The Role of Ground Beetles (Coleoptera: Carabidae) in Weed Seed Consumption: A Review

Sharavari S. Kulkarni, Lloyd M. Dosdall, and Christian J. Willenborg*

Weed management is a challenge in all agroecosystems. Given the negative consequences associated with herbicide-based weed management, it is important to consider integrated weed management options with emphasis on strategies such as biological control. Postdispersal weed seed predation by granivorous and omnivorous carabid beetles results in substantial natural suppression of weed populations. Although the role of ground beetles as “generalist predators” in various agroecosystems is known, their contribution to weed management is not well recognized. In this context, this review presents an account of carabids and their granivorous nature, the importance of a seed diet in the life histories of different carabid groups, factors affecting granivory, and their potential role in weed seed management. Below, we discuss the interrelationships among various factors influencing weed seed consumption by carabids, its consequences for weed management, and the need for future research.

Key words: Biological control, carabids, integrated weed management, postdispersal seed consumption, weeds.

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 yr⁻¹ (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.) Scop., can cause up to 60% yield reduction in canola (Brassica napus L. and Brassica rapa L.) (Canola Council of Canada 2014a). 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 (Derkson et al. 2002). Excessive dependence on herbicides has resulted in problems such as selection for 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 such 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 alternative to herbicide applications, and also serves as a sustainable option for long-term weed management (Boyetchko et al. 2009). Biological control can be combined harmoniously with other weed management practices. Some predispersal insect seed consumers have already been used for biological control of weeds (Julien 1992). Postdispersal seed consumption can cause direct death of weedy plants (Crawley 2000; Harper 1977), and serves as a critical factor determining the population dynamics of weeds in agroecosystems (Crawley 2000; Lundgren 2009).

DOI: 10.1614/WS-D-14-00067.1

*First and second authors: Graduate student, Professor, Department of Agricultural, Food, and Nutritional Science, 410 Ag/Forestry Building, University of Alberta, Edmonton, Alberta, Canada T6G 2P5; third author: Assistant Professor, Department of Plant Sciences, College of Agriculture and Bioresources, University of Saskatchewan, 51 Campus Drive, Saskatoon SK, Canada. Corresponding author’s E-mail: sharavar@ualberta.ca
In agroecosystems, 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; Louda 1989; Menalled et al. 2007; Ward et al. 2011). Among vertebrates, rodents are an important group of seed feeders (Hulme 1998, 2002; Kollmann et al. 1998), and some studies suggest that rodents contribute to an equal or greater proportion of seed consumption than invertebrates (Brust and House 1988; Cardina et al. 1996; Harrison et al. 2003; Menalled et al. 2000b; Watson et al. 2003; Westerman et al. 2003a). However, rodents might not prefer disturbed habitats such as agricultural fields (Brust and House 1988; Hulme 1998; 2002; Kollmann et al. 1998). For example, Brust and House (1988) compared seed predation rates under zero tillage and conventional tillage conditions and found that rodents actually contributed significantly more weed seed removal in the zero-tilled (less disturbed) fields.

Among invertebrates, insects comprise an important group of seed feeders (Gallandt et al. 2005; Hulme 1998; Lundgren 2005; Mauchline et al. 2005; Menalled et al. 2000b; Nystrand and Granstrom 2000), and their role in weed seed consumption has gained attention in recent years due to their prominence in agroecosystems (Lundgren 2009). The granivorous taxa of the temperate region are dominated by crickets and carabid beetles (Honek et al. 2003; Lundgren et al. 2006; O’Rourke et al. 2006), and to a lesser degree include some caterpillars (Lepidoptera), weevils (Curculionidae), rove beetles (Staphylinidae) and isopods (Lundgren et al. 2013; Saskia 2008a). In the tropics (Albert et al. 2005; Chauhan et al. 2010; Motzke et al. 2013), semiarid (Baraibar et al. 2009), and arid habitats (Hulme 1998), ants play an important role in seed feeding.

Among invertebrate seed consumers, carabid beetles are an important taxonomic group in temperate agroecosystems (Zhang et al. 1997), and are the focus of this review paper in view of their abundance and importance in Canadian agroecosystems. Their role as arthropod predators is well-known in various agroecosystems, and carabids are considered important biological control agents (Holland and Luff 2000; Kromp 1999; Marko and Kadar 2005). However, evidence from recent studies underlines their potential effectiveness as postdispersal seed feeders of many important agricultural weeds (Bohan et al. 2011; Honek et al. 2003; Jonason et al. 2013; Lundgren 2005; Lundgren et al. 2013; O’Rourke et al. 2006), capable of exerting significant constraints on weed population size. For example, seed consumption by carabids can help to reduce seed stock of a weed species in the range of 65 to 90% (Honek et al. 2005). Weed seed consumption rates of up to 74% have been documented for three weed species: field violet, Viola arvensis Murr.; chickweed, Stellaria media (L.) Vill., and shepherd’s-purse, Capsella bursa-pastoris (L.) Medik., in agricultural habitats (Jonason et al. 2013). Estimates of seed consumption rates by carabid species differ among various agroecosystems, and depend on crop type, activity–density, seasonality, presence of noncrop habitats, and extent of disturbance (Gaines and Gratton 2010). Reports indicate that rates of consumption also vary from moderate consumption rates of 200 seeds m$^{-2}$ day$^{-1}$ (Gaines and Gratton 2010) up to 1,000 seeds m$^{-2}$ day$^{-1}$ in some cases (Honek et al. 2003). More importantly, some carabid species are capable of removing weed seeds that are dispersed on the ground, as well as those that are buried in the soil as a result of agricultural operations (White et al. 2007). This provides an advantage to carabids over other seed consumers that lack the capacity to track buried seeds (Van der Wall 1998). Seed consumption by carabids at the soil surface intercepts the entry of seeds into the soil seed bank after seed rain (Bohan et al. 2011). Capacity to consume buried seeds can further reduce the net seed stock of the soil (Bohan et al. 2011). Such seed consumption thus influences soil seed banks, consequently influencing the community structure of weed populations (Bohan et al. 2011). An understanding of the factors that influence weed seed consumption by ground beetles is very important for facilitating natural suppression of weed populations.

To date, most studies on ground beetles have focused on their distribution (Holland et al. 1999; Honek and Jarosik 2000; Saskia et al. 2008; Thiele 1977), various aspects of their life histories and ecology (Lóvei and Sunderland 1996), species composition, and the effects of agricultural practices on their distribution (Booij and Noorlander 1996; Cárcamo et al. 1995; Dritschilo and Wanner 1980; Ellsbury et al. 1998; Kromp 1989; Lundgren et al. 2006). However, there is a growing interest in habits of primarily granivorous and omnivorous species, and recent studies have focused on weed seed consumption under field conditions (Gaines and Gratton 2010; Honek et al. 2003, 2005;
Carabid Beetles and Granivory

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 Zettoun-Brandmayr 1979; Tréfás 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 (Lövei 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 (Hammond 1979). 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 yr (Lövei and Sunderland 1996).

**Ground Beetles and Seed Diets.** Carabids are generally polyphagous and feeding habits vary from carnivory to omnivory to granivory (Hůrka and Jarosik 2001). Forbes (1883) first reported the granivorous behavior of carabid beetles, but 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 (Lövei and Sunderland 1996). The general
assumption regarding the carnivorous nature of many carabid species is exaggerated (Lindroth 1992). In fact, Lindroth (1992) found that about 35% of the species he studied exhibited omnivorous feeding habits.

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; Saska 2005; 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 generally considered highly carnivorous, including Bembidion quadriraculatum (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 (Gylenthal) (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 (Lövei and Sunderland 1996). Within carabid groups, there are significant variations in larval feeding habits. In an evolutionary context, granivory is an apomorphic character in the larvae of Carabidae and evolved independently in several groups of the family (Húrka and Jarosík 2003; Klimes and Saska 2010; Saska and Jarosík 2001; Zetto-Brandmayr 1990), whereas carnivory is considered plesiomorphic (Húrka 1996).

Within the Carabidae, granivory, as a derived character, occurs in relatively few species. Larvae of the granivorous genus Amara were considered primarily carnivorous (Luff 1993), until Thompson (1979) and Húrka (1998) demonstrated that Amara larvae could be reared on a diet of oat flakes. Recent evidence suggests that larvae of Amara could be granivorous (Fawki and Toft 2005; Jørgensen and Toft 1997; Klimes and Saska 2010), or omnivorous (Húrka and Jarosík 2001, 2003; Saska 2005). Larvae of species from genera Ditomus, Ophonus, and Harpalus have also been reported to be primarily granivorous (Briggs 1965; Kirk 1972; Zetto-Brandmayr 1990). Larvae of Ophonus puncticeps (Stephens) and O. ardosiacus (Lutshnik) are exclusive seed feeders and generally consume umbelliferous seeds (Zetto-Brandmayr 1976, 1983). Despite variations in extent to which granivory has evolved among larval groups, their role in weed seed consumption is important and has implications for weed management.

Adaptations to Granivory. Seed-feeding carabids have several behavioral, morphological, and physiological adaptations for granivory. For example, seed-caching behavior is prominently observed in the adults of Ditomus spp. (Schremmer 1960) and in larvae of Harpalus and Ophonus species (Hartke et al. 1998; Kirk 1972; Luff 1980; Zetto-Brandmayr 1983). However, size and depth of these burrows are species-specific and can vary according to larval stage. For example, first- and second-instars can burrow 10 to 13 cm in the soil (Alcock 1976; Hartke et al. 1998; Luff 1980), but the third-instars can burrow up to 17 cm (Luff 1980). Burrowing habits help to protect the larvae from predators and other natural enemies and also help to maintain better conditions for growth, such as regulating humidity and avoidance of water loss. The seeds cached can be maintained in good condition for a long time (Tooley and Brust 2002).

Apart from seed caching, another behavioral adaptation is climbing on plants. Sasakawa (2010a) observed that several carabid species belonging to the genera Amara and Harpalus climb on weeds and feed on flowers and seeds. For instance, Amara gigantea (Motschulsky) climbed preferentially on plants of Japanese hops [Humulus japonicus (Sieb. & Zucc.)]. The climbing and foraging behavior was observed mainly in females, and females consumed more seeds than males (Saska et al. 2010). Males climbed on plants primarily for copulation rather than for foraging or seed feeding.

To crush the hard seeds, larvae of Amara have developed broad and triangular mandibles with the presence of a subapical tooth in some species (Klimes and Saska 2010). In contrast, larvae of Harpalus possess stout mandibles (Luff 1993), and
the adults of these genera possess broad mandibles (Forbes 1883; Forsythe 1983; Zetto-Brandmayr et al. 1998). Acorn and Ball (1991) studied mouth parts of adult granivorous carabids, and noted that these beetles possess robust mandibles with highly modified structures. For example, the terebral ridge of the mandibles is more sinuate in occlusal aspect to give additional strength to the mandibles. Similarly, a chisel-shaped incisor region provides vertical shear, and the retinacular region is well-modified in a way such that the ridges of retinaculum form a compact basin for the production of the bolus of the chewed food.

Digestion of solid plant material is facilitated by the evolution of sclerotized structures in the adult proventriculus (Evans and Forsythe 1985). Microbial communities in the gut play an important role in digestion of plant-based food in omnivorous insects (Campbell 1989; Jones 1984). Knowledge of the physiological adaptations for digestion of seed material in carabid beetles is currently limited. The presence of endosymbiotic communities in the gut of Harpalus pensylvanicus (De Geer) is known, and they possibly have a role in facilitating digestion of seed material (Lundgren and Lehman 2010).

Importance of Seed in the Carabid Life Cycle. Seed is a more nutritious food source for granivores compared to any other plant structure due to its high protein content and nitrogen levels (Bewley and Black 1994; Crawley 2000; Lundgren 2009). Seeds in the diet can influence female fecundity, survival of preimaginal stages, overall growth and developmental rate (Saska 2005; Saska and Jarosik 2001), and larval survival (Fawki and Toft 2005; Sasakawa 2010).

Species-specific differences exist in the importance of seed vs. animal food in the diet of carabids. For instance, larvae of Ophonus spp. feed exclusively on seeds, and supplementing their diet with animal food affects their survival and development (Zetto-Brandmayr 1990). Larvae of Harpalus honestus (Duftschmid) developed faster when fed solely with seeds of dandelion (Taraxacum officinale F.H.Wigg.) compared with animal-based diets (Zetto-Brandmayr 1990). By contrast, larval developmental and survival rates were higher for the omnivorous species, Amara aenea De Geer (Hürka and Jarosik 2003), and Amara convexiuscula Marsham (Saska 2005) for a seed- and animal-based diet mixture vs. a pure seed-based diet. Jorgensen and Toft (1997) determined that larval survival and development of Amara similata were higher on a mixed seed-based diet than on seeds mixed with an animal diet. Likewise, adding animal components such as earthworms or slugs reduced the chances of larval survival for Amara similata, and larvae performed better on a pure seed diet (Fawki and Toft 2005).

Food quality can also affect female fecundity in carabids. For example, Amara similata females laid more eggs when fed a mixed seed diet or when an animal-based diet was supplemented with seeds. The species of weed seed can significantly influence life parameters in granivorous carabids. Females of Amara similata fed seeds of scentless chamomile, Tripleurospermum perforatum (Mérat) M. Lainz and dandelion, Taraxacum sp. had higher fecundities than those that fed seeds of annual bluegrass, Poa annua L. (Jorgensen and Toft 1997). Larvae responded differently than adults and their survival rate was highest on smaller seeds of C. bursa-pastor over the larger seeds of T. perforatum and Taraxacum sp. This was probably due to larger seed size of T. perforatum and Taraxacum sp., which are difficult for the first instars to consume (Jorgensen and Toft 1997). Thus, nutritional preference depends on the seed species and animal prey involved, which optimize nutritional gain required to complete the physiological process of granivorous species (Lundgren 2009).

Weed Seed Preferences of Carabids. Carabids can exhibit specific preferences for seeds of certain weed species. Such preferences are influenced by carabid species as well as seed characteristics. Important factors determining weed seed consumption are the size of the seed consumer and the size of the seed, both of which influence seed consumption rates (Brown et al. 1979; Brust and House 1988; Hartke et al. 1998).

Preferences of weed seed consumers could have impacts on weed communities. Preferences for specific weed seeds could lead to changes in the population dynamics of the preferred weed species and also of the weed community in general. Brust (1994) observed that under greenhouse conditions, carabid species preferred seeds of dicot over monocot species, thus altering the relative yield of broadleaf weeds compared to grassy weeds. Such a preference and the resulting yield losses would create a competitive advantage for the nonpreferred over preferred weed, thus influencing the population composition and community structure of weed species under field conditions. On the contrary, some other studies reported that monocot weeds...
were preferred over the broadleaf weeds (Saska 2008b; Heggenstaller et al. 2006). Davis et al. (2013) determined that variation in long-term seed consumption is largely determined by the weed species. Hence, if a seed-feeding species exhibits a strong preference for an economically important weed species in a particular agroecosystem, it might play an important role in management of that weed population.

Carabid beetle body size is among the major determinants of weed seed preferences. Honek et al. (2003, 2007, 2011) experimented with adults of several carabid species and found that the preference for the seed depended on carabid body size.

The abundances of granivorous and omnivorous species in a given agroecosystem also determine weed seed consumption. Furthermore, the composition of species assemblages in terms of carabid body size would ultimately influence seed preferences under field conditions. Preferences of large-bodied species such as *H. pensylvanicus* for large weed seeds are thus most likely to influence weed communities producing relatively large seeds. Such preferences can favor other weed species if the composition of the carabid fauna is dominated by one or a few species with highly specific preferences. However, size-based seed preferences can also facilitate co-existence of different granivorous carabid species and reduce intraguild competition (Lundgren 2009). Such reduced intraguild competition in the presence of small- and large-bodied carabids has been documented under field conditions. With few exceptions, large carabids preferred larger seeds and vice versa. For example, large carabids are known to feed on dandelion seeds of large size whereas the smaller carabids prefer smaller dandelion seeds (Honek et al. 2011). Although seed consumption is positively associated with the body size of the granivorous carabids (Honek et al. 2006), the rates of seed consumption among large-sized carabids can vary. For example, individual adults of species such as *Pseudophonus rufipes* (De Geer) have been reported to consume 10 to 12 seeds d⁻¹ of canola, whereas *Pterostichus melanarius* (Illiger) consumed 2 to 8 seeds d⁻¹ (Koprdová et al. 2012). However, several factors including, and not limited to, the diet of omnivorous species, physical state of seed (exhumed, imbibed vs. dry), and taxonomic preferences for seed consumption might bring about such differences in observed rates of weed seed consumption among bigger carabid groups (Koprdová et al. 2012). In fact, Gaines and Gratton (2010) determined under field conditions that small carabid species consumed seeds that were smaller (3.26 mm diam), whereas large carabid species consumed seeds that were larger (4 mm diam). Prior research indicates that there is a certain seed size beyond which the seeds are unacceptable (Lundgren and Rosentrater 2007). However, once this size limit is set, other seed traits govern carabid seed preferences. These other traits include seed coat hardness, seed density, nutritional quality, or other morphological traits. Such seed characters are seed defensive traits (Lundgren 2009), and are the mechanisms utilized by seeds to deter predation. For example, a hard seed coat restricts granivory because the granivore needs to invest substantial energy to break the seed coat and reach the endosperm (Brust and House 1988; Carmona et al. 1999; Kremer and Spencer 1989; Tooley and Brust 2002). Preference for softer and smaller seeds of redroot pigweed (*Amaranthus retroflexus* L.) and giant foxtail (*Setaria faberi* Herrm.) over hard-coated and large seeds such as velvet leaf, *Abutilon theophrasti* Medik., were attributed both to the physical properties of the seed coat and to seed size (White et al. 2007). Nevertheless, certain carabid species prefer seeds with hard seed coats over those with soft seed coats. For example, *H. pensylvanicus* preferred smaller, tough seeds with hard seed coats whereas *Anisodactylus sanctaecrucis* (Fabricius) preferred seeds that were hard internally (Lundgren and Rosentrater 2007). Although some earlier studies indicate that hard seed coats restrict granivory (Cardina et al. 1996; Pausch and Pausch 1980; Ready and Vinson 1995), this cannot be generalized for all seed types because the strength of, and adaptations possessed by, a particular carabid species determine seed preferences. Similarly, seeds with external appendages and projections offer mechanical resistance to predation. Further, chemical seed defenses include concentrated secondary metabolites such as alkaloids, lectins, phenolic compounds, and glucosinolates (Lundgren 2009).

The origin of weed species can also affect predation. Under a choice scenario, carabid beetles from the Czech Republic preferred dandelion seeds from the Czech Republic over the seeds originating from Italy (Honek et al. 2011). However, the information on population preferences and the mechanisms involved in such preferences is currently limited.

Nutritional quality of the seed is also an important criterion determining seed preferences (Crist and McMohan 1992; Inouye 1980). However, few studies have explored the effects of
nutritional quality on carabid weed seed preferences. The nutritive value of seeds can directly affect life history parameters of the consumer, and nutritional gains and the associated advantages can vary among seed types, influencing the performance of the granivore. Higher fecundity and larval growth rates of *Harpalus rufipes* (DeGeer) on the seeds of common lambsquarters (*Chenopodium album* L.) than those of other cereals and rye grass are indicative of nutritional advantages associated with common lambsquarters seeds. As a consequence, larvae of *H. rufipes* tended to aggregate in field patches with high common lambsquarters density (Briggs 1965). This demonstrates that nutritional quality is not only a determinant of seed preferences but can also determine field dynamics and foraging behavior of seed consumers.

It is not only carabid adults that show specific weed seed preferences because even the larvae can prefer one seed type over another. These preferences are mainly expressed by the early larval instars and might be governed by morphological traits such as the size of the larval head capsule. For example, first-instar larvae of *Amara similata* fed exclusively on seeds of common chickweed (Paarmann et al. 2006) and shepherd’s purse (Klimes and Saska 2010), whereas the later instars had generalist feeding habits that lacked discrete preferences. First-instar larvae of the generalist species, *Amara aenea*, had more difficulty in crushing the hard seed coat of dandelion compared with the late instars, which supports the idea that morphological constraints are an important factor in the seed preferences of granivores (Paarmann et al. 2006). Larvae with burrowing habits and seed-caching strategies also demonstrate specific seed preferences (Alcock 1976). For instance, larvae of *H. pensylvanicus* and *Harpalus erraticus* Say mainly prefer foxtail seeds for storing in a seed cache (Kirk 1972). It is not clear whether factors such as nonperishability over long storage durations might influence the preference of carabids for specific weeds.

Finally, mobility of seed consumers such as carabids has been considered to influence rates of weed seed predation (Cromar et al. 1999). Adults of Carabidae are highly mobile, but the larvae are relatively less mobile than adults; in some species, adults cache the seeds as a part of maternal care to provide seeds to immature stages (Lundgren 2009). However, not much is reported on how the mobility affects the seed tracking behavior. For example, it is not documented whether the beetles can track seeds away from their habitat efficiently, and how far they can move in tracking seed sources. Previous studies have reported that carabids did not respond specifically to weed density manipulations, which suggests that they do not respond to stimuli such as seed density (Westerman et al. 2008).

**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 the 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 (Bohan et al. 2011; Westerman et al. 2003b).

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 even conspecifics can differ in terms of seed consumption. In some cases, predation rates can be as low as 4% d⁻¹ (Brust and House 1988) but in other studies, carabids can consume the majority of seeds in a system, sometimes consuming 70% of all seeds in a given season (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, 2011), abiotic factors such as 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).

Under greenhouse conditions, a reduction in seed number of common lambsquarters and redroot pigweed by 56 and 63%, respectively, has been reported for eight carabids species belonging to *Amara*, *Anisodactylus*, *Harpalus*, and *Stenolophus* (Brust 1994). Likewise, carabid species such as *Harpalus affinis* Schrank and *Pseudophonus rufipes* have been shown to feed on as many as 120 seeds of Canada thistle [*Cirsium arvense* (L.) Scop.] in a 5-d
Table 1. An overview of studies focusing on weed seed consumption by different granivorous taxa under field conditions.

<table>
<thead>
<tr>
<th>Seed consumer</th>
<th>Weed species</th>
<th>Removal rate</th>
<th>Crop</th>
<th>Study duration</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>and crickets</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vertebrate exclusion</td>
<td><em>Alopecurus myosuroides</em> Huds., <em>Bromus sterilis</em> L., <em>Avena fatua</em> L.</td>
<td>1.43–7.2% d⁻¹</td>
<td>Grassy margins of cereal fields</td>
<td>1 mo</td>
<td>Povey et al. 1993</td>
</tr>
<tr>
<td>Carabids, crickets</td>
<td><em>Ablation theophrasti</em> Medik.</td>
<td>11% d⁻¹</td>
<td>Corn</td>
<td>4 yr</td>
<td>Cardina et al. 1996</td>
</tr>
<tr>
<td>Invertebrates</td>
<td><em>Echinochloa crus-galli</em> (L.) Beauv., <em>Chenopodium album</em> L.</td>
<td>28–31% d⁻¹</td>
<td>Corn; soybean and wheat</td>
<td>2 yr</td>
<td>Cromar et al. 1999</td>
</tr>
<tr>
<td>Invertebrate</td>
<td><em>Digitaria sanguinalis</em> (L.) Scop., <em>Setaria faberi</em> Herrm., <em>A. retroflexus</em>, <em>A. theophrasti</em></td>
<td>11% d⁻¹</td>
<td>corn</td>
<td>2 wk</td>
<td>Menalled et al. 2000</td>
</tr>
<tr>
<td>Mainly cricket, ground</td>
<td><em>S. faberi</em></td>
<td>58% d⁻¹</td>
<td>Wheat with red clover</td>
<td>3 mo</td>
<td>Davis and Liebman 2003</td>
</tr>
<tr>
<td>beetles also captured</td>
<td></td>
<td></td>
<td>cover crop</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Harpalus pensylvanicus</em></td>
<td><em>Ambrosia trifida</em> L.</td>
<td>57–70% yr⁻¹</td>
<td>No-till corn</td>
<td>12 mo</td>
<td>Harrison et al. 2003</td>
</tr>
<tr>
<td>Carabids</td>
<td><em>C. album</em>, <em>Stellaria media</em> L., <em>A. fatua</em></td>
<td>35% wk⁻¹</td>
<td>Spring barley</td>
<td>2 wk</td>
<td>Mauchline et al. 2005</td>
</tr>
<tr>
<td>Carabids</td>
<td><em>C. album</em>, <em>Sinapis arvensis</em> L.; <em>S. media</em>, <em>Polygonum aviculare</em> L.</td>
<td>17% d⁻¹</td>
<td>Corn–soybean</td>
<td>2 yr</td>
<td>Westerman et al. 2005</td>
</tr>
<tr>
<td>Carabids</td>
<td><em>A. theophrasti</em></td>
<td>32%/d⁻¹</td>
<td>Corn–soybean–Triticale + alfalfa–alfafa</td>
<td>4 yr</td>
<td></td>
</tr>
<tr>
<td>Invertebrates</td>
<td><em>S. faberi</em>, <em>A. theophrasti</em></td>
<td>16–30% d⁻¹</td>
<td>Different crop rotations of cereals and legumes</td>
<td>4 mo for 2 yr</td>
<td>Heggenstaller et al. 2006</td>
</tr>
<tr>
<td>Carabids</td>
<td><em>C. album</em>, <em>Panicum dichotomiflorum</em> Michx.</td>
<td>10–90% d⁻¹</td>
<td>Corn (organic; no-till and conventional)</td>
<td>4 August–7 September 2000</td>
<td>Menalled et al. 2007</td>
</tr>
<tr>
<td>Carabids and Isopoda</td>
<td><em>T. officinale</em></td>
<td>34–40% yr⁻¹</td>
<td>Grassland</td>
<td>2 yr</td>
<td>Honek et al. 2009</td>
</tr>
<tr>
<td>Carabids</td>
<td><em>S. faberi</em>, <em>A. trifida</em>, <em>A. theophrasti</em>, <em>A. retroflexus</em></td>
<td>11% d⁻¹</td>
<td>Potato fields</td>
<td>4 wk</td>
<td>Gaines and Gratton 2010</td>
</tr>
<tr>
<td>Invertebrates</td>
<td><em>S. faberi</em></td>
<td>5% d⁻¹</td>
<td>Surrounding noncrop habitat</td>
<td>4 yr</td>
<td></td>
</tr>
<tr>
<td>invertebrates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Downloaded from https://www.cambridge.org/core. IP address: 54.70.40.11, on 27 Jan 2019 at 04:35:51, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
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). In Indiana, *H. pensylvanicus* was a major seed consumer on 12 weed species (Lund and Turpin 1977), whereas *Amara* spp. and *Harpalus* spp. have been shown to contribute to more than 70% of weed seed consumption in other studies (Table 1) (Mauchline et al. 2005).

Although laboratory studies demonstrate the weed seed-feeding potential of carabids, the relationship between seed consumption rates and the activity–density (numbers captured trap$^{-1}$ day$^{-1}$) of granivorous ground beetles has proven to be ambiguous under field conditions. Several studies have observed a positive relationship (Gaines and Gratton 2010; Honek et al. 2003, 2005; Jonason et al. 2013; Menalled et al. 2007; Trichard et al. 2013), whereas other studies have shown a lack of spatio-temporal association between the two factors (Mauchline 2005; Saska et al. 2008). A lack of relationship between activity–density and seed consumption activity might be attributed to the method of sampling (Lundgren et al. 2013), and site-specific variations in rates and activity of seed consumption (Davis et al. 2013). For example, most studies used pitfall traps to sample carabid beetles, but these are known to be biased towards the preferential capture of large, surface-active species (Arneberg and Andersen 2003; Spence and Niemelä 1994). The activity–density of carabid beetles trapped in pitfall traps fluctuates as a result of climatic factors (mainly temperature), which should be considered (Saska et al. 2013). Hence, interrelations between activity–density and carabid weed seed consumption should be interpreted with caution and with consideration, given to biases that can skew estimations. Despite this, pitfall trapping is a relatively common method used in most studies due to the relative ease in handling the traps, and the efficiency in trapping carabid beetles. Activity–density as an indicator of carabid abundance alone might not, however, be the best predictor of carabid weed seed-consumption activity.

Many of the studies reported here measured surface weed seed predation; only one study has examined the actual relationship between carabid activity–density and its effect on seeds deeper within the soil seed bank. A study by Bohan et al. (2011) examined the relationship between activity–density of carabids and the seed bank in spring maize (*Zea mays* L.) and winter oilseed rape in fields across the United Kingdom. The results showed that the

<table>
<thead>
<tr>
<th>Weed species</th>
<th>Carabids</th>
<th>Vertebrates and invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Viola arvensis</em></td>
<td><em>C. trivialis</em>, <em>S. media</em>, <em>C. bursa-pastoris</em></td>
<td><em>V. arvensis</em>, <em>S. media</em>, <em>C. bursa-pastoris</em>, <em>A. myosuroides</em>, <em>S. faberi</em>, <em>A. trifida</em>, <em>A. theophrasti</em></td>
</tr>
<tr>
<td>Removal rate</td>
<td>16.5% d$^{-1}$</td>
<td>30% wk$^{-1}$</td>
</tr>
<tr>
<td>Crop</td>
<td>Organic, conventional farms, main cereal fields</td>
<td>28 winter cereal fields</td>
</tr>
<tr>
<td>Study duration</td>
<td>2 wk</td>
<td>5 wk</td>
</tr>
<tr>
<td>Period</td>
<td>Organic; conventional farm over 1 km radius; mainly studied landscape factors</td>
<td>28 winter cereal fields</td>
</tr>
</tbody>
</table>

Table 1. Continued.
granivorous and omnivorous carabid species are efficient in managing seed banks of monocot weed seeds, and omnivorous *Pterostichus melanarius* had a density-dependent response to monocot weed seed banks. In addition, the activity–density of three *Pterostichus* spp. was efficient in consuming post-dispersal seeds and reduced the number of seeds entering the soil seed bank.

Synchronization between the weed seed availability on the ground surface and phenologies of carabid species is also important for effective weed seed removal (Mauchline et al. 2005; Westerman et al. 2012). Several carabid beetles such as *H. pensylvanicus* and *Pterostichus melanarius* are autumn-breeding, whereas species such as *Amara littoralis* (Mannerheim) are spring breeders. The seasonal phenologies of these species would thus influence weed seed consumption.

Many carabid species that feed on weed seeds are omnivorous, and the presence of alternate food sources could decrease seed feeding over the growing season. This omnivorous behavior can lead to variable seed consumption; omnivory is higher earlier in the season than later due to the high availability of alternate prey (Marino et al. 2005; Mauchline et al. 2005). Trichard et al. (2013) determined that the weed seed consumption rate was positively related to the diversity of granivorous species and negatively related to the diversity of omnivorous species. This association might be due to variable preferences of some omnivorous species between animal and plant food sources. In another study, the omnivorous carabid beetles responded positively to seed subsidies in the field (Frank et al. 2011). Therefore, seed consumption is dependent on the availability of alternate resources, carabid species preferences (granivory vs. omnivory), and any potential deterrents utilized by the seed (Lundgren 2009).

Seed burial is a major factor hindering post-dispersal seed consumption (Chambers and McMahon 1994; Crawley 2000). Several processes, including tillage, the development of cracks and pores due to changes in soil physical properties, and the activities of terrestrial fauna (burrowing, caching) can result in seed burial at a depth where they are no longer available to surface active-predators (Chambers and McMahon 1994; Westerman et al. 2006).

Carabid species differ in their ability to consume seeds that are buried at different depths (Klimes and Saska 2010). Some species such as *Amara aenea* and *Anisodactylus sanctae crucis* showed reduced seed consumption as the depth of the seed burial increased. In contrast, predation by *H. pensylvanicus* remained unaffected by seed burial depth. *H. rufipes* preferred wild mustard (*Sinapis arvensis* L.) seeds dispersed on the ground compared to buried or half-buried seeds; both the seed consumption rates and efficiency were affected by seed burial (Harrison and Gallandt 2012). Despite such differences in weed seed consumption, the role of seed-feeding carabid species in weed seed removal and soil seed bank management is important, and need to be investigated further.

Earlier studies have reported that weed seed consumption can be density-independent (Brust and House 1988), inversely density-dependent (Cardina et al. 1996), or positively density-dependent (Cromar et al. 1999). Weed populations are patchy under field conditions and this spatial aggregation plays a role in weed dispersal (Cousens et al. 2006; Rew et al. 1996). This can be positive because density-dependent seed consumption in weed patches is beneficial in terms of weed management. For example, if the rate of seed consumption increases with increasing seed density in patches, it can significantly limit future weed dispersal and persistence (Cousens et al. 2006; Lundgren 2009). Two limitations exist, however: (1) density-dependent weed seed consumption is more prominent in ants than in carabids; and (2) absolute seed density alone does not determine weed seed removal by carabids, although they prefer aggregated seed patches (Marino et al. 2005; Noroozi et al. 2012). As a result, higher weed seed removal rates were measured in fields with highly aggregated seed distributions than when seeds were available in high densities (Marino et al. 2005; Noroozi et al. 2012).

Seasonality in weed seed availability also determines seed consumption behavior. Westerman et al. (2008) determined there was more positive density-dependent seed consumption late in the season than earlier in the season. However, density-dependent seed consumption patterns cannot be established as a norm in the case of carabid species because seed consumption is a result of several functionally diverse granivorous communities acting variably at different spatial and temporal scales (Hulme 1998; Marino et al. 2005). High seed density can result in satiation and lead to an inverse density-dependent response (Janzen 1971), and under such circumstances biological control might not be an effective strategy (Lundgren 2009). Even under laboratory conditions, carabids showed early satiation at high
seed densities that resulted in reduced seed consumption (Honek et al. 2003, 2006). This suggests that when seeds are available in excess of what seed-consuming carabids can eat, there is a gradual decline in rates of seed consumption once that satiation level has been reached (Lundgren 2009). Hence, high seed availability might not always coincide with high seed-removal rates. However, attainment of satiation largely depends on the time of year (Westerman et al. 2008), the overall hunger level of consumers, and the community composition. Synchronization of carabid activity with seed production and dispersion patterns can help carabid communities maintain their seed consumption activity, and carabid communities are frequently well-synchronized with weed seed consumption patterns (Lundgren 2009). Consequently, higher satiation patterns and a subsequent decline in carabid weed consumption rates are often documented in late fall (Davis and Raghu 2010; Westerman et al. 2008).

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, we present an account of the major factors that affect weed seed consumption under field conditions.

Agricultural Management Practices. Because of their epigeal habit, carabid activity in agroecosystems is affected by agricultural management practices such as crop species, cultivation intensity, and crop diversification. Factors such as species habitat preference (Thomas et al. 1997), soil cultivation pattern (Cárcamo et al. 1995; Holliday and Hagley 1984; Tyler and Ellis 1979), cropping system (Blubaugh et al. 2011; Booij and Noorderlander 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 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. A good sod layer maintains aeration and serves as an amenable site for overwintering because it maintains favorable temperature and microclimate (Desender et al. 1981) compared to compact sod with poor aeration. However, the influence of disturbance caused by cropping practices depends on species habitat requirements and behavior. Here we have focused on important agricultural management practices that influence the activity of seed-consuming carabid groups. The practices we have emphasized include tillage, crop diversification, and other management practices such as pest management, and their direct and indirect influences on carabid activity.

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. 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 can vary among carabid species. One of the important factors causing this variation is synchronization between timing of tillage operations and the presence of sensitive life stages of carabid species. The autumn-breeding *Pterostichus melanarius* overwinters as a larva in the soil, and hence spring conventional tillage could negatively affect its populations (Cárcamo 1995; Fadl 1996; Hatten et al. 2007; Lalonde et al. 2012; Shearin et al. 2007). The extent to which a carabid species is affected by tillage is also determined by species habitat preferences and habits. For example, the larvae of *H. rufipes* overwinter deep in the soil at a depth of about 45 cm (Briggs 1965; Speight and Lawton 1976), a habit that can help them to escape the deleterious effects on their populations of tillage operations in early spring (Baguette and Hance 1997; Shearin et al. 2008). Tillage performed at a shallow depth is therefore less likely to damage the larvae and pupae of *H. rufipes*. In contrast, the eggs, adults, and neonate larvae of this species are most prone to tillage operations performed in late spring because they are present in the upper soil layer and exposed to tillage operations directly. Hence, how a
particular operation is likely to affect a given carabid species depends upon the overlap of agricultural operations with phenological parameters and species characters.

The equipment used for tillage operations determines the extent of soil disturbance and its ultimate effect on carabid populations. Studies indicate that soil disturbance and subsequent damage to granivorous beetles was lower when a chisel plow was used under a minimum tillage regime, compared to the disturbance caused by a mouldboard plow and rotary hoe (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 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). Menalled et al. (2007) reported that both the activity–density of seed-feeding species and the rate of seed predation were higher in zero tillage fields than in conventionally tilled fields. Contrary to this, Cromar et al. (1999) reported that weed seed consumption rates were higher in fields subjected to a zero tillage regime as well as those tilled with a mouldboard plow, compared with those fields that were tilled with a chisel plow. This indicates that not only does the type of tillage influence seed consumption, but too does the equipment used for tillage.

Further, zero tillage regimes create undisturbed conditions, which sustain high arthropod diversity (House and Parmelee 1985). This also ensures higher prey availability, and thus, 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. On the contrary, fields subjected to intensive tillage operations (for example, using a mouldboard plow) can cause extensive disturbance, destroy sheltered habitats for various arthropod species, and hence negatively affect arthropod biodiversity (House and Parmelee 1985; Stinner et al. 1988). As a consequence, the availability of alternate food resources is reduced and higher rates of seed predation are measured (Cromar et al. 1999). Given the above observations, the interrelations among tillage, carabid population dynamics, and weed seed consumption are obviously complex (Shearin et al. 2007).

**Cropping Diversity.** Diversity of carabid beetles under different cropping systems has been studied extensively. Studies have usually demonstrated that carabid populations are increased 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 (Cárcamo 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, the crop phenology, and the habitat requirement of the granivorous taxa present in that field. Previous results conclude that a cover crop and its residue can have a positive impact on predator communities by providing a favorable microhabitat, which protects them from extreme climatic conditions and provides for greater food resources (Carmona and Landis 1999; Manley 1996; Rivard 1966; Speight and Lawton 1976). Some carabid species, such as *Bembidion* spp., are xerophilous, preferring dry areas with sparse vegetation (Hummel et al. 2012), whereas some are hygrophilous, such as *Pterostichus melanarius*, which prefers a dense crop canopy and might benefit from cover crops such as clover (*Trifolium* spp.). Understanding interactions among major granivorous species from particular agroecosystems and their habitat requirements can help to conserve beneficial species. This can be achieved by maintaining suitable shelter areas and vegetation that can provide supplementary food resources and microhabitats for different species.

Among the abiotic conditions that support higher carabid faunas are soil temperature and relative humidity (Shearin et al. 2008). The type of crop grown significantly alters soil temperatures and humidity, and can influence carabid abundance and seed consumption. For example, a cover cropping system of oat (*Avena sativa* L.) and pea (*Pisum sativum* L.) in summer followed by a fall crop of winter rye (*Secale cereale* L.) and hairy vetch (*Vicia villosa* Roth) will lower soil temperature and increase relative humidity, thereby favoring the abundance of *H. rufipes*, compared to a system consisting of a fallow season followed by the cover crops of clover and oat (Shearin et al. 2008). Fallowing for one season relies on disturbance-based weed management and is most likely to impact carabid abundance and activity, thereby creating conditions that are less favorable than those created by suitable crop regimes.

The amount of vegetation cover varies with crop phenology, which in turn affects populations of
granivorous taxa and the rate of seed removal under field conditions (Heggenstaller et al. 2006; Westerman et al. 2011). For example, higher seed removal rates in a phenologically late-maturing crop of sugar beet (Beta vulgaris L.) have been observed compared to early-maturing cereals (Westerman et al. 2011). This can be attributed to two factors: high activity–density of granivorous taxa late in the season due to abundant vegetation cover in the late-maturing sugar beet field compared to cereals, as well as high temporal overlap between carabid activity and seed rain. This example demonstrates that diversifying cropping systems by incorporating crops with different phenologies can help to provide a long activity window for granivorous carabids to consume weed seeds. Similarly, weed cover and diversity can impact seed predation. Blubbaugh et al. (2011) determined that weed cover conserves more omnivorous species that probably feed on weed seeds. Likewise, the activity–density of two major granivorous species in Pennsylvania [Amara aenea (De Geer)and H. pensylvanicus] was higher under a cover crop regime compared to a fallow and soybean [Glycine max (L.) Merr.] crop (Ward et al. 2011).

In a crop rotation, seed losses can vary over different phases of the rotation as a result of crop type, crop age, and weeds associated with specific crops. For example, in a crop rotation sequence of corn–soybean–triticale (Triticosecale spp.) + alfalfa (Medicago sativa L.)–alfalfa, seed losses for weeds such as velvetleaf (Abutilon theophrasti Medik) attributed to carabid activity were as high as 40% in the soybean phase but only 27% in the other phases due to the change in associated weeds and crop growth stages (Westerman et al. 2005). The predicted losses can reduce weed populations substantially, and any further seed loss would result in a significant decrease in weed species such as velvetleaf in these cropping systems (Westerman et al. 2005).

In a crop rotation, a preceding crop can significantly influence the activity–density of granivorous carabids in succeeding crops. For example, in a canola–corn crop rotation system, more species from the granivorous genus Amara were recorded than in corn monocrops (Bourassa et al. 2010). Availability of canola seeds lost during harvesting operations in the preceding season could have resulted in the high numbers of this granivorous genus (Bourassa et al. 2010).

Other Disturbances. Among other factors that can influence carabid activity, the use of chemicals for agricultural pest management can be an important factor, although the effects of pesticides in crop management on seed-consuming communities such as carabids have not been extensively investigated (O’Rourke et al. 2006). 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). Omnivorous species such as Pterostichus melanarius have been known to be affected by insecticide applications (Holland and Luff 2000), and are known to be susceptible to the organophosphate insecticides such as dimethoate (Holland et al. 2000). Some insecticides such as synthetic pyrethroids, which are considered less toxic to nontarget organisms, have been reported to cause sublethal toxicity among carabid species (Tooming et al. 2014).

The studies investigating effect of insecticides indicate insecticidal application negatively affects carabid population (Brown et al. 1983; Floate et al. 1989). Some studies indicate that the effects of insecticidal applications can be short-lived, and populations can recover in time (Holland 1998; Holland and Luff 2000). Factors such as species dispersal ability, availability of shelterbelts, and unsprayed buffer zones determine the ability of beneficial species to recover from insecticide applications and repopulate field areas (Holland and Luff 2000). Further, reduced dosage of field applications of insecticides and herbicides can help to maintain carabid activity (Navntoft et al. 2006). At reduced applications rates (0.25 of the recommended application rates) of herbicides and insecticides, a 25% increase in overall carabid activity has been documented in Europe; however, the activity of one species, Pterostichus spp., improved by 62% under these reduced rates (Navntoft et al. 2006). This underlines the importance of judicious applications of agricultural chemicals as it pertains to the conservation of beneficial insects such as those that consume weed seeds, and in particular, the ground beetles of the Carabidae family.

Timing of application of agrochemicals, particularly of insecticides, is critical in context of maintaining carabid populations. For example, nocturnal species are less exposed to insecticide applications (Navntoft et al. 2006). Synchronization
of adult emergence with time of insecticide applications further determines susceptibility of adults to such applications. Adults of omnivorous species such as *Pterostichus melanarius* emerge in spring, which coincides with the timing of insecticidal applications, and this could result in higher sustainability of teneral adults to various insecticides (Navrot et al. 2006).

Typically, the application of herbicides and fungicides has few direct adverse effects, but herbicide applications indirectly influence carabid populations through reduced food availability and habitat suitability (Brust 1990; Holland and Luff 2000). Previous studies indicate a lack of acute or chronic toxicity effects of commonly used herbicides (atrazine, simazine, paraquat, and glyphosate) on carabid fauna (Brust 1990). However, indirect effects of herbicide applications can be particularly prominent for strictly granivorous members that rely on weed seeds as a food source. Moreover, changes in composition, weed density, and seed availability can affect their activity (Holland and Luff 2000). The extent of the effects of herbicide applications further depends on species habitat requirements. Species that prefer open habitats can disperse better and are less affected by herbicide applications compared to species such as *Amara* spp. that require weedy patches and cropped habitats (Holland and Luff 2000). For example, smaller carabids that show burrowing behavior have been reported to be less affected by herbicide applications (Brust 1990) compared to large carabids.

Negative effects of fungicides can be measured in the form of reduced diversity of carabid groups. Trichard et al. (2013) recorded a negative impact of fungicides used for disease management on the Shannon diversity indices of granivorous species, whereas insecticides negatively affected total seed predation rates and the activity–density of omnivorous species. However, very few studies have attempted to understand such effects. Thus, the scales at which local management practices are implemented determine the impact on weed seed consumption of carabids. Consequently, higher weed seed removal rates are observed under organic farming regimes that lack pesticides use (Diekotter et al. 2010).

Current knowledge of the effects of pest management strategies on carabids is limited to general carabid taxa. Very few studies have focused on how granivorous species and their activities are influenced by pest management regimes. Further research to elucidate such effects is needed to devise pest management strategies that can conserve populations of seed-feeding carabids, thereby enhancing seed consumption and biological weed management.

**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 noncrop habitats surrounding field areas and the resulting shortage of specific food resources for strictly carnivorous or granivorous species. Further, simple landscapes lack structural heterogeneity, and the agricultural management practices in such landscapes can negatively affect carabid activity (Fischer et al. 2011; Tscharntke et al. 2005, 2012). This is mainly due to the effects of extensive crop management practices on immigration and emigration rates of species between fields and surrounding areas. However, the level of disturbance determines habitat heterogeneity and its ultimate effects on environmental services such as seed consumption. For example, intensively managed conventional fields in simple landscapes surrounded by less intensively managed organic fields are known to...
harbor high carabid diversity compared to organic fields surrounded by conventional fields (Diekotter et al. 2010).

The type of noncrop habitat is also important. For example, seed removal rates are higher in fields surrounded by temporary pastures than fields surrounded by permanent pastures and forest (Trichard et al. 2013). Temporary pastures are more likely to be dynamic in terms of crop associations and availability of food and shelter than permanent habitats. Similarly, granivorous taxa are more abundant in grassland and open agricultural habitats than in forest habitats (Vanbergen et al. 2010). However, effects of habitat complexity are locally specific and can range from having a very high effect to no effect at all on habitat complexity (Winquist et al. 2011). A study from Sweden determined that complex habitats did not play a role either in fostering populations of carabid beetles or in influencing seed consumption rates; instead, both were higher in a simple landscape with a greater proportion of arable crops (Jonason et al. 2013). Consequently, an understanding of species dynamics at a given landscape scale with reference to landscape characters is important.

**Mortality from Natural Enemies and Predation.** A detailed account of natural enemies of carabids and the defense mechanisms of carabids in response to predation has been provided by Brandmayr et al. 2009. The major sources of natural mortality in carabids are natural enemies and environmental abiotic factors (Lovéi 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.

**Effects of Climatic Factors on Weed Seed Consumption.** 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. 2013). Climatic factors can influence seed consumption rates in several ways, including a reduction in seed traceability through seed burial (Westerman et al. 2009), or by altering the life cycle or life stages of carabids (Kotze et al. 2011). For example, ambient temperature beyond the optimum temperature range of 4 to 35°C can hamper reproductive status, larval development (Kotze et al. 2011; Saska et al. 2010), and seed feeding behavior. Increased seed consumption patterns with respect to increased temperature is known in species such as _H. affinis_ and _Pseudophonus rufipes_ (Saska et al. 2010). Precipitation and relative humidity can affect egg maturation, larval development, and hibernation success, and therefore are also critical factors determining population dynamics (Kotze et al. 2011) and seed removal (Lundgren et al. 2006).

**Future Research**

Given the intensive nature of crop cultivation and crop management practices in modern agriculture and their negative consequences on the ecosystem biodiversity, implementation of biological control of weeds using arthropods such as carabids can be challenging. However, an integrated weed management approach that incorporates agronomic practices that favor conservation of beneficial bioagents such as carabids can improve ecological services such as weed seed consumption. The studies reviewed here indicate that practices such as reduced tillage, habitat diversification, and judicious use of agrochemicals might have potential implications for enhancing granivory in agroecosystems. In a weed management context, it is important to acknowledge the fact that bioagents such as carabids cannot eliminate all the seed stock in a given area (Menalled et al. 2000a). However, their activity brings about substantial reduction in net seed stocks in seed banks over time, and biological control cannot be considered a stand-alone approach for weed management but should be integrated as an effective tool in harmony with other weed management practices (Lundgren 2009). A broader understanding of interactions between agroecosystem processes, disturbances, and the ecology of different carabid groups is essential to estimate the extent to which services such as granivory can be used to manage weed seeds. The studies reported here cover trends observed in carabid granivory in diverse regions, climates, and agroecosystems consisting of...
diverse carabid assemblages. Hence, the observed trends should be interpreted with caution. For effective weed management, studying long term seed consumption processes in different agroecosystems and regions might help to develop a better understanding of the patterns and factors governing such services. This can help to develop a long-term strategy to improve weed consumption services (for example, thorough planning of appropriate crop rotations, crop types, management of surrounding habitats etc.).

Although the role of carabids as “generalist” predators of arthropod pests is well-recognized, several knowledge gaps exist in understanding their role as biological control agents of weeds. Overall, laboratory studies have demonstrated the importance of carabid size, seed size ratios, (Honek et al. 2003, 2007, 2011), and other seed characteristics such as seed coat hardness (Lundgren and Rosentrater 2007) in determining carabid preferences for particular weed seeds. However, other seed characteristics, such as nutritional quality of the seed and seed surface chemistry, might also play important roles in seed consumption. These mechanisms are not well-studied and need further investigation. Further, very limited attention has focused on the potential of carabid larvae in weed seed consumption. Developing efficient field sampling methods for carabid larvae could facilitate estimation of the possible role of carabid larvae in weed seed consumption.

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; Triéfás 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. Insights into foraging behavior and seed-tracking mechanisms can improve our current understanding of species assembly dynamics, behavior, and time of the season for active foraging. 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 considered further.

Several studies have investigated the potential of carabid beetles for weed management across Europe (Westerman et al. 2003a, Honek et al. 2005, 2007; Mauchline et al. 2005) and the United States (Gaines and Gratton 2010; Lundgren et al. 2013; Menalled et al. 2000b, 2007; Shearin et al. 2007, 2008; White et al. 2007). Despite having a rich carabid fauna in Canadian agroecosystems (Goulet 2003; Levesque and Levesque 1994; Lindroth 1957), the role of omnivorous and granivorous species in weed management has not been extensively studied. Although the effects of tillage on weed seed consumption by carabid beetles has been reported by Cromar et al. (1999), there is a large gap in studies focusing on different aspects of seed predation. In the last two decades, cropping practices have undergone major changes in the northern Great Plains region, such as intensive canola production (Canola Council of Canada 2014b), the use of herbicide-tolerant crops (Harker et al. 2000), and adoption of zero-tillage practices (Smyth et al. 2010). Studying weed seed consumption under these circumstances could help in understanding the weed seed consumer community and weed seed consumption patterns in this region.

**Acknowledgments**

We are grateful to the Alberta Canola Producers Commission and the Natural Sciences and Engineering Research Council (NSERC) for their generous funding to this project.

**Literature Cited**


Downloaded from https://www.cambridge.org/core. IP address: 54.70.40.11, on 27 Jan 2019 at 04:35:51, subject to the Cambridge Core terms of use, available at https://www.cambridge.org/core/terms.
Pterostichus melanarius (Illig) in three cropping
Weed Science 63, April–June 2015
Amara similata (Gyll) (Col
Harpalus rufipes De Geer: an important weed seed predator
Setaria faberi and Erwin TL, Ball GE, Taraxacum officinale agg)
Holm FA, Johnson EN (2009) The history of herbicide use for
management apple orchard. Can Entomol 116:165–171
Holm FA, Johnson EN (2009) The history of herbicide use for
management apple orchard. Can Entomol 116:165–171
Honek A, Jarosik V (2000) The role of size taxonomic
affiliation and geographic origin of dandelion (Taraxacum agg)
chicks (Alectoris rufa and Perdix perdix) on arable farmland in
Hammond PM (1979) Wing-folding mechanisms in beetles with
special reference to investigations of adephagan phylogeny
(Coleoptera) Pages 113–180 in Erwin TL, Ball GE, Whitehead D, Halpern AL, eds. Carabid Beetles: Their
Evolution, Natural History, and Classification. The Hague,
The Netherlands: Dr. W. Junk Publishers
Harker KN, Blackshaw RE, Kirkland KJ, Derksen DA, Wall D
Academic Press. 892 p
Harrison SK, Gallandt ER (2012) Behavioural studies of
Harpalus rufipes De Geer: an important weed seed predator
in northeastern US agroecosystems. Int J Ecol. DOI:101155/
2012/846546, 6 p
Harrison SK, Regnier EE, Schmoll JT (2003) Postdispersal
predation of giant ragweed (Ambrosia trifida) seed in no-tillage
corn. Weed Sci 51:935–964
Hartke A, Drummond FA, Liebman M (1998) Seed feeding,
seed caching and burrowing behaviors of Harpalus rufipes De
Geer larvae (Coleoptera: Carabidae) in the Maine potato
agroecosystem. Bio Control 13:91–100
Hatten TD, Bosque-Perez NA, Labonte JR, Guy SO, Eigenbrode SD (2007) Effects of tillage on the activity density and
biological diversity of carabid beetles in spring and winter
crops. Environ Entomol 36:356–368
Heggenstaller AH, Menalled FD, Liebman M, Westerman PR
(2006) Seasonal patterns in post-dispersal seed predation of
Abrutilon theophrasti and Setaria faber in three cropping
Holland JM (1998) Comparative impact of insecticide
applications on beneficial invertebrates in conventionally and
integrated farming systems. Pages 267–278 in Haskell PT,
McEwen P, eds. Ecotoxicology: Pesticides and Beneficial
Publishers
on Carabidae in temperate agroecosystems. Integrated Pest
Manag Rev 5:109–129
Holland JM, Perry JN, Winder L (1999) The within field spatial
and temporal distribution of arthropods in winter wheat. Bull
Entomol Res 89:499–513
Ann Appl Biol 136:93–105
Holliday NJ, Hagley EAC (1984) The effect of sod type on the
occurrence of ground beetles (Coleoptera: Carabidae) in a pest
management apple orchard. Can Entomol 116:165–171
Holm FA, Johnson EN (2009) The history of herbicide use for
weeds management apple orchard. Can Entomol 116:165–171
Honek A, Jarosik V (2000) The role of crop density, seed and
aphid presence in diversification of field communities of
(Carabidae) as seed predators. Eur J Entomol 100:531–544
predation of Taraxacum officinale (dandelion) seed. J Ecol
93:310–318
affiliation and geographic origin of dandelion (Taraxacum agg)
seeds on predation by ground beetles (Carabidae Coleoptera).


Larocelle A (1990) The Food of Carabid Beetles (Coleoptera: Carabidae, including Cicindelinae). Fabreries Suppl 5. Quebec City, Quebec, Canada: Sillery: Association des entomologistes amateurs du Québec. 132 p


Lund RD, Turpin FT (1977) Carabid damage to weed seeds found in Indiana cornfields. Environ Entomol 6:695–698


Sasaki K (2010a) Field observations of climbing behavior and seed predation by adult ground beetles (Coleoptera: Carabidae) in a lowland area of the temperate zone. Environ Entomol 39:1564–1560

Sasaki K (2010b) Laboratory studies on the larval food habits of the ground beetle Amara (Curtonotus) gigantea (Motschulsky) (Coleoptera: Carabidae: Zabrini). Entomol Sci 13:358–362


Thomas CFG, Green F, Marshall EJP (1997) Distribution, dispersal and population size of the ground beetle, Pterostichus melanarius (Illiger) and Harpalus rufipes (Degeer) (Coleoptera, Carabidae), in field margin habitats. Biol Agric Hortic 15:337–352

Thompson RG (1979) A systematic study of the larvae in the tribes Pterostichini, Morionini and Amarini (Coleoptera: Carabidae). University of Arkansas Bulletin No. 837. Fayetteville, AR: Agricultural Experiment Station. 105 p


Received April 28, 2014, and approved November 21, 2014.