An Edge Effect Caused by Adult Corn-Rootworm Beetles on Sunflowers in Tallgrass Prairie Remnants

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Abstract: *The once-extensive tallgrass prairie community of North America has been reduced to small remnants, many of which are surrounded by intensive corn (*Zea mays*) agriculture. We investigated adult corn-rootworm beetles (Chrysomelidae:* Diabrotica *spp.), important pests of corn, on sunflowers (Asteraceae:* Helianthus *spp.) in prairie remnants in southeast Minnesota. Large numbers of beetles invaded the prairie from surrounding corn fields in late summer.* D. barberi *and* D. virgifera *were captured on sticky traps in all locations in the prairie, but abundance was much greater near the edge adjacent to corn. We observed* D. barberi *(but not* D. virgifera*) feeding extensively on sunflower pollen and occasionally on other flower parts, such as petals. Sunflowers located nearer corn fields sustained more floral damage than those farther from corn. To determine the effect of beetle damage on seed set, we enclosed sunflower heads in bags with either zero, two, or four* D. barberi *adults. Seed set was reduced in heads enclosed with* D. barberi. *Thus, this agricultural pest may interfere with the successful reproduction of sunflowers and possibly other prairie composites that flower in late summer. Given the small size of most prairie remnants and the abundance of this flower-feeding beetle in landscapes dominated by corn agriculture,* D. barberi *may affect the sustainability of prairie plant populations.*

Un Efecto de Borde Causado por Escarabajos Adultos sobre Girasoles en Remanentes de Pastizales de Praderas

Resumen: *La que fuera alguna vez una comunidad de pastizales altos de pradera de Norteamérica ha sido reducida a remanentes pequeños, muchos de los cuales están rodeados de tierras de cultivo intensivo de maíz (*Zea mays*). Investigamos los adultos del escarabajo (Chrysomelidae:* Diabrotica *spp.), una plaga importante del maíz, en los girasoles (Asteraceae:* Helianthus *spp.) en remanentes de pradera del sureste de Minesota. Grandes cantidades de escarabajos provenientes de los cultivos de maíz adyacentes invadieron la pradera hacia finales del verano.* D. barberi *y* D. virgifera *fueron capturados en trampas pegajosas en todas las localidades de la pradera, pero la abundancia fue mucho mayor cerca del borde adyacente a los cultivos de maíz. Observamos que* D. barberi *(pero no* D. virgifera*) se alimentaron extensivamente del polen de girasoles y ocasionalmente en otras partes de las flores, como son los pétalos. Los girasoles ubicados cerca de los campos de maíz presentaron un mayor daño floral que aqúellos alejados del maíz. Para determinar el efecto del daño de los escarabajos en las semillas, encerramos cabezas de girasol en bolsas que contenían cero, dos o cuatro* D. barberi *adultos. Los juegos de semillas fueron reducidos en las cabezas encerradas con* D. barberi. *Por lo tanto, esta plaga agrícola puede interferir con la reproducción exitosa de los girasoles y posiblemente de otros elementos de las praderas que florean hacia el final del verano. Dado el pequeño tamaño de la mayoría de los remanentes de la pradera y a la abundancia de estos escarabajos que se alimentan de flores en paisajes dominados por el cultivo de maíz,* D. barberi *podría afectar la sostenibilidad de las poblaciones de plantas de la pradera.*

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Introduction

The fragmentation of once-continuous habitats by human activity has been a focus of concern for conservation biologists (Saunders et al. 1991; Murcia 1995; Didham et al. 1996; Laurance & Bierregaard 1997). When habitat fragments are small or irregularly shaped, most of their area is near a boundary (Laurance & Yensen 1991). A variety of negative effects of such edges have been documented, both abiotic (e.g., greater tree mortality due to differences in microclimate and wind; Laurance et al. 1997) and biotic (e.g., prevalence of nest predators and parasites near edges; Hartley & Hunter 1998). Such edge effects may cause accelerated loss of species in habitat fragments (Woodroffe & Ginsberg 1998).

Tallgrass prairie covered more than 68 million ha in central North America at the time of European settlement, but has now been reduced to scattered remnants (Weaver 1954; Samson & Knopf 1994; Robertson et al. 1997). The decline in area of tallgrass prairie is greater than for any other major community type in North America (Samson & Knopf 1994). Almost all tallgrass prairie has been converted to agriculture, now mostly corn (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr).

The rate of extinction of plant species in prairie remnants is alarmingly high (Leach & Givnish 1996), and edge effects are among the potential causes (Leach & Givnish 1996). The few fragments of tallgrass prairie that remain are mostly small. Robertson et al. (1997) report that 83% of the high-quality prairie remnants in Illinois are <10 acres (approximately 4 ha) in area. As a result, almost all remaining prairie is near an edge. Therefore, it is essential to understand edge effects that occur on the boundary between prairie and agriculture. Most research on edge effects concerns forests; grassland edges have not been studied extensively (but see Johnson & Temple 1990; Tyser & Worley 1992; Burger et al. 1994).

Agricultural insect pests could be the cause of a major biotic edge effect in prairie remnants, potentially disrupting reproduction in prairie plants. Throughout the "corn belt," which now occupies former tallgrass prairie, two of the most damaging insect pests of corn are the chrysomelid beetles *Diabrotica barberi* Smith and Lawrence (northern corn rootworm) and *Diabrotica virgifera* LeConte (western corn rootworm) (Chiang 1973; Krysan 1986; Krysan & Smith 1987; Levine & Oloumi-Sadeghi 1991). The two *Diabrotica* species share a similar life cycle (Chiang 1973; Krysan & Branson 1983): they are univoltine; eggs overwinter in the soil of corn fields and hatch in the spring; larvae feed almost exclusively on the roots of corn (the "rootworm" stage); and pupation occurs in the soil. Adults emerge in July (Elliott et al. 1991; Naranjo 1991) and begin to feed on corn pollen, silks, and immature ears.

The two *Diabrotica* species differ in their feeding behavior after corn pollination is complete and the reproductive tissues dry out. *D. barberi* adults disperse from corn fields starting in August and feed on the pollen and other floral parts of a variety of plants (Cinereski & Chiang 1968; Ludwig & Hill 1975; Hill & Mayo 1980 Lance et al. 1989; Naranjo 1991, 1994). Yellow composites (Asteraceae) such as *Helianthus* spp. seem to be a preferred food source for *D. barberi. Helianthus* spp. are among the most common plants that bloom in late summer in prairie communities (Curtis 1959; Weaver 1968). In controlled feeding experiments, *D. barberi* females fed on a diet of composite flowers have similar longevity and fecundity to those fed on a diet of corn (Lance & Fisher 1987; Siegfried & Mullin 1990; Mullin et al. 1991). *D. barberi* females return to corn fields to oviposit (Cinereski & Chiang 1968; Lance et al. 1989; Naranjo 1991).

Adults of *D. virgifera* are also capable of widespread dispersal (Hill & Mayo 1980; Coats et al. 1986) but rarely feed on plants other than corn. Once corn reproductive tissues have dried, *D. virgifera* continues to feed on corn tissues, including leaves (Ludwig & Hill 1975; Branson & Krysan 1981). In contrast to the situation for *D. barberi*, composite flowers are a poor diet for adult *D. virgifera* (Siegfried & Mullin 1990; Mullin et al. 1991).

Native prairie beetles also feed on composite flower heads. *Chauliognathus pennsylvanicus* (DeGeer) (Coleoptera: Cantharidae) is widespread in the eastern and midwestern United States and adjacent Canada (Fender 1964). Adults are commonly found in late summer on flowers of a variety of species, especially members of the Asteraceae (Gross & Werner 1983; McLain 1984; Dickinson & McKone 1992). There is no specific association known between *C. pennsylvanicus* and corn, so its distribution in prairies relative to the proximity of corn makes an informative comparison with that of *Diabrotica* spp.

We investigated the potential effects of adult *Diabrotica* spp. dispersing from corn into prairie, with emphasis on the effect of the beetles on the pollination of sunflowers. We asked three experimental questions: (1) How do the densities of *D. barberi* and *D. virgifera* change as a function of distance from the edge between a corn field and prairie, and how does this pattern compare with the distribution of the native beetle *C. pennsylvanicus*? (2) What is the feeding behavior of *Diabrotica* spp. on *Helianthus* heads, particularly in relation to diurnal changes in pollen availability? (3) Does the feeding by *Diabrotica* affect seed set in *Helianthus*?

Methods

Spatial Distribution of Beetles and Damage

We measured the distribution of *Diabrotica* spp. and *C. pennsylvanicus* at McKnight Prairie in Goodhue County, southeastern Minnesota (lat. 44°30′04″N, long.

93°01′40″W). This prairie remnant contains gravelly ridges and adjacent lowland areas, with a diverse flora of prairie plants. Dominant grasses include *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, *Panicum virgatum* L., *Schizachyrium scoparium* (Michx.) Nash, and *Stipa spartea* Trin. Management has included spring burns since the property was purchased by Carleton College in 1963. Some portion of the prairie is burned almost every year, with any particular area being burned every 3-5 years.

McKnight Prairie is an isolated remnant surrounded on all sides by agricultural areas, with little prairie in the surrounding landscape. The prairie boundaries (Fig. 1) are nearly rectangular, approximately 170 m (east and west sides) by 780 m (north and south sides). Most of the northern boundary is adjacent to a large agricultural field, which was planted with corn during the 1994 field season. The southern boundary is adjacent to a commercial plantation of small conifers (mostly *Pinus* spp.) grown for use as Christmas trees.

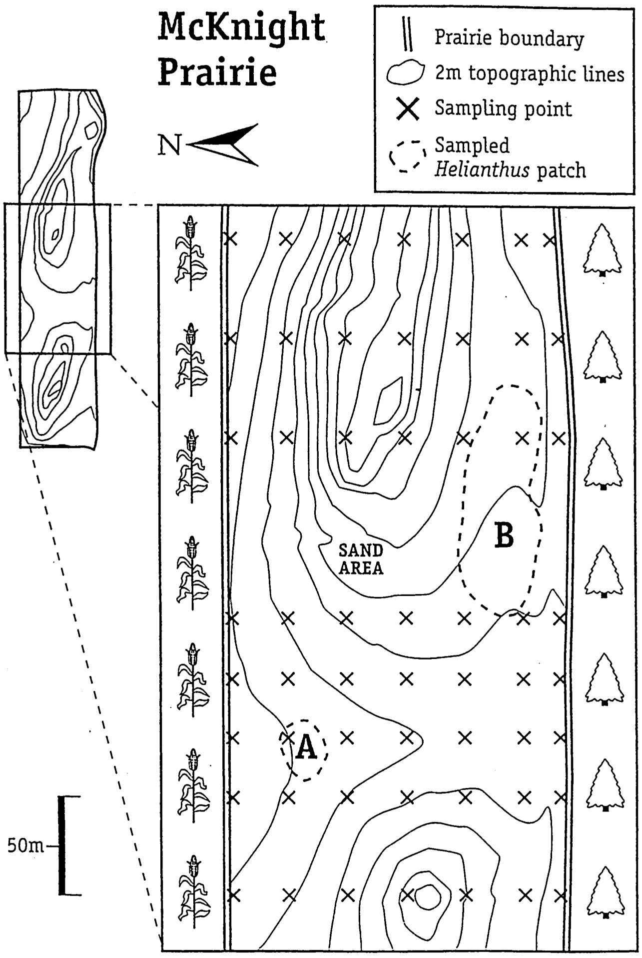

Figure 1. Map of the study site, McKnight Prairie, Goodhue County, Minnesota. Sampling points are where sticky traps and potted sunflowers were placed to sample insects. Four of the north-south transects were placed in a relatively flat area between the hills, and four were placed so they crossed hilltops. The areas marked A (near the corn) and B (away from the corn) contained flowering Helianthus *that were surveyed for insect abundance and ray-petal damage during August.*

We established an insect sampling grid across the central portion of the prairie (Fig. 1). Eight north-south transects spanned the distance from the corn edge to the conifer edge. Four of these crossed ridge tops and four crossed more gradual terrain. Each transect contained seven sample points, which were 30 m apart.

Starting on 30 July, 15 August, and 3 September 1994, we used commercial sticky traps (Scentry Multigard Trap, Ecogen Inc., Langhorne, Pennsylvania) to sample the grid. The rectangular traps were made of a bright green-yellow cardboard that is highly attractive to *Diabrotica* spp. (Hesler & Sutter 1993; Youngman et al. 1996). The colored area of each trap was 28 × 23 cm; the central 20 x 15 cm was covered with a sticky, waterproof substance similar to Tanglefoot. The sticky traps were folded in half and placed 1 m above the ground at each sample point. After 2 days, we counted the number of captured *Diabrotica* and *C. pennsylvanicus* individuals on the traps. For the September sample, the first day the traps were out was rainy and unseasonably cool, so few beetles were captured. For this sample we left the traps up for 2 more days, counted the beetles, and subtracted the number of beetles captured on day 1.

To sample the distribution of living beetles on flowers dispersed evenly across the prairie, we used potted sunflowers placed at the same grid points as the sticky traps. Wild-type *Helianthus annuus* L. plants were grown from seed in the greenhouse in pots 15 cm in diameter. The pots were transported to the prairie and placed on the grid on the afternoon of 1 September 1994. On the afternoon of 3 September, we visually surveyed the beetles on the heads of the potted *H. annuus*. Almost all of the plants had only one head; if there were two, we counted insects on only one arbitrarily chosen head. A single observer approached each plant with as little disturbance as possible and counted the insects visible on the head. The beetles seemed to have little reaction to the approaching observers, but we may have undercounted if beetles dropped to the ground (their typical response to disturbance) before they could be counted.

We also used naturally occurring *Helianthus* plants to compare the density of beetles in parts of the prairie at varying distances from the corn edge. Identification of individual *Helianthus* plants to species was difficult at the study site. Following Gleason and Cronquist (1991), we keyed some plants to *H. pauciflorus* Nutt. and some to *H. tuberosus* L., but intermediates were common. Hybrids between these two species are well known (Heiser et al. 1969). Therefore, individuals of *H. tuberosus*, *H. pauciflorus*, and intermediates from McKnight Prairie are herein referred to simply as *Helianthus*.

On 26 August 1994, we counted the beetles on flowering heads of *Helianthus* growing in two areas of McKnight Prairie (Fig. 1). The near-corn patch (A) had fewer plants, was smaller in area, and seemed to be more exclusively *H. tuberosus*; possible hybrid individuals were more common in the larger patch farther from corn (B). Beetles were counted in all of the open flowers in each patch as described above for the potted plants. In addition, the condition of the ray petals of each head was classified visually into the following categories: light damage, 0–25% of area of ray petals missing or shriveled; medium damage, 25–75% of area of ray petals missing or shriveled; and heavy damage, >75% of area of ray petals missing or shriveled.

Feeding Behavior

Observations of the behavior of *D. barberi* individuals took place at Hillside Prairie in the Cowling Arboretum of Carleton College, Northfield, Minnesota (lat. 44°28′15″N, long. 93°08′50″W). This site was restored to prairie and was planted in various years starting in 1978. Our observations took place mostly in plots planted in 1979 and 1981.

Data were recorded from 25 to 28 August 1997, when *H. pauciflorus* was flowering. As in most composites, the disk florets of *Helianthus* are protandrous. Most of a floret's pollen is presented in the morning (Neff & Simpson 1990; Minckley et al. 1994), whereas nectar is produced throughout the day (Neff & Simpson 1990). Because of the changing floral resources available during the day, we observed the behavior of *D. barberi* both in the morning (mostly between 0900 and 1100 hours) and in the afternoon (mostly between 1430 and 1700 hours).

Observers walked through the site and chose flowering heads haphazardly. Once a head was chosen from a distance, the plant was approached carefully to avoid disturbing the beetles. Individuals were recorded as (1) on stamens, feeding on pollen; (2) nectar feeding, as judged by beetles with their heads inserted deeply into the corollas of the disk florets; (3) on stigmas, which included individuals feeding on pollen that had been deposited on the stigmas; (4) on the rays, feeding or not; or (5) in other locations or behaviors.

Enclosure Experiment

To assess the effect of *Diabrotica* on seed set of *H. pauciflorus*, we performed a bag-enclosure experiment at Hillside Prairie. We used *D. barberi* because *D. virgifera* was essentially absent from *Helianthus* in our counts at McKnight Prairie and elsewhere. There were five treatments: unbagged control (no manipulation; $n = 21$); hand-pollinated control (never exposed to *D. barberi*; $n = 19$); and bagged heads with either zero ($n = 19$), two ($n = 12$), or four ($n = 18$) *D. barberi* enclosed in the bag. Before the experiment, all available unopened heads were chosen from plants along a transect in the prairie. Each head was randomly assigned to one of the five treatments, and all but the unmanipulated control heads were bagged with bridal-veil cloth.

The experiment took place between 20 and 31 August 1994. Manipulations to a head began on the day the first ray florets opened and continued until all of the disk florets had flowered. Except for the hand-pollinated controls, the bags were removed on alternate days for about 4 hours starting at approximately 0900 hours to allow for natural pollination of bagged heads. Unpollinated stigmas of *H. annuus* can remain receptive for up to 4 days (Neff & Simpson 1990), so we assumed that pollination on alternate days would be sufficient for complete pollination of all florets. When bags were replaced in the afternoon, any beetles remaining on the heads were removed, and the appropriate number of newly collected beetles were enclosed in the bag. The *D. barberi* individuals used for the experiment were collected earlier in the day from a nearby source and chilled in a cooler to allow the beetles to be handled easily. As a result of this treatment, individual beetles were in the bags for no more than 48 hours.

Because even the bagged heads could be visited by *D. barberi* during the period of open pollination, we included a hand-pollinated control that was never exposed to *D. barberi*. All perennial members of the genus *Helianthus* are self-incompatible (Heiser et al. 1969), so *H. pauciflorus* required pollen from another individual to set seed. We hand-pollinated plants in the early afternoon. Bags were removed, the heads were pollinated with pollen collected on small paintbrushes, and bags were replaced immediately. To avoid using self pollen from different shoots of the same *H. pauciflorus* clone, we pollinated heads from sources well beyond the nearest neighbors of a particular shoot.

Heads from all treatments were collected at the end of the season. The number of seeds (technically achenes, one-seeded fruits) per head was large, so the heads were subsampled to determine seed set. Each head was cut in two longitudinally, exposing a row of seeds; this row was counted completely. If there were <30 florets in the row, a second row was exposed and counted. We classified each ovary as either a set seed (expanded since anthesis) or unexpanded. Many of the heads contained small insect larvae that damaged the ovaries by hollowing them out at various stages of expansion. We attempted to count the number of insect-damaged ovaries, but this was not always possible because the feeding took place inside the ovary wall (for discussion of a similar situation in *H. grosseserratus*, see Stuessy et al. 1986). Regardless of insect damage, ovaries were considered expanded if they had elongated significantly since anthesis.

Statistics

We used nonparametric tests (Mann-Whitney test, Kruskal-Wallis test) for our analysis because insect counts often deviated from normality or had unequal variances among treatments. After the Kruskal-Wallis test, we performed multiple pairwise comparisons between treatments with Dunn's nonparametric test for unequal sample sizes (Zar 1996).

Results

Within McKnight Prairie, the rate of capture of *D. barberi* in sticky traps was strongly dependent on proximity to the boundary with corn (Fig. 2). The effect of position was highly significant for all three sample periods (Kruskal-Wallis test, df = 6, $p < 0.001$). The edge effect was most pronounced when the *D. barberi* population peaked in mid-August, at which time there were approximately 18 times as many beetles captured at the corn edge as at the locations farthest from the edge.

D. virgifera showed a similar pattern of capture in sticky traps (Fig. 3), although the total number of beetles captured was much lower than for *D. barberi.* The effect of proximity to the corn edge was highly significant for all three sample periods (Kruskal-Wallis test, df = 6, $p < 0.001$, for samples starting 30 July and 15 August; $p = 0.003$ for sample starting 4 September).

The number of *C. pennsylvanicus* captured (Fig. 4) was not affected by position relative to the corn edge in samples starting on 30 July (Kruskal-Wallis test, df = 6, $p = 0.10$) or 4 September (Kruskal-Wallis test, df = 6, $p = 0.10$). There was a significant effect of position in the mid-August sample (Kruskal-Wallis test, df = 6, $p < 0.01$), but the peak density was on sticky traps farthest from the corn.

When we used potted sunflowers on the grid to sample beetles on 3 September, we frequently found *D. barberi* on the sunflower heads (Fig. 5). The position of sunflowers relative to corn had a highly significant (Kruskal-Wallis test, df = 6, $p < 0.001$) effect on *D. barberi* abundance. We found no *C. pennsylvanicus* and only one *D. virgifera* on the heads of the 56 potted plants.

On 26 August, we found more damage to rays of *Helianthus* heads near corn than far from corn (χ^2 test, df = 2, $p < 0.005$; see Table 1). We found no *D. virgifera* on 213 sampled heads of *Helianthus* that grew in patches near and far from corn. There was a significant difference in the number of *D. barberi* per head in the two patches (Mann-Whitney test, $U = 1795$, $p < 0.01$), with more beetles in the patch near corn (mean ± SE =

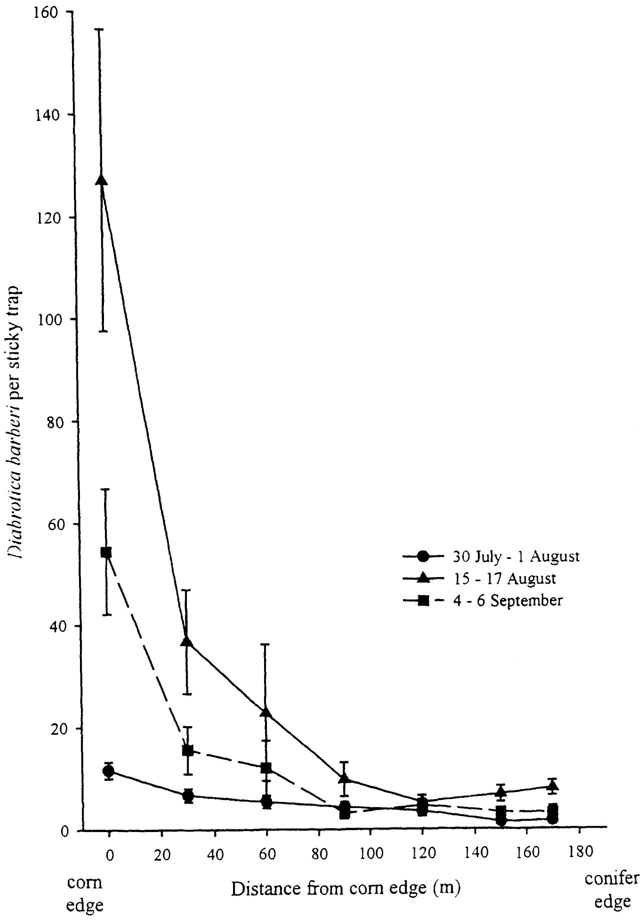

Figure 2. Number of Diabrotica barberi *from 56 sticky traps exposed for 48 hours at three times during the season. Averages across eight transects (Fig. 1) are shown. Bars are ±1 SE.*

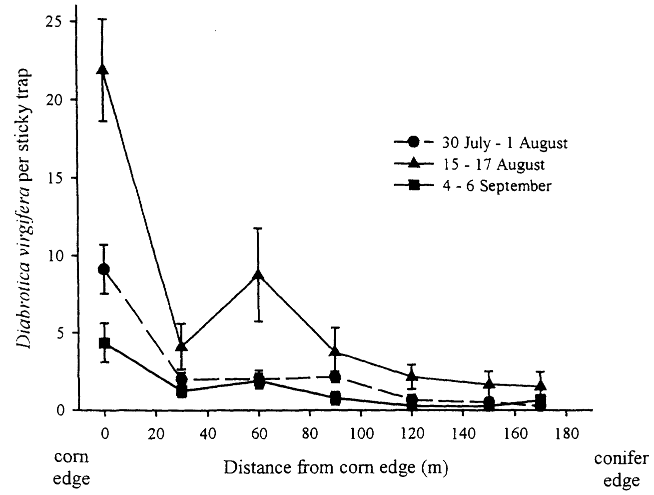

Figure 3. Number of Diabrotica virgifera *from 56 sticky traps exposed for 48 hours at three times during the season. Averages across eight transects (Fig. 1) are shown. Bars are ±1 SE.*

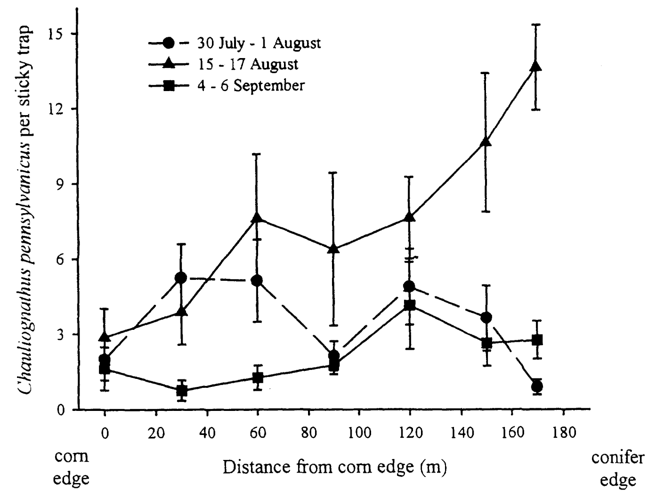

Figure 4. Chauliognathus pennsylvanicus *counts from 56 sticky traps exposed for 48 hours at three times during the season. Averages across eight transects (Fig. 1) are shown. Bars are ±1 SE.*

Table 1. Damage to rays of *Helianthus* in patches[a] at different distances from a corn edge at McKnight Prairie, Minnesota, in August.

Damage category[b]	*Heads in patch A, near corn edge (%)*	*Heads in patch B, far from corn edge (%)*
Light	46.4	68.6
Medium	25.0	23.8
Heavy	28.6	7.6
Sample size	28 heads	185 heads

[a] *The patch locations are shown in Fig. 1. Patch A was smaller, and near the corn edge, and all available heads were counted there. Patch B was far from the corn edge.*

[b] *Damage was categorized as light (0 - 25% of area of ray petals missing or shriveled), medium (25% - 75% of area of ray petals missing or shriveled), or heavy (75% of area of ray petals missing or shriveled).*

3.86 ± 0.41, *n* = 28) than in the patch far from corn (2.74 ± 0.18, *n* = 185). *C. pennsylvanicus* numbers were much lower than those for *D. barberi.* Because almost all heads had either one or no *C. pennsylvanicus* individuals, data were analyzed categorically (i.e., heads categorized as having the species present or absent). There was no difference (χ^2 test, df = 1, $p > 0.10$) in the number of heads with *C. pennsylvanicus* between the patch near corn (11% of heads, *n* = 28) and the patch far from corn (20% of heads, *n* = 185).

At Hillside Prairie we observed *D. barberi* actively feeding on floral parts of *H. pauciflorus*, including pollen, nectar, and ray petals. In the morning, when the pollen was presented in newly opened florets, most individuals fed on pollen (Fig. 6). By afternoon, most of the pollen had been removed from the heads, and the beetles were more often seen feeding on nectar, stigmas (where they appeared to remove pollen that had been deposited there), and ray florets (Fig. 6). The difference in behavior between morning (*n* = 514 individuals) and afternoon (*n* = 230) was highly significant (χ^2 test, df = 4, $p < 0.001$). *D. barberi* individuals were reluctant fliers throughout the day and were rarely seen flying between heads.

In the bagging experiment, seed set—the proportion of expanded ovaries, whether or not attacked by predispersal seed predators within the head—was different for

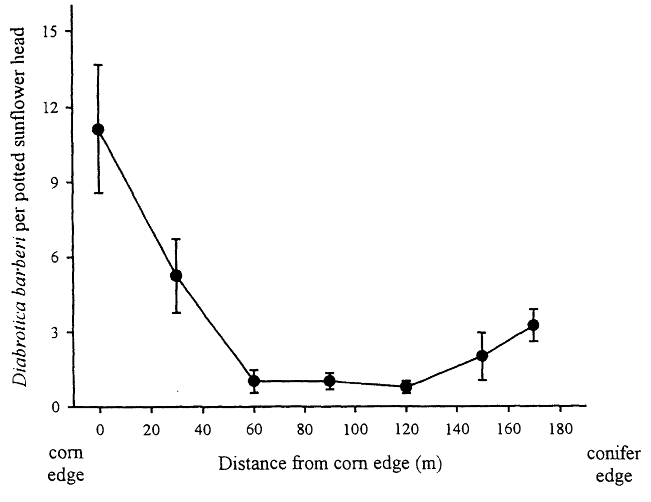

Figure 5. Diabrotica barberi *counts per head on 56 potted sunflowers (wild type* Helianthus annuus*) placed on the sample grid in early September. Averages across eight transects (Fig. 1) are shown. Error bars are ±1 SE.*

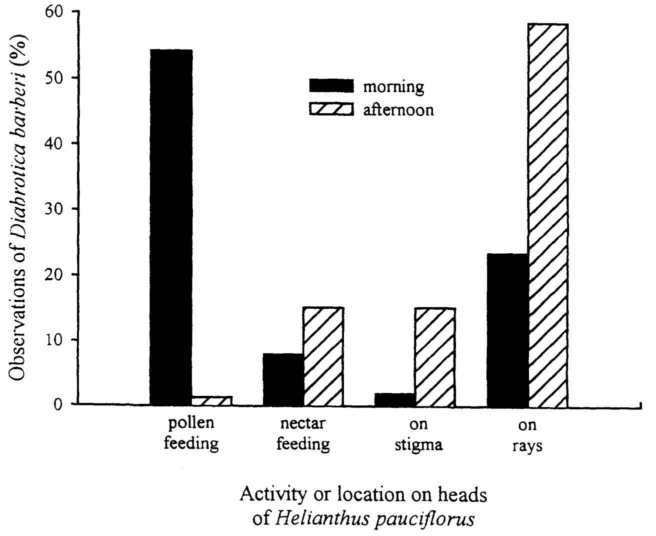

Figure 6. Activity or location of Diabrotica barberi *individuals on heads of* Helianthus pauciflorus *on Hillside Prairie in morning (*n *= 514) and afternoon (*n *= 230) surveys.*

the different *D. barberi* treatments (Kruskal-Wallis test, df = 4, $p < 0.05$). None of the multiple pair-wise comparisons between treatments was significant (Dunn's tests, $p > 0.05$), but heads bagged with beetles generally had lower seed set than those without beetles (Fig. 7).

Discussion

Distribution Relative to Edge

Whether measured by abundance on sticky traps (Fig. 2), on potted sunflowers placed on the prairie (Fig. 5), or on naturally occurring *Helianthus* patches, our data consistently showed greater densities of *D. barberi* near the edge of McKnight Prairie that bordered a corn field. There was a rapid decrease in abundance away from the edge. In the mid-August sticky-trap sample, abundance of *D. barberi* was greatest at the corn edge, and was reduced 70% and 80% at 30 m and 60 m, respectively from the edge. For counts on potted sunflowers, abundance was reduced over 50% relative to the edge at 30 m and 90% at 60 m. But no part of McKnight Prairie was far enough from corn to be completely without *D. barberi.* In a landscape as dominated by corn agriculture as much of the midwestern United States, it seems likely that any location will have at least some *D. barberi* present.

D. virgifera was almost completely absent from the *Helianthus* heads, even though it was commonly present on sticky traps and its density increased near corn (Fig. 3). This difference between the *Diabrotica* spp. is consistent with previous studies: even when *D. virgifera* is abundant in nearby corn, almost all individuals on sunflower heads are *D. barberi* (Hill & Mayo 1980; Siegfried & Mullin 1990).

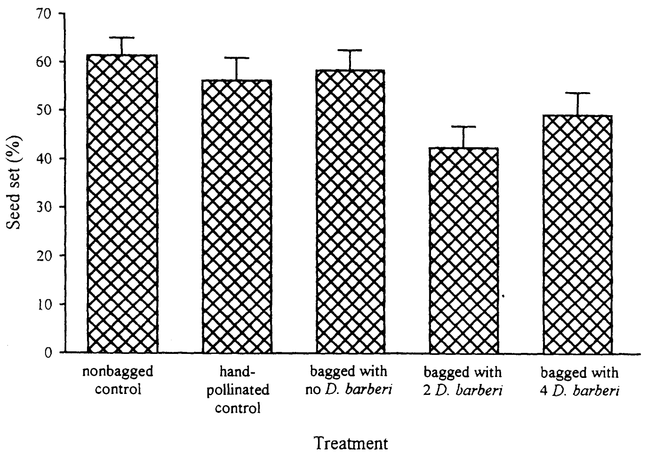

Figure 7. Seed set of Helianthus pauciflorus *heads in the bagging experiment on Hillside Prairie. Mean ± 1 SE shown;* n *ranged from 12 to 21 heads in various treatments. Seed set includes all ovaries that had expanded, even though many had been attacked by predispersal seed predators.*

In the first and last sticky-trap samples, proximity to the corn edge had little effect on the distribution of the native flower-feeding beetle *Chauliognathus pennsylvanicus* (Fig. 4). This suggests that the pattern in *D. barberi* was not caused by a resource or environmental factor that generally favors composite-feeding beetles near the corn. In the mid-August sample, when *C. pennsylvanicus* abundance showed a significant relationship to the edge, the greatest abundance was farthest from the corn (Fig. 4). At this time, a large patch of *Helianthus* was present near the conifer edge (personal observation), and we hypothesize that *C. pennsylvanicus* might have been more common there because it was tracking available floral resources on the prairie. Alternatively, competition from the dense aggregations of *D. barberi* near corn may have driven *C. pennsylvanicus* to flowers far from the corn. This pattern may have appeared only in mid-August because that was when *D. barberi* populations were highest (Fig. 2).

There was greater abundance of *D. barberi* on *Helianthus* heads in the patch near corn (*A*, Fig. 1) than on to the patch near the conifers (*B*). Because all beetle counts were taken from a single patch in each location, it is possible that differences in the patches other than proximity to corn—such as size of patch or density of plants per patch—could explain the difference in *D. barberi* numbers. These were the only patches of *Helianthus* within the study site, so there was no possibility of adding further samples. The lack of difference in *C. pennsylvanicus* density between patches suggests that patch characteristics were at least roughly similar for flower-feeding beetles. Also, the marked increase in *D. barberi* density near corn that was shown by the other means of sampling (Figs. 2 & 5) supports the hypothesis that proximity to corn was the most likely cause of the difference between patches *A* and *B*.

We concentrated our systematic observations of *D. barberi* at McKnight Prairie, but we have observed large numbers of *D. barberi* on composite heads in many prairie remnants elsewhere in the region. We counted the number of *D. barberi* on heads of *Helianthus* and related composites in two other prairie remnants in southeastern Minnesota (Iron Horse Prairie in Dodge County and Wild Indigo Prairie in Mower County). There were greater densities of *D. barberi* at locations nearest corn in both prairies (unpublished data).

Effect of *Diabrotica*

Although *D. virgifera* was common on sticky traps, we conclude that *D. virgifera* had relatively little effect on the pollination of *Helianthus* because it was essentially absent from *Helianthus* heads. This is consistent with previous work showing that *D. virgifera* rarely feeds on anything other than corn. Of course it is possible that *D. virgifera* interacts with some other species in prairies, but we have no data to support this.

Our behavioral observations of *D. barberi* on *Helianthus* heads suggest that *D. barberi* concentrates on pollen feeding, especially in the morning when pollen is newly presented by *Helianthus* florets (Fig. 6). This is consistent with studies of gut contents, which show clearly that *D. barberi* feeds on pollen of the flowers it visits outside cornfields (Cinereski & Chiang 1968; Ludwig & Hill 1975). The shift of *D. barberi* to stigmas in the afternoon was probably a response to changing pollen availability; once the pollen was removed from stamens, the beetles seemed to feed on the pollen deposited on stigmas. We cannot exclude the possibility that the stigmas themselves were being consumed, although they appeared to be largely intact on most heads.

Previous investigators have suggested that *D. barberi* feeds on "floral parts" other than pollen (Krysan & Branson 1983; Siegfried & Mullin 1990), but they have not specified clearly which parts are being eaten. The individuals we observed at Hillside Prairie were frequently on the ray petals (Fig. 6), especially in the afternoon, but were not often directly observed eating ray tissue. The hypothesis that *D. barberi* can feed on rays and cause considerable damage to them is supported by (1) the greater ray damage on *Helianthus* heads at McKnight Prairie near corn (Table 1), where *D. barberi* was more abundant, and (2) the similar ray damage seen on *Helianthus* heads bagged with *D. barberi* (personal observation).

There is evidence from the bagging experiment that feeding by *D. barberi* reduced seed set in *H. pauciflorus* at Hillside Prairie (Fig. 7). We are cautious about this result for several reasons. First, although there was a significant overall effect of the bagging treatment, none of the pairwise post-hoc comparisons between treatments was significant. It would be useful to repeat the experiment and increase the sample size, but the imposition of the treatments and hand-pollinations are labor-intensive. Second, there was heavy damage to the experimental heads by predispersal seed predators, so many of the seeds we counted were probably not viable. Thus, our data may be a good measure of pollination success but not of viable seed production in these plants. Third, the seed set of heads that were unmanipulated (nonbagged control) was more similar to bagged heads without beetles than to bagged heads with two or four beetles (Fig. 7). This was unexpected because the unmanipulated heads were exposed to beetle damage. It is possible that beetles bagged onto heads do more damage than beetles free to move. Also, the control heads in the enclosure experiment were located farther from corn than were the densest populations at McKnight Prairie. *H. annuus* plants placed near the corn edge of McKnight Prairie averaged over 11 beetles per head (Fig. 5). Such plants might experience more substantial reductions in seed production.

There are several means by which *D. barberi* could reduce seed set. If they consume pollen from fertilized stigmas, the beetles could prevent successful fertilization even in florets that received sufficient pollen. In addition, consumption of pollen, nectar, and rays may reduce visitation to *Helianthus* heads by pollinating insects. *D. barberi* feeding is also likely to reduce male reproductive success of *Helianthus* males. Pollen consumption directly reduces the amount of pollen available for export on pollinating insects, and the damaged ray petals of heads attacked by *D. barberi* could make them less attractive to pollinators.

Helianthus spp. are effectively pollinated by a number of native bee species, both specialists and generalists (Robertson 1922; Hurd et al. 1980; Parker 1981; Neff & Simpson 1990). The behavior of *Helianthus* pollinators could be affected by *D. barberi* in at least three ways. First, if pollen and nectar are depleted by *D. barberi*, bees are less likely to visit the heads or to spend much time foraging if they do visit. Second, the presence of many beetles on *Helianthus* heads could cause bees to avoid approaching or landing (Dickinson & McKone 1992). Third, consumption of ray petals by *D. barberi* may also reduce pollinator visitation by reducing the floral display. After removing all the rays from heads of *H. annuus*, Neff and Simpson (1990) found a 90% reduction in bee visitation, although there was no reduction in seed set. Stuessy et al. (1986) observed a reduction in insect visitation, a reduction in the diversity of visitors, and a 64% reduction in seed set after ray removal in *H. grosseserratus*. In addition to possible effects on pollination of *Helianthus*, reduced visitation to heads could affect bees' reproductive success and ultimately their population sizes. This is most likely in specialized bees that are dependent on *Helianthus* pollen for larval food (the "primary oligoleges" of Hurd et al. 1980).

It is difficult to extrapolate the long-term effects of *D. barberi* feeding on *Helianthus* populations in prairie remnants, but there are several possibilities. Pollen consumption by *D. barberi* and reduced visitation by bees could change the pattern of gene flow via pollen, ultimately leading to more genetic isolation and potential inbreeding within *Helianthus* populations. If seed set is consistently reduced by *D. barberi* over many years, recruitment of new individuals into local *Helianthus* populations could be limited. The lack of successful pollination could increase the probability of extinction in small, isolated populations, as has been demonstrated in *Clarkia concinna* (Onagraceae; Groom 1998).

Although we concentrated on *Helianthus*, *D. barberi* is a generalist flower feeder (Hill & Mayo 1980) and could have similar effects on other prairie plants that bloom in late summer. For example, *D. barberi* can be abundant on *Solidago* spp. (Messina & Root 1980; Werner et al. 1980; Siegfried & Mullin 1990; personal observation).

If *D. barberi* has a significant detrimental effect on reproduction of *Helianthus* and other prairie composites, maintenance of these species may depend on core areas of prairie reserves that are relatively buffered from the influx of beetles at the edge. Most theoretical treatments of edge effects require a distance at which the effect is no longer present (e.g., Laurance & Yensen 1991). The density of *D. barberi* is a decreasing function of distance from edge, and there is no point at which density reaches zero at McKnight Prairie (Figs. 2 & 5). For illustration, however, we can assume that the edge effect reaches minimal levels at 60 m from the corn edge. If corn is grown along just one edge of McKnight Prairie, the core would be only 65% of the apparent area. If corn were grown on all four sides of McKnight Prairie, the core would be only 25% of the apparent area. Many tallgrass prairie remnants are smaller than McKnight Prairie, and some (such as railroad rights of way) are shaped so that no portion is more than a few meters from an agricultural edge. Such reserves may have little or no area free from the negative effects of edges with agriculture.

Unfortunately, *D. barberi* is just one of a number of agricultural pests that might have a detrimental effect on prairie plants. Soybeans are often planted in annual rotation with corn in the midwestern United States. A diverse array of insect herbivores can be found in soybean fields (Turnipseed & Kogan 1976; Kogan & Turnipseed 1987), and these might also invade prairie edges and feed on legumes and other plants. Because tallgrass prairie is one of the most reduced and fragmented habitats in North America, an understanding of such edge effects is particularly crucial to maintaining species diversity in the few existing remnants.

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