Effects of crop rotation and genetically modified herbicide-tolerant corn on ground beetle diversity, community structure, and activity density

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Abstract—Ground beetles (Coleoptera: Carabidae) were sampled in conventional and genetically modified herbicide-tolerant (GMHT) corn, *Zea mays* L. (Poaceae), planted under rotation with canola, *Brassica* L. (Brassicaceae), or continuously cropped corn to investigate the influence of corn variety and rotation on the structure of carabid assemblages. Corn variety, cultivation regime, and their interaction all influenced overall carabid activity density. Weed management associated with corn variety influenced the activity density of a few carabid species and this was attributed to changes in vegetation. Some smaller bodied carabids such as *Bembidion quadrimaculatum* L. were less abundant in GMHT plots, probably because weed density was higher in midseason, but the opposite was observed for larger bodied carabids such as *Pterostichus melanarius* (Illiger). Overall, rotating corn with canola had a stronger effect on carabid community structure than did corn variety. We suggest that GMHT corn has little impact on the overall carabid fauna but may influence the activity of certain species through effects on the weed community.

Résumé—Des carabes (Coleoptera : Carabidae) ont été échantillonnés dans des parcelles de maïs conventionnel, *Zea mays* L. (Poaceae), et de maïs génétiquement modifié tolérant à l'herbicide (MGTH), en plantation continue ou en rotation avec du canola, *Brassica* L. (Brassicaceae), dans le but d'étudier l'influence de la variété de maïs et de la rotation sur la communauté de carabes. La variété de maïs et le régime de culture, ainsi que leur interaction, ont tous influencé la densité d'activité des carabes. La gestion des mauvaises herbes associées à la variété de maïs a influencé la densité d'activité de quelques espèces de carabes et ceci a été attribué aux changements dans la végétation. Quelques espèces de carabes de plus petite taille comme *Bembidion quadrimaculatum* L. ont été moins abondantes dans les parcelles MGTH ce qui était probablement due à une plus forte densité de mauvaises herbes durant la mi-saison. Par contre, le contraire fut observé pour quelques espèces de carabes de plus grande taille comme *Pterostichus melanarius* (Illiger). En général, la rotation du maïs avec le canola a eu une plus grande influence sur la communauté de carabes que la variété de maïs. Nous suggérons que le maïs MGTH a un faible impact sur la communauté de carabes mais pourrait influencer l'activité de certaines espèces par le biais des modifications de la communauté de mauvaises herbes.

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Introduction

Weeds impose a major constraint on crop yield and may serve as secondary hosts for pest populations (Norris and Kogan 2000). For these reasons much effort is expended on weed control in agriculture. However, weeds also contribute significantly to biodiversity in agricultural systems (Marshall *et al.* 2003; Altieri and Nicholls 2004). Moreover, there may be advantages, even for overall production efficiency, in maintaining some weeds within or at the margins of agricultural fields to provide habitat and alternative food for beneficial arthropods (Altieri and Whitcomb 1979). Carabids (Coleoptera: Carabidae) prey on many insect pests (Brust *et al.* 1986; Hance and Gregoire-Wibo 1987; Grafius and Warner 1989; Floate *et al.* 1990; Winder 1990; Menalled *et al.* 1999) and may benefit from the shelter and food provided by weeds (Purvis and Curry 1984; Holland 2002). In fact, weeds within or at the margins of a field often increase carabid activity and diversity (Speight and Lawton 1976; Hassall *et al.* 1992; Lys and Nentwig 1992; Lys *et al.* 1994; Pavuk *et al.* 1997; Ellsbury *et al.* 1998; Andersen and Eltun 2000), although a few studies have reported only a moderate effect of weeds on overall carabid activity (Purvis and Curry 1984). An example of an increase in the beneficial action of carabids due to weeds was provided by Speight and Lawton (1976), who caught more carabids and observed more prey attacks in a wheat (*Triticum aestivum* L. (Poaceae)) field wherever *Poa annua* L. (Poaceae) was present. Therefore, weed removal by herbicides or cultivation can affect carabid communities and their beneficial actions.

Although the general effect of herbicide application on arthropods is indirect, *i.e.*, *via* habitat modification (Brust 1990), some types of herbicide have been reported to kill coccinellid larvae (Coleoptera: Coccinellidae) (Adams 1960). Weed removal modifies the plant canopy and the microclimate experienced by carabids; furthermore, different carabid species may respond differently to weed species composition through their specific environmental optima (Barney *et al.* 1984; Armstrong and McKinlay 1997; Pavuk *et al.* 1997).

The recent development of genetically modified herbicide-tolerant (GMHT) crop varieties offers a new tool for weed management. To date, corn (*Zea mays* L. (Poaceae)), soybean (*Glycine max* (L.) Merr. (Fabaceae)), beet (*Beta vulgaris* L. (Chenopodiaceae)), and canola (*Brassica napus* L. (Brassicaceae)) are registered GMHT crops in Canada, despite concerns about their potential long-term effects on biodiversity. For instance, Watkinson *et al.* (2000) predicted a dramatic reduction in the number of weeds with wide adoption of GMHT crops, potentially affecting the survival of some seed-eating birds. However, Hawes *et al.* (2003) and Brooks *et al.* (2003) reported no overall difference in the response of carabids and spiders (Araneae) between GMHT and conventional crops, but among species, activity densities were observed to differ between the treatments. For example, Brooks *et al.* (2003) found more individuals of *Loricera pilicornis* (Fabricius) (Coleoptera: Carabidae) in GMHT crops as a result of an increase in the number of Collembola. However, they found a lower activity density of species of *Bembidion* Latreille (Coleoptera: Carabidae) in GMHT corn. Also, using a suction-sampling approach, Haughton *et al.* (2003) found no difference in carabid responses to conventional and GMHT corn, beet, and canola. In their study, carabids were more abundant in GMHT than in conventional corn on only one sampling date (August). Furthermore, Dewar *et al.* (2003) argued that it is possible to use GMHT crops creatively to enhance both weed and insect populations without compromising yield. Given the lack of the knowledge required for such approaches, it is crucial to study the long-term effects of GMHT crop varieties on nontarget organisms as the use of these crops increases.

In this paper we investigate the diversity, community structure, and activity-density responses of carabids to two corn varieties (GMHT and conventional), each planted under continuous monoculture and rotation. "Corn variety" refers to both the type of culture and its associated weed-management system. Additionally, we predicted that larger

Table 1. Four treatments and their agronomic characteristics in genetically modified herbicide-tolerant (GMHT) and conventional corn in Lethbridge, Alberta, in 2004 and 2005.

Corn variety and regime	Herbicide	Active ingredient (ai)	Rate of application (g ai/ha)	Treatment application in:	
				2004*	2005*
GMHT continuous	Roundup WeatherMax	Glyphosate	890	20.V, 16.VI, 29.VI	27.V, 12.VII
	Pardner	Bromoxynil	345	—	24.VI
	Poast Ultra	Sethoxydim	333	—	24.VI
GMHT rotation†	Roundup WeatherMax	Glyphosate	890	20.V, 16.VI, 29.VI	27.V, 12.VII
	Pardner	Bromoxynil	335	—	27.V, 24.VI, 12.VII
	Poast Ultra	Sethoxydim	333	—	24.VI
Conventional continuous	Atrazine	Atrazine	1186	20.VI	—
	Eradicane 8-E	EPTC	4349	—	26.V
	Buctril	Bromoxynil/ MCPA	554	—	12.VII
	Pardner	Bromoxynil	345	—	24.VI
	Poast Ultra	Sethoxydim	333	—	24.VI
Conventional rotation‡	Eradicane 8-E	EPTC	4349	20.VI	26.V
	Buctril	Bromoxynil/ MCPA	554	16.VI	12.VII
	Pardner	Bromoxynil	345	—	24.VI
	Poast Ultra	Sethoxydim	333	—	24.VI

*Roman numerals denote months.
†Roundup Ready canola grown in the previous year.
‡Conventional canola grown in the previous year.

bodied carabids would be more restrained in their movements under high weed abundance and captured more often under lower weed abundance.

Materials and methods

Site description and agronomic treatments

This study was conducted 10 km east of Lethbridge, Alberta, Canada (approximately 49°41′N, 112°40′W), a region of dark-brown chernozemic soil in the moist grassland ecozone. The investigation was part of a larger study of the environmental impacts of genetically modified corn and canola comprising 4 replicates of 19 plots (15 m × 35 m) arranged in a randomized block design. For the purpose of this study, 4 replicates of 4 plots were used. Plots were 3 m apart and arranged in blocks separated by 20 m of plowed soil in 2004 and mowed fall rye (*Secale cereale* L. (Poaceae)) in 2005. Plots representing four treatments were selected for this study (Table 1). Disc cultivation followed by live rod cultivation and harrow packing was applied prior to seeding all treatments except the GMHT corn variety, which was sprayed with glyphosate for weed control. Both corn varieties were seeded (75 000 plants/ha) in rows 75 cm apart on 28 May in both years. Herbicides were applied according to manufacturers' labels (Table 1) and the entire study field was irrigated as needed. In 2005, flooding associated with 250 mm of rainfall in early June caused high corn mortality and plots were sprayed with Poast Ultra (Sethoxydim) at 300 mL/acre and Pardner (Bromoxinyl) at 500 mL/acre on 24 June to kill all corn. Corn was reseeded on 25 June but the chemical residue reduced corn emergence. Treatments were nonetheless applied as planned, despite the resulting low corn density.

Carabids were sampled using two pitfall traps half-filled with nontoxic propylene glycol placed 10 m into each plot from both ends, near the midline, leaving approximately 15 m between traps. Each pitfall trap consisted of a 1 L plastic sleeve dug into the ground flush with the soil surface, and an inserted 0.5 L cup (11 cm diameter) (Spence and Niemelä 1994). Despite their limitations, pitfall traps are widely used in ecological studies because they provide a simple, inexpensive, and effective way to gain insight into the arthropod communities. Pitfall-trap catches are influenced by the mobility of fauna and it is therefore more appropriate to regard the trap catch as a reflection of activity density rather than absolute density. Sampling periods were 3 May to 30 September in 2004 and 18 April to 1 September in 2005. Pitfall traps were emptied every 7–14 days; contents were preserved in 70% ethanol and refrigerated until identified. Voucher specimens were deposited at the Strickland Entomological Museum and additional reference material is held in the Spence Laboratory Insect Collection, both at the University of Alberta, Edmonton. Carabid nomenclature follows Bousquet and Larochelle (1993).

Weed density in each plot was estimated in 2004 from the number of weeds of each species found in each of fifteen 0.25 m^2 quadrats distributed on each plot at three times: preseeding (May), before herbicide application (June), and after herbicide application (July). Weed species were identified following Bubar *et al.* (2000). In 2005, only the preseeding survey was done, supplemented on 29 July with an estimate of percent weed coverage from photographs of five 1 m^2 quadrats arranged in a cross pattern in each plot. For each of the five quadrats, average percent weed cover was estimated by isolating the green pixels (Image Pro Plus software) and dividing the number of green pixels by the total number of pixels within the quadrat.

To assess the soil moisture level, a soil corer was used to take three soil samples (5 cm diameter, 5 cm depth) around each pitfall trap five times each year (2004: 10 and 26 May, 21 June, 6 July, 16 August; 2005: 11 May, 15 and 28 July, 2 September). Samples were pooled and homogenized and a subsample of about 60 g of soil was weighed before and after drying for 48 h at 105 °C to determine water content.

Analysis

A few species that could not be clearly distinguished using morphological criteria were pooled for analysis, so all specimens were retained. The groups identified as *Amara carinata* (LeConte) and *Harpalus fraternus* LeConte may have also included representatives of *A. lacustris* LeConte and *A. torrida* (Panzer) and *H. reversus* Casey, respectively. Because of severe flooding in 2005 we decided to use only trap catches collected prior to the flood (4 April to 25 May 2005, $n = 3907$ beetles) and compare these results with those obtained from a similar trapping period and sample size in 2004 (3 May to 1 July 2004, $n = 3485$ carabids), referred to herein as spring 2004. The remaining data from 2004 (2 July to 30 September, $n = 4521$ carabids), referred to herein as summer and fall 2004, were analyzed but not compared with those from 2005.

For each sampling date the numbers of individuals of each species caught in each of the two traps present in a plot were summed and divided by their total number of active days to account for the occasional loss of one trap in a plot. Catch rates for each sampling date were summed over each plot to obtain a catch rate for the year.

To investigate species diversity between treatments, individual-based rarefaction analysis was applied to the data before standardization using the Vegan package (Rainio and Niemelä 2003) available in the R package (R Development Core Team 2005). Rarefaction has the advantage of standardizing for trapping effort as an explicit part of the procedure (Gotelli and Colwell 2001). We based individual-based rarefaction curves on 1000 permutations of each subsample and compared the estimated number of species represented by 500 individuals in spring 2004 and summer and fall 2004 and 2005.

Nonmetric multidimensional scaling (NMDS) ordination was used to compare the species characterizing carabid assemblages for each treatment. Dissimilarity between samples was measured as the Sorensen (Bray–Curtis) distance. The final configuration of the NMDS ordination was evaluated in terms of the probability of the observed stress value estimated from 50 runs of Monte Carlo simulation based on randomized data. Similarity in species composition was tested using a multiresponse permutation procedure (MRPP) (McCune and Grace 2002). MRPP calculates a test statistic T and a chance-corrected within-group agreement A reflecting respectively the separation between groups and the variation within groups (McCune and Grace 2002). A Bonferroni correction for multiple comparisons was calculated when required. Species vectors were calculated having a minimum r^2 value of 0.3 and overlaid on the final ordination. The length and angle of each vector denote the strength and direction of the species association.

Carabid catch rates were transformed [$\log_{10}(x + 1)$] prior to statistical analysis. Assumptions of normal distribution and equal variance for parametric analyses were achieved for the total carabid catches in spring 2004 and summer and fall 2004 and 2005 and for catches of most carabid species after data transformations. A two-factor ANOVA including corn variety (GMHT and conventional), cultivation regime (continuous and rotation), and their interaction was performed to compare total carabid catch rates. Log-transformed weed density was used as a covariate and block was added as a fixed factor to remove variability that might be attributed to site. Additionally, for each sampling period, the catch rates for the five most abundant species (which comprised more than 90% of the total catch) were subjected to MANOVA modeled with the factors. When the overall MANOVA was significant (Wilks' λ , $P < 0.05$), the effect of treatment on the activity density of single species was investigated using a planned-comparisons (LSD *post-hoc*) test.

Weed-density data from 2004 and 2005 were not normally distributed, therefore the similarity of treatments for each sampling date was analyzed using Kruskal–Wallis tests followed by a Nemenyi *post-hoc* test. For 2005, we analyzed only weed data from the single period prior to the flooding event and evaluated the relationship between carabid catch and percent weed cover using carabid catches between 25 May and the flood. A linear regression was performed using the transformed [$\log_{10}(x + 1)$] activity density of carabids grouped by body size (small, ≤ 5 mm; medium, 6–9 mm; large, $\geq$ 10 mm) and $\log_{10}(x + 1)$-transformed weed density. This procedure tested the hypothesis that carabids respond to weed abundance according to body size. In 2005 the catch rates for carabids grouped by body size were regressed on percent weed cover to determine whether the relationship was affected by body size. Carabid catches obtained on dates close to those of the weed survey (22 July, 3 and 25 August) were pooled prior to analysis.

In 2004 an ANOVA modeled with corn variety, agricultural regime, and their interaction as factors was performed on percent soil moisture in each plot (mean of two estimates per plot) using sampling date as the repeated measure. In 2005, only data from the preflood sample (11 May) were analyzed using a similar ANOVA model. All statistical analyses were performed using SPSS 11.0 (SPSS Inc. 1999), except the NMDS ordination and MRPP tests, which employed PcOrd (McCune and Mefford 1999).

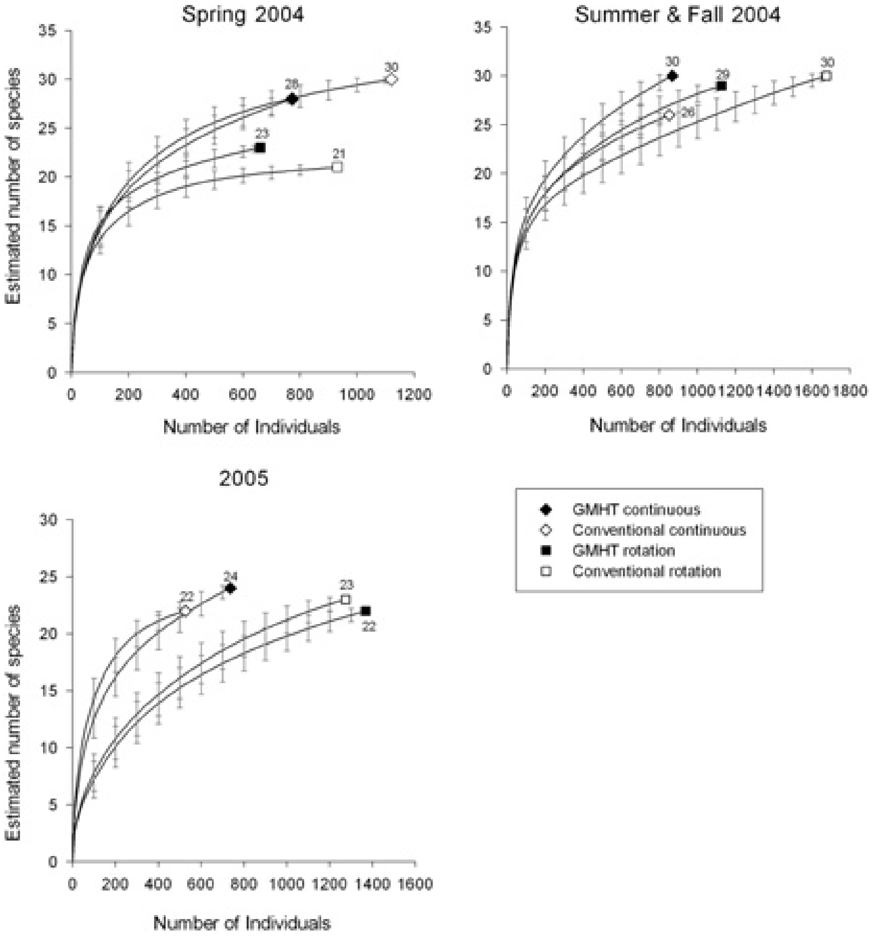
Results

Carabid fauna

Between 3 May and 1 July 2004, 3485 carabid beetles representing 37 species in 15 genera were collected (Appendix A). The most abundant species during this trapping period, *Bembidion quadrimaculatum* L., represented approximately 46% of the total carabid catch and peaked in activity during the last 2 weeks of June. The 10 most abundant species represented 92% of the total catch. Seventeen species were represented by fewer than 10 individuals.

For summer and fall 2004 (2 July to 30 September) we captured 4521 carabids; *Pterostichus melanarius* (Illiger) was the most abundant species, representing approximately

Fig. 1. Rarefaction (species accumulation) curves showing carabid diversity among weed-management treatments in genetically modified herbicide-tolerant (GMHT) and conventional corn and under continuous and rotational cropping regimes in Lethbridge, Alberta, in spring 2004 and summer and fall 2004 and 2005. Error bars represent ± 1 SE of the iteration mean of selected subsamples. The curves show the rotation regime (squares) and the continuous regime (diamonds) for the GMHT (solid symbols) and conventional (open symbols) corn varieties. Each curve ends at the maximum number of individuals caught in each of the four treatments (the numeral at the end of each curve denotes species richness).



40% of the total carabid catch. The 10 most abundant species represented 92% of the catch, and 23 species were captured 10 times or fewer.

In 2005 a total of 3907 carabids from 34 species in 12 genera were caught between 4 April and 24 May (Appendix A). *Amara farcta* LeConte was the most abundant species, representing 69.4% of the total carabid catch. The five most abundant species represented 91.7% of the carabid catch. Seventeen species were represented by fewer than 10 beetles each, and 9 of these species were singletons.

Diversity

Rarefaction curves from spring 2004 and 2005 (Fig. 1) suggested that species diversity in the corn grown under the continuous regime was higher than in the corn grown under rotation. However, this trend did not hold for summer and fall 2004, when species diversity was slightly higher in GMHT corn than in conventional corn. Estimates based on 500 individuals support the following ranking of treatments with respect to carabid diversity in spring 2004: conventional continuous (25.6

species) > GMHT continuous (24.8 species) and GMHT rotation (21.9 species) > conventional rotation (19.7 species). In 2005, estimates based on the same number of individuals suggest a 30% (*vs.* 23% in spring 2004) variation among means (conventional continuous (21.8 species), GMHT continuous (21.5 species), conventional rotation (16.2 species), and GMHT rotation (15.2 species)). Ranking of treatments for summer and fall 2004 is as follows: GMHT continuous (25.5 species), GMHT rotation (23.2 species), conventional continuous (22.7 species), and conventional rotation (20.8 species), with 18% variation among means. Species richness was similar in the corn under the two cultivation regimes except in summer and fall, when four more species were captured in plots under the GMHT continuous treatment than in those under the conventional continuous treatment (Fig. 1).

Species composition

For each sampling period, NMDS ordinations showed plots under rotation to be well separated from the continuously cropped plots (Fig. 2). In spring 2004, when the best fit NMDS ordination was two-dimensional and explained 95.6% of the total variation (stress = 7.270, Monte Carlo randomization test, P = 0.0081), both cultural regime and corn variety influenced species composition (MRPP $<$ 0.05). Overall, treatments had a significant effect on carabid species composition (MRPP, $T = -3.73$, $A = 0.19$, $P = 0.003$), and pairwise comparisons using MRPP showed only GMHT continuous *versus* GMHT rotation (MRPP, $T = -3.47$, $A = 0.13$, $P = 0.004$) and continuous conventional *versus* GMHT rotation (MRPP, $T = -4.13$, $A = 0.34$, $P = 0.006$) to harbour different species. The vectors representing *P. melanarius*, *Amara littoralis* Mannerheim, and *Poecilus corvus* (LeConte) associated with rotation, whereas the vectors for abundance of *B. quadrimaculatum*, *Microlestes linearis* (LeConte), and *Bembidion obscurellum* (Motschulsky) mostly associated with conventional continuous cropping.

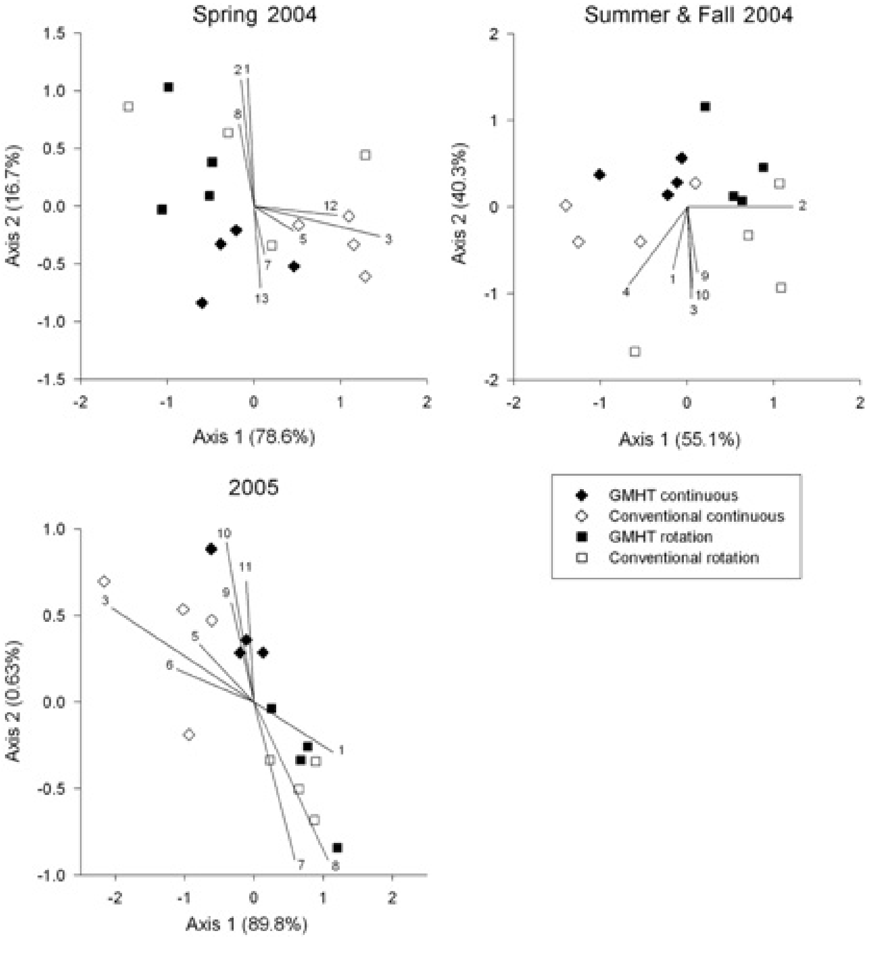
During the sampling period summer and fall 2004, species composition as shown by NMDS revealed a low-stress two-dimensional ordination (stress = 7.332, Monte Carlo randomization test, $P = 0.004$) that explained 95.4% of the variability. This time, only plots under different cultural regimes showed a difference in species composition (MRPP, $T = -4.86$, $A = 0.11$, $P = 0.001$), whereas plots under different corn varieties were similar in species composition (MRPP, $P > 0.05$). When treatments were compared after a significant effect of treatment was shown (MRPP, $T = -4.16$, $A = 0.18$, $P = 0.0009$), only GMHT continuous *versus* GMHT rotation (MRPP, $T = -3.61$, $A = 0.17$, $P = 0.0082$) and GMHT continuous *versus* conventional rotation (MRPP, $T = -3.01$, $A = 0.14$, $P = 0.0077$) showed differences in species composition. As in the earlier sampling period, the vector for *P. melanarius* was associated with rotation plots; however, the vector for *B. quadrimaculatum* was no longer strongly associated with continuous conventional plots.

For 2005, the best fit NMDS ordination was a two-dimensional plot with a stress value of 2.442 (Monte Carlo randomization test, P = 0.0196) that explained 90.4% of the variation in the data (Fig. 2). Once again, only plots of different cultural regimes showed differences in species composition (MRPP, $T = -8.39$, A = 0.30, $P < 0.001$). Overall, there was a significant treatment effect on species composition (MRPP, $T = -5.20$, $A = 0.35$, $P < 0.05$), but when all pairwise comparisons of treatments are considered, only GMHT continuous *versus* conventional continuous and GMHT rotation *versus* conventional rotation were similar in species composition (corrected MRPP, $P >$ 0.0083), suggesting no effect of corn variety. Comparing the vector for 2005 with that for spring 2004, *P. corvus* and *A. littoralis* were again associated with rotation plots, whereas the vectors for *B. obscurellum* and *B. quadrimaculatum* were likewise associated with plots under continuous cropping. The vector for *A. farcta* had a weak association with the continuous plots in spring 2004 but a strong association with the rotation plots in 2005 (Fig. 2).

Activity density

The four spatial blocks and weed covariates had no effect on carabid activity density in

Fig. 2. Nonmetric multidimensional scaling ordination (Bray–Curtis distance) using the entire carabid catch obtained in genetically modified herbicide-tolerant (GMHT) and conventional corn under continuous and rotational cropping regimes in Lethbridge, Alberta, in spring 2004 and summer and fall 2004 and 2005. The percent variation explained by each axis is shown in parentheses. Cropping regimes are represented by squares (rotation) and diamonds (continuous); corn varieties are shown as solid symbols (GMHT) and open symbols (conventional). Vectors for species (thin lines) with a minimum r^2 value of 0.30 are as follows: 1, *Poecilus corvus*; 2, *Pterostichus melanarius*; 3, *Bembidion quadrimaculatum*; 4, *Bembidion timidum*; 5, *Bembidion obscurellum*; 6, *Bembidion rupicola*; 7, *Amara farcta*; 8, *Amara littoralis*; 9, *Amara carinata*; 10, *Agonum placidum*; 11, *Harpalus amputatus*; 12, *Microlestes linearis*; 13, *Harpalus herbivagus*.



either year, therefore these terms were removed from the final model.

Spring 2004

Corn variety significantly affected the total carabid catch rate ($F_{1,12}$ = 6.240, P = 0.028) (Table 2): more carabids were captured in conventional corn than in GMHT corn. The MANOVA results suggested no significant influence of corn variety on the activity density of the five most abundant species (Table 2), although *B. quadrimaculatum* and *Poecilus scitulus* LeConte had higher abundances in plots planted with conventional corn ($P < 0.05$; Table 2). Overall, the MANOVA was significant for cultural regime (Table 2) and for three species. *Poecilus corvus* had a higher abundance in plots under rotation with canola than in plots under continuous corn, whereas the opposite pattern characterized the

Table 2. Activity density (beetle trap-days; mean ± SE (n = 8)) of carabid species in genetically modified herbicide-tolerant (GMHT) and conventional corn varieties and under continuous and rotational cultivation regimes in Lethbridge, Alberta, in spring 2004 and 2005.

	Corn variety			Cultivation regime		
	GMHT	Conventional	*P*	Continuous	Rotation	*P*
Spring 2004						
Total carabid catch	5.59 ± 0.28	8.09 ± 1.22	0.028	7.465 ± 0.69	6.22 ± 0.91	0.140
MANOVA	—	—	0.112	—	—	0.050
Poecilus corvus	1.24 ± 0.13	1.27 ± 0.14	0.896	1.05 ± 0.11	1.47 ± 0.11	0.030
Amara farcta	0.46 ± 0.09	0.29 ± 0.06	0.103	0.50 ± 0.08	0.25 ± 0.05	0.019
Microlestes linearis	0.27 ± 0.07	0.50 ± 0.11	0.106	0.47 ± 0.11	0.30 ± 0.08	0.232
Bembidion quadrimaculatum	2.19 ± 0.25	3.98 ± 0.61	0.019	3.74 ± 0.45	2.43 ± 0.59	0.026
Poecilus scitulus	0.26 ± 0.06	0.52 ± 0.09	0.043	0.38 ± 0.10	0.39 ± 0.08	0.844
2005						
Total carabid catch	12.2 ± 1.96	10.3 ± 1.89	0.194	7.32 ± 0.80	15.2 ± 1.86	<0.001
MANOVA	—	—	0.142	—	—	0.001
Harpalus amputatus	0.48 ± 0.12	0.24 ± 0.06	0.010	0.56 ± 0.11	0.16 ± 0.09	<0.001
Poecilus corvus	1.89 ± 0.19	1.16 ± 0.23	0.024	1.26 ± 0.29	1.79 ± 0.34	0.060
Amara farcta	8.30 ± 1.95	7.11 ± 1.84	0.213	3.60 ± 0.53	11.8 ± 1.68	<0.001
Amara littoralis	0.41 ± 0.18	0.40 ± 0.18	0.997	0.01 ± 0.01	0.80 ± 0.16	<0.001
Bembidion quadrimaculatum	0.18 ± 0.03	0.52 ± 0.18	0.013	0.57 ± 0.17	0.12 ± 0.18	0.001

activity density of *B. quadrimaculatum* and *A. farcta*.

Summer and fall 2004

There was a significant interaction effect of corn variety and cultural regime on the total carabid catch in summer and fall 2004 ($F_{1,12} = 5.128$, $P = 0.043$), with more carabids captured in the conventional continuous treatment than in any other treatment (Table 3). Similarly, the MANOVA also showed a significant interaction ($F_{5,8} = 4.483$, $P = 0.03$), with only *Agonum placidum* (Say) showing a preference for conventional continuous corn (Table 3).

2005

Only cultivation regime affected the total carabid catch rate in 2005, when more carabids were captured in corn rotated with canola than in corn under continuous cultivation ($F_{1,12} = 26.033$, $P < 0.001$; Table 2). Using a MANOVA restricted to early-season carabid capture, four of the five most abundant species were significantly affected by cultivation regime ($F_{5,8} = 15.177$, $P = 0.001$). *Amara farcta* ($F_{1,12} = 41.262$, $P < 0.001$) and *A. littoralis* ($F_{1,12} = 35.886$, $P < 0.001$) were more abundant in plots under the rotation regime, whereas *Harpalus amputatus* Say ($F_{1,12} = 28.03$, $P < 0.001$) and *B. quadrimaculatum* ($F_{1,12} = 17.172$, $P = 0.001$) were more abundant in plots planted continuously with corn (Table 2). Although the results of the MANOVA for corn variety was not significant, the results for 2005 were similar to those for spring 2004, when the activity density of *B. quadrimaculatum* was higher in conventional than in GMHT corn.

Weed abundance and carabid activity density

Weed abundance was significantly affected by our treatments on each sampling date in 2004 (Kruskal–Wallis test, May: $T_{3,\ 0.05} = 8.16$, $P = 0.043$; June: $T_{3,\ 0.05} = 12.791$, $P = 0.002$; July: $T_{3,\ 0.05} = 10.354$, $P = 0.016$) (Fig. 3). Weed abundance in plots planted with conventional corn, regardless of rotation, decreased from May to June and July. Weed abundance in plots planted with GMHT corn (continuous and rotation) was low in May, increased in June, and decreased in July. Average weed abundance was lowest in

Fig. 3. Weed density (mean ± SE; $n = 4$ for each column) in genetically modified herbicide-tolerant (GMHT) and conventional corn under continuous and rotational cropping regimes in Lethbridge, Alberta, on three survey dates in 2004 and one in 2005. The letters above the bars represent the grouping within each survey date after a significant Kruskal−Wallis test ($P < 0.05$) followed by a Nemenyi *post-hoc* test.

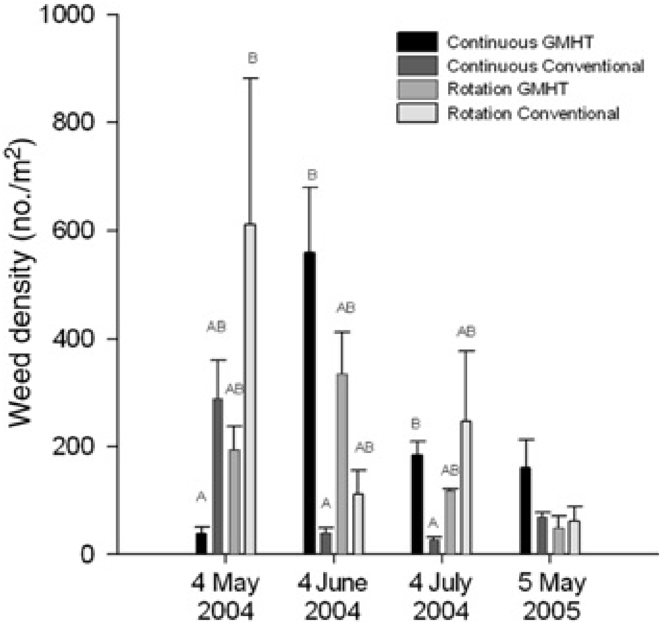


Table 3. Activity density (beetle trap-days; mean ± SE ($n = 8$)) of carabid species in genetically modified herbicide-tolerant (GMHT) and conventional corn varieties and under continuous and rotational cropping regimes in Lethbridge, Alberta, in summer and fall 2004.

	Continuous regime		Rotation		
Summer and fall 2004	GMHT corn	Conventional corn	GMHT corn	Conventional corn	P^*
Total carabid catch	5.72 ± 0.55	5.30 ± 0.69	7.17 ± 0.90	11.41 ± 1.48	0.043
MANOVA	—	—	—	—	0.030
Amara carinata	0.94 ± 0.27	0.94 ± 0.21	0.65 ± 0.08	1.86 ± 0.65	0.135
Pterostichus melanarius	2.70 ± 0.39	1.91 ± 0.66	5.04 ± 0.45	5.37 ± 1.58	0.624
Agonum placidum	0.30 ± 0.01	0.03 ± 0.01	0.18 ± 0.13	1.25 ± 0.49	0.003
Bembidion quadrimaculatum	1.28 ± 0.20	1.48 ± 0.18	1.04 ± 0.26	2.26 ± 0.47	0.142
Bembidion timidum	0.50 ± 0.13	0.95 ± 0.18	0.34 ± 0.08	0.67 ± 0.25	0.984

*The α value of the interaction between corn variety and cultural regime.

conventional continuous treatments in June and July. High weed abundance in rotated plots of conventional corn observed in May was due principally to kochia (*Bassia scoparia* (L.) A.J. Scott (Chenopodiaceae)). High average weed abundance in GMHT (both continuous and rotation) in June was almost exclusively due to redroot pigweed (*Amaranthus retroflexus* L. (Amaranthaceae)). In 2005, treatment had no significant effect on average weed abundance before the June flood. However, there seemed to be a trend for GMHT continuous to show higher weed abundance, on average, than did the other three treatments.

In 2004 there was a significant negative correlation between activity density of

Fig. 4. Activity density of small-bodied carabids with increasing weed abundance in 2004 ($r^2 = 0.284$, $P = 0.034$) (*a*) and large-bodied carabid species with increasing weed cover in 2005 ($r^2 = 0.368$, $P = 0.013$) (*b*) (see the text) in corn plots in Lethbridge, Alberta. Each data point corresponds to one experimental plot.

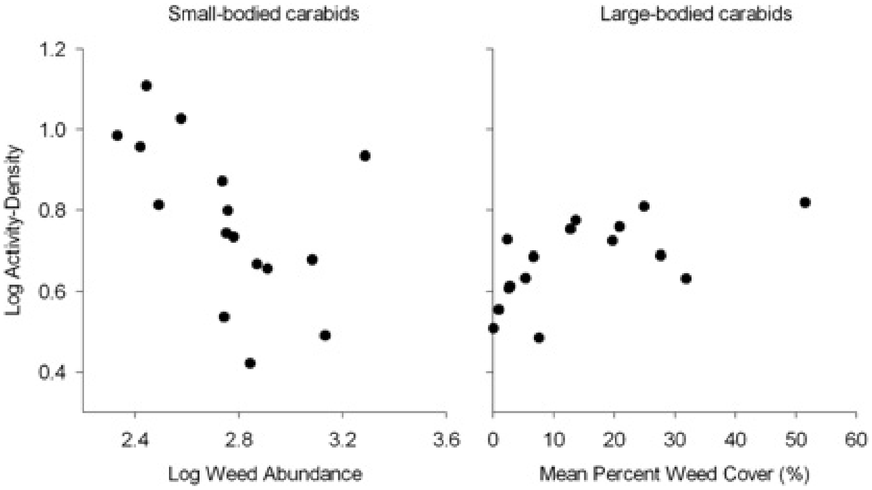
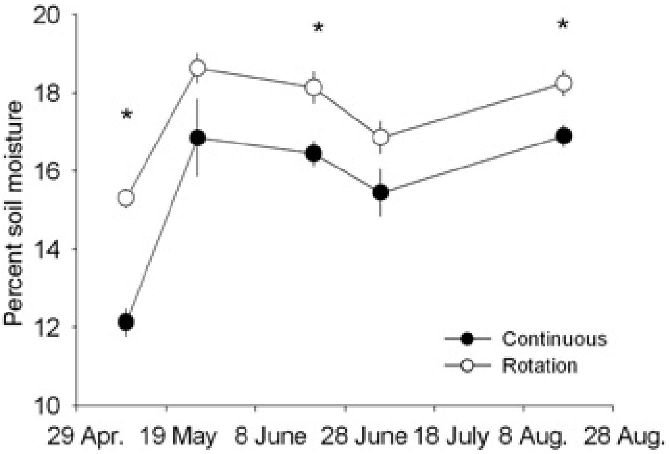


Fig. 5. Percent soil moisture (mean ± SE; $n = 8$) in corn plots under rotational and continuous cropping regimes in Lethbridge, Alberta, in 2004. Asterisks indicate dates when percent soil moisture differed significantly between the two cropping regimes ($P < 0.05$).



small-bodied carabids and weed abundance ($P = 0.034$, $r^2 = 0.28$; Fig. 4*a*). In contrast, only large-bodied carabids responded significantly to weed cover ($P = 0.013$, $r^2 = 0.368$) during 2005, the capture rate increasing with weed cover (Fig. 4*b*).

Soil moisture

In 2004, the soil moisture level was significantly higher in plots under rotation than in those under the continuous cropping regime ($F_{1,28} = 27.33$, $P < 0.001$). On three of five sampling dates (10 May, 21 July, and 16 August), plots under rotation had a significantly higher soil moisture level than did those under the continuous system (Fig. 5). This result also held for 2005, when moisture in the rotation plots was 10.4 ± 0.6% compared with 8.5 ± 0.4% in the continuous plots ($F_{1,28} = 7.296$, $P = 0.012$).

Discussion

Corn variety

The effects of corn variety on the carabid community in our study were likely mediated through the associated weed-management strategies. Hence, variations in weed density could have altered habitat quality for certain carabid species. However, when we looked at the overall carabid catch, we only observed a decrease in activity density in plots seeded with GMHT corn in spring 2004. In the summer and fall sampling period, corn variety and cultural regime interacted to influence the total catch in favour of the conventional continuous treatment. No effect of corn variety was observed in 2005. Furthermore, *Bembidion quadrimaculatum*, the most abundant species in spring 2004, is a xerophilous species associated with weed-free environments (Rivard 1964; Kromp 1990). Interestingly, in 2004, during peak activity of *B. quadrimaculatum*, we observed a strong emergence of redroot pigweed (almost exclusively in the GMHT plots, which considerably increased weed abundance. This late-emerging weed was not controlled by the first preburn herbicide spray in GMHT plots because it was present only as seeds at that time. In a normal year with higher spring temperatures, a field planted to a GMHT crop would have lower weed abundance and a corresponding higher activity of xerophilous carabids. In fact, the average seed bank after 7 years of these treatments in our study plots was lower in GMHT than in conventional plots (R.E. Blackshaw unpublished data). Higher weed biomass in GMHT corn than in conventional corn was also reported by Hawes *et al.* (2003). Higher weed density in GMHT plots may have considerably modified the microenvironment of the GMHT plots and influenced the distribution of the abundant species, *B. quadrimaculatum*. Lower activity density of *B. quadrimaculatum* in weedier plots was also reported by Bourassa *et al.* (2008) and Floate *et al.* (1990). Additionally, *Bembidion timidum* (LeConte) (data not shown) and *Microlestes linearis*, species with habitat associations similar to those of *Bembidion quadrimaculatum,* were also less abundant in the GMHT corn plots in spring 2004. However, *B. quadrimaculatum* was the only species showing this pattern in spring of both 2004 and 2005. Brooks *et al.* (2003) also reported higher abundance of *Bembidion* species in conventional corn than in GMHT corn. *Poecilus scitulus* also responded negatively to the GMHT plots in spring 2004; however, less is known about the habitat preferences of this species. Two species, *Harpalus amputatus* and *Poecilus corvus*, showed a preference for GMHT corn in 2005. Although many studies have reported no overall effects of GMHT corn on carabid assemblages (Brooks *et al.* 2003; Hawes *et al.* 2003), our results support reports of subtle species-specific responses (Brooks *et al.* 2003; Roy *et al.* 2003).

Contrary to our initial hypothesis, corn variety had only a minor effect on carabid diversity; no carabids, except for the few species mentioned above, responded to corn variety and, overall, there was no major difference in species richness between the two corn varieties. Thus, this study provided no evidence that planting GMHT corn would have a detrimental effect on carabid diversity relative to that of conventional corn.

Crop rotation

Rotating corn with canola had a much stronger influence on carabid community structure in each sampling period than did corn variety. Additionally, in each sampling period, more carabids were captured in corn plots under rotation, a result also reported by Brust *et al.* (1986). In a study conducted in Lethbridge and Lacombe, Alberta, Butts *et al.* (2003) found that canola provides a good habitat for many carabids, especially species of *Amara* Bonelli (which are known to eat seeds of cruciferous plants such as canola (Thiele 1977)). In 2005 the dominance of *A. farcta* and *A. littoralis* in plots under rotation was probably due to an increase in canola residues at the soil surface. The opposite trend was observed for *A. farcta* in spring 2004, although its overall abundance was much lower that year. Activity density of other species was also enhanced by the rotation treatment. Mean activity density of *Pterostichus melanarius* and *Poecilus corvus*, for example, was higher in plots under rotation than in those under continuous cropping. This trend may reflect the potentially higher prey availability in rotation treatments. In fact, an increased amount of organic matter can increase microarthropod abundance under some conditions (Jagers op Akkerhuis *et al.* 2008).

Although the catch rate was higher in rotation plots, carabid diversity was lower in those plots in two of the three sampling periods. This contrasts with a report that species richness in corn grown in rotation with wheat was higher than in continuous corn (Lövei 1984). Lower diversity in spring in plots under rotation may have been caused by a higher abundance of soil-surface canola residue, which may have obstructed the movement of some species and reduced their representation in pitfall-trap catches. In fact, many small-bodied carabids, such as *Bembidion* species, were less abundant in plots under rotation, and some, such as *Bembidion nitidum* (Kirby), were never captured in those plots. An increase in vegetative debris, impeding carabid movement, was also reported by Greenslade (1964). Additionally, a higher soil moisture level in the plots under rotation may also have reduced the capture of xerophilous species such as *B. quadrimaculatum*.

Carabid body size and weed abundance

Intuitively, large-bodied carabids should be more constrained in their movements under dense vegetation than are small-bodied carabids. Therefore, trapping carabids in dense vegetation should provide a more accurate estimate of activity density for small-bodied than for large-bodied carabids. Thus, one might expect that large-bodied carabids would be underrepresented in traps in dense vegetation. Contrary to these expectations, in 2005 more large-bodied carabids were captured as weed density increased. In 2004, fewer small-bodied carabids were captured under dense vegetation. Although weed-survey methods and trapping periods differed between years because of the unexpected problems with weather, we argue that our data accurately represent carabid habitat use. For instance, our data are consistent with observations that larger carabids leave areas subjected to herbicide application, suggesting that dense weed cover may be an important component of their habitat (Brust 1990).

Habitat use by large- or small-bodied carabids could reflect their feeding guild. Prey of large-bodied carabids are generally larger than those of small-bodied carabids (Wheater 1988), and because dense weed stands will generally attract a greater diversity of prey (Strandberg *et al.* 2005), there would be more opportunities for large-bodied carabids to find appropriately sized prey items. Additionally, larger bodied beetles are more vulnerable to bird predation than are smaller ones and weed cover may offer good protection. Also, many smaller bodied *Bembidion* species are primarily diurnal hunters that may use visual cues to find insect eggs or larvae, and high weed density may reduce their ability to locate prey. Chiverton (1990) reported that searching for prey increases with temperature, a variable that is usually reduced under dense weed cover.

Conclusions

Crop rotation affects carabid diversity, species composition, and activity density more significantly than does corn variety (conventional *vs.* GMHT). Rotating corn with canola increased the amount of mulch on the soil surface, which in turn increased soil moisture. This aspect probably affects species in different ways: for example, large-bodied carabids may find more food items as the amount of mulch increases, whereas the movement of smaller bodied carabids both into and within such plots may be physically restricted. The use of conventional herbicides in weed management may also affect carabids indirectly because weed abundance differentially influences activity density in relation to beetle body size. Therefore, tolerating a moderate amount of weeds within a corn field may help reduce pest density and maintain acceptable, cost-efficient yields. In addition, rotating canola with corn may conserve endemic natural enemies that contribute to biological control of insect pests and, possibly, some weeds.

Although rotation decreased carabid species evenness, it did not reduce species richness. In this short-term study, the use of GMHT corn had no negative effects on the carabid community except for a few species such as *B. quadrimaculatum* that were negatively impacted by an anomalous weedier environment in the GMHT plots relative to conventional corn during their peak activity period. Studies at larger spatiotemporal scales are required to fully assess the environmental impacts of the use of GMHT crops, and the associated weed-management technology, on the Canadian prairies. Short-term results such as ours need to be interpreted with caution and point to the need for longer term studies using commercial fields of more realistic size.

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Appendix A

Table A1. Carabid species caught in corn plots in Lethbridge, Alberta, in 2004 and 2005, showing counts and percentages.

	Spring 2004		Summer and fall 2004		2005	
	No.	Percentage	No.	Percentage	No.	Percentage
Agonum corvus (LeConte)	1	0.03	5	0.11	2	0.05
Agonum cupreum Dejean	—	—	2	0.04	1	0.02
Agonum placidum (Say)	20	0.57	200	4.42	16	0.4
Amara apricaria (Paykull)	5	0.14	33	0.73	2	0.05
Amara carinata (LeConte)	36	1.03	557	12.32	9	0.23
Amara confusa LeConte	6	0.17	—	—	29	0.74
Amara ellipsis (Casey)	1	0.03	—	—	1	0.02
Amara erratica (Duftschmid)	2	0.06	—	—	—	—
Amara farcta LeConte	183	5.25	159	3.52	2714	69.4
Amara latior (Kirby)	—	—	22	0.49	1	0.02
Amara littoralis Mannerheim	43	1.23	3	0.07	133	3.4
Amara obesa (Say)	2	0.06	9	0.20	—	—
Amara patruelis Dejean	1	0.03	—	—	—	—
Amara quenseli (Schönherr)	26	0.75	152	3.36	2	0.05
Amara torrida (Panzer)	—	—	3	0.07	—	—
Axinopalpus biplagiatus (Dejean)	2	0.06	—	—	—	—
Bembidion bimaculatum (Kirby)	—	—	3	0.07	—	—
Bembidion nitidum (Kirby)	2	0.06	—	—	1	0.02
Bembidion nudipenne Lindroth	13	0.37	12	0.27	1	0.02
Bembidion obscurellum (Motschulsky)	39	1.12	4	0.09	2	0.05
Bembidion quadrimaculatum (L.)	1598	45.85	641	14.18	132	3.37
Bembidion rapidum (LeConte)	—	—	1	0.02	1	0.02
Bembidion rupicola (Kirby)	51	1.46	10	0.22	22	0.56
Bembidion timidum (LeConte)	96	2.75	249	5.51	2	0.05
Bradycellus congener (LeConte)	13	0.37	1	0.02	5	0.12
Calosoma obsoletum Say	1	0.03	3	0.07	—	—
Carabus granulatus L.	1	0.03	2	0.04	2	0.05

Table A1. (*concluded*).

	Spring 2004		Summer and fall 2004		2005	
	No.	Percentage	No.	Percentage	No.	Percentage
Chlaenius sericeus (Forster)	2	0.06	8	0.18	—	—
Clivina fossor (L.)	81	2.32	49	1.08	50	1.27
Dicheirotrichus cognatus (Gyllenhal)	—	—	1	0.02	—	—
Diplocheila obtusa (LeConte)	1	0.03	—	—	—	—
Harpalus affinis (Schrank)	1	0.03	—	—	—	—
Harpalus amputatus Say	92	2.64	97	2.15	120	3.07
Harpalus fraternus LeConte	—	—	1	0.02	1	0.02
Harpalus fuscipalpis Sturm	13	0.37	10	0.22	16	0.4
Harpalus herbivagus Say	16	0.46	10	0.22	35	0.89
Harpalus nigritarsis Sahlberg	—	—	1	0.02	—	—
Harpalus paratus Casey	—	—	1	0.02	—	—
Harpalus reversus Casey	1	0.03	68	1.50	25	0.63
Harpalus somnulentus Dejean	1	0.03	—	—	—	—
Harpalus ventralis LeConte	—	—	2	0.04	—	—
Microlestes linearis (LeConte)	190	5.45	56	1.24	13	0.33
Poecilus corvus (LeConte)	639	18.34	137	3.03	490	12.5
Poecilus lucublandus (Say)	15	0.43	7	0.15	20	0.51
Poecilus scitulus LeConte	193	5.54	180	3.98	20	0.51
Pterostichus adstrictus Eschscholtz	—	—	1	0.02	1	0.02
Pterostichus melanarius (Illiger)	89	2.55	1816	40.17	23	0.58
Stenolophus comma (Fabricius)	9	0.26	5	0.11	14	0.35
Syntomus americanus (Dejean)	—	—	—	—	1	0.02
Total	3485		4521		3907	