

The impact of plant associations on *Macrostoteles quadrilineatus* management in carrots

Zsafia Szendrei*

Department of Entomology, Michigan State University, 243 Natural Science Bldg., East Lansing, MI 48824, USA

Accepted: 13 February 2012

Key words: aster leafhopper, associational resistance, weed, cereal, border crop, herbicide, generalist, pest management, insect–plant interactions, herbivore, Hemiptera, Cicadellidae

Abstract

Habitat diversification can influence the interactions of insects with plants and this can be used in agroecosystems for the management of pest populations. Plant diversification can be achieved through planting crops, such as trap crops, or by adjusting weed management. Aster leafhopper, *Macrostoteles quadrilineatus* Forbes (Hemiptera: Cicadellidae), is a polyphagous species that uses cereals, vegetables, and weeds as host plants. The influence of weeds on *M. quadrilineatus* abundance was investigated experimentally in carrot [*Daucus carota* L. cv. Canada (Apiaceae)] field plots by adjusting the level of management of two groups of weeds (broadleaf and grass) and by comparing it to weed-free plots. The preference of *M. quadrilineatus* for different cereal and weed species relative to carrots was tested in choice test assays. Habitat context influenced the abundance of *M. quadrilineatus* in the field experiments. The presence of border crops such as oat, rye, barley, wheat, and triticale did not significantly attract or repel this insect to carrot plots compared to the no-border treatment. However, spelt-bordered plots had 42% fewer *M. quadrilineatus* than three treatments, triticale, wheat, and barley, that had the highest insect abundance. The type of weed management affected *M. quadrilineatus* abundance in carrot plots, but not the frequency of herbicide application. Plots that had carrot growing with broadleaf-weeds had about 59% fewer *M. quadrilineatus* compared with those growing with crabgrass or carrot alone. In the greenhouse choice tests, grasses (e.g., cereals) attracted and broadleaf-weeds repelled *M. quadrilineatus* relative to carrots. In summary, carrot growers may be able to manage this pest by reducing the interaction of cereal cover crops with carrots and eliminating grassy weeds in commercial production fields.

Introduction

The context of the surrounding vegetation can influence the outcome of insect–plant interactions, and this phenomenon can be used for improving the success of pest management programs in agroecosystems. Appropriately selected plant species in agricultural fields can be combined to reduce damage by herbivores on the economically valuable focal plant, a practice that has been frequently used in traditional food production systems. By definition, associational resistance is when one species gains protection from its consumer by association with a third species, but more broadly, in agroecosystems, association of the economically valuable focal plant may not always be limited to a single plant species. Root and colleagues (Tahvanainen & Root, 1972; Root, 1973) were among the earliest

to confirm the importance of specific plant–plant associations in reducing herbivory on cabbage. Atsatt & O’Dowd (1976) emphasized the importance of the right kind of diversity by suggesting that not all plant species diversity results in a reduction of herbivory on the focal plant. Reviews of associational resistance in agroecosystems have reported a general reduction of arthropod pests when plants, such as various crops, were associated with taxonomically or genetically different plant species (Risch et al., 1983; Andow, 1991; Tonhasca & Byrne, 1994; Barbosa et al., 2009). As theoretical evidence accumulates in the literature that supports the benefits of plant associations in pest management, the adoption of this practice into modern commercial plant production will hopefully continue to rise in the future.

The method by which associational resistance works depends on the traits of the herbivores and plants involved in the interaction, as well as a range of other abiotic and

*Correspondence: E-mail: szendrei@msu.edu

biotic mechanisms. In the literature there is an overwhelming focus on the influence of biotic mechanisms, including the ability of neighboring plants to camouflage the focal plant via visual or olfactory cues. One of the best-known examples of successful associational resistance in agriculture is the use of trap crops. Trap crops can be located inside or on the perimeter of fields and exert their effect through two major mechanisms: intercepting the movement of a pest into the field and attracting a pest already present in the main crop into the trap crop (Vandermeer, 1989; Asman, 2002; Boucher et al., 2003; Tillman, 2006). Ultimately, to profitably use border crops, there has to be a differential response of the focal herbivore to the trap crop compared to that of the main crop.

Agricultural fields are often colonized by weeds, which may change the environment of the focal plant and thus influence the interactions of insects and plants. Weeds are undesirable pests because they compete for resources with the main crop; nevertheless, the presence of weeds is inevitable in most agricultural production systems and they can have beneficial or detrimental impact on the abundance of herbivores on the focal plant. It is difficult to predict how weeds will impact insect-plant interaction in agroecosystems because weed species appear relatively unpredictably in space and time. Weeds can be reservoirs of pests (Andow, 1988; Altieri, 1995) but, according to the resource concentration hypothesis, diverse (i.e., weedier) plant species assemblages will have lower herbivore populations than those in uniform assemblages (Andow, 1990, 1992). For example, leafhoppers were more abundant in plots that had fewer weeds relative to the monoculture in alfalfa (Oloumi-Sadeghi et al., 1989), bean (Andow, 1992), soybean (Buckelew et al., 2000), and maize (Albajes et al., 2009). On the other hand, a broader review of the literature indicated considerable variation in polyphagous herbivore density when comparing weedy to weed-free agroecosystems (Andow, 1988). Such variation indicates that the outcome of weed-arthropod-crop interactions is dynamic, and the impact of weeds has to be considered in sustainable pest management programs.

Aster leafhopper, *Macrostelus quadrilineatus* Forbes (Hemiptera: Cicadellidae), is a polyphagous pest with over 300 host plant species including important vegetable and cereal crops. In addition, this insect uses numerous weed species as hosts for feeding, oviposition, and overwintering (Hagel & Landis, 1967). Most of the economic damage this insect causes comes from its ability to transmit aster yellows disease, which can render produce unmarketable because of deformed growth and a bitter taste. *Macrostelus quadrilineatus* can disperse effectively over large distances on weather fronts (Chapman, 1971), but can also redistribute locally based on host plant preference (Zhou et al.,

2003). For example, *M. quadrilineatus* dispersed more quickly and frequently from endive, escarole, and maize (non-preferred hosts) compared to lettuce (Meade & Peterson, 1967; Hoy et al., 1999; Zhou et al., 2003). This suggests that host plant preference of this pest can be translated into practical tools to manage its population through practices such as trap cropping and adjusting weed management intensity.

The current study investigated (1) the role of border trap crops in intercepting *M. quadrilineatus* colonization of carrot plots, (2) the interaction of weed management and *M. quadrilineatus* abundance in experimental carrot plots, and (3) the relative preference of this insect when offered a choice between cereal or weed species and carrot in bioassays.

Materials and methods

Border crop study experimental design

To test the effect of borders on *M. quadrilineatus* colonization of carrot plots, seven treatments were replicated four times in a randomized complete block design. The experiment was conducted in 2011, at Michigan State University's Montcalm Research Center in Stanton, MI. Carrot, *Daucus carota* L. cv. Canada (Apiaceae) (Seedway, Hall, NY, USA), was seeded (5×50 cm spacing) into 3×3 m plots using an Earthway® Precision Garden Seeder (Bristol, IN, USA). Plots were spaced 2 m apart and alleyways between plots were kept free of vegetation throughout the growing season using a mechanical cultivator. Plots either received a 0.6-m border treatment on all four sides or were left without a border. Border crop species were selected based on practical agronomic considerations for carrot management and seed availability. Border treatments consisted of the following plant species (all Poaceae): barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.), oat (*Avena sativa* L.) – obtained from Michigan State Seed Solution, Grand Ledge, MI, USA –, spelt (*Triticum spelta* L.), triticale (\times *Triticosecale* Wittm.), and wheat (*Triticum aestivum* L.) – obtained from Albert Lea Seed, Albert Lea, MN, USA.

All border crops were hand-seeded at 600–700 seeds m^{-2} . Carrot and border crop seeds were seeded on 2 June and a pre-emergent herbicide (S-metholachlor, 1 l ha^{-1} a.i.) was applied to the entire experimental field on 6 June. Post-emergence herbicides were applied twice to the entire experimental field to suppress broad-leaf weeds (27 July: metribuzin, 0.625 kg ha^{-1} a.i.; 8 August: linuron, 0.8 l ha^{-1} a.i.). In addition, plots were hand-weeded as needed throughout the growing season to eliminate all weeds. Yellow sticky cards (7.5×12.3 cm; Great Lakes IPM, Vestaburg, MI, USA) were placed in the center of each plot at the level of the carrot foliage on 1 August and

were changed weekly until 29 August. Sticky cards were collected from each plot, placed into transparent plastic bags, labeled, and transported to the laboratory where *M. quadrilineatus* were counted on both sides of the cards and the numbers recorded. Height of each border crop was measured on 15 August (three measurements per plot). Border crop biomass was measured at the end of the experiment by cutting the aboveground plant parts from a 0.5 × 0.6 m section of the border from each plot, drying the plants in the laboratory to constant mass, and by weighing the dry plant material. Carrot for total plant fresh biomass measurement was harvested on 21 October from the two middle rows from each plot and weighed.

Weed management study experimental design

The experiment to examine the impact of weed management on *M. quadrilineatus* abundance in carrot plots was set up in 2011 at the Southwest Michigan Research and Extension Center, Benton Harbor, MI, USA. Carrot (cv. Canada; 5 × 50 cm spacing) was seeded using the same method as above on 20 May. Plots were 6 × 7.6 m with no alleyways between adjacent plots. Carrot plots were either hand-weeded or sprayed using a backpack sprayer with a broadleaf (linuron, 0.8 l ha⁻¹ a.i.) or a grass herbicide (clethodim, 0.15 l ha⁻¹ a.i.) or both. Herbicide-treated plots were either sprayed twice or three times post-emergence, and hand-weeding was done as needed (herbicide application dates: 22 and 29 June, and 12 August for plots that received three herbicide applications). The seven treatments (broadleaf, grass, or both herbicides at two application times and hand-weeding) were replicated five times in a randomized complete block design. Yellow sticky cards (7.5 × 12.3 cm) were placed in the center of each plot at the level of the carrot foliage on 14 July and were changed weekly until 1 September. A 1-m radius around each yellow sticky card was kept vegetation-free by hand-weeding weekly throughout the growing season. Sticky cards were collected from each plot, placed into transparent plastic bags, transported to the laboratory where *M. quadrilineatus* were counted on both sides of the card, and the numbers were recorded. Weed cover (%) in each plot and species of weeds present in plots were visually estimated and recorded on 28 July and 5 August. Carrot for total plant fresh biomass measurement was harvested on 13 October from the two middle rows from each plot and foliage was weighed together with roots.

Greenhouse choice tests

Choice tests were set up in the greenhouse to test the host plant preference of *M. quadrilineatus*. Carrots, weeds, and border crops were grown in plastic pots (10 × 10 × 12 cm) in plant medium (Sure-Mix Perlite; Michigan

Grower Products, Galesburg, MI, USA) in the greenhouse between 1 April and 27 July 2011, at L16:D8 and 23–28 °C. Carrots and border crops were purchased from the same seed sources as described above. The following eight weed species were used in the choice tests: chicory (*Cichorium intybus* L.), milkthistle [*Silybum marianum* (L.)], common dandelion (*Taraxacum officinale* F.H. Wigg), pineapple weed (*Matricaria discoidea* DC), wild lettuce (*Lactuca serriola* L.), corn chamomile (*Anthemis arvensis* L.) (all Asteraceae), common plantain (*Plantago major* L.) (Plantaginaceae), and Queen Anne's lace (*Daucus carota* L.) (Apiaceae). All weeds were obtained from Local Harvest (Santa Cruz, CA, USA), except corn chamomile, seeds of which were collected in 2010 from plants growing at an agricultural field on the campus of Michigan State University (East Lansing). All these species occur commonly in Michigan and are known host plants of *M. quadrilineatus* (Schultz, 1979; Jensen, 1982; USDA PLANTS Profile Database, 2011: <http://plants.usda.gov/java/>). Choice tests were conducted between 26 April and 27 July in the greenhouse at L16:D8 and 23–28 °C, 2011 in insect rearing cages (47.5 × 47.5 × 93 cm; Megaview, Taichung, Taiwan).

Ten cages were placed horizontally on greenhouse benches, and two potted plants were positioned 30 cm apart from each other on the floor of each cage. *Macrostelus quadrilineatus* were reared in the laboratory on greenhouse-grown oats (at L16:D8 and 23–25 °C in 47.5 × 47.5 × 47.5 cm Megaview rearing cages), and transported in groups of 10 in plastic aspirator vials (25 × 70 mm; BioQuip, Rancho Dominguez, CA, USA) from the laboratory to the greenhouse without food or water. Vials were placed into a Styrofoam cooler to maintain 23–25 °C during the 10-min transportation. After a carrot plant and another plant were positioned in the cage, 20 adult *M. quadrilineatus* were released between the two plants on the cage floor. Choice tests consisted of a carrot and weed or border crop comparison; the position of the two plants in the cages was randomized and treatments were replicated over time. The number of replications for treatment combinations varied between 8 and 27 (Figure 4A). Insects were left in the cages for 24 h, after which a Styrofoam board was carefully inserted into the middle of each cage to divide it into two equal halves and an insect vacuum (BioQuip) was used to collect *M. quadrilineatus*. More than 90% of *M. quadrilineatus* were settled on plants after 24 h, but during vacuuming some insects jumped from the plant onto the cage walls, which were then vacuumed up together with those collected from the plant. Once all *M. quadrilineatus* were vacuumed up from one side of the cage, the insects were transferred into a re-sealable transparent plastic bag and labeled with the treatment information. Plastic bags with *M. quadrilineatus* were placed at –20 °C for 30 min before

counting. Height and weight of the fresh aboveground biomass were recorded for each plant.

Statistical analysis

Prior to statistical analysis (SAS 9.2, 2002–2008; SAS Institute, Cary, NC, USA), insect count data were log-transformed to meet assumptions of analysis of variance (ANOVA). The effect of border treatments on *M. quadrilineatus* abundance was analyzed with an ANOVA using date as a repeated measure, border treatment type as the dependent variable, and block as random factor in the model. Differences among treatments were determined using the lsmeans statement with Tukey adjustment. The correlation between the seasonal average of *M. quadrilineatus* and border crop biomass or height was evaluated using a regression analysis.

The effect of weed treatments on *M. quadrilineatus* abundance was analyzed with an ANOVA with date as a repeated measure, weed management method and herbicide application frequency as dependent variables, and block as random effect in the model. Differences among treatments were determined using the lsmeans statement with Tukey adjustment. Correlation between seasonal average of *M. quadrilineatus* and carrot biomass was evaluated using a regression analysis.

For statistical analysis the response ratio (number of *M. quadrilineatus* on the carrot/total number of *M. quadrilineatus* recovered from the cage), and height and weight of the carrot plant relative to the other plant was calculated (carrot height or weight/other plant's height or weight). The value of the response ratio was between 0 and 1, with 0.5 representing equal preference for the two choices, and values higher than 0.5 representing preference for the carrot plant over the other plant. The response ratio was arcsine-transformed before statistical analysis. An analysis of covariance was done using the response ratio as the dependent variable, choice type as independent variable, date as a blocking factor, and the relative height and weight of the carrot plant as covariates in the model. Differences among treatments were determined using the lsmeans statement with Tukey adjustment. For each choice type, a G-test with William's correction (Sokal & Rohlf, 1995) was conducted on the numbers of insects, which tested the null hypothesis of no preference.

Results

Border crop study

The number of *M. quadrilineatus* was significantly different among border crop treatments ($F_{6,83} = 3.87$, $P < 0.01$), with significantly fewer insects found on yellow cards in carrot plots bordered by spelt than in plots bordered by

barley, wheat, or triticale ($P < 0.05$; Figure 1). Carrot weight among plots with different border treatments was not significantly different ($F_{6,24} = 0.90$, $P = 0.52$). Border crop biomass ($F_{5,23} = 6.78$, $P < 0.01$) and height ($F_{5,23} = 426.46$, $P < 0.01$) were significantly different among treatments, with rye and spelt being the smallest, and wheat and triticale being the largest plants. There was a positive although not statistically significant relationship between *M. quadrilineatus* numbers on yellow cards and border crop biomass ($r^2 = 0.31$, $P = 0.19$; Figure 2A), and a marginally significant relationship with border crop height ($r^2 = 0.58$, $P = 0.05$; Figure 2B).

Weed management study

The weed management impact on *M. quadrilineatus* abundance was significant ($F_{2,177} = 55.07$, $P < 0.01$), but herbicide application frequency (two or three applications in the growing season) did not significantly impact abundance ($F_{1,177} = 0.02$, $P = 0.96$). Approximately 56% fewer *M. quadrilineatus* were found on yellow cards placed in plots treated with grass herbicide compared to all the other treatments (lsmeans with Tukey adjustment: $P < 0.05$), but there were no significant differences among treatment effects when comparing treatments with broadleaf herbicide, both herbicides, and hand-weeding (Figure 3A). Weed management significantly affected carrot biomass ($F_{6,33} = 8.98$, $P < 0.01$); using one type of herbicide significantly reduced biomass compared to plots that were hand-weeded or treated with both types of herbicides (lsmeans with Tukey adjustment: $P < 0.05$; Figure 3B). There was no significant correlation between carrot biomass and *M. quadrilineatus* abundance ($r^2 = 0.36$, d.f. = 1,6, $P = 0.08$).

The naturally occurring broadleaf-weed species in the carrot field were corn chamomile, prostrate pigweed (*Amaranthus albus* L.), Powell's amaranth (*Amaranthus powellii* S. Watson), annual ragweed (*Ambrosia artemisiifolia* L.), lambsquarters (*Chenopodium album* L.), Canadian

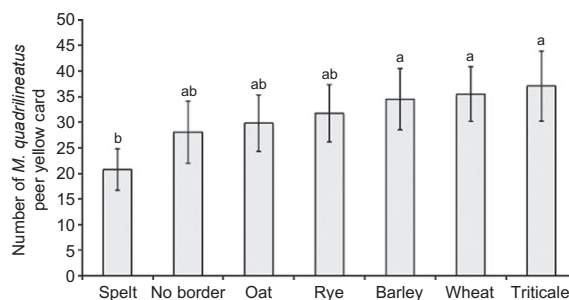


Figure 1 Seasonal mean (\pm SEM) number of *Macrosteles quadrilineatus* on yellow sticky cards placed in carrot plots bordered by various cereal crops. Means with the same letter are not significantly different (lsmeans with Tukey adjustment: $P > 0.05$).

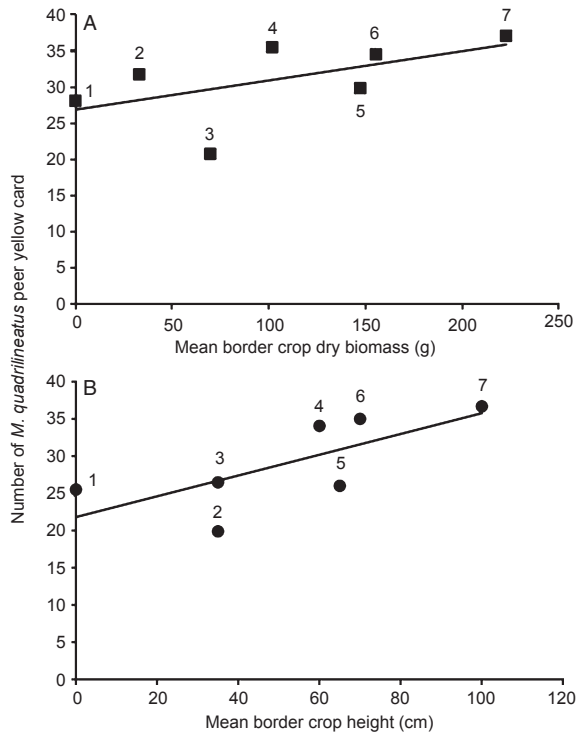


Figure 2 Relationship between the seasonal mean *Macrosteles quadrilineatus* density on yellow sticky cards placed in carrot plots and (A) border crop biomass (g), and (B) border crop height (cm). Numbers near symbols represent the following border crops: 1, no-border; 2, rye; 3, spelt; 4, wheat; 5, oat; 6, barley; and 7, triticale.

horseweed [*Conyza canadensis* (L.) Cronquist], green carpetweed (*Mollugo verticillata* L.), little hogweed (*Portulaca oleracea* L.), common plantain, curly dock (*Rumex crispus* L.), and hairy crabgrass [*Digitaria sanguinalis* (L.) Scop.]. Except for green carpetweed and little hogweed, all the weed species listed are known host plants of *M. quadrilineatus* (Schultz, 1979; Jensen, 1982). On average, in grass herbicide-treated plots 38% of the area was covered in broadleaf-weeds, and in broadleaf herbicide-treated plots 75% of the area was covered with grassy weeds. In plots that received both herbicides 39% of the area was covered with a mix of broadleaf and grassy weeds and <1% of the area in hand-weeded plots were covered in weeds.

Choice tests in greenhouse

The fresh biomass of plants was a significant covariate in the model ($F_{1,260} = 32.95$, $P < 0.01$), but their height was not ($F_{1,260} = 3.26$, $P = 0.07$); therefore, the latter term was not used in subsequent statistical analyses. The interaction between biomass and treatment was not significant ($F_{13,238} = 1.7$, $P = 0.06$). In the choice tests there was a

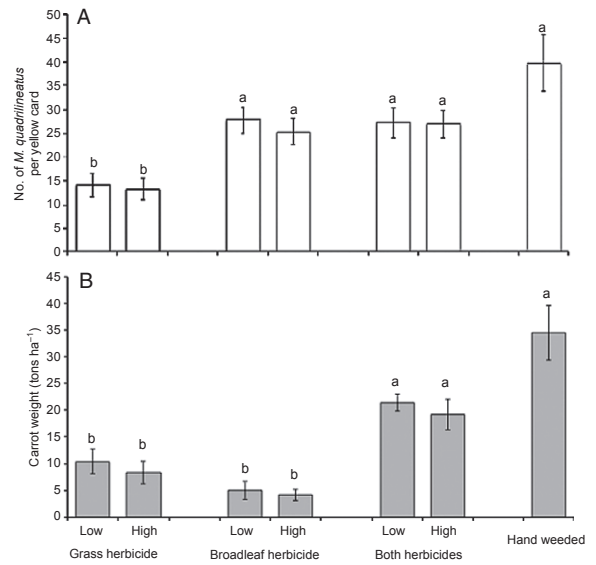


Figure 3 (A) Seasonal mean (\pm SEM) number of *Macrosteles quadrilineatus* on yellow cards placed in carrot plots with different types of weed management. (B) Mean (\pm SEM) biomass (tons ha⁻¹) of carrots from plots with different weed management methods. Herbicides were either applied twice (low) or three times (high) in the growing season. Means within a panel with the same letter are not significantly different (lsmeans with Tukey adjustment: $P > 0.05$).

significant difference in the response of *M. quadrilineatus* to various plants relative to carrots ($F_{13,224} = 2.10$, $P < 0.01$). In general, they chose cereals over carrots and carrots over weeds, but there was no statistically significant difference within these two groups of plants in the response ratio (Figure 4A). Carrot was significantly more preferred over all the tested weed species, except for wild lettuce, and less preferred compared to the cereals ($G_{adj} > 14.89$, d.f. = 1, $P < 0.01$; Figure 4B).

Discussion

Habitat diversification with cereals and weeds can influence the population abundance of *M. quadrilineatus* in carrot plots. Carrot is often grown on sandy soils that are prone to wind erosion, thus commercial carrot growers frequently use rye planted between rows to mitigate this effect. When rye and carrots develop simultaneously in the field, insect abundance may be influenced by both species. Therefore, understanding the preference of *M. quadrilineatus* for cereals, such as rye, has practical implications for pest management. In the border crop study, abundance of *M. quadrilineatus* in carrot plots varied depending on species of cereal bordering these plots, with spelt-bordered plots having reduced abundance of this insect. It is unclear

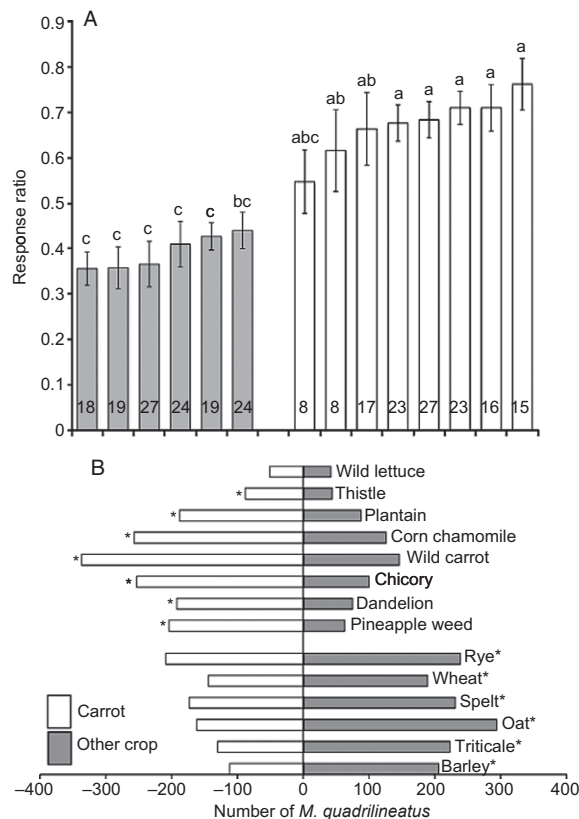


Figure 4 (A) Mean (\pm SEM) response ratio of *Macrosteles quadrilineatus* responding to various plants vs. carrot in a choice test assay. Numbers in bars represent the number of replications for each treatment. Values less than 0.5 correspond to a preference for the alternative plant relative to carrot. Means with the same letter are not significantly different (lsmeans with Tukey adjustment: $P > 0.05$). (B) Number of *M. quadrilineatus* responding in a choice test. Asterisks denote statistically significant preference for a resource (G-test with William's correction: $P < 0.05$).

whether this was the result of attracting insects out of the carrot or by intercepting immigrating populations. Spelt did not stand out from among the other tested cereal species in the greenhouse choice tests for differential preference by *M. quadrilineatus* and although it was one of the smaller border plants, it was similar in height and biomass to rye. This indicates that the factor responsible for the effect of spelt seen in the field experiment may be due to traits particular to this plant growing under field conditions, or that it has a behavior-modifying feature that *M. quadrilineatus* perceive at a distance greater than ca. 20 cm. In the field experiment, spelt-bordered plots had 42% less *M. quadrilineatus* than wheat- or barley-bordered carrot plots. Spelt is a close relative of wheat and is comparable to it in development time (about 120 days to harvest for both), which is about double the time required

for barley to reach harvest; therefore, it is unlikely that the difference in insect numbers was due to a temporal effect of the border crop. It is also possible that increased *M. quadrilineatus* abundance in triticale- and wheat-bordered plots was due to a spill-over effect into the carrot plot from the border, but determining this would have required separate measurements of the herbivore's abundance on the carrot and on the border crops.

Border crops such as oat, rye, barley, wheat, and triticale did not significantly attract or repel *M. quadrilineatus* to carrot plots compared to the no-border treatment, although all these border crop plots had slightly higher numbers of *M. quadrilineatus*. The consistent but slight preference for cereals over carrots from the field experiment and the bioassay indicates that cereals may not be ideal as trap crops for leafhoppers, because the response of the insect to the two plants has to be markedly different for a trap crop to function effectively. Vandermeer (1989) emphasized that high enough trap crop concentration is critical to attract pests away from the main crop. Given the results of the greenhouse choice test experiments, the concentration of the cereals would have to exceed that of carrots to work as effective trap crops, which may be unrealistic for commercial carrot production purposes. One possible application of cereals in carrot fields for *M. quadrilineatus* management is to apply an insecticide (possibly as a seed treatment) to the trap crop that would kill insects immigrating into the field. In fact, in a pilot study there was a slight reduction in *M. quadrilineatus* abundance in carrot plots bordered by insecticide-treated barley compared to untreated barley (Z Szendrei, unpubl.).

The type of weed management affected *M. quadrilineatus* abundance in carrot plots, but the frequency of herbicide application did not. Plots where grasses were completely eliminated with herbicides but broadleaf-weeds were not controlled had the fewest *M. quadrilineatus*. Plots that either had carrot with crabgrass (broadleaf herbicide or both herbicide-treated plots) or carrot alone (hand-weeded plots) had the most abundant *M. quadrilineatus* populations. The greenhouse choice tests displayed similar trends, where broadleaf-weeds were less preferred by *M. quadrilineatus* relative to carrots. This result supports the resource concentration hypothesis (Root, 1973), which states that herbivores will be abundant in habitats where the concentration of a preferred host plants is high. In the case of *M. quadrilineatus*, both grasses and carrots are more suitable and preferred host plants relative to broadleaf-weeds. The biomass of carrots in plots did not explain *M. quadrilineatus* abundance on yellow cards; for example, plots that had the most crabgrass (broadleaf herbicide-treated plots) had similar numbers of

M. quadrilineatus as hand-weeded plots but yielded significantly less carrot biomass, indicating that both these plants are attractive hosts for *M. quadrilineatus*.

Broadleaf-weeds can be sources of colonization of carrot fields by *M. quadrilineatus* early in the season when carrots are just beginning to develop, but these types of weeds in carrot fields later in the season will likely not attract more *M. quadrilineatus* into the field. From a practical pest management standpoint this means that it is more important to appropriately manage grassy weeds and hosts in and around carrot fields than it is to completely eliminate broadleaf-weeds. This study indicated that having two or three herbicide applications does not significantly change carrot biomass or *M. quadrilineatus* abundance in plots, which in theory could lead to a reduction in herbicide use in commercial carrot production provided that these results apply on a larger scale.

There has been a considerable amount of research published on the effect of habitat diversification on pest abundance in agroecosystems and much of the controversy over the subject has centered on the question of diet breadth of the focal herbivore. One assumption is that associational resistance is more likely with polyphagous insects because they are able to respond to cues from multiple plants. On the other hand, specialist herbivores are repelled by cues that are not recognized as coming from the host plant. In fact, there are published meta-analyses that support both sides: Barbosa et al. (2009) found that polyphagous and monophagous insects respond similarly to plant associations, but Andow (1991) and Jactel et al. (2005) concluded that in diverse habitats monophagous herbivores have lower abundance than polyphagous insects. It is challenging to predict the impact of habitat management based on diet breadth, which is the case with the polyphagous *M. quadrilineatus* that responds differently to cereals and weeds. As this study was conducted over one growing season at a small spatial scale, findings will be tested further in the future on a larger spatial scale with the ultimate goal of using habitat management as a tool to suppress *M. quadrilineatus* in carrot fields.

Acknowledgements

Thanks to Dr. Daniel Brainard [Michigan State University (MSU), Department of Horticulture] for donating the corn chamomile seeds and for the weed identifications in the field plots. I thank the team of undergraduate students at MSU who helped out with parts of this project, especially Erica Brown and Suze LaGory who were instrumental for the management of the greenhouse choice tests. I am also grateful to Adam Byrne, Alexandria Bryant, Bruce Sackett, and Dave Francis who provided help with various

aspects of fieldwork. Thanks also to Matt Greenstone and Cesar Rodriguez-Saona for comments on a previous version of this manuscript. This research was supported by MSU AgBioResearch and Project GREEN (#GR10-058).

References

- Albajes R, Lumbierres B & Pons X (2009) Responsiveness of arthropod herbivores and their natural enemies to modified weed management in corn. *Environmental Entomology* 38: 944–954.
- Altieri MA (1995) *Agroecology: The Science of Sustainable Agriculture*. Westview Press, Boulder, CO, USA.
- Andow DA (1988) Management of weeds for insect manipulation in agroecosystems. *Weed Management in Agroecosystems: Ecological Approaches* (ed. by MA Altieri & M Liebman), pp. 265–301. CRC Press, Boca Raton, FL, USA.
- Andow DA (1990) Population dynamics of an insect herbivore in simple and diverse habitats. *Ecology* 71: 1006–1017.
- Andow DA (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36: 561–586.
- Andow DA (1992) Population density of *Empoasca fabae* (Homoptera: Cicadellidae) in weedy beans. *Journal of Economic Entomology* 85: 379–383.
- Asman K (2002) Trap cropping effect on oviposition behaviour of the leek moth *Acrolepiopsis assectella* and the diamondback moth *Plutella xylostella*. *Entomologia Experimentalis et Applicata* 105: 153–164.
- Atsatt PR & O'Dowd DJ (1976) Plant defense guilds. *Science* 193: 24–29.
- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A & Szendrei Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution and Systematics* 40: 1–20.
- Boucher TJ, Ashley R, Durgy R, Sciabarrasi M & Calderwood W (2003) Managing the pepper maggot (Diptera: Tephritidae) using perimeter trap cropping. *Journal of Economic Entomology* 96: 420–432.
- Buckelew LD, Pedigo LP, Mero HM, Owen MDK & Tylka GL (2000) Effects of weed management systems on canopy insects in herbicide-resistant soybeans. *Journal of Economic Entomology* 93: 1437–1443.
- Chapman RK (1971) Predictions of aster leafhopper migrations and the resultant aster yellows problem in Wisconsin. *Proceedings of the North Central Branch of the Entomological Society of America* 26: 96–98.
- Hagel GT & Landis BJ (1967) Biology of the aster leafhopper, *Macrostelus fascifrons* (Homoptera: Cicadellidae), in eastern Washington, and some overwintering sources of aster yellows. *Annals of the Entomological Society of America* 60: 591–595.
- Hoy C, Zhou X, Nault L, Miller S & Styer J (1999) Host plant, phytoplasma, reproductive status, and aster leafhopper (Homoptera: Cicadellidae) flight behavior. *Annals of the Entomological Society of America* 92: 523–528.
- Jactel H, Brockerhoff E & Duelli P (2005) A test of the biodiversity-stability theory: meta-analysis of tree species diversity

- effects on insect pest infestations, and re-examination of responsible factors. *Forest Diversity and Function* (ed. by M Scherer-Lorenzen, C Korner & ED Schulze), pp. 235–262. Springer, Berlin, Germany.
- Jensen JO (1982) Management of the Aster Leafhopper and Aster Yellows in Wisconsin. PhD Dissertation, University of Wisconsin, Madison, WI, USA.
- Meade AB & Peterson AG (1967) Some factors influencing population growth of the aster leafhopper in Anoka County, Minnesota. *Journal of Economic Entomology* 60: 936–941.
- Oloumi-Sadeghi H, Zavaleta LR, Lamp WO, Armbrust EJ & Kapusta G (1989) Interactions of the potato leafhopper (Homoptera: Cicadellidae) with weeds in an alfalfa ecosystem. *Environmental Entomology* 16: 1175–1180.
- Risch SJ, Andow DA & Altieri MA (1983) Agroecosystem diversity and pest control: data, tentative conclusions, and new research directions. *Environmental Entomology* 12: 625–629.
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43: 95–124.
- Schultz GA (1979) Epidemiology of the Aster Leafhopper and Aster Yellows in Relation to Disease Control. PhD Dissertation, University of Wisconsin, Madison, WI, USA.
- Sokal RR & Rohlf FJ (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*. Freeman, New York, NY, USA.
- Tahvanainen JO & Root RB (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta crucifera* (Coleoptera: Chrysomelidae). *Oecologia* 10: 321–346.
- Tillman PG (2006) Sorghum as a trap crop for *Nezara viridula* L. (Heteroptera: Pentatomidae) in cotton in the southern United States. *Environmental Entomology* 35: 771–783.
- Tonhasca A & Byrne DN (1994) The effects of crop diversification on herbivorous insects – a meta-analysis approach. *Ecological Entomology* 19: 239–244.
- Vandermeer J (1989) *The Ecology of Intercropping*. Cambridge University Press, Cambridge, UK.
- Zhou X, Hoy CW, Miller SA & Nault LR (2003) Marking methods and field experiments to estimate aster leafhopper (*Macrosteles quadrilineatus*) dispersal rates. *Environmental Entomology* 32: 1177–1186.