The Effects of a Winter Cover Crop on *Diabrotica virgifera* (Coleoptera: Chrysomelidae) Populations and Beneficial Arthropod Communities in No-Till Maize

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ABSTRACT The effects of an autumn-planted, spring-killed, grass cover crop (*Elymus trachycaulus* [Link] Gould ex Shinners) on populations of *Diabrotica virgifera virgifera* LeConte and its predator community were evaluated in South Dakota maize fields over two seasons. Abundance and size of *D. virgifera* larvae and adults and sex ratio of adults were measured in maize produced under two treatments (i.e., a winter cover crop or bare soil), as were maize root damage and the abundance and diversity of the predator communities collected on the soil surface and in the soil column. First and second instars and adults of *D. virgifera* were similarly abundant in the two treatments, but third instars were significantly fewer in maize planted after a winter cover crop. Larvae developed at different rates in the two treatments, and second instars were significantly smaller (head capsule width and body length) in the maize planted after a cover crop. First and third instars and adults were of similar size in the two treatments, and adult sex ratios were also similar. Although initially similar, predator populations increased steadily in the cover-cropped maize, which led to a significantly greater predator population by the time *D. virgifera* pupated. There was significantly less root damage in the cover-cropped maize. Predator communities were similarly diverse in both treatments. Predator abundance per plot was significantly and negatively correlated with the abundance of third instars per plot. Clearly, winter cover crops reduce *D. virgifera* performance and their damage to the crop, and we suspect that this reduction is caused by both environmental effects of the treatment on *D. virgifera* size and development, and of increased predation on the third instars of the pest. Additional data on the impact of cover crops on actual predation levels, grain yield and quality, and farmer profitability, and correlations among pest performance, crop characteristics, and predator populations and behaviors are key components of this system that remain to be addressed.

KEY WORDS biodiversity, biological control, conservation, western corn rootworm, *Elymus trachycaulus*, generalist predators, IPM

Vegetation diversity within farmland can lead to lower insect pest populations when the habitat is altered in ways that affect herbivore performance (e.g., host plant quality or abundance, ability to locate the host plant, altered microclimates, etc.) (Root 1973), or when natural enemies of the pest are favored by increased biodiversity (e.g., increased availability of alternative resources, greater niche differentiation in complex habitats, favorable microclimates, etc.) (Altieri and Letourneau 1982, Andow 1991, Landis et al. 2000). A major challenge for farmers is integrating biodiversity into cropland without sacrificing agricultural productivity. Two general approaches for integrating vegetation diversity into cropland involve distributing the vegetation in strips or uniformly throughout a field, with costs and benefits to both strategies (Lundgren 2009). Autumn-planted cover crops fall within the latter category, and are being adopted for the many agronomic benefits they provide (Wyland et al. 1996, Clark 1998, Snapp et al. 2005). The benefits of cover crops for insect pest management are recognized for numerous systems (Bugg et al. 1991; Bugg and Waddington 1994; Hooks and Johnson 2003, 2004; Tillman et al. 2004; Prasifka et al. 2006; Jackson and Harrison 2008; Broad et al. 2009), including pests of maize (*Zea mays* L.) (House and Del Rosario Alzugaray 1989, Brust and House 1990, Laub and Luna 1992, Buntin et al. 1994). This notwithstanding, the effects of winter cover crops on a key pest of maize in North America and Europe, *Diabrotica virgifera virgifera* LeConte (western corn rootworm, Coleoptera: Chrysomelidae), have never been documented.

D. virgifera is a severe and longstanding pest of maize in North America (Gray et al. 2009, Spencer et al. 2009). Its subterranean larvae consume maize roots, which disrupts the plant's physiological processes (Riedell 1990, 1993; Riedell and Reese 1999) and increases their susceptibility to damage from mechani-

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cal forces (e.g., wind and harvesting equipment) (Riedell and Evenson 1993). Current management of *D. virgifera* involves granular soil insecticides, insecticidal seed treatments, adult insecticide applications, Bt maize hybrids, crop rotation, and adult sprays to prevent egg laying the next year. Management costs to farmers are extensive. A further problem is that *D. virgifera* readily evolves resistance to many chemical insecticides (Miller et al. 2009), and a rotation tolerant variant of *D. virgifera* is currently spreading throughout much of the maize-producing region of North America (Gray et al. 2009, Miller et al. 2009). Developing cost-competitive, nonchemical tools for managing *D. virgifera* would reduce pressure on current options and be in line with an integrated pest management (IPM) philosophy.

Despite the fact that *D. virgifera* has been a pest for >100 yr, very little is published on the natural enemies of its preimaginal stages (Toepfer et al. 2009). Thirty-five years ago, Vernon Kirk conducted extensive surveys of potential *D. virgifera* predators in the northern Great Plains of North America, but did not evaluate their impact on the pest (Kirk 1971; 1973a, b; 1975; 1977). Laboratory and field manipulations suggest that predators can impact the immature stages of *Diabrotica* spp. (Toepfer et al. 2009), but the importance of predation on the population dynamics of *D. virgifera* has largely escaped attention. Recently, at least 18 predator taxa that are sympatric with eggs and larvae of *D. virgifera* in South Dakota maize fields were found to consume these life stages of the pest under natural conditions (Lundgren et al. 2009b, c). However, *D. virgifera* inflicts crop damage despite incurring these ambient levels of predation, and reducing pest populations below economic levels will only be attainable if predation levels can be increased within cropland.

In the current research, we evaluated the effects of planting a winter grass cover crop on populations of *D. virgifera* and its predator community in South Dakota maize. In addition to measuring the numerical responses of these insect communities to the cover crop, we examined the seasonal population dynamics of the pest and predators, maize root damage, and beetle size and sex ratio. Our approach allowed us to separate direct mechanisms of habitat alterations on the pest from the indirect, predator-mediated effects of cover crops.

Methods

Experimental Conditions. All research was conducted in Brookings Co., SD, (latitude, longitude: 44.348, −96.811) in a spatially divided 12.5-ha field under continuous maize-soybean (*Glycine max* L.) rotation. The field was untilled following the soybean phase of the rotation that preceded the experimental research. Maize (glyphosate-tolerant DeKalb 44–92; Monsanto Company, St. Louis, MO) was planted at 77,000 plants ha^{-1} on 29 May 2007 and 30 May 2008; seeds were planted ≈4 cm deep, with 76 cm between rows. The maize was fertilized at 169 kg N ha^{-1} before planting, and glyphosate was applied at 3.3 liters ha^{-1} (Roundup Weathermax, Monsanto Company) to all research plots near the time of planting. In spring of the experimental years, the 6- to 12-m wide alleyways between plots were planted with a small grain mixture, which was mowed regularly throughout the season.

Experimental plots (n = 6 and eight in 2007 and 2008, respectively; 18 × 24 m each) were established in the soybean half of the field before the experiment. Plots were randomly and evenly assigned to one of two treatments that either received a winter cover crop or remained bare soil. In the cover crop treatment, slender wheatgrass, *Elymus trachycaulus* (Link) Gould ex Shinners (Poaceae) (cultivar. Revenue, Milborn Seeds, Brookings, SD), seed was broadcast at 34 kg ha^{-1} on 7 September 2006 and 10 September 2007 (Osborne et al. 2010).

Assessing Pests, Predators, and Root Damage. Before maize planting, all experimental plots were artificially infested with known densities of *D. virgifera* eggs according to protocols described in Sutter and Branson (1986). Briefly, eggs of *D. virgifera* were obtained from a continuous colony started with beetles collected in Trent, SD, and maintained at the North Central Agricultural Research Laboratory (USDA-ARS) in Brookings, SD. Eggs were suspended in 0.15% agar solution, and were infested using a tractor-mounted egg infester into rows at calculated rates of 3,000 (2007) and 3,300 (2008) viable eggs m^{-1}. *D. virgifera* is a univoltine pest that currently does not lay eggs into soybean crops of our region; thus our methodology ensures that the *D. virgifera* populations came exclusively from our infestation. Eggs were infested on 3 May 2007 and 8 May 2008, roughly 3.5 wk before planting maize, which was planted directly into the egg-infested furrows.

D. virgifera larval populations were monitored using core samples and adult populations were monitored using emergence cages. Weekly core samples were collected beginning on 11 June 2007 (four total sample dates) and 20 May 2008 (10 total sample dates). Golf-cup cutters were used to collect soil cores (10 cm diameter and 10 cm deep) at the bases of randomly selected plants (n = 10 plants plot^{-1} date^{-1}). Cores per plot were homogenized into a single sample, and were placed in a Berlese funnel; insects were collected in 70% ethanol as the sample dried over a 7 d period. The number of larvae collected per plot and the maximum head capsule width of each individual (for staging purposes) were recorded. As a general rule, larvae with head capsules measuring <0.25 mm were considered first instars, those with 0.25–0.40 mm were second instars, and those with capsules >0.40 mm were third instars (Hammack et al. 2003). In 2008, the body length of each larva was recorded as an additional size metric. Adult emergence cages (0.61 × 0.76 m, 8 cm tall, n = 5 plot^{-1}) were placed equidistant along a linear transect through the length of each plot on 10 July 2007 and 21 July 2008, soon after core samples revealed diminishing populations of third instars (these cages were functionally similar to those described by Tollefson 1986). Emerging adults were collected weekly, sexed using external morphology

(Hammack and French 2007), dried at room temperature to constant weight, and weighed to the nearest 0.0001 g on a microbalance (only in 2008).

Arthropod predator populations were monitored over the season using surface collection of predators within quadrats, and soil core samples (in 2008 only). In both years, insects were hand-collected from quadrat samples ($n = 3$ plot^{-1}) at ≈09:00 on six dates between 18 May and 5 July. In 2008, quadrat samples were collected on seven dates between 21 May and 18 July (see Fig. 4 for 2007 and 2008 sample dates). For each sample, a 0.5 m^2, sheet-metal quadrat (15 cm tall) was pressed into the soil at a randomly selected site (e.g., Lundgren et al. 2006). All predators within the quadrat were hand-collected using mouth aspirators, and were frozen at −20°C in 70% ethanol until processing. In 2008, predators collected from the Berlese funnels containing the *D. virgifera* larval soil cores, as described above, were preserved at −20°C in 70% ethanol until processing.

Predators were identified to the lowest taxonomic unit possible, and morphospecies were assigned to many of the taxa for community analysis. Carabids were identified to the species level according to keys listed in Ball and Bousquet (2001). Coccinellids were identified to species using keys of Gordon (1985). Spiders were identified to family level, with a few identified to species level by Dr. SE. Romero (University of Kentucky, Lexington, KY). Ants were identified to genus level according to keys listed in Fisher and Cover (2007). The numerous Staphylinidae species were grouped into small (<3 mm), medium (3–10 mm), and large taxa (>10 mm). The remaining predators were identified from previous experience of the author, or were left as morphospecies. Although mites were abundant in the core samples, they were not included in the analyses. The mean number of each taxon per plot was calculated, as were the total number of predators per plot.

In each year, 15 maize plants were randomly selected from each plot, and were destructively subjected to a root damage assessment. Each plant was dug from the ground, the soil was washed from the root ball, and the roots were characterized using the 1–6 Iowa rating scale (Hills and Peters 1971). A mean root rating value was generated per plot.

Data Analysis. For all analyses involving predator communities, separate analyses were conducted for hand-collected quadrat samples and soil core Berlese samples (2008 only) per plot. Changes in predator abundance over the season were compared between treatments using repeated measures (rm)-analysis of variance (ANOVA). Predator diversity indices, total species captured, Shannon Index (H), and species evenness (J) (calculated according to Smith 1992), were calculated for each plot and compared between treatments using nonparametric Kruskal-Wallis ANOVA because diversity indices do not conform to parametric ANOVA assumptions. A complete discriminant analysis (and associated MANOVA) was used to distinguish differences in the predator communities found in the two treatments.

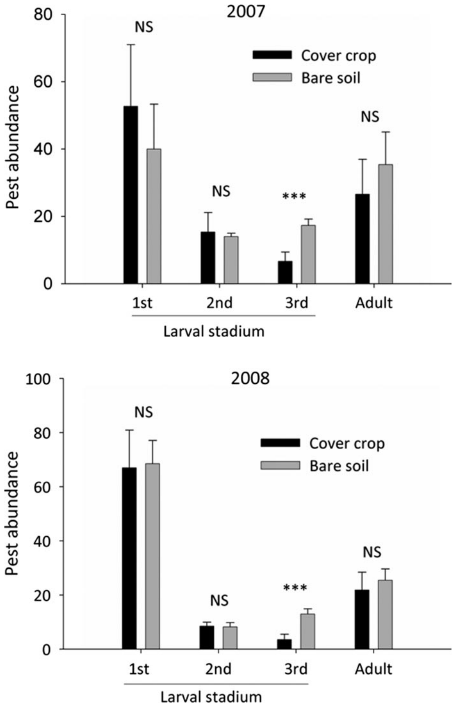

Fig. 1. The effects of maize following winter cover crops on mean (SEM) larval and adult populations of *D. virgifera.* Data represent seasonal total larval populations per ten core samples per plot (four sample dates in 2007, 10 sample dates in 2008). Seasonal total adult populations per emergence cage per plot ($n = 3$ and four replicates in 2007 and 2008, respectively). The results of significance tests (ANOVA) for each life stage are presented above bar couplets; NS indicates nonsignificant differences ($\alpha = 0.05$), and *** indicates highly significant treatment differences ($P = 0.001$).

Changes in mean pest abundance (total larvae, first instars, second instars, third instars, adults) per plot were compared between treatments for each year using independent rm-ANOVAs. Mean head capsule width and larval sizes (body length, 2008 only) for each stadium and adult dry weights and sex ratios (proportion male) were compared between treatments using independent ANOVAs. Mean root damage ratings per plot were compared between treatments using ANOVA (separate analyses for each sample year). Relationships between total predators captured per plot and the total abundance of each larval stadium and adults per plot were derived using a general linear model. An exponential decay model was fitted to any significant relationships uncovered in the general linear model. All statistical analyses were conducted using Systat 11 Software (Richmond, CA).

Results

Pest Populations and Root Damage. The availability of vegetation residue affected the development of *D. virgifera* larvae and their relative abundances (Figs. 1 and

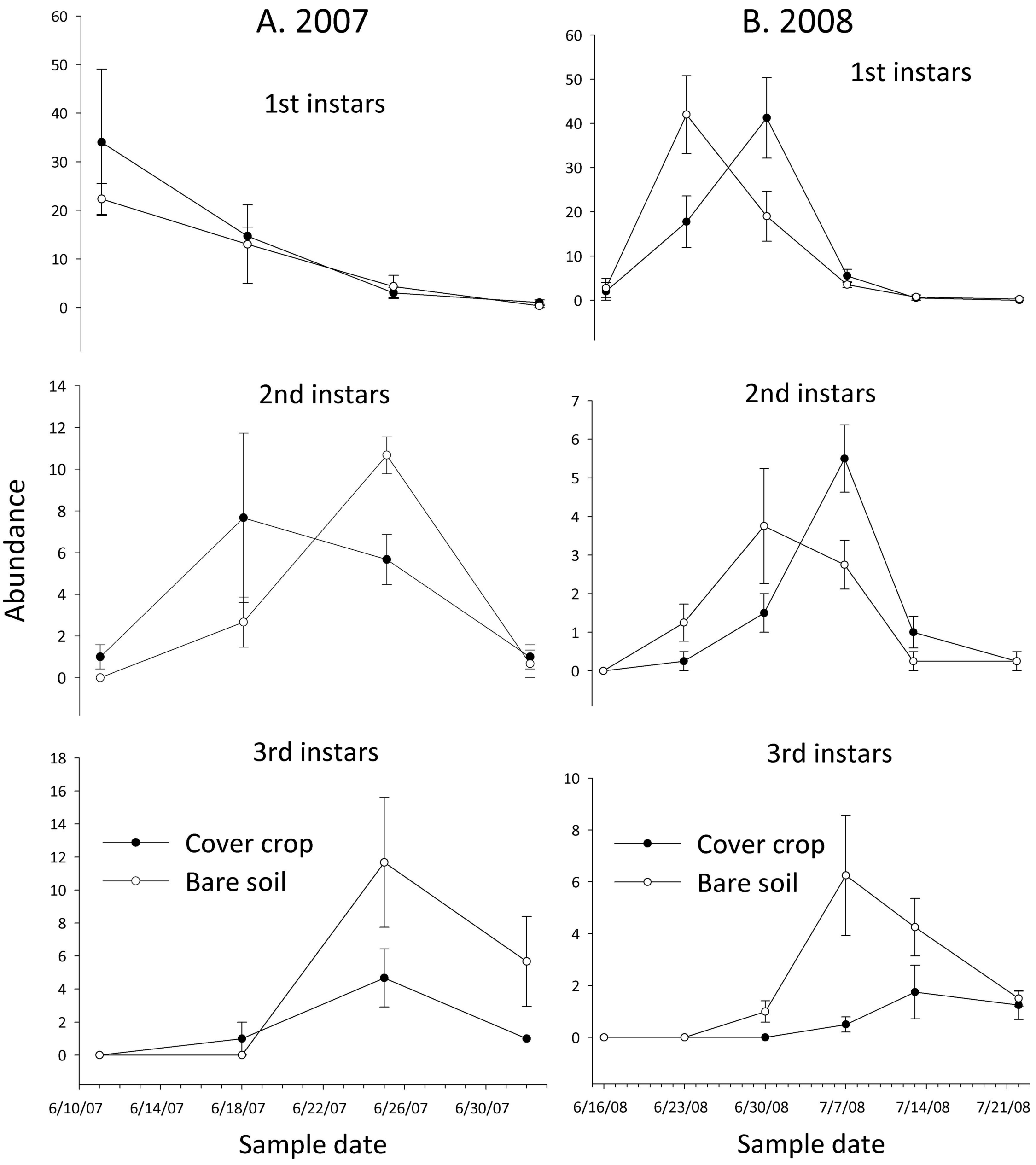

Fig. 2. Seasonal population dynamics of *D. virgifera* larvae collected per plot (mean ± SEM) from maize following a winter cover crop or bare soil. $N = 3$ and four replicates in 2007 and 2008, respectively.

2). In 2007, first instar abundances and seasonal population dynamics were similar in the two treatments throughout the sampling period (trmt: $F_{1, 4} = 0.31$, $P = 0.61$; date: $F_{3, 12} = 10.03$, $P = 0.001$; interaction: $F_{3, 12} = 0.55$, $P = 0.66$). Although there were similar numbers of second instars in the two treatments during 2007, second instars were most prominent earlier in the cover cropped treatment than in the bare soil (trmt: $F_{1, 4} = 0.05$, $P = 0.83$; date: $F_{3, 12} = 12.95$, $P < 0.001$; interaction: $F_{3, 12} = 4.04$, $P = 0.03$) (Figs. 1 and 2). There were significantly more third instars in the bare soil treatment than in the cover cropped treatment in 2007 (trmt: $F_{1, 4} = 10.45$, $P = 0.03$; date: $F_{2, 8} = 5.14$, $P = 0.04$; interaction: $F_{2, 8} = 1.45$, $P = 0.29$) (Fig. 1 and 2). In 2008, treatment did not affect the abundance of first and second instars, but insects developed more quickly in the bare soil treatment than in the cover cropped treatment (first instars: trmt: $F_{1, 6} = 0.01$, $P = 0.94$; date: $F_{5, 30} = 21.99$, $P < 0.001$; interaction: $F_{5, 30} = 5.62$, $P < 0.001$; second instar: trmt: $F_{1, 6} = 0.01$, $P = 0.91$; date: $F_{4, 24} = 12.91$, $P < 0.001$; interaction: $F_{4, 24} = 4.20$, $P = 0.01$) (Figs. 1 and 2). There were significantly more third instars captured in the bare soil treatment in 2008, and the larvae were marginally more prevalent earlier in the bare soil treatment than the cover cropped treatment (trmt: $F_{1, 6} = 11.64$, $P = 0.01$; date: $F_{3, 18} = 3.32$, $P = 0.04$; interaction: $F_{3, 18} = 2.68$, $P = 0.07$) (Figs. 1 and 2). To summarize, the cover-crop induced changes to the maize system significantly reduced the abundance of third instars in both years, and affected the development rate of larval populations (but in different ways in 2007 and 2008).

Adult emergence was statistically similar in the two treatments (2007: trmt: $F_{1, 4} = 0.39$, $P = 0.57$; date: $F_{7, 28} = 12.69$, $P < 0.001$; interaction: $F_{7, 28} = 0.67$, $P = 0.70$. 2008: trmt: $F_{1, 6} = 0.22$, $P = 0.66$; date: $F_{6, 36} = 18.41$, $P < 0.001$; interaction: $F_{6, 36} = 0.64$, $P = 0.70$.) (Fig. 1).

Second instars were significantly larger in the bare soil plots than in the cover cropped treatments. First and third instars had similar head capsule widths in the two treatments (first instars: $F_{1, 12} = 0.23$, $P = 0.64$; third instars: $F_{1, 10} = 1.04$, $P = 0.33$; note that the reduction in degrees of freedom were because third instars were not captured in two of the plots). Mean SEM head widths were 0.21 ± 0.001 and 0.49 ± 0.004 mm for first and third instars, respectively (pooled across treatments and years). Second instars from the bare soil treatment had significantly wider head capsules per plot than those collected from the cover cropped treatment (second instars: $F_{1, 12} = 4.83$, $P = 0.048$). Mean ± SEM head capsule widths were 0.31 ± 0.003 and 0.32 ± 0.003 mm in second instars collected from the cover cropped and bare soil treatments, respectively. In 2008, first and third instars had similar body lengths per plot (first instars: $F_{1, 6} = 0.68$, $P = 0.44$; third instars: $F_{1, 4} = 2.45$, $P = 0.19$). Mean ± SEM body lengths were 1.62 ± 0.02 and 7.10 ± 0.45 mm in first and third instars, respectively (pooled across treatments and years). Second instars from the bare soil plots were marginally longer than those collected in the cover cropped plots ($F_{1, 6} = 4.59$, $P = 0.07$); mean SEM body lengths were 3.13 ± 0.19 and 3.70 ± 0.19 mm for second instars collected from the cover cropped and bare soil treatments, respectively. Adults from the two treatments had similar dry weights ($F_{1, 6} = 0.16$, $P = 0.70$), and there was a similar proportion of males that emerged per plot in each treatment ($F_{1, 12} < 0.001$, $P = 0.99$). Mean ± SEM adult dry weight was 10.63 ± 0.09 mg, and proportion males (pooled across treatments and years) was 0.21 ± 0.02. There was significantly lower root ratings in the cover cropped maize than in the maize from the bare soil in both study years (2007: $F_{1, 4} = 7.84$, $P = 0.049$; 2008: $F_{1, 6} = 28.19$, $P = 0.002$) (Fig. 3).

Predator Populations. There were significant effects of treatment and date on the number of predators collected from the soil-surface in quadrats during 2007 (trmt: $F_{1, 4} = 23.44$, $P = 0.008$, date: $F_{5, 20} = 3.07$, $P = 0.03$, interaction: $F_{5, 20} = 2.46$, $P = 0.07$) (Fig. 4). The same patterns were seen in 2008, except that there was an additional significant interaction between treatment and sample date (trmt: $F_{1, 6} = 42.49$, $P = 0.001$, date: $F_{6, 36} = 12.41$, $P < 0.001$, interaction: $F_{6, 36} = 12.02$, $P < 0.001$). Predator abundance per plot was initially similar in the two treatments in 2008, but then diverged as the season progressed (Fig. 4). There was a marginally significant effect of treatment on number of predators collected in the core samples per plot, and the number of predators varied significantly among the sample dates (trmt: $F_{1, 6} = 3.86$, $P = 0.098$, date: $F_{9, 54} = 6.66$, $P < 0.001$, interaction: $F_{9, 54} = 1.07$, $P = 0.40$) (Fig. 4).

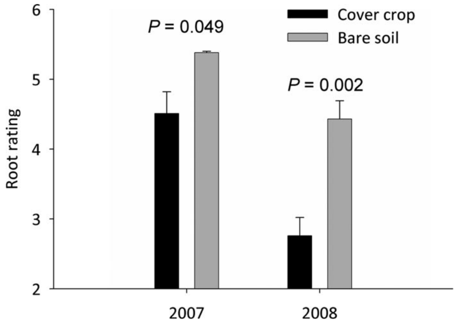

Fig. 3. Root damage ratings (mean ± SEM per plot; 1–6 Iowa rating scale) for maize plants following a winter cover crop or bare soil. Lower root ratings indicate less root damage (Hills and Peters 1971). $N = 3$ and four replicates in 2007 and 2008, respectively. Additional statistics can be found in the text.

There were 63 predator taxa identified from the soil core samples, and 86 predator taxa collected on the soil surface in quadrat samples (Table 1). By far, the most speciose groups found in our samples were spiders (33 species) and carabid beetles (20 species), although Staphylinidae were not identified to species level, and mites were not included at all. In the soil surface samples (both years pooled), 924 total predators were collected from maize planted after the winter cover, and 991 were captured in the bare soil treatment. In the soil core samples (2008 only), 1,093 total predators were collected in the cover cropped plots, and 874 predators were collected in the bare soil treatments. Diversity indices (total species captured, Shannon Index, and Evenness) were statistically similar in the two treatments (Table 1).

The predator communities were structurally similar in the two treatments. From Table 1, it is clear that some species were significantly more abundant in certain treatments; however, discriminant analysis did not uncover clear relationships between treatments and community structure. Complete discriminant analysis of the predator communities captured on the soil surface in the quadrat samples revealed similar communities found in the two treatments (Wilk's $\lambda = 0.14$; $F_{12, 1} = 0.49$, $P = 0.82$). The eigenvalue used to describe this community was 5.92, and described 100% of the dispersion in the data. In the resulting model, 12 taxa were used to describe the dispersion of the data. Similarly, complete discriminant analysis did not reveal different communities in the two treatments collected in the core samples of 2008 (Wilk's $\lambda = 0.32$; $F_{6, 1} = 0.35$, $P = 0.86$). The eigenvalue used to describe this community was 2.09, and described 100% of the dispersion in the data. Only six taxa were used in the model to describe the overall patterns in the community.

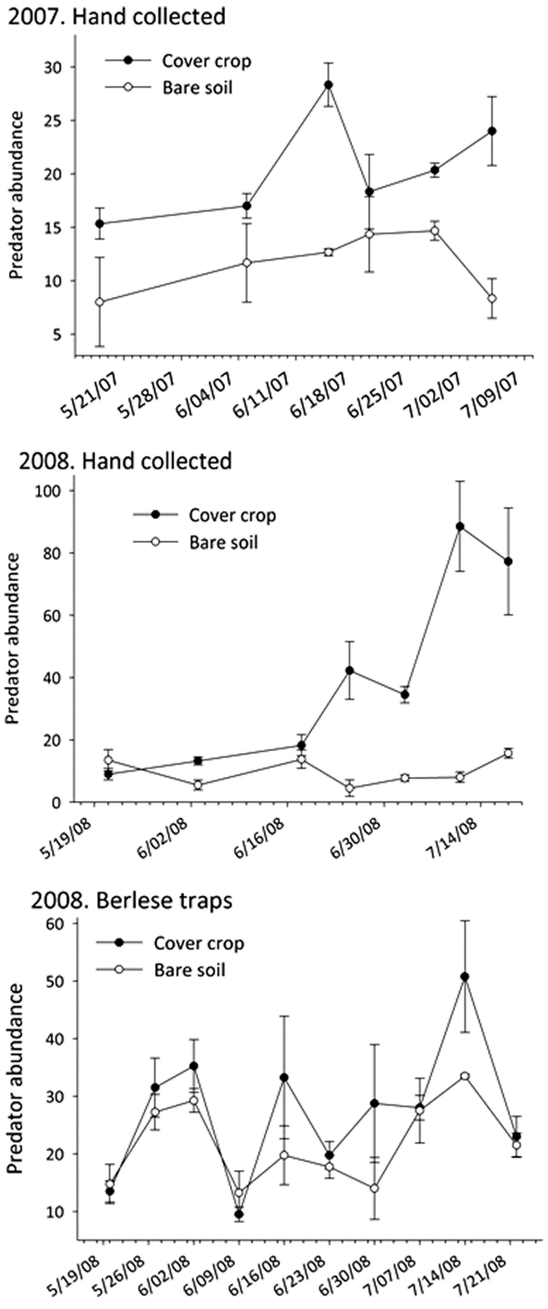

Fig. 4. Seasonal occurrence of mean (SEM) predator abundance hand-collected from the soil surface in quadrat samples or from soil cores collected in maize fields following a winter cover crop or bare soil (n = 3 and four replicates in 2007 and 2008, respectively).

Correlations Between Predators and Pest Populations. Over the 2 yr, total predators captured at the soil surface in quadrat samples per plot and pest third instars captured in a plot were negatively correlated ($F_{1,\,12}$ = 13.25, P = 0.003). An exponential decay model describes this relationship particularly well (Fig. 5). In contrast, predator numbers per plot were not linearly correlated with total pest first or second instars (first: $F_{1,\,12}$ = 1.06, P = 0.32; second: $F_{1,\,12}$ = 0.05, P = 0.83) or adults ($F_{1,\,12}$ = 1.25, P = 0.29). In 2008, total predators recovered from soil core samples per plot were not linearly correlated with any of *D. virgifera*'s life stages found in the respective plots (first: $F_{1,\,6}$ = 0.21, P = 0.67; second: $F_{1,\,6}$ = 0.15, P = 0.72; third: $F_{1,\,6}$ = 1.45, P = 0.27; adult: $F_{1,\,6}$ = 0.88, P = 0.38).

Discussion

Cover crops changed the maize habitat in ways that directly affected pest performance and reduced the pests' impact on the crop plant, and increased the abundance of natural enemies of the pest. The seasonal population dynamics and size of *D. virgifera* larvae were affected by the cover crop treatment, primarily in the abundance of *D. virgifera* third instars. The effects of this treatment were manifested in the reduced root damage inflicted to maize plants in the cover-cropped fields. Although diversity and structure of the predator communities were similar in the two treatments, predator abundance increased substantially in the cover cropped treatment over the period when *D. virgifera* larvae were present. Moreover, predator abundances per plot were strongly and negatively correlated with *D. virgifera* performance, implying that predation and direct effects of the cover crop to the suitability of the maize habitat were both contributing to the population declines observed in this treatment. The effects of cover crops on the efficacy of predators as biological control agents, the ability of *D. virgifera* to reduce yields, and the profitability of maize production should be explored more fully.

Adding vegetation to a crop environment can reduce pest performance by changing the microclimate of the habitat and reducing the suitability of the host plant (Costello and Daane 2003, Bukovinszky et al. 2004, Schmidt et al. 2007). In the current study, larval phenologies were different in the two treatments (Fig. 2), and larvae (at least second instars) were generally larger in the bare soil treatment, suggesting direct effects of the cover crop–induced changes to the environment on the larvae. Crop plants are often affected physiologically by the presence of cover crops or their residue, and our research showed that maize plants in the cover crop were of different size and quality, compared with plants in the bare soil treatment (J.G.L., unpublished data). We did not quantify the effects of treatment on the roots themselves, but crop root abundance, size and nutritional quality are often affected by cover crops (Hulugalle 1988, Sainju et al. 2001) and these host characteristics are extremely important for the successful development of *D. virgifera* larvae (Moeser and Vidal 2004b, Olmer and Hibbard 2008, Agosti et al. 2009). The symptoms that we observed in the larvae of the cover-cropped treatment also have been reported for this species raised on hosts of sub-optimal quality (Branson and Ortman 1967a, b, 1970; Johnson et al. 1984; Clark and Hibbard 2004; Moeser and Vidal 2004a; Oyediran et

Table 1. The diversity of hand-collected predator taxa collected from the soil surface in quadrat samples (2007 and 2008) or from the soil column in soil core samples (2008) from maize grown after a winter cover crop or bare soil

Higher order classification	Morphotaxon	Soil surface samples			Soil column predators		
		Cover crop	Bare soil	Total	Cover crop	Bare soil	Total
Chilopoda	Centipede 1	11	8	19	3	5	8
Chilopoda	Centipede 2	10	8	18	20	28	48
Chilopoda	Centipede 3	0	1	1	9	18	27
Diplura	Dipluran 1	0	0	0	309	314	623
Opiliones: Phalangiidae	*Phalangium opilio*	32	22	54	1	0	1
Araneae	Spiderling	13	22	35	142	86	228
Araneae	Araneae sp.1	2	0	2	0	0	0
Araneae	Araneae sp.2	2	5	7	0	0	0
Araneae: Anyphaenidae	Anyphaenidae sp.1	3	0	3	0	0	0
Araneae: Anyphaenidae	Anyphaenidae sp.4	3	2	5	0	0	0
Araneae: Araneaeidae	Araneaeidae sp.1	1	3	4	0	0	0
Araneae: Araneaeidae	Araneidae sp.2	19	16	35	0	0	0
Araneae: Araneaeidae	Araneidae sp.4	1	0	1	0	0	0
Araneae: Clubionidae	Clubionidae sp.1	1	2	3	0	0	0
Araneae: Dictynidae	Dictynidae sp.1	4	7	11	26	7	33
Araneae: Gnaphosidae	Gnaphosidae sp.1	1	1	2	0	0	0
Araneae: Gnaphosidae	Gnaphosidae sp.2	5	6	11	0	0	0
Araneae: Gnaphosidae	*Callilepis* sp.	3	3	6	0	0	0
Araneae: Linyphiidae	*Agynota* sp.	55	71	126	7	5	12
Araneae: Linyphiidae	*Erigone dentigera*	29	32	61	11	7	18
Araneae: Linyphiidae	*Eridantes* sp.	15	11	26	0	0	0
Araneae: Linyphiidae	Linyphiidae sp. 1	59	72	131	0	2	2
Araneae: Linyphiidae	Linyphiidae sp.2	16	15	31	1	2	3
Araneae: Linyphiidae	Linyphiidae sp.3	2	0	2	0	0	0
Araneae: Liocranidae	*Agroeca* sp.	1	0	1	0	0	0
Araneae: Lycosidae	*Pardosa* sp.	5	6	11	0	0	0
Araneae: Lycosidae	*Pirata* sp.	1	0	1	0	0	0
Araneae: Lycosidae	*Schizocosa* sp. 1	3	5	8	0	0	0
Araneae: Lycosidae	*Schizocosa* sp. 2	0	0	0	1	0	1
Araneae: Oecobiidae	Oecobiidae sp.1	2	4	6	0	0	0
Araneae: Philodromidae	*Philodromus* sp.	13	12	25	0	0	0
Araneae: Pimoidae	Pimoidae sp.1	0	1	1	0	0	0
Araneae: Pisauridae	Pisauridae sp.1	4	2	6	0	0	0
Araneae: Salticidae	Salticidae sp.1	8	12	20	0	0	0
Araneae: Tetragnathidae	*Pachygnatha* sp.	0	1	1	0	0	0
Araneae: Tetragnathidae	*Glenognatha foxi*	2	0	2	0	0	0
Araneae: Tetragnathidae	*Tetragnatha* sp.1	25	33	58	1	0	1
Araneae: Thomisidae	*Coriachne utahensis*	2	1	3	1	0	1

Table 1. Continued

Higher order classification	Morphotaxon	Soil surface samples			Soil column predators		
		Cover crop	Bare soil	Total	Cover crop	Bare soil	Total
Araneae: Thomisidae	*Misomena* sp.	2	2	4	0	0	0
Araneae: Thomisidae	*Ozyptila* sp.	4	4	8	5	0	5
Orthoptera: Gryllidae	*Allonemobius* nymph	119	101	220	0	0	0
Orthoptera: Gryllidae	*Allonemobius*	1	1	2	8	1	9
Orthoptera: Gryllidae	*Gryllus* nymph	46	49	95	12	9	21
Hemiptera: Geocoridae	*Geocoris* nymph	19	20	39	1	0	1
Hemiptera: Geocoridae	*Geocoris* adult	7	6	13	0	0	0
Hemiptera: Miridae	Mirid nymph	0	2	2	1	0	1
Hemiptera: Nabidae	Nabid nymph	6	4	10	0	0	0
Hemiptera: Nabidae	Nabid adult	2	0	2	1	0	1
Coleoptera: Carabidae	Carabid larva	7	9	16	91	73	164
Coleoptera: Carabidae	*Abacidus permundus*	3	0	3	0	4	4
Coleoptera: Carabidae	*Agonum placidum*	0	0	0	4	3	7
Coleoptera: Carabidae	*Amara apricaria*	0	0	0	0	1	1
Coleoptera: Carabidae	*Amphasia sericea*	0	0	0	0	1	1
Coleoptera: Carabidae	*Anisodactylus discoideus*	0	0	0	1	0	1
Coleoptera: Carabidae	*Anisodactylus pennsylvanicus*	0	1	1	0	0	0
Coleoptera: Carabidae	*Anisodactylus rusticus*	1	0	1	0	0	0
Coleoptera: Carabidae	*Badister transversalis*	0	0	0	1	0	1
Coleoptera: Carabidae	*Bembidion affine*	4	14	18	1	1	2
Coleoptera: Carabidae	*Bembidion bifossulatum*	0	0	0	1	0	1
Coleoptera: Carabidae	*Bembidion quadrimaculatum*	3	3	6	2	1	3
Coleoptera: Carabidae	*Bembidion rapidum*	18	15	33	7	0	7
Coleoptera: Carabidae	*Clivina* impressefrons	0	1	1	18	14	32
Coleoptera: Carabidae	*Colliurus pennsylvanica*	1	3	4	3	1	4
Coleoptera: Carabidae	*Cyclotrachelus alternans*	3	0	3	0	0	0
Coleoptera: Carabidae	*Elaphropus* sp.	33	55	88	8	16	24
Coleoptera: Carabidae	*Harpalus pensylvanicus*	0	0	0	0	1	1
Coleoptera: Carabidae	*Microlestes linearis*	8	8	16	1	0	1
Coleoptera: Carabidae	*Poecilus chalcites*	2	3	5	1	0	1
Coleoptera: Carabidae	*Poecilus lucublandus*	1	2	3	1	0	1
Coleoptera: Carabidae	*Polyderis* sp.	0	2	2	75	36	111
Coleoptera: Carabidae	*Pterostichus femoralis*	1	1	2	1	0	1
Coleoptera: Carabidae	*Scarites* larva	1	0	1	0	0	0
Coleoptera: Carabidae	*Scarites quadriceps*	2	0	2	0	0	0

Table 1. Continued

Higher order classification	Morphotaxon	Soil surface samples			Soil column predators		
		Cover crop	Bare soil	Total	Cover crop	Bare soil	Total
Coleoptera: Carabidae	*Stenolophus comma*	0	0	0	1	0	1
Coleoptera: Carabidae	*Stenolophus ochropezus*	0	0	0	0	2	2
Coleoptera: Carabidae	*Stenolophus rotundatus*	0	1	1	1	0	2
Coleoptera: Coccinellidae	Coccinellid larva	7	4	11			
Coleoptera: Coccinellidae	*Brachyacantha ursine*	0	0	0	0	1	1
Coleoptera: Coccinellidae	*Coccinella septempunctata*	2	1	3	0	0	0
Coleoptera: Coccinellidae	*Coleomegilla maculata* larva	1	3	4	1	0	1
Coleoptera: Coccinellidae	*Coleomegilla maculata*	6	4	10	1	0	1
Coleoptera: Coccinellidae	*Harmonia axyridis*	1	0	1	0	0	0
Coleoptera: Coccinellidae	*Hippodamia convergens*	0	0	0	0	1	1
Coleoptera: Coccinellidae	*Hippodamia parenthesis*	2	0	2	0	0	0
Coleoptera: Coccinellidae	*Hippodamia tredecimpunctata*	4	3	7	0	0	0
Coleoptera: Coccinellidae	*Scymnus rubricaudus*	149	194	343	7	3	10
Coleoptera: Elateridae	Elaterid larva	0	0	0	2	2	4
Coleoptera: Elateridae	Elaterid 1	0	0	0	1	2	3
Coleoptera: Lampyridae	Lampyrid larva	0	1	1	0	0	0
Coleoptera: Lampyridae	Lampyrid 1	0	0	0	0	1	1
Coleoptera: Staphylinidae	Staphylinid 1 (<3 mm)	12	13	25	114	75	189
Coleoptera: Staphylinidae	Staphylinid 2 (<3 mm)	9	7	16	3	0	3
Coleoptera: Staphylinidae	Staphylinid (>3 mm, <12 mm)	2	5	7	16	12	28
Coleoptera: Staphylinidae	Stapylinid (>12 mm)	5	1	6	0	2	2
Hymenoptera: Formicidae	*Amblyopone pallipes*	0	0	0	4	5	9
Hymenoptera: Formicidae	*Lasius* sp. (*niger* grp)	53	20	73	74	12	86
Hymenoptera: Formicidae	*Leptothorax*	0	0	0	1	2	3
Hymenoptera: Formicidae	*Solenopsis* subg. *Diplorhoptrum*	0	2	2	0	0	0
Hymenoptera: Formicidae	Ant sp. 10	7	3	10	61	72	133
Hymenoptera: Formicidae	Ant sp. 11	0	29	29	2	0	2
Hymenoptera: Formicidae	*Ponera pennsylvanica*	15	9	24	23	44	67
Hymenoptera: Formicidae	*Formica* subg. *Fusca*	1	1	2	0	0	0
Hymenoptera: Formicidae	Queen Ant	1	0	1	1	1	2
	Total species[a]	29.57 ± 3.74	28.57 ± 4.27	Mann-Whitney $U = 25.00$, $\chi^2_1 = 0.004$, $P = 0.95$	28.75 ± 2.75	25.00 ± 2.65	Mann-Whitney $U = 11.00$, $\chi^2_1 = 0.79$, $P = 0.38$
	Shannon Index (H)[a]	4.02 ± 0.15	3.92 ± 0.12	Mann-Whitney $U = 30.00$, $\chi^2_1 = 0.49$, $P = 0.48$	3.49 ± 0.16	3.22 ± 0.16	Mann-Whitney $U = 11.00$, $\chi^2_1 = 0.75$, $P = 0.39$
	Evenness (J)[a]	1.21 ± 0.05	1.20 ± 0.05	Mann-Whitney $U = 26.00$, $\chi^2_1 = 0.04$, $P = 0.85$	1.04 ± 0.03	1.01 ± 0.02	Mann-Whitney $U = 11.00$, $\chi^2_1 = 0.75$, $P = 0.39$

[a] Mean ± SEM diversity indices calculated for each plot ($n = 7$ for soil surface; $n = 4$ for soil column).

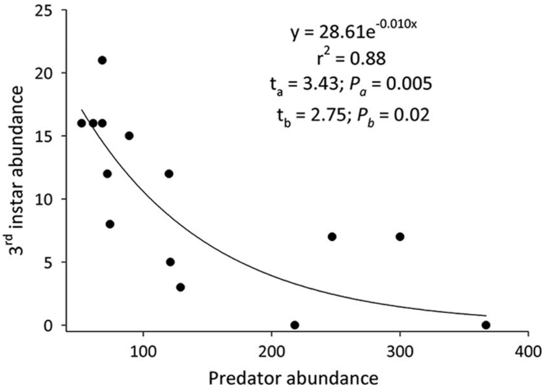

Fig. 5. Exponential decay model describing the relationships between total third instars of *D. virgifera* and total predators recovered from the soil surface in quadrat samples in each maize plot. Equation for the model is $y = ae^{(-bx)}$. Each data point represents data from a single plot (pooled across years).

al. 2004a, b; Wilson and Hibbard 2004; Chege et al. 2005; Ellsbury et al. 2005; Oyediran et al. 2005), which adds further support for our hypothesis that maize plants in the cover-cropped treatment were a less suitable host for developing *D. virgifera* larvae. In addition, intraspecific competition among the larvae may be affected by the environment produced by the cover crop residue, and merits further examination as a possible mechanism for our observations on larval population characteristics. Finally, cover crops and residue often affect the microclimate of the soil (e.g., soil temperature) (Flerchinger et al. 2003, Zibilske and Makus 2009), which could also have altered the development of the herbivore. At this point, we are unable to separate whether the changes in larval performance are caused by environmental characteristics, quality of the host plant, or both.

There was a particular effect of treatment on the abundance of third instars, suggesting a physiological or behavioral shift in the pest that increases its susceptibility to mortality sources in cover cropped maize. We speculate that the differences in third instars did not produce a corresponding significant reduction in adult emergence in the cover cropped treatment because there was insufficient replication of the adult emergence traps, and lower statistical power associated with this sampling technique. Prior life table analyses have shown that egg and first instars of *D. virgifera* incur high levels of mortality, and that third instars under typical growing conditions do not incur high levels of mortality (Toepfer and Kuhlmann 2005, 2006). However, previous studies, and our unpublished data, have shown that third instars move from the protection of maize roots to find food (Hibbard et al. 2004, 2005) and pupation sites (Branson et al. 1975). Moreover, an anti-predator hemolymph defense is highly active in third instar *D. virgifera* (Lundgren et al. 2009a, Lundgren et al. 2010), and may have evolved to protect these susceptible older instars from predation. However, this protection is not universally effective against all predator groups (Lundgren et al. 2009c, Lundgren et al. 2010), and larvae are consumed by a broad group of natural enemies. We suspect that predation is a likely explanation for the reduction in third instar abundance experienced in the cover-cropped maize.

The abundance of natural enemy communities is frequently favored by vegetation diversity in cropland, and this was certainly the case for soil predator communities in maize. Although initially similar at the onset of the field season, a gulf widened between the treatments in predator abundance as the season progressed, with substantially more predators being found in the cover-cropped treatment by the end of the sample period. Noncrop vegetation within cropland favors natural enemies by providing alternative foods, favorable microclimates, and preferred oviposition sites (Landis et al. 2000, Lundgren 2009). The contributions of vegetation diversity to natural enemy function is less studied than the effects of diversity on predator abundance, although the majority of research on the topic suggests that vegetation and resource diversity is a source of biological control rather than a sink under realistic conditions (Bugg et al. 1991, Eubanks and Denno 2000, Lundgren et al. 2006, Prasifka et al. 2006, Lundgren and Harwood 2010). Given that the cover crop is killed early in the season, we suspect that the soil predator community in maize is favored by a more diverse or abundant detritivore community or an enhanced microclimate (e.g., more cover or more favorable temperatures) present in the cover-cropped treatment. Finally, the numerical abundance of predators per plot is well correlated with reductions in *D. virgifera* third instars, which implies causation (i.e., predators are reducing the number of third instars). However, more explicit examination of these trophic interactions is necessary before a firm conclusion on predator contributions to pest management can be attained.

Before cover crops can be viewed as a viable option for managing *D. virgifera* in maize, a series of additional questions that are often overlooked in biological control research (Wratten et al. 1998, van Emden 2003, Lundgren 2009) must be addressed. First, how does planting cover crops and predation affect crop damage and grain yield and quality? Reducing pest populations does not necessarily affect crop performance, and this topic will be discussed for the cover crop-*D. virgifera*-maize system in a companion paper. Finally, the costs and benefits of cover crops must be weighed in relation to other forms of rootworm management (e.g., insecticidal seed treatments, Bt maize hybrids, no treatment) for the profitability of this nonchemical strategy to be fully realized. Examining the community responses of the herbivore and its natural enemy assemblage is the first crucial step in developing conservation biological control as a tool for pest management.

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