Selection and Evaluation of a Companion Plant to Indirectly Augment Densities of Coleomegilla maculata (Coleoptera: Coccinellidae) in Sweet Corn

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ABSTRACT Coleomegilla maculata (DeGeer), which is a frequent predator of Helicoverpa zea (Boddie) eggs on sweet corn, prefers to oviposit on plants that have glandular trichomes. These plants provide C. maculata eggs a refuge from cannibalism and other predation. Previous work showed that interplanting glandular pubescent weeds in corn increases C. maculata density and predation on H. zea eggs. We conducted an oviposition preference screening to identify a cultivated species that could provide the same augmentation of C. maculata and possibly increase biological control. In our experiment, tomato had 2.5 times more C. maculata eggs found on it than Acalypha ostryifolia Ridell, a weed documented to be preferred for oviposition over corn. In a separate experiment, 9.6 times more C. maculata eggs were found on a tomato companion crop than on corn, and eggs on tomato had 2.6–5.9 times higher survival than those on corn. In corn plots with a companion crop of tomato, C. maculata larvae were 5–10 times more abundant near the companion crop than in an equivalent location in the corn monoculture. Augmentation of larval densities declined as distance from the companion tomato crop increased, but the augmentation effect persisted for at least 5 m away from the companion crop. In 1 yr of our study, there was a trend toward higher densities of C. maculata adults in the plots with a companion crop of tomato. The observed augmentation of C. maculata did not result in an increase in H. zea egg predation or decrease in ear infestation.

KEY WORDS Coleomegilla maculata, Helicoverpa zea, biological control, companion planting, habitat modification

The native coccinellid Coleomegilla maculata (DeGeer) is the most frequent predator of Helicoverpa zea (Boddie) eggs in Kentucky sweet corn, accounting for 44–56% of observed predation events on sentinel eggs (Cottrell and Yeargan 1998a, Pfannenstiel and Yeargan 2002). C. maculata is also an important predator of other sweet corn insect pests such as the corn leaf aphid, Rhopalosiphum maidis (Fitch), and European corn borer, Ostrinia nubilalis (Hübner) (Wright and Laing 1980, Phoofolo et al. 2001). C. maculata is found in a wide range of field, horticultural, and tree crops throughout North America (Warren and Tadic 1967, Nault and Kennedy 2000, Wright and DeVries 2000). Within these crops, C. maculata feeds on important pests including Heliothis virescens (F.) and H. zea in cotton; the fall webworm, Hyphantria cunea (Drury), in pecan; the cereal leaf beetle, Oulema melanopus L., in oats; the Colorado potato beetle, Leptinotarsa decemlineata (Say), and the green peach aphid, Myzus persicae (Sulzer), in potato; the greenbug, Schizaphis graminum (Rondani), in sorghum and wheat; and various aphid species on other crops (Whitcomb and Bell 1964, Warren and Tadic 1967, Shade et al. 1970, Bryson 1974, Mack and Smilowitz 1980, Groden et al. 1990). In addition to arthropod prey items, C. maculata feeds on nectar, fungal spores, and pollen (Stone et al. 1984, Hodek and Honek 1996, Patt et al. 1997). C. maculata feeds heavily on pollen and is capable of completing its development on this food source; the beetles also tend to aggregate where pollen is available (Smith 1965, Groden et al. 1990, Harmon et al. 2000, Nault and Kennedy 2000, Landgren and Wiedenmann 2004).

Within the corn system, the presence of pollen diverts C. maculata’s diet away from carnivory, but in alfalfa, the presence of a pollen source leads to greater net predation on aphids by C. maculata (Cottrell and Yeargan 1998b, Harmon et al. 2000, Pfannenstiel and Yeargan 2002). Plant resources that are not pollen-based also affect C. maculata’s abundance and impact on other arthropods. Andow and Risch (1985) found higher C. maculata abundance and predation in monoculture corn than in corn grown with bean and squash. Weedy soybeans have been reported to have a higher abundance of C. maculata than weed-free soybeans (Shelton and Edwards 1983). In sweet corn patches in which the annual weed hophornbeam coperleaf, Acalypha ostryifolia Ridell, was present, there were higher densities of C. maculata larvae and in-
increased predation on sentinel *H. zea* eggs (Cottrell and Yeargan 1998a).

When plants with abundant glandular trichomes are available, they are preferred oviposition sites for *C. maculata* (Obrycki and Tauber 1985, Cottrell and Yeargan 1998a, Griffin and Yeargan 2002a, Staley and Yeargan 2005). Eggs on these plants suffer less cannibalism and other predation than those on nonglandular pubescent plants (Cottrell and Yeargan 1998a, Griffin and Yeargan 2002b). Predation of *C. maculata* eggs on corn plants is as high as 77% (Wright and Laing 1982). Cottrell and Yeargan (1998a) reported that 25–30% of *C. maculata* egg clusters on corn were cannibalized every 3 h. Over 24-h periods, predation on *C. maculata* egg clusters on corn averaged >80% (Griffin and Yeargan 2002b). When *C. maculata* egg clusters were placed on glandular pubescent weeds, *A. ostryifolia* or *Abutilon theophrasti* Medicus, cannibalism was only 0–5% per 3 h, and only ≈25% were attacked in a 24-h period (Cottrell and Yeargan 1998a, Griffin and Yeargan 2002b). These glandular pubescent weeds provide a refuge from cannibalism and other predation because predators, particularly coccinellid larvae, have difficulty moving on these surfaces and tend to avoid them (Elsey 1974). Another predaceous insect, *Aphidoletes aphidimyza* (Rondani), avoids egg predation by *C. maculata* by preferentially ovipositing in areas of high pubescence (Lucas and Brodeur 1999).

Including a glandular pubescent weed in sweet corn plantings led to increased density of *C. maculata* larvae on sweet corn plants. This effect was caused by a high proportion of eggs being laid on the weed and having higher survival than if they had been laid on corn (Cottrell and Yeargan 1998a). Coccinellid larvae themselves have a difficult time moving on glandular pubescent surfaces so they disperse from these weeds by dropping to the ground ≈24 h after hatching and disperse onto corn (Cottrell and Yeargan 1999).

The inclusion of a glandular pubescent weed, to serve as a refuge from egg predation, has been shown to increase *C. maculata* densities and decrease survival of *H. zea* eggs on sweet corn (Cottrell and Yeargan 1998a). The tolerance or encouragement of weeds in cropping systems can have pest management benefits (Altieri and Whitcomb 1979, Norris and Kogan 2005). However, nonweed components of habitat diversity are more agronomically acceptable and thus more likely to be adopted by growers. Our first objective was to identify a desirable cultivated plant that would provide a refuge from cannibalism and predation of *C. maculata* eggs and possibly have additional benefits (e.g., nitrogen fixation or being a harvestable crop). Additionally, we wanted to determine if interplanting such a glandular pubescent domesticated plant with sweet corn has a positive effect on *C. maculata* densities and *H. zea* egg predation, thereby reducing crop infestation by *H. zea*.

### Materials and Methods

**Oviposition Choice Experiments.** Four 11 by 14-m plots of ‘Golden Queen’ sweet corn were planted on 14 May 2003 at the University of Kentucky North Farm near Lexington. Spacing between rows was 0.9 m, and each plot contained 12 rows. On the day of planting, an application of preemergence herbicide (atrazine [1.52 kg/ha] + S-metolachlor [1.18 kg/ha]) was made to the field. Weeds that escaped chemical control were mechanically removed through tilling and hoeing throughout the experiment.

Domesticated plants tested for *C. maculata* oviposition preference were chosen because they either contained a high degree of glandular pubescence or were traditional companion crops of corn (Table 1). Hophornbeam copperleaf was included as a positive control as it was previously documented to be preferred for *C. maculata* oviposition (Cottrell and Yeargan 1998a). Candidate plants were grown in a greenhouse and placed in the field in a randomized complete block design with seven replicates. All candidate plants were ≈20 cm tall at the time they were taken to the field. Plants were placed in the sweet corn field on 8 July 2003 before corn tasseling. Individual plants in pots were placed in holes such that the lip of the pot was flush with the soil surface. One of the plots contained only one block of candidate plants, but the other three contained two blocks of all candidate plants, one between the 3rd and 5th rows and the second between the 5th and 10th rows. Plants were placed at least 2 m from the next nearest candidate plant and at least 3 m from the plot edge. Within a block, a particular row middle contained either four or five plants.

### Table 1. Common and scientific names of candidate plants screened for *C. maculata* oviposition preference and mean no. (±SE) of egg clusters and eggs laid on each species when interplanted with sweet corn during anthesis.

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Egg clusters/ plant/48 h</th>
<th>Eggs/plant/48 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ornamental tobacco (var. unknown)</td>
<td><em>Nicotiana alata</em> Link and Otto</td>
<td>1.5 ± 0.2a</td>
<td>22.0 ± 3.2a</td>
</tr>
<tr>
<td>Tomato 'Brandywine’</td>
<td><em>Lycopersicon esculentum</em> Miller</td>
<td>1.4 ± 0.2a</td>
<td>20.4 ± 3.1a</td>
</tr>
<tr>
<td>Petunia (var. unknown)</td>
<td><em>Petunia hybrida</em> Vilimor</td>
<td>0.6 ± 0.1b</td>
<td>8.7 ± 1.8b</td>
</tr>
<tr>
<td>Snail medic ‘SA 28738’</td>
<td><em>Medicago satellata</em> L.</td>
<td>0.5 ± 0.1b</td>
<td>8.1 ± 2.0b</td>
</tr>
<tr>
<td>Chickpea ‘Dewelly’</td>
<td><em>Cicer arietinum</em> L.</td>
<td>0.3 ± 0.1b</td>
<td>6.2 ± 2.0b</td>
</tr>
<tr>
<td>Hophornbeam copperleaf</td>
<td><em>Acalypha ostryifolia</em> Ridell</td>
<td>0.5 ± 0.1b</td>
<td>5.8 ± 1.6b</td>
</tr>
<tr>
<td>Squash ‘Early Prolific Straightneck’</td>
<td><em>Cucurbita pepo</em> L.</td>
<td>0.3 ± 0.1b</td>
<td>3.3 ± 1.1b</td>
</tr>
<tr>
<td>Cucumber ‘Spacemaster’</td>
<td><em>Cucumis sativus</em> L.</td>
<td>0.1 ± 0.1b</td>
<td>1.5 ± 0.9b</td>
</tr>
<tr>
<td>Potato ‘Hairy Prince’</td>
<td><em>Solanum tuberosum</em> L.</td>
<td>0.0 ± 0.0c</td>
<td>0.0 ± 0.0c</td>
</tr>
</tbody>
</table>

Means within columns followed by the same letter are not significantly different (*P > 0.05, Ryan–Einot-Gabriel-Welsch multiple range test).
Plants were examined for coccinellid egg clusters on 18 July 2003 and every 2 d afterward until 28 July 2003. These dates fell during corn anthesis or soon after its cessation when *C. maculata* adults occur in high numbers and oviposition is at its peak. The number of egg clusters per plant and number of eggs per cluster were recorded. Eggs were removed and reared in the laboratory to verify species identity. The number of clusters per plant and total number of eggs per plant were compared among plant species using a repeated-measures analysis of variance (ANOVA), and means were compared with a Ryan-Gabriel-Einot-Welsch test (SAS Institute 2003).

In 2004, a *C. maculata* oviposition preference test was conducted using four tomato varieties. This was done because 'Brandywine', the variety used in the 2003 preference test among different plant species, has a peculiar potato-shaped leaf unlike many conventional varieties of tomato. Three tomato varieties with conventionally shaped leaves—'Mountain Spring', 'Sunbeam', and 'Sunleaper'—were tested along with 'Brandywine'. Greenhouse raised tomato plants, all ≈25 cm tall, were placed in a 30 by 30-m plot of 'Golden Queen' sweet corn on 26 July 2004, before tassel emergence. Five replicates of each tomato variety were present in a completely randomized placement within the plot. Each plant was at least 2 m from the next nearest tomato plant and at least 3 m from the plot edge. With the onset of anthesis plants were examined every 48 h, and the number of clusters and eggs per cluster were recorded. Egg counts began on 30 July and ended on 12 August. Count data from seven dates over 13 d were analyzed using a repeated-measures ANOVA (SAS Institute 2003).

**Companion Planting Experiments.** Sweet corn ‘Golden Queen’ plots were established at the University of Kentucky North Farm near Lexington on 10 May and 23 May in 2004 and 2005, respectively. Sweet corn plots were 32 by 32 m in 2004 and 32 by 10 m in 2005. Herbicide treatments followed the same procedure as before except locations in the field that were designated for the companion crop were protected with a layer of heavy plastic. Weeds that escaped chemical control were removed mechanically throughout the experiment.

Each plot was randomly assigned to one of two treatments. The first treatment was a sweet corn monoculture plot to serve as a control. Plots assigned to the second treatment had a 3 by 4-m block of tomato, consisting of four rows of eight plants each, placed in the middle. Tomatoes were greenhouse raised and transplanted into the plot centers on 26 June 2004 and 2 July 2005. Four replicates of each treatment were used, and each experimental unit had an equal chance of being either treatment; thus, this was a completely randomized design. In the companion crop treatment tomato plants were visually examined for *C. maculata* oviposition on three dates from 7 July to 20 July 2004 and on three dates from 17 July to 28 July 2005. The number of egg clusters and number of eggs per cluster were recorded on each date. In 2004, the first sampling date, 7 July, occurred before pollen shed, and all 128 plants, 32 per plot, were examined. On the next two sampling dates, 12 and 20 July, eight randomly selected tomato plants were sampled from each plot that contained tomato plants. In 2005, *C. maculata* oviposition was monitored on the tomato companion crop by examining every other plant in one randomly selected outside row, immediately bordering sweet corn, and one randomly selected inside row, which was bordered on both sides by other rows of tomato. Sampling dates in 2005 were 17, 21, and 28 July. As in 2004, the first sampling date occurred before anthesis. In 2005, concurrent sampling of sweet corn in the monoculture treatments took place to quantify *C. maculata* eggs in that treatment. Two randomly selected row meters at least 4 m from the plot edge were visually examined in each monoculture plot, and the numbers of *C. maculata* egg clusters and eggs per cluster were recorded. Orthogonal contrasts were used to determine if differences existed in the amount of *C. maculata* oviposition on the tomato companion crop between the different sampling dates in both years, and a repeated-measures ANOVA was used to determine if differences existed between oviposition amounts on tomato and corn in 2005 (SAS Institute 2003).

A *C. maculata* colony was maintained in the laboratory as described by Griffin and Yeargan (2002b). Mated females were kept singly in petri dishes. The lid of the petri dish was lined with florist’s paper (green). Eggs laid on this paper were collected daily and kept at 12 ± 1°C until used. Egg clusters were accumulated for 2 d and used when they were <3 d old. Sentinel egg clusters (average of 13.5 eggs per cluster) attached to ≈0.6 cm² of florist paper were placed on the underside of a tomato leaf in plots containing tomato and on sweet corn at an equivalent height and location (i.e., near center) in monoculture plots. One or two egg clusters per plot were used in 2004 and 2005, respectively, and signs of predation on eggs were recorded after 24 h. Eggs were placed on the plants on two dates in 2004, 9 July and 12 July, and three dates in 2005, 25 July, 1 August, and 8 August. The square root of the proportion of eggs surviving after 24 h was arcsine transformed and analyzed using a repeated-measures ANOVA (SAS Institute 2003).

On three dates each year, beginning in early anthesis, adult and immature *C. maculata* densities were sampled. Each randomly selected 1-m² sampling site was centered on a row of sweet corn; thus, each sample contained a linear meter of one row of corn, average of 4.5 plants, and the ground surface extending 0.5 m into adjacent row middles on each side. A randomly selected site was chosen in each plot at three different distances, 2.5, 5, and 7.5 m, from the companion crop of tomato or the equivalent location in the monoculture treatments. On the second sampling date in 2004, sites 10 m away from the companion crop or the equivalent distance also were examined. In 2004, with the larger plot size, sampled sites were taken from one randomly selected cardinal direction from the companion crop in each plot. In 2005, with the reduced width of plots, samples were taken from one of two cardinal directions (north or south of the com-
Comp antibacterial period 3, 112.

To compare the proportion of infested ears after the data were analyzed using proc GLM to determine the cardinal directions (in 2005, distances were to the north and south of companion crop in all plots because才干ant planting). A colony of H. zea was kept in the laboratory at room temperature and a 15:9 (LD) h photoperiod. Adults were kept in a 3.8-liter paper carton lined with florist’s paper (green) and provided sugar water for food. Eggs were collected by removing the florist’s paper daily. If necessary, eggs were stored at 12 ± 1°C until a sufficient number for a test was accumulated. All eggs used in the experiments were 3 d old when taken to the field. Pieces of florist’s paper, ~6.5 cm², were cut from the larger sheets with each piece containing 10 singly laid eggs. On three dates in both 2004 and 2005, beginning with the onset of anthesis and occurring at 7-d intervals, survival of H. zea eggs was examined. Egg stations were placed at four different distances (2.5, 5, 7.5, and 10 m) away from the companion planting of tomatoes or in equivalent locations in the monoculture plots. The egg stations were placed on the developing corn ears by stapling them to the husk near the silks. Eggs were examined 24 h after placement for absence or presence and signs of predation. An individual egg was considered a survivor if it was present and had not been damaged. The square root of the proportion surviving was arcsine transformed and analyzed using a repeated-measures ANOVA (SAS Institute 2003).

Sweet corn ears were shucked and the number of caterpillars was recorded to determine H. zea infestation. Five ears were examined at 2.5, 5, 7.5, and 10 m away from the companion corn or an equivalent location in the monoculture in two randomly chosen cardinal directions (in 2005, distances were to the north and south of companion crop in all plots because of reduced plot size); thus, 40 ears were examined in each plot. Data were analyzed using proc GLM to compare the proportion of infested ears after the data were arcsine transformed (SAS Institute 2003).

Results

Oviposition Choice Experiments. Over the 12-d examination period 3,112 C. maculata eggs in 210 clusters were laid on the study plants. No other coccinellid species were reared from eggs on the plants. Significantly more C. maculata egg clusters and total number of eggs were laid on tomato and ornamental tobacco compared with the other seven species examined (clusters: F8,43 = 13.31, P < 0.01; total eggs: F8,43 = 12.13, P < 0.01; Table 1). Potato, ‘Hairy Prince’, had no C. maculata eggs laid on it during the examination period and thus had significantly lower mean number of eggs and clusters than all other examined plants (Table 1).

In the tomato variety test, 832 C. maculata eggs in 57 clusters were laid on the interplanted tomatoes. The three tomato varieties with typically shaped leaves did not have significantly more or less C. maculata egg clusters or total number of eggs than the Brandywine variety with its potato-like leaf shape (cluster: F3,16 = 2.23, P = 0.12; total eggs: F3,16 = 2.20, P = 0.13; Table 2).

Companion Planting Experiments. In both 2004 and 2005, large numbers of C. maculata eggs (30–70/ plant) were found on the tomato companion crop during sweet corn anthesis (Table 3). The first sampling dates in both years had fewer eggs on tomato than when examined after the beginning of anthesis (2004: F1,11 = 71.64, P < 0.01; 2005: F1,11 = 195.56, P < 0.01). Eggs were abundant on tomato after anthesis, but less so than when examined during anthesis (2004: F1,11 = 29.70, P < 0.01; 2005: F1,11 = 27.56, P < 0.01). In 2005, when corn in monoculture was sampled concurrently, few C. maculata eggs were found on corn, with most samples having no eggs. Mean counts per row meter during anthesis were 0.37 ± 0.26 egg clusters and 5.12 ± 3.61 eggs. Significantly more C. maculata eggs were found on the tomato companion crop than on sweet corn in the monoculture plots (F1,6 = 221.58, P < 0.01).

Coleomegilla maculata eggs placed on sweet corn in monoculture plots had low survival (from 15 to 39% in 24 h). Eggs placed on tomato suffered little predation and had significantly higher survival (from 88 to 100%) than those placed on corn in both years (2004: F1,6 = 20.40, P < 0.01; 2005: F1,6 = 31.30, P < 0.01; Fig. 1).

On the first sampling date of 2004, which was within the first 2 d of anthesis, no differences were seen in the density of C. maculata larvae between sweet corn with a tomato companion crop and a monoculture of sweet corn (F1,6 = 0.41, P = 0.54). There were significantly more C. maculata larvae in the sweet corn with a tomato companion crop than the monoculture plantings on the remaining sampling dates in 2004 and in

Table 2. Mean (±SE) C. maculata egg clusters and eggs on four different varieties of tomato planted in association with sweet corn during anthesis

<table>
<thead>
<tr>
<th>Variety</th>
<th>Egg clusters/plant/48 h</th>
<th>Eggs/plant/48 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brandywine</td>
<td>0.3 ± 0.1a</td>
<td>6.9 ± 0.8a</td>
</tr>
<tr>
<td>Mountain spring</td>
<td>0.6 ± 0.2a</td>
<td>9.3 ± 2.8a</td>
</tr>
<tr>
<td>Sunbeam</td>
<td>0.2 ± 0.1a</td>
<td>3.0 ± 1.8a</td>
</tr>
<tr>
<td>Sunleaper</td>
<td>0.3 ± 0.1a</td>
<td>4.4 ± 1.4a</td>
</tr>
</tbody>
</table>

Means within columns with the same letter are not significantly different (P > 0.05, Ryan-Einot-Gabriel-Welsch multiple range test).

Table 3. Mean no. (±SE) of C. maculata egg clusters and total no. of eggs laid on a tomato companion crop interplanted in sweet corn

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Egg clusters/plant/48 h</th>
<th>Eggs/plant/48 h</th>
</tr>
</thead>
<tbody>
<tr>
<td>7 July 2004</td>
<td>0.4 ± 0.1</td>
<td>5.1 ± 0.8</td>
</tr>
<tr>
<td>12 July 2004</td>
<td>5.1 ± 0.4</td>
<td>70.5 ± 5.2</td>
</tr>
<tr>
<td>20 July 2004</td>
<td>2.9 ± 0.5</td>
<td>34.0 ± 5.8</td>
</tr>
<tr>
<td>17 July 2005</td>
<td>0.5 ± 0.1</td>
<td>2.4 ± 0.7</td>
</tr>
<tr>
<td>21 July 2005</td>
<td>5.1 ± 0.5</td>
<td>54.8 ± 6.1</td>
</tr>
<tr>
<td>28 July 2005</td>
<td>2.9 ± 0.3</td>
<td>31.5 ± 3.8</td>
</tr>
</tbody>
</table>

Second sampling dates of each year (12 July 2004 and 21 July 2005) were during anthesis.
2005 (2004: $F_{1,6} = 10.24, P = 0.02$; 2005: $F_{1,6} = 19.57, P < 0.01$; Fig. 2). In both years, excluding the first sampling date in 2004, there was a significant interaction between treatment type and distance the sample was taken from the companion planting or equivalent location between treatment type and distance the sample date in 2004, there was a significant interaction between vertical bars within the same year ($P < 0.05$).

Survival of $H. zea$ eggs was low in both treatments and in both years, but especially so in 2005 (Fig. 4). In both 2004 and 2005, there was a time effect on the survival of $H. zea$ eggs in that survival was higher during anthesis in comparison to after anthesis (2004: $F_{2,12} = 11.36, P < 0.01$; 2005: $F_{2,12} = 14.24, P < 0.01$). Larvae were abundant at 2.5 m from the companion tomatoes and progressively decreased in density in samples farther from the companion planting (Fig. 2). In 2004, densities of $C. maculata$ larvae in the monoculture plantings slightly increased at greater distances from the center of the plot, but in 2005 were similar at all sampling distances (Fig. 2).

In 2004, there was a trend toward higher adult $C. maculata$ density in the plots with a tomato companion crop than in monocultures ($F_{1,6} = 5.00, P = 0.07$; Fig. 3). There were higher densities of adult $C. maculata$ in 2005 in all treatments compared with 2004, but no difference between the two treatments was detected ($F_{1,6} = 0.01, P = 0.94$; Fig. 3).

Survival of $H. zea$ eggs was low in both treatments and in both years, but especially so in 2005 (Fig. 4). In both 2004 and 2005, there was a time effect on the survival of $H. zea$ eggs in that survival was higher during anthesis in comparison to after anthesis (2004: $F_{2,81} = 34.72, P < 0.01$; 2005: $F_{2,49} = 52.26, P < 0.01$). The first sampling date in both years occurred within the first several days of anthesis. No differences in the survival of $H. zea$ eggs were seen between the sweet corn monoculture and those planting with a tomato companion crop (during anthesis: 2004: $F_{1,6} = 0.32, P = 0.59$; 2005: $F_{1,6} = 0.16, P = 0.71$; postanthesis: 2004: $F_{1,6} = 0.29, P = 0.61$; 2005: $F_{1,6} = 0.11, P = 0.76$; Fig. 4).

Ear infestation rates were low in both treatments in both years (2004: monoculture: 10 ± 2%, with tomato companion: 11 ± 2%; 2005: monoculture: 9 ± 2%, with tomato companion: 15 ± 3%). In neither year was any difference in percent ear infestation detected between sweet corn that had a tomato companion crop and a sweet corn monoculture (2004: $F_{1,6} = 0.02, P = 0.96$; 2005: $F_{1,6} = 1.21, P = 0.31$). The distance a corn plant was from the companion crop or center of the plot had no impact on the percentage of ears infested either (2004: $F_{3,50} = 0.98, P = 0.41$; 2005: $F_{3,50} = 1.23, P = 0.31$).

**Discussion**

Previous studies have shown that $C. maculata$ prefers oviposition on plants with a high density of glandular trichomes compared with nonglandular pubescent plants (Obrycki and Tauber 1985, Cottrell and Yeargan 1998a, Griffin and Yeargan 2002a, Staley and Yeargan 2005). In our oviposition preference test, $C. maculata$ oviposited more frequently on tomato and ornamental tobacco in comparison with the other tested plants. Both of these plants have dense glandular pubescence to the extent that their leaves feel viscous. Additional studies focused on tomato because, in many cases, it is already grown on the same
farms that grow sweet corn, it produces an edible fruit that can be marketed, and many growers are more familiar with its production practices than with those for ornamental tobacco. The tomato variety Brandywine was used for the companion cropping experiments because its leaf shape facilitates searching for *C. maculata* eggs. Our results suggest that other tomato varieties are likely to be as suitable as ‘Brandywine’ for use as companions to sweet corn.

The large quantities of *C. maculata* eggs found on tomato lends further evidence to its being a preferred oviposition plant in comparison to sweet corn. The present and previous studies have shown that glandular-pubescent plants in three different plant families (Euphorbiaceae, Malvaceae, and Solanaceae) are preferred by *C. maculata* for oviposition (Cottrell and Yeargan 1998a, Griffin and Yeargan 2002a). The preference for these plants is caused by their physical characteristics and not the presence of alternative prey or plant-based food (e.g., pollen), although larval dispersal from these plants may be delayed if a food source is present (Cottrell and Yeargan 1999, Griffin and Yeargan 2002a). This is an oviposition preference with a greater number of *C. maculata* eggs being laid on these types of plants, despite *C. maculata* adults spending very little time on them (Staley and Yeargan 2005).

Increased *C. maculata* larval densities on sweet corn with a companion crop of tomato was caused by high numbers of eggs being laid on and increased survival of these eggs on the tomato plants. Eggs on tomato suffered little predation compared with those on sweet corn. Previous work showed low survival of *C. maculata* eggs placed on corn attributable mostly to cannibalism (Wright and Laing 1982, Cottrell and Yeargan 1998a, b, Griffin and Yeargan 2002b). The few predators seen on the tomato plants were mainly *Orius insidiosus* (Say) and spiders, and no older *C. maculata* larvae were observed there. Those few eggs that were attacked on tomato seemed to have been consumed by a mandibulate predator. The paucity of predators on tomato may have been because of the taller sweet corn acting as a barrier to insects that would otherwise colonize tomato. Larvae of *C. maculata* usually disperse from a glandular pubescent plant by dropping from that plant onto the soil surface (Cottrell and Yeargan 1999). These first instars are capable of dispersing across bare soil up to 8 m, but most travel shorter distances (Cottrell and Yeargan 1999). We observed elevated densities of *C. maculata* larvae up to 5 m away from the companion crop in comparison to a similar location in the monoculture sweet corn, which generally agrees with distances previously documented for *C. maculata* dispersing from *A. ostryifolia* (Cottrell and Yeargan 1999). We suggest that larvae that have dispersed from a glandular pubescent plant on which they hatched will be more likely to climb onto and remain on corn than a companion plant, because corn lacks glandular pubescence and often contains suitable food for the larvae (e.g., pollen, prey). Thus, our companion plants served as a source for this natural enemy stage and not a sink. This dispersal mechanism and a larval preference for foraging on corn likely led to the increased densities of larvae found on corn in the companion-planting treatment.

Based on the duration of our sampling and the time required for *C. maculata* to complete a generation, it is likely that most of the adults sampled during our experiments represented individuals that colonized the plots as adults. In 2004, there was a trend (0.05 < P < 0.1) toward higher *C. maculata* adult densities in
the companion cropped sweet corn. If this is a true effect, it may be that gravid female *C. maculata* became concentrated in areas with preferred oviposition sites. In 2005, the density of adult *C. maculata* was much higher than in 2004 (Fig. 3), with no differences on sweet corn with or without a companion crop. There is evidence that adult coccinellids emigrate more rapidly from patchy habitats, and *C. maculata* in particular tends to aggregate in corn monocultures (Wetzler and Risch 1984, Kareiva 1986). Although plants with heavy glandular pubescence are a preferred oviposition location, *C. maculata* adults spend little time foraging on them (Staley and Yeargan 2005). Thus, our corn plots with companion plantings would be favorable for adult *C. maculata* in that there were refuges for eggs, but also would be a patchier habitat. This may have led to quicker adult emigration in 2005, when the corn to companion plant ratio was lower than it was in 2004. Given the lack of dramatic differences in adult densities between treatments, it seems that differences in larval densities between these types of plantings (Fig. 2) had little, if anything, to do with adult densities.

Despite augmenting densities of *C. maculata* larvae in our companion cropped sweet corn, there was no increase in the mortality of sentinel *H. zea* eggs. When *H. zea* egg survival was reduced in earlier companion planting studies (Cottrell and Yeargan 1998a), the companion plants (*A. ostryifolia*) were growing throughout the plots, whereas in our experiment, the companion crop was concentrated in one area. Survival of *H. zea* eggs was higher in both years during anthesis when there was an abundance of alternative food, corn pollen, available to *C. maculata* and *Orius insidiosus*, both of which are common predators on *H. zea* eggs and heavy pollen feeders. It is notable that survival of *H. zea* eggs seems to have been lower in 2005 compared with 2004 across all sampling times and treatments; this corresponds with higher densities of *C. maculata* adults and larvae in 2005.

The proportion of ears infested by *H. zea* in both years (9–15%) was lower than that which has been previously reported for early planted sweet corn in central Kentucky (Garman and Jewett 1914). The low *H. zea* infestation rates make it difficult to show any true differences between treatments if they exist, but it must be acknowledged that *H. zea* is a difficult target for biological control. The main factors creating difficulty in control are the high number of eggs laid on the silks, the physical protection larvae have from natural enemies once in the ear, and the very low tolerance for damage from this pest. It may therefore be unrealistic to expect biological control to further reduce low infestation rates as occurred in our study.

Although we chose tomato as the companion crop for this study, our results suggest that several more of the screened domesticated plants are at least equally preferred for oviposition by *C. maculata* as *A. ostryifolia*, which has been documented to increase the density of *C. maculata* when interplanted in sweet corn. There are numerous ways in which plant diversity can be introduced into a cropping system (e.g., intercropping, companion planting, living mulches). How this is done depends largely on the introduced plant’s characteristics and whether it will serve additional functions besides natural enemy augmentation. For example, chickpea and snail medic most likely would be planted between rows to provide nitrogen fixation and cover throughout the planting, whereas petunia and ornamental tobacco would more likely be incorporated through companion planting. Growers would likely incorporate tomato into sweet corn as an intercrop (e.g., alternating strips). However, for our experiments, we incorporated it as a concentrated companion crop to study the distance an augmentation of *C. maculata* larvae would occur from the companion planting (i.e., a refuge from egg predation).

The knowledge that a tomato companion crop can augment *C. maculata* larval density for at least 5 m will facilitate testing of other planting arrangements and ratios of companion crop to sweet corn to possibly enhance biological control of *H. zea*. For example, strips of sweet corn embedded between strips of tomato would have a source of *C. maculata* larvae on both sides. If the corn strips were 10 m wide, our results predict that the entire planting would have augmented densities of *C. maculata* larvae. Augmenting *C. maculata* may also prove beneficial in suppressing other sweet corn pests such as corn leaf aphid and European corn borer.

Knowledge about how natural enemies use plant-based resources may lead to the ability to indirectly augment natural enemy populations to increase biological control. We have shown that the addition of a cultivated species with glandular trichomes augments the density of *C. maculata* larvae in sweet corn for at least 5 m away from the companion crop. *C. maculata* occurs in several agroecosystems and is considered an important predator on many significant economic pests. Our results suggest that it may be possible to augment this natural enemy in crops in which it already occurs, through adding a cultivated plant species with glandular trichomes. Furthermore the inclusion of floral resources in crop systems have been documented to increase the abundance of and predation by *C. maculata* (Patt et al. 1997, Harmon et al. 2000), so it may be possible to combine an oviposition refuge plant with flowering plants that provide alternative food (i.e., pollen, nectar) in a multi tactic strategy to augment *C. maculata* abundance in crops. An easily envisioned manifestation of this would be a dual companion planting of a flowering plant to attract adults and a plant with glandular trichomes to serve as a refuge from egg predation.

**Acknowledgments**

We thank R. Reuter, C. Allard, B. Wallin, K. Decker, B. Seagraves, and D. Slone for assistance with field studies and R. Bessin for guidance on statistical analyses. K. Haynes and D. Potter provided helpful reviews of an earlier draft of the manuscript. This study (paper 06-08-023) was conducted in connection with a project of the Kentucky Agricultural Experiment Station.
References Cited


Bryson, C. T. 1974. The efficiency of the spotted lady beetle, Coleomegilla maculata (DeGeer) (Coleoptera: Coccinellidae), as a predator of Heliothis on cotton. MS thesis, Mississippi State University, Starkville, MS.


Received for publication 17 February 2006; accepted 15 July 2006.