

Effects of Tillage on the Activity Density and Biological Diversity of Carabid Beetles in Spring and Winter Crops

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Environ. Entomol. 36(2): 356–368 (2007)

ABSTRACT The effects of tillage regimen (conventional [CT] and no-tillage [NT]) on the activity density and diversity of carabid beetles (Coleoptera: Carabidae) was studied by pitfall trapping within a rain-fed cropping system in northwestern Idaho, 2000–2002. The cropping rotation consisted of a spring cereal (barley, *Hordeum vulgare* L., in 2000 and 2001; and wheat, *Triticum aestivum* L., in 2002), spring dry pea (*Pisum sativum* L.) 2000–2002, and wheat (*T. aestivum*), spring in 2000 and 2001, and winter in 2002. A total of 14,480 beetles comprised of 30 species was captured, with five numerically dominant species [*Poecilus scitulus* L., *Poecilus lucublandus* Say, *Microlestes linearis* L., *Pterostichus melanarius* Ill., and *Calosoma cancellatum* (Eschscholtz)], accounting for 98% of all captures. All species including the dominants responded idiosyncratically to tillage regimen. Adjusting for trapping biases did not significantly change seasonal activity density of *Poecilus* spp. or *Pt. melanarius* to tillage. More beetles were captured in CT than in NT crops because of the dominance of *P. scitulus* in CT, whereas species richness and biological diversity were generally higher in NT crops. Observed patterns suggest that direct effects of tillage affected some species, whereas indirect effects related to habitat characteristics affected others. CT may provide habitat preferable to xerophilic spring breeders. A relationship was found between beetle species size and tillage regimen in pea and to a lesser extent across all spring crops, with large species (>14 mm) conserved more commonly in NT, small species (<7 mm) in CT, and intermediate species (7–14 mm) conserved equally between tillage systems.

KEY WORDS Carabidae, wheat, conservation tillage, no-till, activity density

Carabid beetles (Coleoptera: Carabidae) spend most of their lives in the soil, on the soil surface, or in surface litter (epigeal). Carabids are numerous and diverse in temperate agricultural habitats (Potts and Vickerman 1976) and are important biocontrol agents of pest species, especially when occurring in an assemblage of generalist natural predators (Sunderland 2002).

Conventional tillage (CT) practices (moldboard plowing or intensive tillage operations) disturb the physical, chemical, and biological properties of cropland soils (Kladivko 2001), detrimentally affecting soil biota including carabids (Holland and Luff 2000). In no-tillage (NT) agriculture, a form of conservation tillage, the plow and secondary tillage have been eliminated, and seed is drilled into existing crop residues (Veseth and Karow 1999). Eliminating tillage reduces production costs and the risks of soil compaction, while in some cases increasing crop productivity (Gebhardt et al. 1985). NT preserves the vertical structure of the soil profile, moderates soil temperature, and conserves soil organic matter (SOM) and biota (Hendrix et al. 1986, Kladivko 2001). Although NT agricul-

ture is increasing in the Palouse region of northwestern Idaho and southeastern Washington (Veseth 1999), little is known about how the region's carabid fauna responds to different tillage regimens.

Carabid beetles are typically sampled by pitfall trapping. The number of beetles captured in pitfall traps (i.e., trap catch) is a function of the density, but also the activity of the sampled organisms and their behavior (Halsall and Wratten 1988) on encountering a trap. Hence, the term "activity density" is used to refer to population estimates obtained using pitfall traps. Many authors have reported higher activity density of carabids under NT than under CT (Brust et al. 1985, House and Parmelee 1985, Stinner and House 1990, Weiss et al. 1990, Brust 1994, Digweed et al. 1995, Heimbach and Garbe 1995, Kendall et al. 1995, Purvis and Fadl 1996, Andersen 1999, Holland and Reynolds 2003), but others have reported lower activity density of carabids under NT (Barney and Pass 1986, Cárcamo 1995, Baguette and Hance 1997), or no discernible differences between tillage systems (Tyler and Ellis 1979, Huusela-Veistola 1996). However, conclusions drawn from pitfall trapping studies must be tempered by the possible influences of sampling biases inherent to this method (Sunderland et al. 1995). Activity of carabids and thus capture rate of traps for the beetles may differ among tillage systems, even though actual

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abundances do not (Sunderland et al. 1995, Hatten 2006). For example, in mark-recapture experiments, Hatten et al. (2007) found that pitfall trap capture rates for *Poecilus scitulus* LeConte were greater in NT than in CT pea, whereas capture rates of *Pterostichus melanarius* Illiger were greater in CT than in NT spring wheat. Where possible, corrections for such treatment-dependent biases should be used to improve the accuracy of pitfall sampling to compare relative abundances and treatment effects.

The response of carabids to tillage depends on many interacting factors. Tillage may affect carabid populations in a direct manner by mechanically injuring or killing individuals (Holland and Luff 2000), or in an indirect manner by modifying their habitat and altering prey availability (Hance 2002, Holland 2004). Tillage effects are mediated by species-level traits of carabids including phenology, diel activity, and preference for microclimate and habitat (Holland and Luff 2000).

In this study, we compared the effects of different tillage regimens (CT and NT) in Palouse cropland on the activity density and diversity of Carabidae in spring crops and a winter crop. Trapping biases for *Poecilus lucublandus* Say, *P. scitulus*, and *Pt. melanarius* were accounted for, and the corrected versus uncorrected patterns were compared. We hypothesized that species richness and diversity of carabids would be greater under NT than under CT but that the abundance of individual species would differ idiosyncratically between the two treatments.

Materials and Methods

Study Site and Experimental Design. The study was conducted at the University of Idaho's (UI) Kambitsch Research Farm (Kambitsch) in Latah Co., 3 km northeast of Genesee in the Palouse region of Idaho. This long-term study established in 2000 was designed to assess the influence of tillage on pests, natural enemies, soil organisms, soil quality, and crop varieties. The study consists of two tillage treatments, NT and CT, randomized in four replications (each tillage strip is 20 by 80 m). Three sections (one 27 by 157-m section for each crop) oriented perpendicular to and across the tillage strips were planted to winter wheat (*Triticum aestivum* L.), a spring cereal (either barley [*Hordeum vulgare* L.] or wheat [*T. aestivum*]), or spring dry pea (*Pisum sativum* L.), with eight plots per crop section: four in CT and four in NT. Because crops at Kambitsch are planted separately, this design enables tillage but not crop comparisons. Since 2000, the crops have rotated annually, such that pea is seeded into spring small grain residue, spring cereal is seeded into winter wheat residue, and winter wheat is seeded into pea residue. This is a commonly used rotation in the region. In 1999, winter wheat was cropped over the entire experiment area, so in 2000, only spring crops were seeded, and spring wheat replaced winter wheat in the rotation to control volunteer winter annual weeds on the site. In 2001, winter wheat planted in the rotation was destroyed over winter by meadow vole (*Microtus pennsylvanicus* Ord), and the plots were

reseeded to spring wheat. Thus, for 2000 and 2001, barley was the spring cereal in the rotation sequence.

Tillage and Seeding. Conventional tillage plots were established on winter wheat fields by moldboard plowing in October 1999 to a depth of ≈ 18 cm, and in following years were chisel plowed to a depth of 22 cm on 18 October 2000 and 26 October 2001. To prepare the seedbed, CT plots were cultivated and harrowed each spring on the same day or 1 d before seeding with two passes using a field cultivator. The NT plots were not disturbed before planting, and both CT and NT were seeded on the same days and received the same amounts of fertilizer. Spring crops were planted 1 May 2000, 25 April 2001, and 24 April 2002. Winter wheat was planted on 27 October 2001. All plots were seeded and fertilized using a Great-Plains NT drill with turbo-colters and disc openers for fertilizer and seed placement (Great Plains Manufacturing, Salina, KS). Seeding rates were 300 seeds/m² of spring wheat, 85 seeds/m² of spring pea, and 260 seeds/m² of spring barley and of winter wheat.

Fertilizer and Pesticide Applications. In cereal crops, liquid fertilizer was applied at planting in all years. Fertilizer rates in 2000 and 2001 were 95N-22P-0K-17S kg/ha. After the winter wheat was destroyed in 2001, glyphosate (DuPont, Wilmington, DE) was applied in March 2001, and plots were seeded with spring wheat and given an additional application of 15N-49P-0K-0S kg/ha fertilizer at seeding. Fertilizer rates in 2002 were 103N-22P-0K-4S kg/ha. The 2002 winter wheat plots received 106N-25P-0K-19S kg/ha fertilizer at fall planting, and an additional 50N-0P-0K-8S kg/ha were broadcast in the spring. Pea received no fertilizer in any year of the study.

In plots planted to spring cereals, glyphosate (Monsanto, St. Louis, MO) was applied in the fall of 1999 and 2000 at the rate of 840.6 g acid equivalent (a.e.)/ha. No glyphosate was applied in the fall of 2001. Each spring, glyphosate was applied at a rate of 525 g (a.e.)/ha before planting. Once spring cereals were established, 280.2 g (AI)/ha of bromoxynil, 280.2 g (AI)/ha (4-chloro-2-methylphenoxy) acetic acid (MCPA), 96.3 g (AI)/ha of fenoxaprop-*p*-ethyl (all from Bayer Crop Science AG, Research Triangle Park, NC), 1.4 g (AI)/ha of thifensulfuron, and 0.7 g (AI)/ha of tribenuron (both from DuPont) were applied. In plots planted to spring pea, esfenvalerate (DuPont) was applied at a rate of 44 g (AI)/ha to control pea-leaf weevil (*Sitona lineatus* L.) on 24 May 2000, 17 May 2001, and 17 May 2002; bifenthrin (FMC, Philadelphia, PA) was applied during bloom at a rate of 112 g (AI)/ha to control pea weevil (*Bruchus pisorum* L.) and pea aphid (*Acyrtosiphon pisum* Harris) on 2 July 2000, 21 May 2001, and 3 July 2002. In plots planted to winter wheat, downy brome (*Bromus tectorum* L.) was hand weeded, and prickly lettuce (*Lactuca serriola* L.) was sprayed preharvest with glyphosate and 2,4-D (Agrilience, St. Paul, MN). For additional details on plot management, see Castle del Conte et al. (2005).

Pitfall Sampling. Carabids were sampled from 2000 to 2002 using pitfall traps. In 2000, the sampling period extended from June until early August, whereas in 2001

and 2002, it extended from early May until mid-August. In 2002, pea plots were also sampled throughout April, allowing us to determine which spring breeders were present during the very early season and to assess the effects of spring tillage (24 April 2002) on this fauna. Hence, in April 2002, the traps were removed the day before spring tillage and replaced the day after. To capture the arthropods, in all years two 6-cm-diameter pitfall traps were placed 10 m apart in each plot. Traps consisted of 266-ml plastic drink cups set in plastic liners flush with the soil surface. Each trap was filled weekly with 30–60 ml of low-toxicity antifreeze. Arthropods that fell into the traps were preserved by the antifreeze and collected on a weekly basis. Trap contents were processed by transferring all specimens into 70% methanol. We identified adult beetles using the taxonomic keys of Lindroth (1961–1969) and Noonan (1991) and by comparing beetles collected during the study to specimens in the W. F. Barr Entomological Museum at the University of Idaho, Moscow, ID, and the entomology collection at the Oregon Department of Agriculture, Salem, OR. Voucher specimens were deposited in both museums.

Analysis. Trap catches (i.e., numbers of individuals) from each plot were averaged (i.e., counts divided by two traps per plot) by week and $\log(x + 1)$ transformed. Mean differences in trap catch by week and season were tested for significance using repeated-measures analysis of variance (ANOVA; PROC MIXED; SAS Institute 2001), with trap and week coded as the subject and repeat variables, respectively, tillage (two treatment levels, CT and NT) as the independent variable, and beetles (by species) as the response variable. Six pitfall traps (three in barley, two in pea, one in spring wheat) were destroyed by crop husbandry practices in CT during the study. To perform our biodiversity assessment on an equal number of traps per system, we randomly deselected six traps from the NT data set. Doing so had only a minor effect on the data set, reducing the total number of carabids captured during the study by 80 beetles (of a total of >14,000), but leaving the number of species captured per crop tillage system unchanged. The number of carabid species per crop tillage system (S) was tallied, and the true number of species (S^*) per system was estimated for each habitat with the first-order jackknife using EstimateS (Colwell 2000):

$$S^* = S_{\text{obs}} + L(n - 1/n)$$

where n = the number of samples and L = the number of unique species occurring in only one sample (Heltshel and Forrester 1983). In the jackknife procedure, the model randomly selects a sample unit and estimates the number of species present, a second sample is selected at random, and richness is recalculated using the pooled data from both samples and so on for x number of randomizations (in this case, 50). Jackknifing often reduces sampling bias and improves estimate precision (Colwell and Coddington 1994). The underlying distribution of jackknife estimates tends to be normally distributed, with the variance and confidence intervals calculated in the normal way (Heltshel and Forrester 1983). In this study, mean differences in

S^* for each CT and NT comparison at maximum sample size were compared with a t -test (independent samples with equal sample size).

Biological diversity of the carabid fauna was calculated using the Shannon-Weaver (H') index:

$$H' = - \sum p_i \ln p_i,$$

where H' = biological diversity, p_i = the observed relative abundance of species i , and \ln = natural logarithm (Southwood and Henderson 2000). Species equitability or evenness (E) (Southwood and Henderson 2000) was calculated as:

$$E = H' / \ln S.$$

Randomization tests were used to test whether H' or E differed significantly between tillage systems. As described by Solow (1993), the CT and NT trap counts used to calculate H' and E were combined into single data sets for each crop. Each combined data set was randomly partitioned by shuffling the data (without replacement) into two subsets of size n (where n = number of individuals trapped per tillage system). We calculated H' and E for each subset and recorded the differences (δ) between subsets. Calculated δ and observed δ (from field sampling) were compared. This procedure was repeated 1,000 times (www.resample.com) and tallied each time simulated $|\delta| > \text{observed } |\delta|$ (two-tailed test) or simulated δ was $>$ observed δ (one-tailed test), with P values calculated per Manly (1991).

Accounting for Trapping Biases. Activity densities of *P. lucublandus*, *P. scitulus*, and *Pt. melanarius* were adjusted to account for treatment-related biases in capture rates in CT and NT. Treatment biases for these species were first obtained by Hatten et al. (2007) who (1) measured capture rates over the season in CT and NT crops through a mark-recapture study in the same plots as in this study and (2) divided the capture rates measured in CT by those in NT to obtain a bias adjustment factor (BAF). We multiplied the BAFs of Hatten et al. (2007) by the weekly trap counts obtained during this study. For example, capture rates for *Pt. melanarius* were found by Hatten et al. (2007) to be 1.81 times greater in CT than in NT spring wheat. Therefore, we multiplied NT counts in spring wheat for this species by a 1.81 BAF. Also, the different capture rates for *P. scitulus* in CT and NT pea required multiplying NT counts by a 0.43 BAF. In contrast, capture rates of *P. lucublandus* were not adjusted because the BAF for this species = 1.

Index V and Beetle Size. The relative response of carabid species to tillage (CT and NT) was assessed with index V (Wardle 1995):

$$V = (2M_{\text{CT}} / [M_{\text{CT}} + M_{\text{NT}}]) - 1,$$

where M_{CT} and M_{NT} = total trap catch in CT or NT, respectively. Index V ranges from 1 (species captured only in CT) to -1 (species captured only in NT), with 0 indicating equal trap catch in CT versus NT. Kendall et al. (1995) found a relationship between beetle size and tillage regimen, with larger species conserved in NT relative to CT systems and vice versa. We explored this

Table 1. Number and cumulative percentage of Carabidae collected from pitfall traps in CT and NT spring pea, wheat, barley, and winter wheat at the Kambitsch Research Farm, northern Idaho, 2000–2002

Species	Crops								Total		Percent ^a
	Spring pea		Spring wheat		Spring barley		Winter wheat		CT	NT	
	CT	NT	CT	NT	CT	NT	CT	NT			
<i>Poecilus scitulus</i>	4352	1066	1740	634	781	165	761	136	7,634	2,001	66.5
<i>Poecilus lucublandus</i>	565	966	409	502	149	225	578	269	1,701	1,962	25.3
<i>Microlestes linearis</i>	139	40	106	85	28	19	10	8	283	152	3
<i>Pterostichus melanarius</i>	51	58	15	58	28	45	17	5	111	166	1.9
<i>Calosoma cancellatum</i>	60	36	32	35	37	27	25	13	154	111	1.8
<i>Harpalus amputatus</i>	1	2	0	0	0	0	0	0	1	2	—
<i>Harpalus fraternus</i>	2	5	6	10	2	3	3	0	13	18	—
<i>Harpalus fuscipalpis</i>	0	0	0	0	1	0	0	1	1	1	—
<i>Harpalus opacipennis</i>	1	0	0	0	0	0	0	0	1	0	—
<i>Harpalus somnulentus</i>	0	0	0	0	1	1	0	0	1	1	—
<i>Amara apricaria</i>	1	2	1	8	0	0	1	1	3	11	—
<i>Amara blanchardi</i>	0	1	0	0	0	0	0	0	0	1	—
<i>Amara californica</i>	1	1	2	1	0	0	0	0	3	2	—
<i>Amara conflata</i>	0	0	0	1	0	0	0	0	0	1	—
<i>Amara cupreolata</i>	0	0	0	0	0	1	0	0	0	1	—
<i>Amara farcta</i>	2	2	2	0	0	0	0	0	4	2	—
<i>Amara littoralis</i>	5	6	5	7	0	1	5	5	15	19	—
<i>Amara sp.</i>	0	1	1	0	0	0	0	0	1	1	—
<i>Acupalpus meridianus</i>	6	2	3	0	0	0	0	1	9	3	—
<i>Anisodactylus californicus</i>	0	0	0	0	0	0	2	0	2	0	—
<i>Anisodactylus sanctaerucis</i>	5	1	3	1	0	1	0	1	8	4	—
<i>Anisodactylus similis</i>	1	2	3	0	8	9	3	1	15	12	—
<i>Bembidion ruficollis</i>	2	2	1	1	1	1	1	0	5	4	—
<i>Bradycellus congener</i>	3	0	5	2	0	0	0	0	8	2	—
<i>Calosoma tepidum</i>	1	2	0	2	0	3	2	0	3	7	—
<i>Carabus nemoralis</i>	0	2	0	0	0	0	0	0	0	2	—
<i>Dicheirus piceus</i>	1	0	0	1	0	0	0	0	1	1	—
<i>Discoderus parallelus</i>	0	0	0	1	0	0	0	0	0	1	—
<i>Stenolophus lecontei</i>	4	0	0	0	0	0	0	0	4	0	—
<i>Trechus obtusus</i>	2	3	1	4	0	0	0	1	3	8	—
Sum	5,205	2,200	2,335	1,353	1,036	501	1,408	442	9,984	4,486	100
Observed no. of species	21	20	17	17	10	13	12	12	25	27	

Spring pea and wheat were sampled from 2000 to 2002, spring barley from 2000 to 2001, and winter wheat during 2002.

^a Cumulative percentage (%) of captures, where — is <1% of captures.

potential relationship by plotting index V against mean body length of all species captured during the study.

Results

Trap Catch and Diversity. In total, 14,480 carabid beetles from 15 genera and 30 species were captured during the study (Table 1). Twenty-seven species were captured in NT and 25 in CT (Table 1), with the relative response of these beetles to tillage differing by species (Fig. 1). Activity density of all beetles combined was generally higher during the early season in CT than in NT plots, but differences between systems diminished as each season progressed, resulting in a year × tillage × week interaction ($F_{58, 446}, P < 0.001$). For example, trap catch was significantly higher during 2002 on 18 June in pea ($t = 4.25, P < 0.01$), spring wheat ($t = 2.61, P = 0.01$), and winter wheat ($t = 3.77, P < 0.01$) but not during the same year on 30 July in pea ($t = 0.11, P < 0.91$), spring wheat ($t = 0.09, P < 0.91$), or winter wheat ($t = 0.03, P < 0.91; df = 14,84$ for all 2002 comparisons). Differences between systems were caused primarily by the high numbers of *P. scitulus* captured in CT plots. Without the inclusion of *P. scitulus* in the analysis, overall trap catch did not differ between tillage systems during 2002 on 18 June

in pea ($t = 0.22, P = 0.83$), spring wheat ($t = 0.20, P = 0.84$), and winter wheat ($t = 1.73, P = 0.09$), nor did it differ on 30 July in pea ($t = 0.14, P = 0.88$), spring wheat ($t = 0.26, P = 0.79$), and winter wheat ($t = -0.12, P = 0.95$).

Observed richness (S) differed little between tillage systems (Table 1), whereas estimated richness (S^*) was higher in NT versus CT cereals but was lower in NT versus CT pea (Fig. 2). Evenness (E) was greater in NT than in CT spring crops (wheat, barley, pea) but did not differ in winter wheat (Table 2). The activity density of *P. scitulus* in CT crops was the principal cause of the lower E in CT. The Shannon diversity index (H'), which increases with S and E, was lower in CT than in NT crops (Table 2). Randomization tests indicated that differences in diversity between NT and CT were highly significant (Table 3).

Dominant Species. More than 98% of all trap catches across tillage and crops was comprised of five species (in order of numerical dominance): *P. scitulus*, *P. lucublandus*, *Microlestes linearis* LeConte, *Pt. melanarius*, and *Calosoma cancellatum* (Eschscholtz). All these species except *Pt. melanarius* are spring breeders (Lindroth 1961–1969). All tend to be zoophages, although like many carabids, they exhibit a degree of omnivorous behavior (Toft and Bilde 2002), with the

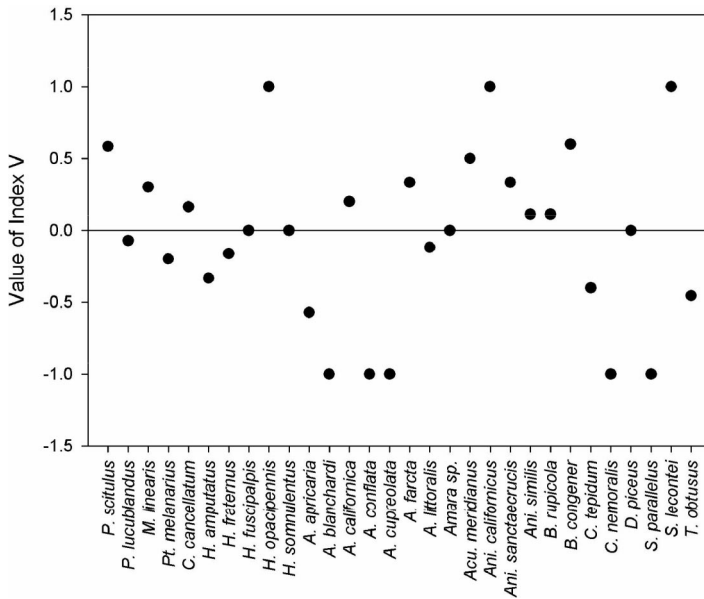


Fig. 1. Values of index V ($V = [2M_{CT}/M_{CT} + M_{NT}] - 1$, where M_{CT} and M_{NT} = total trap catch in CT or NT, respectively) for carabid beetles captured in CT versus NT crops at the Kambitsch Research Farm, 2000–2002 (see Table 1 for catch data). Index V ranges from 1 (species captured only in CT) to -1 (species captured only in NT), and 0 indicates equal trap catch in CT versus NT.

exception of *C. cancellatum*, which seems to be purely predaceous (Laroche and Larivière 2003). Trap catch of the dominants fluctuated weekly, and the patterns differed with tillage. The activity period of most species ranged from at least early May to mid-July, after which time summer temperature reached a maximum (Hatten 2006) and the crops senesced. Some species, including *M. linearis* and *Pt. melanarius*, were active at least until harvest. As with the entire fauna, decreasing activity by the dominants in July resulted in converging time series and significant tillage \times week interactions (Tables 4–6). Interactions also resulted from oscillating time series and changes in rank order of means between weeks, especially for *C. cancellatum* and *M. linearis*.

The two *Poecilus* spp. captured during the study responded in the opposite manner to tillage in pea compared with cereal crops. Catches of *P. scitulus* were consistently higher in CT than in NT pea on many sample dates from 2000 to 2002, whereas in the same crop and over the same time period, catches of *P. lucublandus* were often higher in NT pea (Fig. 3). Adjusting for trapping biases accentuated the mean differences between tillage systems for *P. scitulus* but not for *P. lucublandus* (with a BAF = 1.0). During April 2002 (the only year we sampled in April), we detected *P. lucublandus* several weeks before the other spring breeders and before spring tillage that occurred on 24 April. Trap catch of *P. lucublandus* was significantly higher in CT than in NT pea the week after spring tillage (23 April, $df = 1,18$, $t = 1.84$, $P < 0.082$; 30 April, $df = 1,18$, $t = 4.09$, $P < 0.001$; Fig. 3).

A similar but less consistent divergent pattern for *Poecilus* spp. was also observed in the cereal crops, especially in barley in 2001 and winter wheat in 2002 (data not shown). The response of the other three dominant species to tillage was less consistent between years than observed for *Poecilus* spp., but some notable patterns were detected. Weekly catches of *M. linearis* tended to be higher in CT crops, a pattern that was most evident in pea in 2001 and 2002 (Fig. 4). Catch of *C. cancellatum* also tended to be higher on some dates in CT than in NT crops, especially in pea in 2001 and winter wheat in 2002, although catch of this species was also higher on occasion in NT (Fig. 4). Weekly catches of *Pt. melanarius* were higher in NT than in CT wheat and barley during 2000, especially on 25 June (barley and wheat) and 9 July (wheat) (Fig. 4). Mean differences of *Pt. melanarius* increased in wheat after adjusting for trapping biases.

Index V on Beetle Size. We found an inverse significant relationship between index V and beetle size in spring pea (Fig. 5) and a similar trend ($P = 0.06$) across all spring crops. Small species (<7.0 mm) within spring crops were captured more frequently in CT plots, large species (>14 mm) were captured more frequently in NT, whereas the catch patterns of intermediate sized species (7–14 mm) were less divergent between systems, especially across all spring crops. The relationship between index V and beetle size was nonsignificant across all crops ($n = 30$, $P = 0.14$, adjusted $R^2 = 0.08$), largely because of the slightly positive and nonsignificant relationship between these variables in winter wheat.

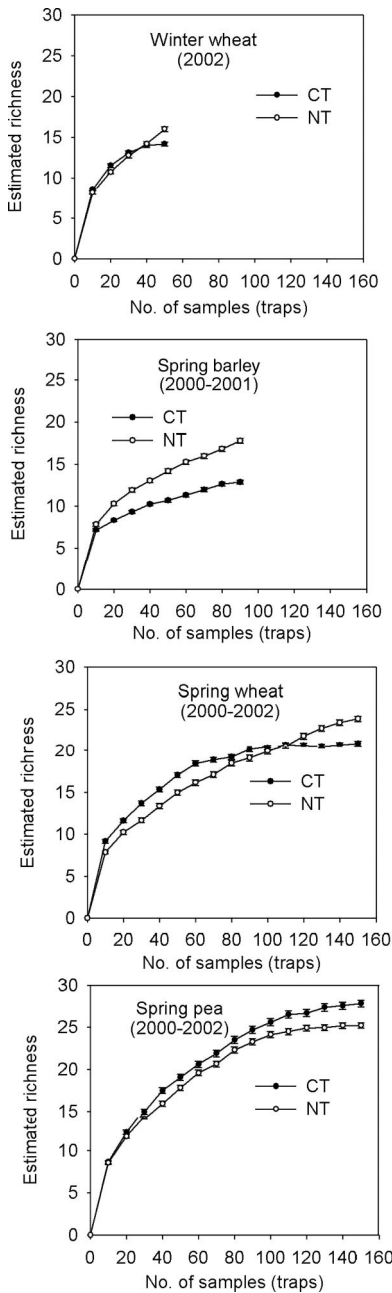


Fig. 2. Species accretion curves for carabid assemblages in spring wheat, barley, pea, and winter wheat under CT and NT agriculture at the Kambitsch Research Farm, North Idaho, 2000–2002. All values (mean richness \pm SEM) were extrapolated using a first-order Jackknife richness estimator, with each point on the curve jackknifed 50 times. Spring pea and wheat were sampled from 2000 to 2002 ($n = 152$), spring barley from 2000 to 2001 ($n = 92$), and winter wheat during 2002 ($n = 60$). Differences in total mean estimated richness (i.e., last pair of points on the curve) between tillage systems were highly significant ($df = 1,49$ for each comparison: winter wheat; $t = 13.26$, $P < 0.001$; barley, $t = 9.05$, $P < 0.001$; wheat, $t = 4.94$, $P < 0.001$; pea, $t = -3.57$, $P < 0.001$).

Table 2. Biodiversity statistics for Carabidae collected from pitfall traps in CT and NT crops at the Kambitsch Research Farm, northern Idaho, 2000–2002

Statistic	Crop							
	Spring pea		Spring wheat		Spring barley		Winter wheat	
	CT	NT	CT	NT	CT	NT	CT	NT
Evenness (E)	0.21	0.35	0.30	0.45	0.38	0.56	0.38	0.41
Shannon-Weaver (H')	0.64	1.06	0.85	1.29	0.88	1.43	0.93	1.02

Spring pea and wheat were sampled from 2000 to 2002, spring barley from 2000 to 2001, and winter wheat during 2002.

Discussion

This study provides the first comprehensive examination of Carabidae in cropping systems on the Palouse. Our finding of 30 species of Carabidae is consistent with reports from other agroecosystems, irrespective of cropping system or continent (Luff 2002). Most species reported herein have not been detected previously in Palouse cropland, and approximately one half of this fauna appears different from that reported in cropping system studies of the northern Great Plains (Weiss et al. 1990, Tonhasca 1993, Cárcamo 1995, Cárcamo et al. 1995, Ellsbury et al. 1998, Denke and Blodgett 2002, Melynychuk et al. 2003).

Carabid species richness was greater in NT than in CT cereals (spring wheat and barley, winter wheat), and diversity (H') of the carabid fauna was higher in all NT crops, including pea. These results generally support the hypothesis that NT enhances the diversity of epigeal arthropods such as carabids (Stinner and House 1990, Holland and Luff 2000). Greater trap catches of carabids in crops under CT versus NT management suggests that tillage enhances the activity

Table 3. Results of randomization tests to determine whether diversity (H') and species equitability (E) of carabid beetles differed between CT and NT crops at the Kambitsch Research Farm, northern Idaho, 2000–2002

Test	Crops							
	SP		SW		SB		WW	
	H'	E	H'	E	H'	E	H'	E
Observed δ	0.42	0.14	0.44	0.15	0.55	0.18	0.3	0.03
No. simulated $ \delta >$ observed $ \delta $	0	0	0	0	0	0	0	210 ^a
No. simulated $\delta >$ observed δ	0	0	0	0	0	0	0	217 ^a

In each comparison, the data from CT and NT were combined into a single data set, labeled by species, and randomly reassigned to two subsets of size n ($n =$ no. of observations from CT and NT, respectively). Diversity (H') and evenness (E) were calculated for each subset, and the differences (δ) were recorded and compared with observed δ (calculated from H' and E values in Table 2). This procedure was repeated 1,000 times and tallied each time simulated $|\delta| >$ observed $|\delta|$ or simulated $\delta >$ observed δ (i.e., two-tailed and one-tailed test, respectively, with P values calculated per Manly 1991). All mean differences were significant ($P \leq 0.05$) unless ^a $P > 0.05$.

Spring pea and wheat were sampled from 2000 to 2002, spring barley from 2000 to 2001, and winter wheat during 2002.

SP, spring pea; SW, spring wheat; SB, spring barley; WW, winter wheat.

Table 4. Repeated-measures ANOVA testing the effects of tillage on the activity density of five numerically dominant species of carabids in CT and NT crops at the Kambitsch Research Farm, northern Idaho, 2000

Species	Crop	Week (Wk)		Tillage (Till)		Wk × Till	
		$F_{8,48}$	P	$F_{1,6}$	P	$F_{8,48}$	P
<i>P. scitulus</i>	Pea	22.90	<0.01 ^a	32.40	<0.01 ^a	5.45	<0.01 ^a
<i>Pt. melanarius</i>		9.12	<0.01 ^a	0.52	0.45	0.72	0.67
<i>P. lucublandus</i>		86.75	<0.01 ^a	2.88	0.14	2.25	0.04 ^a
<i>C. cancellatum</i>		4.37	<0.01 ^a	0.76	0.42	1.48	0.19
<i>M. linearis</i>		3.46	0.01 ^a	2.71	0.15	4.22	<0.01 ^a
All species		36.52	<0.01 ^a	18.92	<0.01 ^a	2.99	0.01 ^a
<i>P. scitulus</i>	Wheat	7.84	<0.01 ^a	0.68	0.44	2.85	0.01 ^a
<i>Pt. melanarius</i>		8.56	<0.01 ^a	12.44	0.01 ^a	5.10	<0.01 ^a
<i>P. lucublandus</i>		11.76	<0.01 ^a	0.05	0.82	1.32	0.26
<i>C. cancellatum</i>		5.86	<0.01 ^a	0.93	0.37	2.45	0.03 ^a
<i>M. linearis</i>		1.61	0.15	1.39	0.28	2.14	0.05 ^a
All species		13.91	<0.01 ^a	0.05	0.83	2.06	0.06
<i>P. scitulus</i>	Barley	4.08	<0.01 ^a	1.08	0.34	0.73	0.67
<i>Pt. melanarius</i>		3.25	0.01 ^a	3.50	0.11	2.77	0.01 ^a
<i>P. lucublandus</i>		22.49	<0.01 ^a	7.86	0.03 ^a	6.02	<0.01 ^a
<i>C. cancellatum</i>		13.15	<0.01 ^a	0.30	0.60	3.64	<0.01 ^a
<i>M. linearis</i>		1.00	0.45	1.00	0.36	1.00	0.45
All species		17.48	<0.01 ^a	0.97	0.36	2.87	0.01 ^a

All tests were performed on $\ln(x + 1)$ transformed data.

^a Mean differences are significant at the $P \leq 0.05$ level. See Figs. 3 and 4 for tillage effects.

density of carabids. However, a single species (*P. scitulus*) accounted for >66% of all captures, and catch of this species was consistently higher in CT than in NT, strongly influencing overall patterns, whereas most other species did not respond consistently to tillage.

Individual carabid species responded differently (idiosyncratically) to tillage, as has been previously reported in agroecosystems (Tyler and Ellis 1979, Barney and Pass 1986, Hance and Grégoire-Wibo 1987, Weiss et al. 1990, Cárcamo 1995, Cárcamo et al. 1995, Holland and Luff 2000). In a review of the literature, Holland and Luff (2000) found that, of 47 taxa examined, trap catches of 20 were higher in CT fields, catches of 21 were higher in conservation tillage fields,

and catches of 7 species did not differ between CT and conservation tillage.

Sampling biases associated with pitfall trapping have hindered efforts to quantify the response of carabids and other invertebrates to anthropogenic disturbance (Sunderland et al. 1995, Melbourne 2002). In this study, we adjusted the trap counts of three dominant carabid species (accounting for $\approx 94\%$ of all captures) to estimate better their relative abundances and response to tillage. Although the required adjustments were relatively large (0.43 times for *P. scitulus* and 1.81 times for *Pt. melanarius*), catch patterns were not substantially changed (P values were little changed). This suggested that during the timeframe of the study

Table 5. Repeated-measure ANOVA testing the effects of tillage on the activity density of five numerically dominant species of carabids in CT and NT crops at the Kambitsch Research Farm, northern Idaho, 2001

Species	Crop	Week (Wk)		Tillage (Till)		Wk × Till	
		$F_{13,78}$	P	$F_{1,6}$	P	$F_{13,78}$	P
<i>P. scitulus</i>	Pea	52.10	<0.01 ^a	74.20	<0.01 ^a	3.91	<0.01 ^a
<i>Pt. melanarius</i>		3.16	<0.01 ^a	0.10	0.76	1.51	0.13
<i>P. lucublandus</i>		21.92	<0.01 ^a	9.02	0.24	2.67	0.01 ^a
<i>C. cancellatum</i>		4.22	<0.01 ^a	4.15	0.09	1.12	0.35
<i>M. linearis</i>		2.77	0.01 ^a	10.74	0.02 ^a	2.77	<0.01 ^a
All species		59.36	<0.01 ^a	47.11	<0.01 ^a	2.01	0.03 ^a
<i>P. scitulus</i>	Wheat	16.00	<0.01 ^a	2.82	0.14	0.98	0.48
<i>Pt. melanarius</i>		1.96	0.04 ^a	0.27	0.62	0.90	0.55
<i>P. lucublandus</i>		28.56	<0.01 ^a	2.19	0.19	0.44	0.95
<i>C. cancellatum</i>		4.85	<0.01 ^a	0.08	0.78	3.05	<0.01 ^a
<i>M. linearis</i>		4.63	<0.01 ^a	3.80	0.10	0.90	0.56
All species		17.00	<0.01 ^a	1.83	0.225	0.58	0.86
<i>P. scitulus</i>	Barley	28.70	<0.01 ^a	53.50	<0.01 ^a	4.76	<0.01 ^a
<i>Pt. melanarius</i>		2.70	<0.01 ^a	0.58	0.47	0.59	0.85
<i>P. lucublandus</i>		33.80	<0.01 ^a	1.96	0.21	0.85	0.61
<i>C. cancellatum</i>		4.59	<0.01 ^a	3.45	0.11	1.01	0.45
<i>M. linearis</i>		8.23	<0.01 ^a	1.34	0.29	1.91	0.04 ^a
All species		77.64	<0.01 ^a	43.40	0.01 ^a	4.11	<0.01 ^a

All tests were performed on $\ln(x + 1)$ transformed data.

^a Mean differences are significant at the $P \leq 0.05$ level. See Figs. 3 and 4 for tillage effects.

Table 6. Repeated-measures ANOVA testing the effects of tillage on the activity density of five numerically dominant species of carabids in CT and NT crops at the Kambitsch Research Farm, northern Idaho, 2002

Species	Crop	Week (Wk)		Tillage (Till)		Wk × Till	
		F _{14,84}	P	F _{1,6}	P	F _{14,84}	P
<i>P. scitulus</i>	Pea	14.55	<0.01 ^a	3.56	0.11	1.78	0.06
<i>Pt. melanarius</i>		1.92	0.04 ^a	0.00	1.00	0.83	0.64
<i>P. lucublandus</i>		28.00	<0.01 ^a	2.37	0.18	0.56	0.89
<i>C. cancellatum</i>		1.44	0.15	3.59	0.11	0.46	0.95
<i>M. linearis</i>		5.51	<0.01 ^a	11.99	0.01 ^a	2.57	<0.01 ^a
All species		24.55	<0.01 ^a	3.47	0.11	1.93	0.35
<i>P. scitulus</i>	Wheat	13.81	<0.01 ^a	7.75	0.03 ^a	2.37	<0.01 ^a
<i>Pt. melanarius</i>		1.29	0.23	0.49	0.51	0.53	0.91
<i>P. lucublandus</i>		10.91	<0.01 ^a	0.48	0.52	0.69	0.78
<i>C. cancellatum</i>		1.53	0.12	0.69	0.44	1.47	0.14
<i>M. linearis</i>		8.46	<0.01 ^a	3.54	0.11	1.27	0.24
All species		20.12	<0.01 ^a	2.77	0.15	1.58	0.10
<i>P. scitulus</i>	Winter wheat	17.08	<0.01 ^a	34.53	<0.01 ^a	4.19	<0.01 ^a
<i>Pt. melanarius</i>		1.60	0.10	1.74	0.23	1.25	0.26
<i>P. lucublandus</i>		18.82	<0.01 ^a	9.07	0.02 ^a	2.69	<0.01 ^a
<i>C. cancellatum</i>		4.05	<0.01 ^a	4.38	0.08	0.83	0.64
<i>M. linearis</i>		3.79	<0.01 ^a	0.32	0.59	1.21	0.28
All species		22.77	<0.01 ^a	25.56	0.01 ^a	2.33	<0.01 ^a

All tests were performed on ln(x + 1) transformed data.

^a Mean differences are significant at the P ≤ 0.05 level. See Figs. 3 and 4 for tillage effects.

pitfall data yielded reasonable estimates of carabid abundance in CT relative to NT crops.

Trap catches of *P. scitulus*, *M. linearis*, and to a lesser extent, *C. cancellatum* were higher in CT (Figs. 3 and 4), and the opposite pattern occurred in some spring crops for *P. lucublandus* and on occasion *Pt. melanarius*. The different responses of the two *Poecilus* spp. to tillage are striking. In North Dakota, Weiss et al. (1990) also found that catch of *P. lucublandus* was higher in NT, whereas catch of *P. scitulus* was higher in CT (spring wheat). In contrast, Denke and Blodgett (2002) found no effect of tillage on *P. scitulus* across various crops in Montana. Our findings are in accordance with Tyler and Ellis (1979), Clark et al. (1993), and Cárcamo (1995), who found that catches of *P. lucublandus* were higher in NT (corn, corn, and barley, respectively), although Cárcamo et al. (1995) and Ferguson and McPherson (1985) detected no tillage effect (in barley and soybeans, respectively) on *P. lucublandus*. Trap-catch patterns of *Pt. melanarius* during the study are generally consistent with those of Cárcamo et al. (1995), who found significantly higher catch of *Pt. melanarius* in NT than in CT barley, contrasting with Clark et al. (1993), who found this species exhibited little response to tillage treatments. Denke and Blodgett (2002) found trap catches of *M. linearis* to be generally higher in CT (2 of 3 yr) than in NT crops in Montana, which is consistent with patterns we observed.

Whether the patterns we observed were caused by direct mechanical effects of tillage on the insects or by tillage-related changes in the soil habitat cannot be determined from our data. Nonetheless, there are patterns suggesting that spring breeders including *Poecilus* spp. are not directly affected by tillage. Two to 3 wk after spring tillage operations, carabid populations were relatively low, as shown for *Poecilus* spp in Fig. 3, after which they peaked in mid-June. Trap catches

during this time period did not differ between tillage systems, as would have occurred had the tillage caused greater mortality in CT plots. Moreover, early season sampling of pea plots during April 2002 revealed that *P. lucublandus* is relatively active compared with *P. scitulus* before tillage, yet catch of this species increased immediately after tillage, indicating that *P. lucublandus* populations were not reduced by tillage. Holland and Reynolds (2003) also found no effect of spring tillage on spring breeders, although spring tillage in their study occurred considerably earlier in the season than in our trials.

Pesticide treatments were the same in CT and NT plots; thus, it is unlikely that they influenced response patterns to tillage. Nonetheless, esfenvalerate applications for the control of the pea leaf weevil seemed to have suppressed carabid populations in pea, as reflected by the temporal dynamics of the *Poecilus* spp. shown in Fig. 3. Populations were reduced for a period of 1–2 wk after pesticide applications were made on 17 May 2001 and 17 May 2002, after which populations climbed above pretreatment levels, perhaps because of immigration from cereal plots or from adjacent fields.

Carabids exhibit strong preferences for specific microclimate and habitat (Thiele 1977, Wallin 1986), influencing their spatial and temporal distribution patterns within and between fields. Hence, tillage regimens may have indirectly influenced carabid composition and populations during the study. Spring breeders tend to be thermophilic, day-active species preferring open habitats, whereas autumn breeders are generally meso- or hygrophilic, night-active species preferring more closed habitats (Thiele 1977). The bare soil from plowing and secondary tillage may create conditions preferable to thermophilic species in spring months (Holland and Reynolds 2003, Holland 2004). Three of four dom-

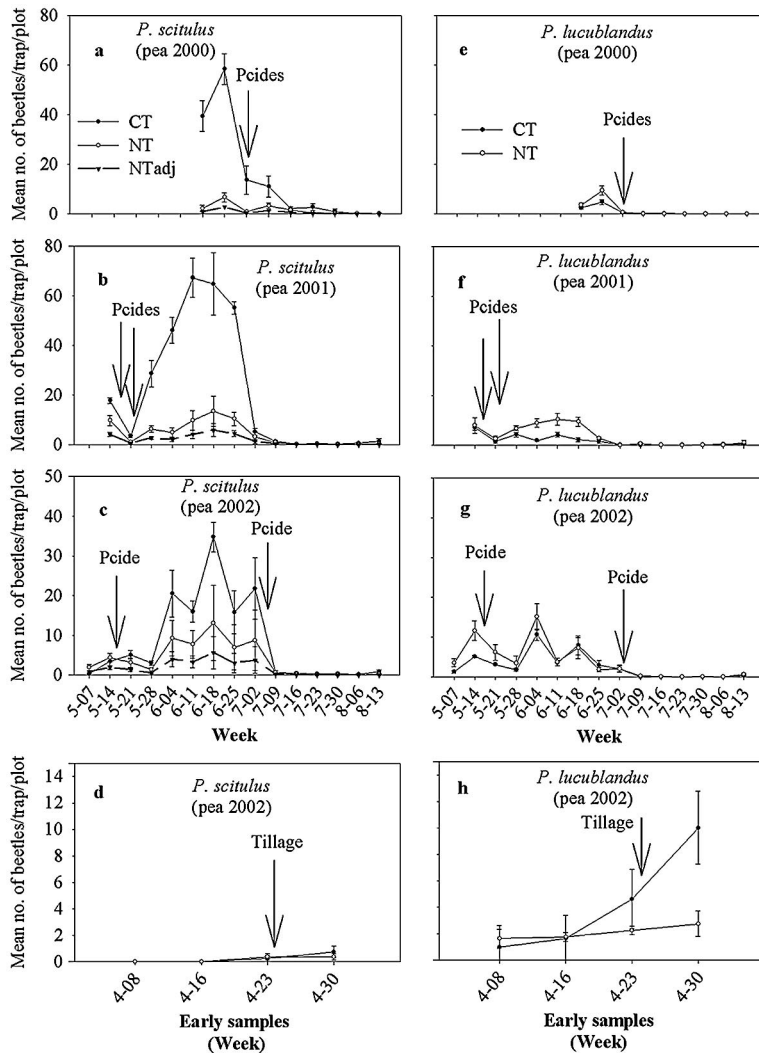


Fig. 3. Effect of tillage on weekly activity density (trap catch) of *P. scitulus* (a–c) and *P. lucublandus* (e–g) in spring pea at the Kambitsch Research Farm, 2000–2002. Tillage effects on these species pre- and posttillage during 2002 are presented in Fig. 4d (*P. scitulus*) and 4h (*P. lucublandus*). NTadj. are NT counts adjusted for trapping biases (note: bias adjustment factor for *P. lucublandus* = 1.0; hence, catch data were not adjusted). Arrows denote application of pesticides (pcides); first arrow for esfenvalerate on 17 May, 2001–2002, and second arrow for bifenthrin on 21 May 2001 and 3 July 2002. Entries are mean beetles \pm SEM.

inant spring breeders captured in our studies exhibited greater activity densities in CT than in NT spring crops, perhaps because of habitat affinity for CT. We also found an enhancement effect of CT on spring breeders in winter wheat, albeit observations in this crop were made over a single season. Other authors have detected a preference by spring breeders for CT (Clark et al. 1993, Tonhasca 1993) or the occurrence of such species within fields in sunny locations or on bare soils (Baker and Dunning 1975, Wallin 1985, Honek 1988). These patterns may be artifacts, however, because trap catch can be correlated with ambient or soil surface temperatures

(Honek 1988, Hatten 2006) or humidity (Hatten 2006), independent of any differences in abundance (Hatten et al. 2007). Despite attempts to account for trapping biases in this study, sampling biases likely still occurred, especially with species for which trap counts were not adjusted. Microclimatic preferences might explain higher trap catch of *Pt. melanarius* in NT cereals, but not higher catch of *P. lucublandus* in NT crops. Circumstantial evidence for the affinity of autumn breeders to the microclimate and surface conditions created by NT systems is provided by Cárcamo and Spence (1994) and Armstrong and McKinlay (1997), who found that

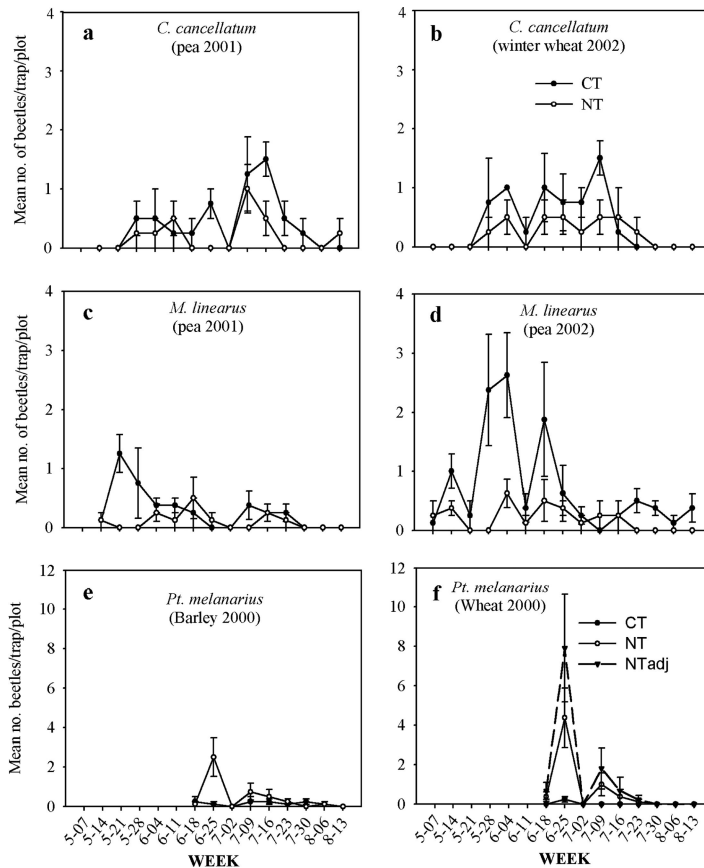


Fig. 4. Effect of tillage on weekly activity density (trap catch) of *C. cancellatum* (a and b), *M. linearis* (c and d), and *Pt. melanarius* (e and f) in select crops and years at the Kambitsch Research Farm, 2000–2002. NTadj. are NT counts adjusted for trapping biases. Entries are mean beetles \pm SEM. Mean differences of *Pt. melanarius* were increased in wheat after adjusting for trapping biases.

shady conditions created by polycultures may attract and accumulate autumn breeders, specifically *Pt. melanarius*.

We found a linear relationship in spring pea between beetle size and tillage regimen, with the relative proportion of beetles captured in NT versus CT systems increasing with beetle size. A similar trend was observed across all spring crops, whereas in winter wheat, we found no such relationship. Luff and Sanderson (1992) argued that large carabids are more capable of escaping from the unfavorable conditions created by plowing, owing to greater surface mobility relative to smaller species. It has also been suggested that larger beetles are buried, injured, or killed more readily by tillage machinery than smaller ones (Kladivko 2001). Our results are similar to those obtained by Kendall et al. (1995), although Baguette and Hance (1997) found that conservation tillage favored small over large species, whereas Holland and Reynolds (2003) found no effect. Our results are consistent with the broader literature indicating that intensive agriculture and habitat degradation disproportionately affect large over small carabids (Lebrun et al. 1987, Price 1997).

No-till management creates more structurally complex habitats and may provide alternative food resources for carabids (Langellotto and Denno 2004). Crop residue (i.e., litter) on the Palouse measured as percent ground cover can be 10–15 times greater during the growing season under NT than under CT crops (Guy and Cox 2002, Guy and Lauver 2006). Crop residue provides habitat for the epigeal fauna and may facilitate prey capture, refuge from intraguild predation, and shelter from extreme abiotic conditions (Langellotto and Denno 2004). Regional studies show that conservation tillage relative to CT systems on the Palouse and inland Pacific Northwest conserve the physical and chemical properties of soil, soil organic matter, soil microbial biomass (Bezdicsek et al. 2003), and saprophytic and detritus feeding species (Peterson 1982, Borden 1991, Wuest 2001). The detritus food web provides year-round food resources for carabids (Stinner and House 1990), suggesting that food web enrichment under NT management may attract and retain these beetles.

In conclusion, our findings indicate that the structure and composition of the carabid community is strongly influenced by tillage regimen on the Pal-

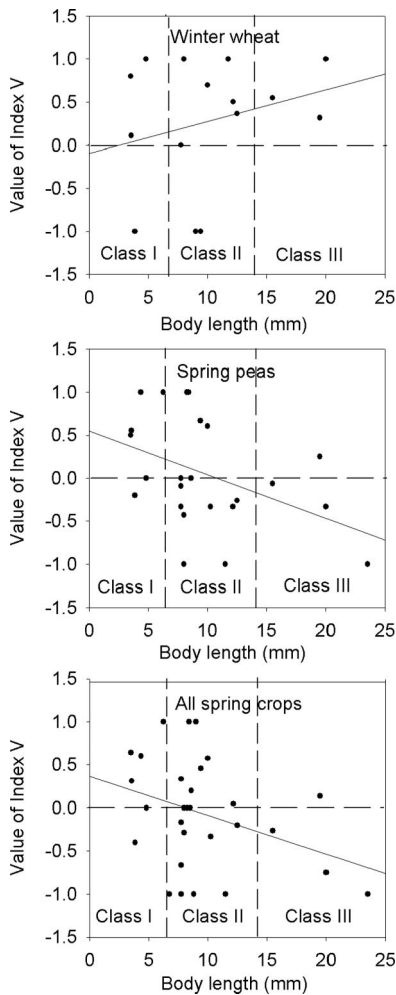


Fig. 5. Values of index V ($V = [2M_{CT}/M_{CT} + M_{NT}] - 1$), where M_{CT} and M_{NT} = total trap catch in CT or NT, respectively) regressed against mean body length of carabids captured in winter wheat, spring pea, and all spring crops under CT and NT management at the Kambitsch Research Farm, 2000–2002. Index V ranges from 1 (species captured only in CT) to -1 (species captured only in NT), and 0 indicates equal trap catch in CT versus NT. Size class reflects average body length of the beetle based on Lindroth (1961–1969), with class I containing small beetles (<7 mm), class II containing intermediate beetles (7–14 mm), and class III containing large beetles (>14 mm). The relationship between index V and body length of beetles was nonsignificant in winter wheat ($n = 16$, $P = 0.34$, adjusted $R^2 = 0.07$), significant in spring pea ($n = 24$, $P = 0.04$, adjusted $R^2 = -0.18$), and nonsignificant across all spring crops ($n = 29$, $P = 0.06$, adjusted $R^2 = -0.12$).

ouse. Carabid diversity and richness were generally greater in NT crops, whereas abundance of these beetles was greater in CT crops. Tillage-related differences in the carabid community may have important implications for ecological services provided by the beetles including pest control. Pest suppression may be strengthened (Aquilino et al.

2005) or weakened (Prasad and Snyder 2004, 2006) by predator biodiversity, depending in part on the identity of predator species in the community (Straub and Snyder 2006). Additional research is needed to determine whether the carabid community responds the same to tillage on commercial farms as observed at Kambitsch and to identify underlying mechanisms for the observed patterns.

Acknowledgments

We thank J. B. Johnson for encouragement and laboratory support, R. Sprague for laboratory and technical assistance, W. Price for help with statistical analysis, W. E. Snyder, J. McCaffrey, T. Prather, and J. Johnson-Maynard for helpful reviews and suggestions on this manuscript, and the USDA STEEP Program, the National Science Foundation IGERT Program, and the Idaho Wheat Commission for generous financial support. This is a publication of the Idaho Agricultural Experiment Station.

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Received for publication 24 July 2006; accepted 9 January 2007.