Factors influencing dispersal of larval *Coleomegilla maculata* from the weed *Acalypha ostryaefolia* to sweet corn

Ted E. Cottrell* & Kenneth V. Yeargan
*S-225 Agricultural Sciences Building-North, Department of Entomology, University of Kentucky, Lexington, KY 40546, USA; *Current address: USDA-ARS, Southeastern Fruit and Tree Nut Research Laboratory, 21 Dunbar Road, Byron, GA 31008, USA*

Abstract

The polyphagous predator, *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), commonly oviposits on the native weed, *Acalypha ostryaefolia* Riddell (Euphorbiaceae), in and around Kentucky sweet corn fields. Cannibalism of eggs by *C. maculata* adults and larvae is drastically lower on *A. ostryaefolia* than on nearby sweet corn plants. We examined ovipositional preference of *C. maculata* for *A. ostryaefolia* plants or sweet corn plants, dispersal of larvae from *A. ostryaefolia* plants, capability for dispersal of larvae across bare soil (e.g., to nearby plants), ability of larvae to climb from ground level up *A. ostryaefolia* plants or sweet corn plants, and effect of *A. ostryaefolia* borders adjacent to sweet corn plots on *C. maculata* population density in sweet corn. The ovipositional preference study revealed that *C. maculata* laid more eggs on *A. ostryaefolia* than on corn. First-instar *C. maculata* that hatched from egg clusters on *A. ostryaefolia* dispersed predominantly by falling, rather than crawling, to the ground. Glandular trichomes on *A. ostryaefolia* petioles and stems apparently inhibited intraplant movement of first instars, resulting in those larvae falling directly from leaves to the ground. Some first instars were capable of moving at least 8 m across bare soil in 24 h. From the ground, significantly more first instars climbed sweet corn plants than climbed *A. ostryaefolia* plants. Significantly more larvae were present in sweet corn plots bordered by *A. ostryaefolia* plants than in sweet corn plots without an *A. ostryaefolia* border. These findings show that physical attributes of companion plants can significantly influence natural enemy populations on crop plants by affecting interplant dispersal of natural enemies.

Introduction

Coleomegilla maculata (DeGeer) is one of the most omnivorous species of Coccinellidae that occur in many agricultural crops, including corn fields, in eastern North America. *Coleomegilla maculata*'s varied diet may include various life stages of insect-pest species (e.g., corn earworm [*Helicoverpa zea* (Boddie)], European corn borer [*Ostrinia nubilalis* (Hübner)]), and Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) (Whitcomb & Bell, 1964; Coll & Bottrell, 1991; Hazzard & Ferro, 1991), corn pollen (Smith, 1960, 1961), and fungal spores (Forbes, 1880; Britton, 1914).

In plots of sweet corn, oviposition by *C. maculata* occurs on sweet corn plants but may also occur on other plant species (i.e., weeds) present within the plots. Previously, we showed that *C. maculata* oviposited on a native weed, *Acalypha ostryaefolia* Riddell (Euphorbiaceae), in plots of sweet corn (Cottrell & Yeargan, 1998b). In addition, it was observed that *C. maculata* eggs on *A. ostryaefolia* were not consistently oviposited in close proximity to a food source (e.g., clumps of aphids) (T. E. Cottrell, personal observation); similarly, *C. maculata* oviposition sites on sweet corn are not closely associated with clusters of prey (Cottrell & Yeargan, 1998a).

When *A. ostryaefolia* was present in sweet corn plots, *C. maculata* egg and larval densities per m^2 (on corn plants + *A. ostryaefolia* plants + ground) were significantly higher than in weed-free sweet corn plots (on corn plants + ground). However, most eggs in weedy plots were found on *A. ostryaefolia* and all eggs in weed-free plots were found on corn plants. This led to fewer eggs on corn plants in weedy plots compared with weed-free plots. An examination of larval densities revealed the converse; fewer larvae occurred on corn plants in weed-free than in weedy plots. In addition, total predation upon sentinel *H. zea* egg groups in weedy plots was significantly lower on *A. ostryaefolia* than on sweet corn plants in weedy or weed-free plots.

We hypothesized that oviposition by *C. maculata* on *A. ostryaefolia* decreased oviposition on corn in weedy plots. However, oviposition on *A. ostryaefolia* (which has simple and glandular trichomes on stems and petioles but only sparse simple trichomes on leaves) in weedy plots resulted in apparent dispersal of *C. maculata* larvae to corn. The following observations strongly suggested interplant dispersal by *C. maculata* larvae in weedy plots: higher *C. maculata* egg densities on *A. ostryaefolia* than on corn, more predispersal *C. maculata* larvae on *A. ostryaefolia* than on corn, lower predation of *H. zea* eggs on *A. ostryaefolia* than on corn, presence of *C. maculata* larvae on the ground, and more older *C. maculata* instars on corn plants than on *A. ostryaefolia* (Cottrell & Yeargan, 1998b).

Our objectives for this study were to examine ovipositional preference of *C. maculata* for *A. ostryaefolia* or sweet corn plants and the mechanisms of larval dispersal from *A. ostryaefolia*. In addition, we examined the ability of *C. maculata* larvae to disperse across bare soil and to climb *A. ostryaefolia* and sweet corn plants from ground level. Lastly, we determined the influence of *A. ostryaefolia* plants, grown adjacent to sweet corn plots, on *C. maculata* population densities in sweet corn.

Materials and methods

Insect colonies. A laboratory colony of *C. maculata* was started from adults collected near Lexington, KY. This colony yielded adult beetles for the oviposition-preference study and egg clusters and larvae for other studies described below. The colony was maintained at 27 ± 1 °C and a photoperiod of L15:D9 in an environmental chamber. Beetles were reared in 9-cm-diameter petri dishes and provided with a blended beef diet (100 g beef liver, 100 g ground beef, and 12 ml of 5% sucrose [wt/vol]) wrapped in laboratory film (Parafilm 'M', American Can Company, Greenwich, CT, USA) and cut into ≈5 mm sections (Cohen, 1985). Water was provided by placing a moistened, cotton dental wick in the petri dish. Lids of petri dishes containing females were lined with green floral paper which provided an ovipositional substrate that was easily removed and replaced. Egg clusters were collected daily.

A colony of *H. zea* was maintained by methods modified from Ignoffo (1965) to provide prey used in studies of *C. maculata* dispersal. The colony was kept at room temperature (≈21 °C) and a L15:D9 photoperiod. Adults were housed in 3.8-liter paper cartons and provided 5% honey-water solution. The sides of these cartons were lined with green floral paper that served as an ovipositional substrate. This paper was collected and replaced daily. Sections of paper (≈6 cm^2) with groups of singly-laid eggs were cut for use in experiments described below.

Ovipositional preference. Ovipositional preference of *C. maculata* for sweet corn or *A. ostryaefolia* plants was examined in cage studies in a greenhouse (17 to 25 °C and L15:D9). Four replicates were run on each of seven dates. Sweet corn plants ('Golden Queen') were grown from seed in 3-liter plastic pots in a greenhouse. Seeds of *A. ostryaefolia* were germinated in trays, and seedlings were transferred to 3-liter plastic pots. Each cage (1.9 × 0.9 × 0.9 m [l × w × h]) contained four sweet corn plants (≈50- to 75-cm tall) and four *A. ostryaefolia* plants (≈15- to 25-cm tall). Differences in heights of the two plant species in this experiment were consistent with growth patterns of these species under field conditions (i.e., corn was always taller than *A. ostryaefolia*). Plants were randomly assigned to positions on an equally-spaced 2 × 4 grid (positions were 40 cm apart). The cage sides and top were screened and the bottom was open. We constructed a cage floor to simulate soil conditions in the field and to prevent the pots from influencing movement of beetles within the cage. The 2 × 4 grid pattern was marked on a 2.1 × 1.2 m plywood board and a 5-cm-diameter hole was drilled through the board to match each grid point. The board was cut (longitudinally) into thirds through the center of the 5-cm-diameter holes. The three floor pieces were reassembled such that they rested on the tops of the eight pots at the plant bases with the plants protrud-

ing through the holes. Sheets of plastic were used to cover the upper surface of the board and, in turn, were covered with ≈5 cm of soil. This soil also was used to fill any remaining space between the plant stalks and the holes in the floor base. To further simulate field conditions, the soil was sprinkled with water and allowed to settle and dry. Four laboratory-reared *C. maculata* females, with no previous exposure to either plant species, were used per cage. Before use in the experiment, these females had mated and were ovipositing daily in petri dishes. The females were put into a 9-cm-diameter petri dish which was then placed on the soil in the center of the floor because oviposition by *C. maculata* typically is near the ground and on corn oviposition occurs on the lower one-third of the plant (Cottrell & Yeargan, 1998a). The cage was then positioned over the plants onto the soil-covered floor. A string, attached to the petri dish lid and running through the screened cage top, was used to open the dish, thereby releasing the females into the cage. After 24 h, cages were opened and beetles were recaptured. Plants, soil, and all interior parts of each cage were searched for *C. maculata* eggs and their numbers were recorded. New plants and beetles were used on each date. Leaf area measurements (LI-COR, model LI-3000, Lambda Instrument Corporation, Lincoln, NE, USA) of all *A. ostryaefolia* and sweet corn plants were taken from one randomly-selected cage on five of the seven dates. The average numbers of eggs oviposited on *A. ostryaefolia* versus sweet corn plants per cage were compared using analysis of variance (ANOVA) (Analytical Software, 1992).

Dispersal of larvae from A. ostryaefolia.   We examined *C. maculata* larval dispersal from *A. ostryaefolia* in laboratory, greenhouse, and field studies. In the laboratory studies, sticky traps were made from plywood boards (30 × 30 cm) and placed around the bases of plants. A 1-cm-wide notch, cut from one edge to the center of the board, was made and used for centering the board around the base of plant stalks. A clear sheet of plastic (30 × 30 cm), with a slit from one edge to the center (i.e., matching the 1-cm-wide notch in the board), was stapled to the board. The board, with the attached plastic sheet, was positioned around the plant stalk and rested on top of the pot. The slit in the plastic, from the edge of the board up to the plant base at the center of the board, was covered with transparent tape. A plastic bag was temporarily placed over the plant while the upper surface of the plastic-covered board was sprayed with insect-trap adhesive (Tangle-

Trap, The Tanglefoot Co., Grand Rapids, MI, USA). The adhesive kept larvae that fell from the plant from climbing back up the plant or off of the board. Outside edges of the plastic-covered board were coated more heavily with a 3-cm-wide band of adhesive (Stikem Special, Seabright Enterprises, Emeryville, CA, USA). The outer border of heavy adhesive was used as a precaution to insure that no larvae could leave the experimental arena. The plant canopy always was directly above the sticky trap. A 4-cm-diameter area at the interface of the board and the base of the plant stalk was covered with wet soil, which was allowed to dry, and was bordered with an ≈0.5-cm-wide band of adhesive (Stikem Special). This heavy band of adhesive near the base of the stalk trapped larvae that dispersed from the plant by crawling down the stalk, thus allowing us to distinguish them from those larvae that had dropped off the foliage. *Acalypha ostryaefolia* plants, prepared as described above, were used to determine the effect of food source (*H. zea* eggs) availability on larval dispersal. Pairs of plants (six replicates) were placed in environmental chambers (27 ± 1 °C and L15:D9). One group of *H. zea* eggs was stapled to the underside of a randomly selected leaf on each *A. ostryaefolia* plant. For each pair of plants, a cluster of *C. maculata* eggs, on ≈6-cm^2 of green floral paper and nearing hatch, was stapled to the underside of a leaf. One plant in each pair had the *C. maculata* egg cluster placed on the same leaf with the food source and on the other plant the *C. maculata* egg cluster was placed on a randomly selected leaf separate from the food source and on the opposite side of the plant. Over a 48 h period, *C. maculata* eggs and the subsequently hatched larvae were observed at approximately 3 h intervals during the photophase. The total number of hatched larvae per plant was recorded. During each observation interval, the number of larvae that had dispersed from the plant was recorded. A 2 × 2 contingency table was used to analyze the total number of larvae that either dispersed from the plant or stayed on the plant when egg clusters either were placed near the food source or placed far from the food source. Cochran's corrected χ^2 was used rather than Yate's correction for continuity because degrees of freedom = 1 and neither row nor column totals for the contingency table were predetermined (i.e., the number of larvae that hatched from egg clusters placed on plants was not predetermined) (Zar, 1996). Data for dispersed larvae are presented as a percentage of the total number of hatched larvae in each treatment.

In another laboratory study we used five replicates of paired plants prepared as described above to determine if placement of *C. maculata* eggs on either the upper or lower surface of a leaf affected dispersal of larvae from the plant. A piece of green floral paper containing a *C. maculata* egg cluster was stapled to the upper surface of a randomly selected leaf on one plant and to the lower surface of a leaf on the other plant. A food source was not provided. Observations were made, only during the light cycle, at ≈3 h intervals over 48 h. Total number of larvae hatching from each egg cluster was recorded. During each observation, first instars found on the ring of soil at the plant base or on the heavy band of adhesive surrounding this soil were removed and recorded as having dispersed by crawling from the plant via the stalk, whereas larvae caught on the remainder of the sticky trap were recorded as having fallen directly from the plant canopy. A 2 × 2 contingency table was used to analyze the total number of first instars that dispersed by crawling from the plant versus those falling from the plant after hatching from egg clusters that were placed on the upper surface versus the lower surface of a leaf. Cochran's corrected χ^2 was calculated (Zar, 1996). Data for first instars that dispersed by falling or crawling are presented as percentages of the total number of dispersed first instars in each treatment.

Dispersal of *C. maculata* larvae from *A. ostryaefolia* was further examined in a greenhouse study to determine if vertical position of a food source, with respect to the larvae, affected their tendency to abandon *A. ostryaefolia*. Potted plants with sticky traps around their bases were prepared similarly to those described above. In this study, the plant canopy was modified by removing, 24 h before the study began, all but three leaves from each plant leaving only a top, middle, and bottom leaf. Eight pairs of plants were set up and the food source was placed on the top leaf of one randomly selected plant and on the bottom leaf of the other plant in each pair. Ten, unfed first-instar *C. maculata* were placed on the upper surface of the middle leaf. First-instar *C. maculata* were transferred to the leaf using a camel-hair brush. After 24 h, the plants were examined and number of larvae that left each plant was recorded. A paired *t*-test was used to compare the number of first instars that dispersed from the plants when the food source was placed above the larvae with the number of first instars that dispersed when the food source was placed below the larvae (Analytical Software, 1992).

Finally, we examined in the field dispersal of all *C. maculata* instars from individual *A. ostryaefolia* plants that had germinated and grown undisturbed in sweet corn plots. All *A. ostryaefolia* plants selected for the study had one or more naturally-oviposited *C. maculata* egg clusters present at the beginning of the study. All *C. maculata* larvae in this study hatched from eggs that were naturally-oviposited on *A. ostryaefolia*. During the study, beetles laid additional egg masses on the plants and many of those eggs hatched. Sticky traps, similar to those described above, were made from plywood boards (40 × 40 cm), with a 2-cm-wide notch cut from one edge to the center of the board. A plastic sheet (40 × 40 cm) with a slit from one edge to the center, was stapled to the board and sprayed with adhesive (Tangle-trap). Outside edges of the board were bordered with a heavy, 3-cm-wide band of another adhesive (Stikem Special) to prevent larvae from crawling onto the board from the ground and to guard against any dispersing larvae leaving the board. Fourth-instar *C. maculata*, the largest larval stage, were not able to cross a 3-cm-wide band of the adhesive (Stikem Special) (T. E. Cottrell, unpubl.). Traps were centered around *A. ostryaefolia* bases with minimal disturbance to the plant. Adhesive (Stikem Special) was used to cover the slit in the plastic and to unite the plastic with the *A. ostryaefolia* plant base. Only foliage of the *A. ostryaefolia* plant beneath which the sticky trap was placed remained directly above the sticky trap. *C. maculata* larvae leaving *A. ostryaefolia* plants were sampled on 9 of 18 days between 4 and 22 August 1997; inclement weather prevented sampling on the other days. The total numbers of first, second, third, and fourth instars recovered on traps beneath each of these eight plants were recorded. Any larvae caught on the outside edge of the adhesive border around the trap were not included because they were presumed to have crawled from the ground onto the trap.

Dispersal of first instars across bare soil. We tested the ability of first-instar *C. maculata* to disperse across bare soil in the field, on four separate dates, by releasing the larvae at the center of circular test sites. Bare soil was tilled immediately before preparing circular test sites on each date. Circles with radii of 1, 2, 4, or 8 m were outlined in the freshly-tilled soil on separate dates, thus, only circles of the same radius were tested concurrently. Circles with radii of 1, 2, and 4 m were replicated four times and circles with a radius of 8 m were replicated twice. Each circle was bordered by

a 30-cm-wide strip of clear plastic with soil covering both the inner and outer edges of the plastic. A 3-cm-wide band of adhesive (Stikem Special) was applied to the middle of the circular plastic border. The area within the circle was compacted manually with a turf roller in an effort to simulate the firm midseason soil texture in sweet corn fields. *C. maculata* eggs from our laboratory colony were collected and allowed to hatch. After $\approx$24 h (i.e., when first instars began to disperse from the egg cluster), first instars were transferred into a 15-cm-diameter petri dish and provided a moistened, cotton dental wick for a water source, but were not fed. First instars were transported to the field and released into a 15-cm-diameter area at the center of each circle between 1700 and 1900 h EDT. After 24 h, the band of adhesive on the circular, plastic border was examined. Only larvae of the same instar as were released (i.e., first instars), and which were caught on the inside edge of the band of adhesive, were recorded as having travelled from the center of the circle to its perimeter.

Ability of first instars to climb plants. We examined the ability of first instars to climb sweet corn plants and *A. ostryaefolia* plants in no-choice tests done in the laboratory and greenhouse. In the laboratory study, potted sweet corn and *A. ostryaefolia* plants were prepared with sticky traps as previously described. Sweet corn plants were paired with *A. ostryaefolia* plants and placed in environmental chambers (27 $\pm$ 1 °C and L15:D9). Four replicates of the plant pairs were used on two separate dates. Ten first-instar *C. maculata* were placed on the 4-cm-diameter ring of soil (surrounded by a band of adhesive) at the base of each plant. Thus, 40 first instars were tested per plant species on each date. The positions of the first instars (on soil, on the plant, in the band of adhesive, or on the adhesive-coated plastic) were examined at 3, 6, 9, and 24 h after release. At each observation time, any larvae found on the plants, at least 2.5 cm above the soil, were recorded as having climbed the plant and were removed. This study was repeated in a greenhouse using eight replicates of paired sweet corn and *A. ostryaefolia* plants on three separate dates. Ten first-instar *C. maculata* were placed on the 4-cm-diameter ring of soil at the base of each plant. Thus, 80 larvae were tested per plant species on each date. First instars were observed at 3, 6, and 24 h after release and their locations recorded. At each observation, if larvae were found on the plant, at least 2.5 cm above the soil, they were recorded as having climbed the plant and were removed from the plants. A paired *t*-test was used to compare data on first instars climbing corn plants compared with those climbing *A. ostryaefolia* plants. Data from the laboratory and greenhouse studies were analyzed separately (Analytical Software, 1992).

Companion planting study. 'Golden Queen' sweet corn plots (4 × 4 m) were planted on 23 June 1997 in a randomized complete block design with four replicates. Weed control in sweet corn plots and alleys was done by treating with alachlor + atrazine (2.5 kg [AI]/ha and 1.5 kg[AI]/ha, respectively) immediately following planting in addition to season-long mechanical removal of all weeds that escaped the herbicide treatment. Each replicate had a weed-free sweet corn plot bordered by *A. ostryaefolia* plants and a weed-free sweet corn plot without the *A. ostryaefolia* border. When sweet corn plants were $\approx$0.5-m tall, *A. ostryaefolia* plants ($\approx$10-cm tall) were transplanted, from a field where they had germinated naturally, alongside designated sweet corn plots. These sweet corn plots were bordered on two sides with *A. ostryaefolia*. The strip of *A. ostryaefolia* plants was 30-cm-wide and separated from the corn plot by a one m wide bare alley. An 8-m-wide strip of bare soil separated the outermost plants (i.e., sweet corn or *A. ostryaefolia*) in one plot from the nearest plants in any other plot. Population densities of all life stages (egg, larva, pupa, and adult) of *C. maculata* were sampled on three dates in both types of sweet corn plots. Three one-m^2 sites per plot, randomly selected along the length of rows 1, 3, and 5 (i.e., each outside row and the center row) were sampled on each date. The ground and corn plants ($\bar{x}$ = 5.6 plants/m^2) were visually inspected for *C. maculata*. In addition, one randomly selected 0.5-m^2 area of each strip of *A. ostryaefolia* plants ($\bar{x}$ = 3.9 plants/0.5-m^2) (i.e., one site on each side of each plot), including the ground, was sampled for all life stages of *C. maculata* each time sweet corn plants were sampled. Individual life stages of *C. maculata* in sweet corn plots with an *A. ostryaefolia* border (but not including any *C. maculata* found in the *A. ostryaefolia* border) and in sweet corn plots without the *A. ostryaefolia* border were compared using repeated measures ANOVA (Analytical Software, 1992).

Results

Ovipositional preference. A significantly higher mean number ($\pm$s.e.) of *C. maculata* eggs was found on *A. ostryaefolia* plants than on sweet corn plants

(3.54 ± 0.59 and 1.75 ± 0.37 eggs per plant, respectively) (F = 6.12; df = 1, 39, P < 0.05). The mean numbers (±s.e.) of *C. maculata* eggs per cluster found on *A. ostryaefolia* plants and on sweet corn plants were 8.0 ± 0.8 and 6.7 ± 0.9, respectively. Mean combined leaf area (±s.e.) of sweet corn plants per cage always was higher than combined leaf area of *A. ostryaefolia* plants per cage (1958.9 ± 121.7 and 840.9 ± 89.5 cm², respectively). Eggs were never found on the soil or interior parts of the cage.

Dispersal of larvae from A. ostryaefolia. In tests of dispersal by first-instar *C. maculata* from *A. ostryaefolia* plants in the laboratory, nearness of *C. maculata* egg clusters to a food source (*H. zea* eggs) significantly affected numbers of first instars dispersing from the plant. Significantly more first-instar *C. maculata* dispersed from *A. ostryaefolia* plants when separated from the food source (79.6%) than when first instars eclosed from eggs placed on the same leaf with the food source (40.4%) (χ^2 = 15.15, df = 1, P < 0.05). When *C. maculata* eggs were on a leaf different from the one containing the food source, first instars never reached the food source; however, first instars emerging on the same leaf with the food source were observed feeding on the *H. zea* eggs. First-instar *C. maculata* did not disperse from the egg cluster until ≈24 h after hatching. Once they started to disperse from the egg cluster, almost all first instars that had not left the plant remained on the *A. ostryaefolia* leaf on which they had hatched. In addition, most first instars that had dispersed from *A. ostryaefolia* were found on the area of the adhesive-sprayed board below the leaf on which they eclosed (i.e., first instars fell from that leaf).

When *C. maculata* egg clusters were placed on the top surface of an *A. ostryaefolia* leaf versus the bottom surface of a leaf, 88.6% and 77.1% of eclosed first instars dispersed from the plants, respectively. There was no effect on the dispersal routes used by these first instars. Of the eclosed first instars that dispersed from the plant after eggs were placed on the top surface of the leaf, 74.2% fell from the plant and 25.8% crawled from the plant, and this was not significantly different from the 75.7% that fell from the plant and 24.3% that crawled from the plant when larvae eclosed on the bottom surface of the leaf (χ^2 = 0.02, df = 1, P > 0.05).

When ten first-instar *C. maculata* were placed on the middle leaves of modified plants that contained only one top, one middle, and one bottom leaf, their
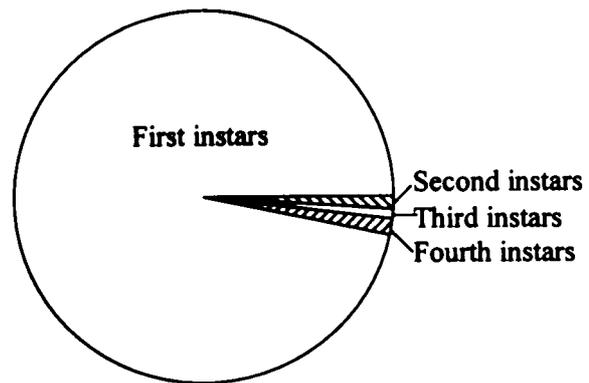

Figure 1. Proportional distribution of *C. maculata* instars captured (*n* = 418) on sticky traps when the larvae dispersed from *A. ostryaefolia* plants in the field.

dispersal from the plant was not affected by presence of food on the upper versus lower leaf (*t* = 1.82, df = 7, P > 0.05). The average number of first instars dispersing from each plant after 24 h when the food source was on the top leaf was 9.6 ± 0.2 whereas the average number dispersing when food was on the bottom leaf was 9.0 ± 0.6. All first instars that dispersed from *A. ostryaefolia* were found on the adhesive-sprayed board below the leaf on which they had been placed (i.e., first instars fell from the plant). However, it is important to note that when first instars were placed on *A. ostryaefolia* leaves, they did not immediately drop from the leaf. In fact many were seen on the same leaf several hours later.

At the start of the field study that examined larval dispersal from individual *A. ostryaefolia* plants, we found an average of 63.6 *C. maculata* eggs/per plant on those plants selected for this experiment. The average temperature during the course of this study was 22.2 °C. Obrycki & Tauber (1978) determined that development of *C. maculata* from egg to pupal stage was ≈18.8 days at 21.1 °C. Therefore, even if all *C. maculata* eggs on the plants had been laid on the day the experiment started, larvae hatching from those eggs (as well as any that hatched from eggs laid earlier) had sufficient time to develop through the fourth instar (if they were capable of surviving while remaining on *A. ostryaefolia* plants). Nevertheless, the vast majority of larvae caught on the sticky traps were first instars, whereas low percentages of the captured larvae were second, third, and fourth instars (Figure 1).

Dispersal by first instars across bare soil. *C. maculata* larvae were capable of traveling considerable

Table 1. Dispersal by first-instar *C. maculata* across bare, compacted soil 24 h after release at the center of circular study areas

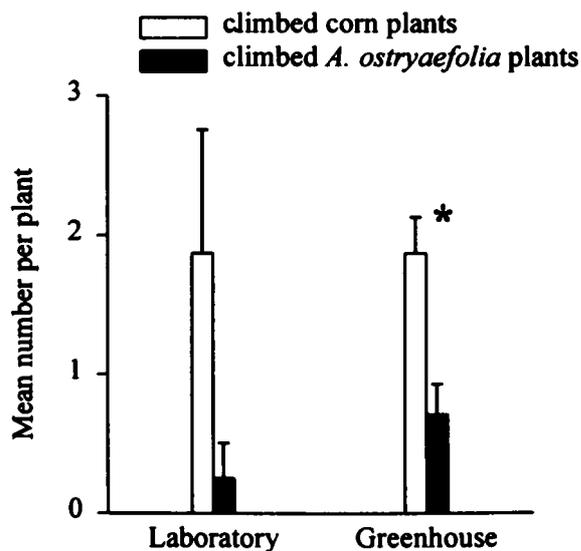| Circle radius (m)	Mean number (±s.e.) released per circle	Mean number (±s.e.) captured per circle
1	107.0 ± 1.4	23.5 ± 5.6
2	113.3 ± 1.1	58.5 ± 3.1
4	175.0 ± 2.3	67.8 ± 6.6
8	253.5 ± 5.5	3.5 ± 1.

Figure 2. Mean number of first-instar *C. maculata* that climbed *A. ostryaefolia* plants versus sweet corn plants. *, indicates significant difference between paired vertical bars (P < 0.05).

distances across bare soil in the field. For all distances tested, at least some of the released larvae were captured on the inside edge of the adhesive band at the periphery of the circles (Table 1).

Ability of first instars to climb plants. In our laboratory experiment, more first-instar *C. maculata* climbed corn plants than climbed *A. ostryaefolia* plants, but the difference was not significant ($t = 1.72$, df $= 7$, P > 0.05) (Figure 2). However, when this study was done in the greenhouse, significantly more first-instar *C. maculata* climbed sweet corn plants than climbed *A. ostryaefolia* plants ($t = 3.62$, df $= 23$, P < 0.05) (Figure 2).

Companion planting study. Sweet corn plots bordered with *A. ostryaefolia* had significantly more

C. maculata larvae ($F = 11.79$, df $= 1, 19$, P < 0.05) per m^2 than sweet corn plots without the *A. ostryaefolia* border (Figure 3) but there were no significant differences in densities of *C. maculata* eggs ($F = 1.28$, df $= 1, 19$, P > 0.05), pupae ($F = 0.15$, df $= 1, 19$, P > 0.05) or adults ($F = 0.00$, df $= 1, 19$, P > 0.05) per m^2 between plot types (Figure 3). *Coleomegilla maculata* population density also was sampled on *A. ostryaefolia* plants (per 0.5 m^2) in the border. *Coleomegilla maculata* eggs, larvae, and adults (but no pupae) were found in the border (Figure 3).

Discussion

We have shown that *C. maculata* oviposits more eggs on *A. ostryaefolia* than on sweet corn. However, first-instar *C. maculata* that eclose on *A. ostryaefolia* are limited in their ability to move about on *A. ostryaefolia,* presumably because of trichomes on the plant and, therefore, fall from the plants to the ground. First-instar *C. maculata* are capable of travelling considerable distances across soil and are more likely to climb corn plants than *A. ostryaefolia* plants. In fact, strips of *A. ostryaefolia* grown at a distance of one m from sweet corn plots significantly increased the population density of *C. maculata* larvae in those sweet corn plots compared with sweet corn plots not bordered by *A. ostryaefolia* strips.

Laboratory-reared *C. maculata* females, which had never been exposed to any plant, laid more eggs on *A. ostryaefolia* than on sweet corn in preference studies. Additionally, Cottrell & Yeargan (1998b) reported that more *C. maculata* eggs occurred on *A. ostryaefolia* plants than on corn plants in field plots of weedy sweet corn. Some egg clusters on corn plants in our greenhouse study may have been cannibalized by *C. maculata* females in the cages, thus affecting the number of eggs found at the end of the experiment, but we saw no evidence of this (i.e., partially eaten egg clusters or chorion remnants).

Oviposition by *C. maculata* in the field was not consistently associated with a food source (e.g., clumps of aphids) on either corn or *A. ostryaefolia.* If adequate food for larval development had occurred near oviposition sites on *A. ostryaefolia* plants, one would expect to find first through fourth instars on the plants or dispersing from the plants (if food supplies became depleted). However, the vast majority of *C. maculata* larvae caught dispersing from *A. ostryae-*
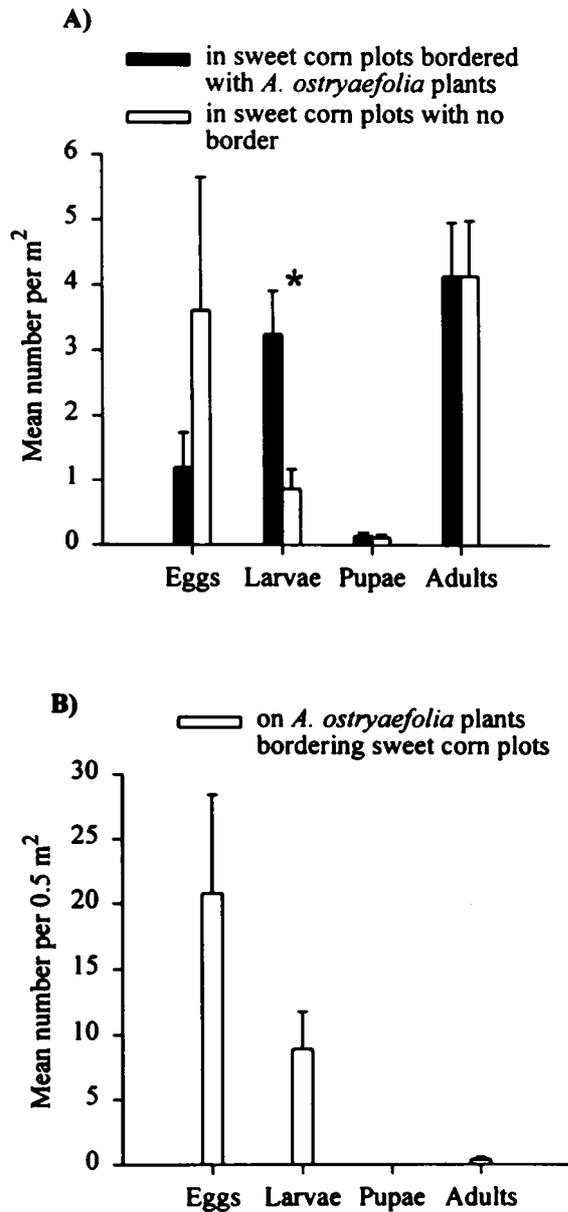
Figure 3. A) Population densities (per m²) of *C. maculata* in sweet corn plots bordered with *A. ostryaefolia* plants versus those in sweet corn plots with no *A. ostryaefolia* borders. *, indicates significant difference between paired vertical bars (P < 0.05). B) Population densities (per 0.5 m²) of *C. maculata* on *A. ostryaefolia* plants in the border alongside sweet corn plots.

folia plants in the field were first instars. *C. maculata* may select habitats for oviposition based, in part, on availability of food, but the diet of this polyphagous predator includes numerous types of arthropods, as well as pollen and fungal spores (Forbes, 1880; Smith 1960, 1961; Hodek and Honěk, 1996). Such diverse foods are likely to be widely dispersed within a given habitat. Once a habitat has been chosen, specific oviposition sites within the habitat may be less dependent on proximity to food sources than on microenvironmental factors such as humidity, light penetration, temperature, and/or physical aspects of potential ovipositional substrates.

Most *C. maculata* larvae that dispersed after hatching from eggs laid on *A. ostryaefolia* did so as first instars, and most of those dispersed by falling. Evidence of first instars falling from leaves, rather than crawling down the stalk, was provided, in part, by the fact that most of those first instars were caught on the sticky trap beneath the leaf upon which the egg cluster or first instars had been placed in laboratory and greenhouse studies. Furthermore, first instars were found similarly clustered on sticky traps in field studies, indicating that these groups of first instars had fallen from localized areas of the plants, presumably from the leaves on which they eclosed. Even though a few first instars were able to crawl down *A. ostryaefolia* stems in one experiment, larvae never were able to find and feed upon prey on any *A. ostryaefolia* plants on which the food source had been placed on a leaf separate from *C. maculata*.

Observations of *A. ostryaefolia* with a light microscope revealed that the petioles and stems were covered with glandular and simple trichomes. Top and bottom surfaces of leaves had sparse, simple trichomes which did not prevent oviposition by adults nor subsequent movement by first instars on that leaf. The petioles and stems did, however, generally inhibit movement by first instars to other parts of the plant. Observations of *C. maculata* on stems and petioles revealed that the legs of first instars were not long enough to prevent the sternum from contacting the trichome exudates (Figure 4). Thus, due to potential contact by the legs, sternal surface, and anal organ of first instars with exudates from trichomes on the petioles and stems, most larvae are apparently faced with two choices: remain on the leaf where they hatched or drop to the ground.

Elsey (1974) showed that the searching speed of first-instar *C. maculata* on tobacco leaves (with glandular trichomes) was slower than on cotton leaves

Figure 4. First-instar *C. maculata* larva on an *A. ostryaefolia* stem. Stems and petioles were similarly covered with glandular and simple trichomes, whereas, leaf surfaces had sparse simple trichomes.

(without glandular trichomes). Additionally, Belcher & Thurston (1982) reported that movement by first-instar *Hippodamia convergens* Guerin (Coleoptera: Coccinellidae) on tobacco plants was negatively affected by trichome exudates. Late-instar *C. maculata* were capable of movement on *A. ostryaefolia* as evidenced by the occurrence of pupae on such plants in the field in an earlier study (Cottrell & Yeargan, 1998b). Belcher & Thurston (1982) reported that older-instar *H. convergens* moved further on tobacco cultivars with various densities of glandular trichomes than did first instars on the same cultivars. In greenhouse studies, Obrycki & Tauber (1984) found that >70% of newly-hatched larvae of coccinellid species commonly found in New York potato fields fell from potato clones that had moderate densities of glandular pubescence. Newly-hatched larvae on a potato clone with a high density of glandular pubescence did not fall to the ground because they became trapped in exudates on the plant surface. In our study, unless a food source was available on the same leaf with the first instars, most fell from *A. ostryaefolia* plants within 48 h after eclosing and the others remained on that same leaf.

Additionally, Obrycki & Tauber (1985) found more coccinellid eggs on a potato clone with more glandular pubescence than on other potato clones. They suggested that female coccinellids might have preferentially oviposited on the highly pubescent clone or that coccinellid eggs on that clone might not have been preyed upon as heavily as those on the less pubescent clones. In contrast, however, when those authors sampled larval coccinellids on the different potato clones, they found higher larval densities on the clone without glandular pubescence. They suggested that some larvae might have moved from clones with higher densities of glandular pubescence (where more coccinellid eggs were found) to a clone without glandular pubescence. Similarly, Cottrell & Yeargan (1998b) found higher densities of older *C. maculata* larvae on sweet corn plants (without glandular trichomes) than on *A. ostryaefolia* plants (with glandular trichomes and where most *C. maculata* eggs occurred) in stands of sweet corn intermingled with *A. ostryaefolia* plants.

One concern with the use of alternate host plants in agricultural systems is that specific natural enemies might spend more time searching for prey on the alternate host than on the crop plant. This was not the case for *C. maculata* on *A. ostryaefolia* in sweet corn fields. Most *C. maculata* larvae fell from *A. ostryaefolia* in the field as first instars, rather than as later instars, again, indicating that these larvae spent little time searching on *A. ostryaefolia*. If an abundant food source had been present on the same *A. ostryaefolia* leaves where *C. maculata* eggs were oviposited, fewer first instars would have been expected to disperse from *A. ostryaefolia* (as we observed in the laborartory). Nonetheless, after falling to the ground, some first instars were capable of moving at least 8 m across bare soil, and more than a third of those tested were able to move at least 4 m within 24 h. In many intercropping or companion planting systems, such larvae could easily reach the crop plants. We further showed that first-instar *C. maculata* were more likely to climb up corn plants than up *A. ostryaefolia* plants from the soil. In fact, when we used *A. ostryaefolia* as a border along two opposite sides of sweet corn plots, larval *C. maculata* densities in *A. ostryaefolia*-bordered sweet corn plots were more than threefold higher than in sweet corn plots without such borders.

Although *C. maculata* preferred to oviposit on *A. ostryaefolia* plants in our greenhouse study, it should be noted that some eggs also were laid on sweet corn plants. Our previous work (Cottrell & Yeargan, 1998b) showed that most *C. maculata* egg mortality in the field was due to cannibalism by adults and larvae, with much higher rates of cannibalism occurring on sweet corn than on *A. ostryaefolia*. The densities of *C. maculata* eggs observed in the field on sweet corn plants and on *A. ostryaefolia* reflect not only the numbers of eggs that had been oviposited, but also the numbers of those eggs that survived the period between oviposition and sampling of egg densities. Therefore, the marked differences in *C. maculata*

egg densities between *A. ostryaefolia* and sweet corn plants in the field probably reflected both preferential oviposition on *A. ostryaefolia* and greater survival of the eggs laid on those plants. We have no basis for asserting that *C. maculata* females preferentially selected *A. ostryaefolia* plants in order to protect their eggs against cannibalism, but such protection is a result.

We chose *A. ostryaefolia* for this and an earlier study (Cottrell & Yeargan, 1998b) based on field observations that *C. maculata* egg densities appeared to be higher on *A. ostryaefolia* plants than on nearby sweet corn plants. Other weedy or cultivated plant species might similarly serve as ovipositional refuges from egg cannibalism, but specific plant characteristics like those identified in the present study (e.g., glandular trichomes) could influence the dispersal, or lack of dispersal, of *C. maculata* from the ovipositional site to nearby sweet corn plants. Our results suggest that companion plants intended to augment *C. maculata* larval densities on sweet corn would be most effective if they inhibit movement of first instars over the plant surface, thus causing the larvae to abandon the companion plants and search for plants with more hospitable foraging surfaces.

Acknowledgments

References

Analytical Software, 1992. Statistix, version 4.0. St. Paul, MN, USA.

Belcher, D. W. & R. Thurston, 1982. Inhibition of movement of larvae of the convergent lady beetle by leaf trichomes of tobacco. Environmental Entomology 11: 91–94.

Britton, W. E., 1914. Some common lady beetles of Connecticut. Connecticut Agricultural Experiment Station Bulletin 181: 21–22.

Cohen, A. C., 1985. Simple method for rearing the insect predator *Geocoris punctipes* (Heteroptera: Lygaeidae) on a meat diet. Journal of Economic Entomology 78: 1173–1175.

Coll, M. & D. G. Bottrell, 1991. Microhabitat and resource selection of the European corn borer (Lepidoptera: Pyralidae) and its natural enemies in Maryland field corn. Environmental Entomology 20: 526–533.

Cottrell, T. E. & K. V. Yeargan, 1998a. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environmental Entomology 27: 1402–1410.

Cottrell, T. E. & K. V. Yeargan, 1998b. Influence of a native weed, *Acalypha ostryaefolia* (Euphorbiaceae), on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environmental Entomology 27: 1375–1385.

Elsey, K. D. 1974. Influence of plant host on searching speed of two predators. Entomophaga 19: 3–6.

Forbes, S. A. 1880. Notes on insectivorous Coleoptera. Bulletin of the Illinois State Laboratory of Natural History 3: 167–176.

Hazzard, R. V. & D. N. Ferro, 1991. Feeding responses of adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to eggs of Colorado potato beetle (Coleoptera: Chrysomelidae) and green peach aphids (Homoptera: Aphididae). Environmental Entomology 20: 644–651.

Hodek, I. & A. Honěk, 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Boston, MA.

Ignoffo C. M., 1965. The nuclear-polyhedrosis virus of *Heliothis zea* and *Heliothis virescens*. II. Biology and propagation of diet-reared *Heliothis*. Journal of Invertebrate Pathology 7: 217–226.

Obrycki, J. J. & M. J. Tauber, 1978. Thermal requirements for development of *Coleomegilla maculata* (Coleoptera: Coccinellidae) and its parasite *Perilitus coccinellae* (Hymenoptera: Braconidae). Canadian Entomologist 110: 407–412.

Obrycki, J. J. & M. J. Tauber, 1984. Natural enemy activity on glandular pubescent potato plants in the greenhouse: an unreliable predictor of effects in the field. Environmental Entomology 13: 679–683.

Obrycki, J. J. & M. J. Tauber, 1985. Seasonal occurrence and relative abundance of aphid predators and parasitoids on pubescent potato plants. Canadian Entomologist 117: 1231–1237.

Smith, B. C., 1960. A technique for rearing coccinellid beetles on dry foods, and influence of various pollens on the development of *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae). Canadian Journal of Zoology 38: 1047–1049.

Smith, B. C., 1961. Results of rearing some coccinellid (Coleoptera: Coccinellidae) larvae on various pollens. Proceedings of the Entomological Society of Ontario 91: 270–271.

Whitcomb, W. H. & K. Bell, 1964. Predaceous insects, spiders, and mites of Arkansas cotton fields. Arkansas Agricultural Experiment Station, Bulletin 690.

Zar, J. H., 1996. Biostatistical Analysis, third edition, Prentice-Hall, Inc., Englewood Cliffs, NJ.