Occurrence of Danaus plexippus L. (Lepidoptera: Danainae) on milkweeds (Asclepias syriaca) in transgenic Bt corn agroecosystems

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Abstract

The potential negative effects of transgenic Bt corn on the monarch butterfly, Danaus plexippus, requires quantification of the presence of D. plexippus in the field and of the effect of Bt corn tissues on oviposition and larval survival. During a 2-year field study, D. plexippus females laid similar number of eggs on Asclepias syriaca in corn fields and on A. syriaca growing in roadside habitats parallel to corn fields. In 1999 and 2000 similar number of D. plexippus larvae were observed on A. syriaca in corn fields and roadside habitats, whereas a greater proportion of A. syriaca in corn fields were infested by at least one D. plexippus larva in 2000. Similar number of eggs were laid in transgenic Bt and non-Bt corn fields, indicating that females did not avoid leaves dusted with anthers and 6–72 Bt pollen grains/cm². Similar number of D. plexippus larvae were found in and near Bt corn fields compared to non-Bt corn fields following corn anthesis. In 2000, transgenic Event MON810 Bt corn pollen and anthers had no measurable effects on D. plexippus oviposition or larval survival.

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1. Introduction

Members of the Asclepiadaceae are the larval food source for Danaus plexippus L. (Lepidoptera: Danaidae), the monarch butterfly (Brower, 1969). Common milkweed, Asclepias syriaca L., is particularly important for the migratory generation of D. plexippus in eastern North America because >90% of adult monarchs wintering in Mexico feed on A. syriaca as larvae (Malcolm et al., 1993) and 50% developed as larvae on A. syriaca growing in the upper mid-west, a region with highly concentrated row crop agriculture (Wassenar and Hobson, 1998).

A native perennial, A. syriaca is the most common milkweed species in cultivated fields of eastern North America (Evetts and Burnside, 1972; Bhowmik and Bandeen, 1976; Malcolm et al., 1993) because of new shoots emerging from root fragments (Cramer, 1977; Minshall, 1977; Bhowmik and Bandeen, 1976; Yenish et al., 1997). Seedling establishment is aided by reduced tillage and cultivation practices that leave seeds near the surface, and the suppression of competitive plant species by herbicides that often do not effectively control A. syriaca (Burnside, 1977; Evets and Burnside, 1975; Bhowmik and Bandeen, 1976; Bhowmik, 1994; Yenish et al., 1996, 1997). In a
survey of 13 mid-western states, Evetts (1977) estimated that 5 million ha of corn and 2.5 million ha of soybeans contained at least 2.5 A. syriaca plants/ha. In roadside surveys conducted in eastern Nebraska from 1976 to 1979 one-third of the corn fields and half the 1200 km of roadsides were infested with A. syriaca (Cramer and Burnside, 1982). In Iowa, A. syriaca was present in 46% of the corn fields and 71% of the roadside habitats (Hartzler and Buhler, 2000). Eastern North America corn fields constitute 19% of the effective D. plexippus breeding habitat. The size of the overwintering adult population in Mexico makes it likely that D. plexippus is utilizing A. syriaca in corn fields (Taylor and Shields, 2000). The occurrence of immature stages on A. syriaca in corn fields, corn field edges, soybean fields, forage crop fields, and non-agricultural land was observed throughout summer at several sites in North America (Oberhauser et al., 2001). The overlap between the peak of the immature migratory generation of D. plexippus in the fall and corn pollination ranged from 15% in Iowa to 62% in Ontario (Oberhauser et al., 2001). In Ontario, non-agricultural habitats contained 100 times more D. plexippus than corn fields on a per area basis, two times more in Minnesota/Wisconsin, and four times in Iowa (Oberhauser et al., 2001). Due to the predominance of agricultural habitats, it is estimated that 73 and 43 times more D. plexippus adults are produced from milkweeds in corn fields than in non-agricultural land in Minnesota/Wisconsin and Iowa, respectively (Oberhauser et al., 2001). Previous studies have shown that high densities of corn pollen and anthers accumulate on milkweeds in corn fields (Jesse and Obrycki, 2000; Pleasants et al., 2001). Larval D. plexippus ingest pollen and anthers and may be negatively affected by the Bt-toxin they contain (Hellmich et al., 2001; Jesse and Obrycki, 2000; Losey et al., 1999).

In a greenhouse study, D. plexippus females laid significantly more eggs on milkweed plants surrounded by non-Bt corn compared to plants surrounded by Bt corn (Tschenn et al., 2001). Because of the low number of eggs laid on A. syriaca surrounded by corn, additional research was needed to determine if D. plexippus females discriminate between types of corn hybrids in the field (Tschenn et al., 2001).

The objectives of this study were to (1) compare D. plexippus oviposition on A. syriaca plants in and bordering corn fields, (2) determine the relative abundance of D. plexippus larvae on A. syriaca plants in and bordering corn fields, and (3) quantify the effects of Bt corn pollen and anthers on D. plexippus oviposition and larval survival.

2. Materials and methods

In 1999, four field sites with relatively high densities of A. syriaca within and adjacent to corn fields were selected from a random survey of sites used to quantify A. syriaca distribution in Iowa (Hartzler and Buhler, 2000). The four sites were located in three counties in north central Iowa. For 7 weeks, beginning 11 July, the number of monarch eggs and each larval stage was counted at each field site by examining the upper and lower surfaces of the leaves and the stem of each A. syriaca plant within 100 m transects in three positions at each site. Plants were sampled in the corn field (0.5 m outside the first row of corn, and between rows 1 and 2, 4 and 5, and 14 and 15). Corn rows being 0.76 m apart, an area of 280 m² was sampled at each site. In roadsides, plants were sampled from an area located <0.5 m from the field to >1 m from the nearest parallel road. Roadside width at the four sites ranged from 4.4 to 10 m, five total area from 440 to 1000 m². Plants growing within 1 m of the road edge were also sampled, a total area of 100 m² per site.

In July 2000, three field sites in central Iowa (Hamilton and Story County) were selected, each with a Bt (MON810 transgenic hybrids: Agropro 9355, Asgrow 730Bt, Pioneer 35NOS) and non-Bt (Agropro 9565, Asgrow 730, Garst hybrids) corn field within 3.2 km of each other. Each site had at least 20 A. syriaca growing within the first 10 rows of corn, and at least 100 A. syriaca growing within a 600 m transect in the roadside parallel to the corn field.

Beginning 3 July, each field site was surveyed weekly for D. plexippus eggs and larvae. The number of A. syriaca plants examined and the distance surveyed in each of the three locations on each sampling date was recorded, so the number of D. plexippus are reported per square meter. A. syriaca growing in the roadside area parallel to the corn field were sampled, roadside width ranged from 6.5 to 9.8 m. Plants growing within 0.5 m of the first row of corn and within rows 1–10 of corn (6.9 m into the corn field) were...
surveyed. The number of eggs and each instar was counted on each *A. syriaca* by examining the upper and lower surfaces of all the leaves and the stem; the location of the *D. plexippus* life stage (upper or lower leaf surface, top, middle, or bottom portion of the plant) was recorded. For each *A. syriaca* with a *D. plexippus* egg or larva, the presence of other arthropods, the height of the plant, and the number of other *A. syriaca* plants within 1 m were recorded.

To determine the density of pollen grains and presence of anthers on *A. syriaca* leaves, 0.79 cm² leaf samples were removed with a #6 cork borer (Jesse and Obrycki, 2000). The presence or absence of anthers was noted for each *A. syriaca* plant with a monarch life stage within the corn fields. Pollen grains and anthers were counted under a dissecting microscope. Leaf disk samples were taken during pollen shed (the week of 10 July) at the three field sites, and additionally during the week of 17 July at field site 1.

During the second to fourth week of *D. plexippus* sampling the characteristics of randomly selected *A. syriaca* were recorded, to compare *A. syriaca* plants with and without *D. plexippus*. Height and diameter of the plant, plant stage, number of other plants within 1 m², and the presence of predacious arthropods and aphids were recorded. Pollen samples were taken from one leaf in the middle of each *A. syriaca* from field sites 1 and 2 during the second week of the survey. Every 15th, 20th, or 25th *A. syriaca* in the roadsides was selected, and every 5th or 10th plant was selected in the corn field depending on the density of plants at each site. Randomly selected *A. syriaca* with *D. plexippus* were recorded, but these plants were removed from the data set prior to analysis since the plant characteristics were already included in the survey for *D. plexippus*.

### 2.1. Data analysis

The occurrence of *D. plexippus* in 1999 and 2000 was analyzed by examining the number of monarch life stages per square meter. This analysis compared the number of *D. plexippus* at different field sites and plant locations, regardless of how many *A. syriaca* plants were present. In 2000, the proportion of plants with a *D. plexippus* was calculated. In this analysis, it was determined if the position of a plant in relation to the corn field influenced the probability for *A. syriaca* to have eggs or larvae. All larval instars of *D. plexippus* were combined for these analyses.

Data from each year were analyzed separately (PROC MIXED, SAS Institute, 2001) using an analysis of variance (ANOVA) for repeated measures. The AR1 (autoregressive) option was used in the repeated measures statement to model the covariant structure (SAS Institute, 2001). Factors and interactions analyzed in the repeated measures design were field site, plant position (road edge, roadside, within corn field), sampling date, and additionally in 2000, corn type (Bt and non-Bt). The two sources of error used for the data from 1999 were (1) field site × plant position and (2) week × field site × plant position. The two sources of error used for the data from 2000 were (1) field site × corn hybrid × plant position and (2) week × field site × corn hybrid × plant position.

A partial life table was constructed for immature *D. plexippus* sampled in 1999, following the methods described by Southwood (1966). The number of eggs, early instars (first and second), and late instars (third to fifth) entering a stage (Iₓ) in the 100 m transects was estimated by integrating the density estimates for each stage over accumulated degree days divided by the development time in degree days for that life stage (Southwood, 1966). The number of individuals dying in a stage (dₓ) and the percentage mortality in a stage (%ₘₓ) was calculated. An average developmental threshold for eggs through fifth instars of 11.65 °C, determined by Zalucki (1982) for *D. plexippus* larvae feeding on *Asclepias fruticosa* L., was used to calculate accumulated degree days in the field. Thermal accumulations (>11.65 °C) used in the life table analysis were 44.5 degree days for eggs, 58.1 degree days for first to second instars, and 117.9 degree days for third to fifth instars (Zalucki, 1982).

A logistic regression (PROC LOGISTIC, SAS Institute, 2001) was used to determine if pollen densities or corn type effected the presence of *D. plexippus* eggs and larva.

### 3. Results

In 1999, the mean number of eggs or larvae per square meter was similar at the four field sites (Table 1). Therefore, data from the field sites were averaged to examine effects of the plant positions.
Fig. 1. The mean number of eggs, first to second and third to fifth instar larvae per square meter in corn fields, roadsides, and road edges in 1999.

The mean number of milkweeds on 11 July was 25 ± 14 A. syriaca (3–65) in the road edge, 104 ± 74 (11–324) in the roadside, and 31 ± 14 (3–59) in the corn fields at the four field sites. On 22 August, the average was 17 ± 11 (1–49) in the road edge, 69 ± 31 (27–160) in the roadside, and 22 ± 7 (6–40) in the corn fields.

Surveyed (road edge, roadside, and corn field) and time (7 weeks) on the mean number of D. plexippus eggs or larvae per square meter (Fig. 1). The mean number of eggs and larvae per square meter was similar in the road edge, roadside, and within the corn field over the 7 weeks of sampling (Table 1). The mean number of milkweeds on 11 July was 25 ± 14 A. syriaca (3–65) in the road edge, 104 ± 74 (11–324) in the roadside, and 31 ± 14 (3–59) in the corn fields at the four field sites. On 22 August, the average was 17 ± 11 (1–49) in the road edge, 69 ± 31 (27–160) in the roadside, and 22 ± 7 (6–40) in the corn fields.
In 1999, the mortality rate for eggs in the corn field, roadside, and road edge was 69, 68, and 58%, respectively (Table 2). Mortality rate for the early instars ranged from 76% in the roadside to 94% in the road edges and was >90% from egg to late instars in all three locations (Table 2).

In 2000, the mean number of *D. plexippus* per square meter and the proportion of a *A. syriaca* plant having an egg or larva was similar on the three sites (Table 1), so the site data was combined to examine other effects. Similar number of eggs per square meter were observed in and near Bt corn fields compared to non-Bt corn and compared to non-Bt corn fields and average number of eggs per square meter within corn fields were similar to numbers in the roadedges (Table 1). The highest number of eggs per square meter was observed during the week of 24–28 July (ANOVA, d.f. = 3, 6, P = 0.0009). Of the 46 plants observed with two eggs, 21 were recorded during that week, nine plants were observed with four eggs, seven of them during that week. The maximum number of eggs observed on a single *A. syriaca* was eight eggs, also during the same week.

The average number of larvae per square meter at the Bt and non-Bt corn sites was similar (Table 1). Similar number of larvae were observed in the roadside compared to within the corn during the 4 weeks of sampling (Table 1). There was a similar probability for eggs to occur on a *A. syriaca* growing in or next to a Bt corn field compared to non-Bt corn (Table 1). There was also a similar probability for eggs to occur on an *A. syriaca* plant growing in the roadside compared to within the corn field (Table 1). The highest probability that an *A. syriaca* would have at least one egg on it occurred during the week of 24–28 July (ANOVA, d.f. = 3, 6, P = 0.03) (Fig. 2).

The probability of one or more larvae occurring on an *A. syriaca* was similar at Bt and non-Bt corn sites over the 4 weeks of sampling (Table 1). There was greater probability of larval occurrence on plants within a field compared to the roadside (Table 1, Fig. 2).

Most *D. plexippus* eggs (95%) were laid on the adaxial surface of *A. syriaca* leaves. Zalucki and Kitching (1982a) also observed 96.5% of eggs on the underside of leaves, Borkin (1982) observed 67%. Forty-six percent of the eggs were laid in the middle

### Table 1

<table>
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<th>Year</th>
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<th>Effect</th>
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<th>Error</th>
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<th>P</th>
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<td>0.00</td>
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<tr>
<td></td>
<td>Week</td>
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<td>6</td>
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<td>0.00</td>
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<td>Week</td>
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<td>6</td>
<td>5.71</td>
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<td>Proportion of plants with eggs</td>
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a Non-significant interactions between factors are not presented.

### Table 2

<table>
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<td>10</td>
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<td>–</td>
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<tr>
<td></td>
<td>Egg-late instars</td>
<td>–</td>
<td>202</td>
<td>95</td>
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<tr>
<td>Roadside</td>
<td>Egg</td>
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<td>200</td>
<td>68</td>
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<td>96</td>
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<tr>
<td></td>
<td>Egg-late instars</td>
<td>–</td>
<td>150</td>
<td>98</td>
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</table>

a Number of individuals entering stage.
b Number of individuals dying in stage.
c Percent mortality in stage.

* Significant effect (P < 0.05).
portion of the plant, 39% in the top, and 15% in the bottom portion.

The majority of the larvae (83%) were also observed underneath A. syriaca leaves, 17% were on the top surface. A similar proportion of larvae were observed in the top (38%) and middle (35%) portions of the milkweed plant, and 27% in the lower portion.

Most of the eggs and larvae (53%) were observed on plants with one to three A. syriaca within 0.5 m, 28% of eggs, 36% of larvae were observed on plants with no other A. syriaca within 0.5 m. The remaining 19% of eggs and 11% of larvae were observed on A. syriaca with more than four additional A. syriaca within 0.5 m.

A. syriaca plants with D. plexippus in Bt corn fields had from 5.9 ± 1.5 pollen grains/cm² at site 1 to 72.3 ± 14.5 pollen grains/cm² at site 3, 79–100% of A. syriaca had at least one anther. In non-Bt corn fields A. syriaca with D. plexippus had from 7.5 ± 3.0 pollen grains/cm² at site 1 to 125.6 ± 41.5 pollen grains/cm² at site 3, at least one anther was found on 75–100% of plants. Pollen densities and type of corn (Bt or non-Bt) did not affect the presence of D. plexippus (LOGISTIC, d.f. = 1, P > 0.05).

The A. syriaca with at least one D. plexippus life stage were taller at Bt corn sites (average height of 58.4 ± 1.6 cm) compared to non-Bt corn sites (50.6 ± 1.5 cm) (ANOVA, d.f. = 1, 2, P = 0.04), and
taller in the roadside (66.0 ± 1.8 cm) compared to the corn fields (48.1 ± 1.2 cm) (ANOVA, d.f. = 1, 2, P = 0.03), except during the third week at one site where milkweed was taller in non-Bt corn field than in the recently mowed roadside. The A. syriaca without D. plexippus were similar in height in Bt (51.3 ± 2.4 cm) and non-Bt corn field sites (47.9 ± 1.7 cm) (ANOVA, d.f. = 1, 2, P = 0.75), and taller in the roadside (55.6 ± 1.8 cm) than in the corn (42.9 ± 2.1 cm) (ANOVA, d.f. = 1, 2, P = 0.02), except at the site where the non-Bt roadside was mowed. At the mowed site, A. syriaca without D. plexippus was taller in the field in both non-Bt and Bt corn. Considering all situations there was no difference in the height of A. syriaca with D. plexippus (54.7 ± 1.1 cm) compared to A. syriaca without D. plexippus (49.3 ± 1.4 cm) (ANOVA, d.f. = 1, 2, P = 0.13).

Araneae, Formicidae, Coccinellidae larva, Chrysopidae eggs and larvae, Reduviidae, Pentatomidae and Aphididae were observed on A. syriaca. Predaceous arthropods or aphids were observed in similar proportions on A. syriaca with or without D. plexippus (ANOVA d.f. = 1, 2 P > 0.48). Of the 294 plants without D. plexippus, 8% had aphids and 12% predaceous arthropods. Of the 331 plants with D. plexippus, 9% had aphids and 15% had predaceous arthropods.

4. Discussion

Oberhauser et al. (2001) reported that D. plexippus females oviposited more frequently on A. syriaca concealed within corn plants (Tschenn et al., 2001). In both 1999 and 2000, however, similar number of eggs were observed on A. syriaca plants growing in non-agricultural habitats. This observation is supported by a greenhouse study showing that D. plexippus females laid eggs less frequently on A. syriaca concealed within corn plants (Tschenn et al., 2001). In 2000, the number of eggs per square meter and the greatest proportion of plants with eggs were significantly higher during the peak in August and the peak D. plexippus egg laying occurred. These results are similar to those of Oberhauser et al. (2001) who observed overlap of monarch larval and corn anthesis in Minnesota and Ontario during 2000; anthesis occurred before peak D. plexippus egg laying in Iowa and Maryland.

Similar number of eggs were counted on A. syriaca in and near transgenic Bt and non-Bt corn fields after pollen shed (second to third week of sampling), indicating that D. plexippus females do not avoid A. syriaca plants with Bt corn pollen and anthers deposited on them. In caged experiments, Tschenn et al. (2001) observed similar number of eggs oviposited on Asclepias curassavica L. plants dusted with Bt and non-Bt corn pollen. However, in a greenhouse experiment, D. plexippus females oviposited less on A.
A. syriaca surrounded by corn (Tschenn et al., 2001). No difference was observed in the number of eggs on A. syriaca in corn fields compared to roadides. Thus, other factors (i.e. cardenolide content, plant height, or nutrient content) have greater influence on oviposition behavior than the presence of Bt corn pollen. In addition, pollen densities recorded on A. syriaca growing in corn fields were below the 500 pollen grains/cm² used in the previous greenhouse study (Tschenn et al., 2001).

After corn anthesis, the number of larvae in and near corn was similar in Bt and non-Bt fields. Pollen from events Bt11 or MON810 did not increase D. plexippus larval mortality, however the added toxin exposure from anther tissue did increase D. plexippus larval mortality in a laboratory study (Hellmich et al., 2001). Larval D. plexippus placed on milkweeds in Bt and non-Bt fields suffer high mortality rates (Stanley-Horn et al., 2001). When A. syriaca were caged to exclude predators, after pollen and anthers had been naturally deposited on them, mortality of D. plexippus larvae tended to be highest in Bt corn fields (Jesse and Obrycki, 2003).

In the mid-western United States immature D. plexippus are exposed to a range of agricultural practices (Obrycki et al., 2001), some with negligible impact, others with potential negative effects. Conservation of D. plexippus larval habitats therefore requires increased scrutiny of the effects of agricultural practices on their populations.

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