in field distribution patterns of seed predatory species; further studies are needed to investigate the nature of associations between vegetation cover and food availability.

Current knowledge about the biology and ecology of seed predatory species can provide insights into designing agroecosystem management strategies that can promote the activity of ground beetles by making the crop environment more favourable for their activity (Blaubaugh et al. 2016). Although several aspects of carabid weed seed predation will likely affect our ability to design conservation biological control strategies that are highly effective, my investigation sheds light on weed seed predatory preferences and factors influencing weed seed predation in canola agroecosystems of central Alberta. Weed seed predation can result in substantial reduction in seed recruitment, so enhancing it will be beneficial. For example, field pennycress is a major brassicaceous weed in North America (Holm et al. 1997) and produces up to 15,000 seeds per plant under heavy field infestations (Best and McIntyre 1975). Wild mustard, *S. arvensis*, is another of the noxious weeds in canola agroecosystems of the Canadian prairies with high competitive ability (Warwick et al. 2000). One plant of *S. arvensis* yields close to 1225 seeds (Lutman 2002), and as many as 5300 to 30000 seeds m^{-1} can be found under high infestations. My field experiments indicate that seed removal was proportional to high activity-density of carabids, therefore, tactics to conserve ground beetle populations can result in greater seed removal and mortality. In this context, carabid weed seed predation as a biological control tactics has potential to manage weed populations when combined with other integrated weed management tactics. From a weed management point of view, findings of my investigation suggest that weed seed predation is governed by a guild of species that is dominated by one or two species with high activity-density. Seed predation rates will be affected by seed burial, but seed predation as such will not be eliminated. Conservation or reduced tillage activities will most likely favor weed seed predation. Moreover, leaving some weedy patches in cropped areas can provide shelter and oviposition sites, and can contribute to conservation of carabid populations. Benefits of maintaining weedy patches may outweigh risks considering the reduction in populations of weeds and arthropod pests due to increased carabid activity.

Although my research focused on aspects of seed preferences, olfactory detection and field dynamics, there are several areas that need further investigation. The themes of my investigation can be further expanded upon to strengthen our understanding about weed seed predation. Carabid larva exhibit seed feeding habits (Klimes and Saska 2010) and very limited attention has focused on the potential of carabid larvae in weed seed consumption. Such quantifications are difficult under field conditions, and therefore laboratory studies to understand developmental parameters of larvae, and their feeding potential and preferences will provide valuable information about their possible role in seed predation (Kolesnikov and Malueva 2015; Talarico et al. 2016).

The quantification of seed predation can be further improved by employing molecular studies (Symondson and Harwood 2014) and gut content analyses using techniques like Enzyme Linked Immunosorbent Assay (ELISA) to establish links among seed predators and seed species (Hagler 2006, Lundgren et al. 2013, Kelly et al. 2014). This improve understanding physiological and nutritional aspects of seed preferences found in my studies, and also the relationships between carabid species or species assemblages and weed communities to design better conservation biological control tactics. In addition, a further role for olfaction in seed detection could be explored by extracting volatile compounds emitted by unimbibed and imbibed seeds and observing the response of carabid species to these volatile compounds. This can enhance our understanding about the use of olfactory stimuli in complex environments with mixed stimuli and how a stimulus perception can lead to seed detection and perception. Finally, I did not study seed predation under different agronomic practices and hence, quantification of field seed predation under different agronomic practices in the Prairies would provide useful data to help in designing appropriate management practices to conserve carabid beetles and optimize ecological services provided by them.

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