

EFFECTS OF WITHIN-FIELD LOCATION OF HOST PLANTS AND
INTERCROPPING ON THE DISTRIBUTION OF *Microtheca ochroloma* (Stål) IN
MIZUNA

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2003

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ACKNOWLEDGMENTS

I would like to thank my committee members for their dedication and assistance in this endeavor. In particular, I am grateful to Dr. Swisher for her overall guidance and instruction in scientific method; to Dr. McSorley for his help with experimental design and statistical analysis; and Dr. Webb for thoughtful and persistent editorial comments and use of her lab facilities.

I would like to thank my family for their continuous love and support.

I would like to thank the Organic Farming Research Foundation for its generous financial support for this project.

I would like to thank Rose Koenig for hours of grant writing assistance and her and her family for use of their farm.

I would like to thank all the farmers in north central Florida who shared their anecdotal evidence and keen observations with me, and whose experiences were the impetus for this research.

I would like to thank my friends and colleagues at UDSA-ARS for their patience and clarification of the finer points of entomology.

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Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
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May 2003

Chair: M.E. Swisher

Major Department: Natural Resources and Environment

The yellowmargined leaf beetle, *Microtheca ochroloma* (Stål), is a pest for organic vegetable farmers in Florida. Very little is known about the ecology of *M. ochroloma*. The yellowmargined leaf beetle is dormant during the warmest part of the year, but it is not clear whether this dormancy constitutes aestivation or quiescence. In field studies, populations of adult *M. ochroloma* were higher on host plants in the field interior than on the field borders, indicating that border areas are not important dormancy habitats. *Microtheca ochroloma* accumulated in monocropped plots of host plants in larger numbers than in intercropped plots, but there was no difference in the number of beetles per plant between the monocropped and intercropped treatments. Therefore, intercropping does not appear to be a useful control strategy for this beetle by organic farmers. The searching behavior of the yellowmargined leaf beetle appears to be density dependent. Small populations of yellowmargined leaf beetles do not congregate or

engage in patch restricted searching. At higher population levels, *M. ochroloma* move *en masse* in response to their own herbivory. More research on the host-plant finding behavior and basic ecology of *M. ochroloma* is necessary to develop control strategies appropriate for organic farmers.

CHAPTER 1 INTRODUCTION

The yellowmargined leaf beetle, *Microtheca ochroloma* Stål, (Coleoptera: Chrysomelidae) is a pest that devastates high value cruciferous crops, such as mizuna (*Brassica rapa*, japonica group), mibuna (*Brassica rapa*, japonica group), napa cabbage (*Brassica rapa*, pekinensis group), turnip (*Brassica rapa*), mustard (*Brassica juncea*), and watercress (*Nasturtium officinale*) (Figure 1-1).



Figure 1-1 Feeding damage to experimental plots of mizuna by *M. ochroloma*

Microtheca ochroloma feeds on these cruciferous host plants, whose primary allelochemical is mustard oil glucosides (Hicks 1974). Jolivet and Hawkeswood (1995) comment that adults of the genus *Microtheca* can feed on the pollen of plants in the Rosaceae family. No reports of *M. ochroloma* feeding on non-crucifers have been made.

Microtheca ochroloma is widespread throughout much of the southeastern Gulf States. The yellowmargined leaf beetle was first identified in the United States in Mobile, Alabama, in 1947 (Chamberlin and Tippins 1948). The yellowmargined leaf beetle was subsequently found in Louisiana, Texas, Mississippi, and Florida. In 1994, *M. ochroloma* was collected in North Carolina (Staines 1999). The yellowmargined leaf beetle is native to South America, where it is found in Argentina, Brazil, Chile and Uruguay (Woodruff 1974).

Description of *M. ochroloma*

The yellowmargined leaf beetle is about 5 mm long (Woodruff 1974), with females generally larger than males. *Microtheca ochroloma* is dark brown, bronze or black, and has orange, yellow or white margins around its elytra (Woodruff 1974). Each elytron has four prominent rows of punctures (Figure 1-2).



Figure 1-2 An adult male *Microtheca ochroloma*

Female *M. ochroloma* deposit bright orange, elongate eggs on plant stems, under fallen leaves or on the soil surface. Eggs are commonly laid in small clutches but may be found singly. Larvae range in color from grayish to yellow-brown and have a sclerotized head capsule (Figure 1-3).



Figure 1-3 Second instar larvae of *Microtheca ochroloma*

According to Oliver and Chapin (1983), there are three larval instars. Jolivet and Hawkeswood (1995) refer to the pre-pupa stage as the fourth instar. Pupal cases are dark brown or black and may be found attached to the undersides of leaves or on the soil surface. Development of *M. ochroloma* from egg to adult takes about 23 days (Oliver and Chapin 1983).

Characterization of *M. ochroloma* in Florida

In 2001, farmers in Florida reported infestations of *M. ochroloma* as far north as Jefferson and Leon counties (George and Margie Cole, pers com.) and as far south as

Charlotte County (David Coles, pers com.). Farmers have reported changing their growing practices due to the severity of yellowmargined leaf beetle infestations (Joe Durando and Charley Andrews, pers com.). Changes reported include not growing susceptible crops at all or decreasing the proportion of susceptible crops grown. Large field populations of this foliage-feeding insect cause significant economic losses to organic farmers.

There are three reasons why *M. ochroloma* causes such problems in Florida. *M. ochroloma*'s cruciferous host plants thrive in the cool months from October to April that comprise most of the growing season for organic vegetable farmers here. During these months, hard frosts or freezes are relatively rare. As a result, the adult beetles continue to feed and reproduce throughout the winter, although larvae are somewhat more susceptible to cold weather. The abundant food supply and above-freezing temperatures create ideal conditions for the yellowmargined leaf beetle. Finally, the yellowmargined leaf beetle is an introduced pest and has no known predators or parasites in the United States. Freed from bio-regulatory interactions, *M. ochroloma* has the potential to spread unchecked. It appears to migrate at a slow rate, which may have thus far prevented it from becoming a nuisance on the order of such introduced pests as whitefly (*Bemisia* spp.), imported fire ants (*Solenopsis invicta*), diamondback moth (*Plutella xylostella*) and others.

In Florida, *M. ochroloma* is part of an invasion of adventive species. Florida is particularly susceptible to the threat of non-native species because of its tropical to sub-tropical climate, its insularity and fragmented natural habitat (Simberloff 1997). There

are nearly a thousand non-native insect species in Florida (Frank *et al.* 1997). Experts estimate that one major new pest arrives every year (Frank *et al.* 1997).

Pesticide Resistance and *M. ochroloma*

Little research has been done on the biology or ecology of *M. ochroloma* because the application of broad-spectrum synthetic insecticides has provided sufficient control for conventional growers. However, the use of insecticides on a large scale will speed up the selection process for individuals with pesticide resistance, as demonstrated by the development of resistance in such pests as Colorado potato beetle (*Leptinotarsa decemlineata*) and tobacco budworm (*Heliothis virescens*). Resistance to insecticides has been reported since the early 20th century, with 447 species of insects and mites resistant to at least one insecticide (Georghiou 1986). Of these resistant insects, 66 species are Coleopterans. Follett and Roderick (1996) list 15 species of chrysomelids that have developed insecticide resistance worldwide. Overall, 59% of the species with known resistance are described as “agriculturally important” pests (Georghiou 1986). The economic costs of resistance are staggering.

The emergence of chemical resistance in *M. ochroloma* will eventually necessitate control measures that are based on an understanding of insect ecology. Many of the newer, reduced-risk insecticides act against a narrower range of pests, but few of these target beetles. If ecological methods can be developed to control *M. ochroloma*, farmers would be able to use these reduced-risk chemicals against aphids and various lepidopteran pests. Currently, with neither the knowledge about its ecology nor the option to use chemical means for its control, organic farmers have been the most affected by this pest (Rose Koenig, pers. comm.).

Organic Research and *M. ochroloma*

This project is a needed addition to the small number of organic and on-farm research projects carried out in the United States southeast region (which includes Florida, Georgia, Alabama, Mississippi, Louisiana, South Carolina, and North Carolina). Florida is the second leading state in the country in vegetable production in the United States, with \$6.95 billion in cash receipts in 2001 (National Agriculture Statistics Service 2002). However, as of 2001, the state had no certified organic research acreage (Sooby 2001). In Florida, only three on-farm research projects have been conducted with the input of certified organic farmers (Sooby 2001). This situation is reflected nationwide as well. Sales of organic products topped \$9 billion in 2001, or about 2% of total market for agricultural products. Publicly funded organic agriculture research comprises only about 0.1% of total agriculture research funding (Lipson 1997).

Research Objectives

This study will describe aspects of emergence and host finding behavior by the yellowmargined leaf beetle and evaluate whether intercropping can be employed by farmers to reduce the severity of beetle outbreaks.

CHAPTER 2 LITERATURE REVIEW

In studying the effect of photoperiod on *M. ochroloma*, Oliver and Chapin (1983) asserted that yellowmargined leaf beetles are multivoltine, with adults entering aestivation from mid-June to October in Louisiana. However, they report finding *M. ochroloma* in ground trash as early as September. They theorized that the ability of *M. ochroloma* to develop continuously in the laboratory (at ca. 27 °C) under an ambient photoperiod indicates that temperature is important in mediating diapause. Oliver and Chapin (1983) did not rear yellowmargined leaf beetles at outdoor ambient temperatures, or vary temperature with photoperiod in order to test this assertion.

In efforts to clarify the aestival behavior of the yellowmargined leaf beetle, I sampled an organic farm in Gainesville, Florida on 1 July 2001. I found a dozen adult yellowmargined leaf beetles on turnip greens. I did not find any eggs or larvae. I took the adult beetles and exposed them to a 14:10 photoperiod and approximately 25° C. The beetles began to mate within 24 hours and oviposition soon followed (Bowers, unpublished).

There are several possible explanations for the disappearance of *M. ochroloma* during the summer. The dormancy pattern of the yellowmargined leaf beetle has not been well described. Pinpointing when and where the yellowmargined leaf beetle emerges and characterizing its host-finding patterns after emergence are the first steps in developing ecologically-based control strategies.

Dormancy and Emergence

The general term dormancy encompasses two distinct types of insect behaviors: diapause and quiescence. Diapause refers to a resting period that is pre-programmed and may be mediated by environmental factors, but is not caused directly by them (Danks 1987). The cues that signal diapause do not limit an insect's development per se, but rather act to set off a series of neuro-hormonal responses known as diapause induction (Danks 1987). Before an aestivating insect can resume activity it must complete the diapause development, a period which restores the ability of an insect to respond to favorable conditions (Danks 1987). A diapausing insect cannot respond to favorable conditions which resume before diapause development is completed. Similarly, Masaki (1980, p.3) comments that aestivation is not only a pattern of dormancy during the summer, but that "there should always be a particular response to environment or programmed sequence of physiological events to complete the dormant stage after the summer."

Quiescence is a dormancy that is a direct response to environmental thresholds (*e.g.*, not enough food, temperature extremes approaching lethal limits) (Danks 1987). Quiescence does not involve the same series of pre-programmed developmental stages involved in diapause, so quiescent insects can resume normal activity as soon as environmental conditions become favorable.

Photoperiod and temperature are often cited as diapause cues, while food quality and quantity are said to provoke quiescence or contribute to diapause in an indirect way. The overlap of these factors and the degree with which they interact are responsible for many of the insect dormancy strategies observed in the field. There are a great number of interactions that control diapause induction.

Photoperiod is the most reliable and easily identifiable diapause cue in temperate climates and terrestrial habitats (Danks 1987). Insect diapause is frequently induced by photoperiods above or below some threshold value, known as the critical photoperiod. The critical photoperiod is the photoperiod under which half of a group of individuals enter diapause (Danks 1987). Insects that respond to long days with diapause (i.e. they diapause in the summer) are known as short-day insects. Long-day insects are those that require long days for their active stages and are cued to diapause by short days.

Although seasonal variations in temperature are predictable, variation in temperature from one day to the next can be drastic. For this reason, temperature is not considered an effective diapause cue, except in a limited number of insects. However, the interaction between temperature and photoperiod plays a fundamental role in mediating diapause (Danks 1987). Temperature can affect photoperiod in several different ways. In some cases, insects are only sensitive to photoperiod cues between certain temperatures. In other insects, low temperatures can strengthen the effect of short days on diapause induction in long-day insects (Danks 1987). Long photoperiods are the cue for summer diapause, or aestivation (Masaki 1980). In general, high temperatures act in concert with long photoperiods in summer diapause induction. The onset of lower temperatures is favorable for diapause development and termination (Masaki 1980). Although relatively little has been written on the subject, summer diapause is more common in insects than the literature might suggest (Masaki 1980). The relationship between temperature and photoperiod in signaling insect diapause is not straightforward, however, as temperatures alone can induce aestivation in the cabbage root fly, *Delia radicum* pupae (Finch and Collier 1985).

In addition to photoperiod and temperature, food plants can influence dormancy in phytophagous insects. Seasonal changes influence the availability of food plants which can have distinct effects on quiescence and diapause. First, lack of food is a direct control (rather than a cue) that causes quiescence (Danks 1987). Secondly, the unavailability of host plants may slow an herbivore's development, exposing the insect to diapause inducing conditions for a longer period of time. This is considered an indirect effect (Danks 1987). Both type and quantity of food can alter an insect's developmental sequence, although the presence or absence of particular food plants is a more reliable cue for monophagous than polyphagous insects (Danks 1987). For the Colorado potato beetle, photoperiod and temperature are the major inductive cues, but access to food plants during long days ensures that beetles do not enter diapause (De Wilde *et al.* 1959). Oliver and Chapin (1983) do not discuss the influence of altered habitat or food resources as a possible explanation for dormancy in *M. ochroloma*.

Most species can enter diapause only in a single specific life cycle stage, according to taxonomic group but two or more dormant stages are possible within diverse groups (Danks 1987). Temperate region chrysomelids were reported to enter diapause as adults (Krause 1982 from Danks 1987), although a few species diapause as eggs, and some genera as larva. A survey of the distribution of summer diapause by stage shows that Coleopterans most often enter summer diapause as adults (38 out of 44 species surveyed) (Masaki 1980). The protection offered by the adult beetles' sclerotized cuticle as well as its ability to move to more favorable microclimates afford adult beetles the best chance for survival during aestivation (Masaki 1980). Oliver and Chapin (1983) report that the yellowmargined leaf beetle enters diapause as an adult, but this observation has

not been substantiated. The adult yellowmargined leaf beetles are the only ones to be seen in the field during the summer and the first to return in the fall, so it seems likely that this is the overwintering stage (Bowers, unpublished). Adult diapause involves the cessation of post-emergence ovarian development. The dormant sub-stage is the newly emerged, non-parous adults (Danks 1987). Oliver and Chapin (1983) do not discuss the possibility of a reproductive diapause as an explanation for the yellowmargined leaf beetle's scarcity during the summer months.

Both summer and winter diapausing insects exhibit the same pre-dormancy behaviors, including seeking shelters, migrating from feeding/ breeding sites and burrowing in the soil (Masaki 1980). Insects may travel between crop plants and non-agricultural landscapes for a number of reasons including changes in food availability, habitat disturbances and natural dispersal patterns (Altieri 1994). Weedy field borders can harbor insect pests until field conditions are appropriate for their return to agricultural hosts (Altieri 1994), particularly when the weeds are closely related to agricultural plants.

Insects display as many variations in diapause habitat as they do in diapause timing. Bean leaf beetles, *Cerotoma trifurcate* (Forster), leave feeding sites for field margins, where they spend their reproductive diapause (Boiteau *et al.* 1979a). Upon emergence, adult Colorado potato beetles can fly or walk back to known feeding sites from overwintering sites, or they may migrate long distances to new feeding sites. For second generation Colorado potato beetles, the usual pattern is to diapause in the field or travel short distances to field margins for overwintering (Voss and Ferro 1990).

In the spring, newly emerged Colorado potato beetle females may oviposit briefly before diapausing or may continue to reproduce without entering diapause. Their

progeny will remain active during the summer months and enter diapause in the fall. The activity of the second generation in the field during the spring and summer tends to obscure the aestival habits of the first generation adults (Tauber *et al.* 1988). Tauber *et al.* 1988 found that the variability in summer oviposition (and subsequent active summer populations) was largely due to temperature and food variability.

Oliver and Chapin (1983) observe that yellowmargined leaf beetle populations drop off dramatically in the hot summer months and attribute this decline in activity to aestivation. Since *M. ochroloma* did not enter dormancy at all under long photoperiod and constant temperature regime in their laboratory, the dormancy of *M. ochroloma* may be mediated by a combination of photoperiod and temperature. It is also possible that the yellowmargined leaf beetle experiences a quiescence during the summer months. Unlike diapause, quiescence is a direct and immediate dormancy response to altered environmental conditions.

Masaki (1980) proposes that summer diapause comprises part of a polymodal emergence strategy by adult insects, whereby a few insects continue to develop and oviposit on a limited basis while others enter dormancy. Multiple diapause responses in a single population would ensure survival during adverse environmental conditions (through the dormancy strategy) while a few insects reproduce, which keeps the population active and growing on a limited basis. If there is no strong selective pressure towards one or the other of these strategies, both will continue to persist in the population. This is a third aestival pattern that could describe the yellowmargined leaf beetle.

In summary, the stage during which diapause induction takes place is highly variable in insects. It can occur as a complete halting of activity in immatures or as the reproductive diapause of adults. Induction cues also vary at the species level and may be the result of unfavorable food or climatic conditions, most often photoperiod, temperature, or the interaction of temperature and photoperiod. Diapause can also vary within a species according to geographical distribution. The induction signals and variability of diapause response in *M. ochroloma* are unknown. It is not yet clear which inductive cues are responsible for dormancy in *M. ochroloma*, or where *M. ochroloma* spends its dormant period.

Host Plant Preferences: Searching and Finding

Chrysomelid Habitats

Ameen and Story (1997a) established that first-instar yellowmargined leaf beetles preferred turnips to other cruciferous vegetation, third instars preferred turnip and mustard greens, while adults consumed turnips, mustard, and radish in equal quantities. Chamberlin and Tippins (1948) Haeussler (1951), Oliver (1956), Spink (1959) all reported that the yellowmargined leaf beetles were found more frequently on their preferred host plants in the field (turnip and mustard) than other crucifers, although this phenomenon has never been quantified. Generally, females of phytophagous insects are able to choose host plants based on characteristics associated with reproductive performance, so that host preference and fecundity are expected to be correlated (Ferguson *et al.* 1991, Ramnath *et al.* 1992). Collard and cabbage were the least preferred host plants of the beetles. In the field, *M. ochroloma* exhibited these same preferences, feeding on cabbage only when no other host plants were available (Chamberlin and Tippins 1948). Cabbage plantings adjacent to a field of turnips heavily

infested with yellowmargined leaf beetles did not become infested with beetles (Chamberlin and Tippins 1948). Ameen and Story (1997) postulate that the texture of host plant leaves may influence feeding; the beetles avoid plants with tough or waxy surfaces.

When a female insect locates an appropriate oviposition habitat, her progeny may find the habitat suitable as well. Lower dispersal rates are generally associated with more specialized phytophagous species (Stinner *et al.* 1983 from Nielsen 1988). Chrysomelids commonly exhibit this phenomenon. For many chrysomelids, mating, oviposition, and adult and larval feeding all take place on the same plant species (Nielsen 1988). Larvae may complete their development on plants only meters away from those that supported their parents' own development (Carne 1966 from Nielsen 1988).

Host Plant Finding in Simple and Complex Environments

While life history characteristics such as monophagy, shared adult and larval resources, and the potential for low dispersal rates all strengthen the relationship between host and insect (Strauss 1988), it is not known exactly how herbivores initially find their preferred host plants. Generally, insects rely on visual, mechanical, and chemical stimuli to locate potential host plants and to determine their acceptability for feeding and oviposition. While insects generally respond to evidence of general habitat like yellow-green reflected light, monophagous herbivores rely on additional, more specific host plant cues (Stanton 1983). Host plant finding is influenced by background vegetation (*e.g.* an adjacent meadow or forest) as well as the distribution of cultivated host and non-host plants, as in an agricultural intercropping pattern. Generally, it is thought that a habitat composed of varied microclimatic, biotic and structural elements supports a greater stability in insect pest populations (Altieri 1994).

While investigating the arthropod community of *Brassica oleracea*, Pimentel (1961) found more herbivores residing in dense host plantings than sparse ones, but host plants in more sparse areas had more herbivores per plant. Herbivores tended to spread themselves out in a dense habitat, so that each plant is less likely to be chosen by an individual herbivore (Pimentel 1961). Dense habitats tended to support fewer taxa overall than the sparse plantings (Pimentel 1961). Also, smaller sized plants spaced far apart were more difficult for herbivores to locate, but once the plants grew larger, they became easier to find, which increased the tendency toward aggregation among the insects (Pimentel 1961).

Dempster (1969) found that crucifers grown in a weedy environment had fewer cabbage butterflies, *Pieris rapae*, than those grown without weeds. Both *Phyllotreta striolata* and *Phyllotreta cruciferae* were found more commonly in the cultivated (weeded) plots than the uncultivated ones, where they were all but absent (Cromartie 1975). Host collards intercropped with tomato and tobacco (*Nicotiana tabacum*) had lower colonization by flea beetles, less leaf damage due to beetle feeding, and lower emergence of subsequent generations (Tahvanainen and Root 1972). There were fewer striped cucumber beetles, *Acalymma vittata*, in polycultures than in cucumber monocultures, even taking into account the smaller plant size in the polyculture plots (Bach 1980). In a similar set of experiments, Bach (1980) found that increasing the cucumber stand purity increased the beetle density per plant. Additionally, the striped cucumber beetle, *A. vittata* preferred cucumber leaves grown in monocultures over those grown with tomato plants (Bach 1980).

Risch (1981) studied several species of beetles (Chrysomelidae: Galerucinae) and found that monocultures had higher numbers of beetles than polycultures, with no significant differences between predation or parasitism between the polyculture and monoculture treatments. Purposeful cultivation of crucifers and non-host plants together in an intercropping system reduced populations of flea beetles, *Phyllotreta crucifera*, in broccoli (Garcia and Altieri 1992).

During the first two seasons of their study, Latheef *et al.* (1984) found no differences in populations of *Phyllotreta cruciferae* between monocultures of collards (*Brassica oleraceae*) and polycultures of collards with non-cruciferous vegetables. The third season, the populations of *P. cruciferae* was smaller on intercropped collards than monocultures. The monocultures also had higher plant damage than the polycultures during the third season. The overall populations of *P. cruciferae* were much higher the first two seasons than the third, and the authors posit that the polyculture did not provide protection to the host plants in the face of much higher populations of flea beetles.

The effects of vegetationally diverse plantings on insect population distribution are far from predictable. Andow (1991) analyzed literature on both additive and substitutive polyculture plantings (a total of 209 studies involving 287 herbivores) and found that just over half (51.9%) of the herbivores studied had lower population densities in polycultures, and 15.2% had higher densities. Andow (1991) concludes that polycultures are likely to support lower individual species densities than monocultures, especially for monophagous insects. However, the range of arthropod responses to plants and the mechanisms responsible for those responses are so varied that generalization is not useful for pest management purposes. Smith and McSorley (2000) concur, observing

that the specific conditions under which polyculture can facilitate pest management or even reduce chemical pest control applications must be tested more rigorously through on-farm research.

Host Plant Finding Theories

Cromartie (1975) found that *Phyllotreta striolata* and *Phyllotreta cruciferae* were more frequent as plot size increased. Kareiva (1983) also found that densities of these two species of flea beetles (*P. striolata* and *P. cruciferae*) increased with patch size. *Pieris rapae*, on the other hand, appeared less frequently with increasing plot size (Cromartie 1975).

The theory of island biogeography (MacArthur and Wilson 1967) suggests that a number of factors, including island size, determine how many species an island can support. Generally, larger islands are able to support larger animal populations than smaller islands. Larger islands are easier for individuals of a species to colonize and once there, those individuals are less likely to leave or die out. Several authors, including Janzen (1968) have suggested that the theory of island biogeography is applicable to host plant finding by insects. Patches of host plants are “islands” among a sea of vegetation to an insect. Janzen (1968) theorized that the number of herbivores is dependent on the size and location of the host plant relative to adjacent vegetation, the similarity of the host plant to that adjacent vegetation, the abundance of the plant in space and the relative insect population on adjacent plants. The insect population in a host plant patch reflects the equilibrium between herbivore emigration and immigration (or colonization in biogeography terms). Janzen (1968) describes this relationship as a co-evolutionary one.

A theory of chemical coevolution between plants and insects was described by Ehrlich and Raven (1964). Although acknowledging that plant mechanical defenses and

ecological considerations are valid parameters within which insects must operate when choosing suitable host plants, Ehrlich and Raven (1964) conclude that it is secondary chemical substances that largely dictate the patterns of herbivory observed in nature. Even so, they caution that experimental verification is required to assess whether or not a particular secondary chemical is an attractant of a feeding stimulant to a specific insect (Ehrlich and Raven 1964).

Subsequent authors have agreed that chemical communication between plant and insect is a key factor with regard to the feeding behavior of phytophagous insects (Matsuda 1988). The relationships between cruciferous plants and crucifer feeding insects illustrate this phenomenon. When crucifers are damaged, enzymes and glucosinolates that are normally stored in different compartments of the plant cells (Luthy and Matile 1984 from Nielsen 1988) are mixed and hydrolysis products (known as mustard oils) are released (Stanton 1983). Glucosinolates and their hydrolysis products are defensive products and are toxic to bacteria, fungi and a number of phytophagous insects (Nielsen 1988). However, glucosinolates and mustard oils act as allelochemicals to some insects, including crucifer-feeding chrysomelid beetles (Stanton 1983, Nielsen 1988). These compounds allow the beetles to distinguish a crucifer host plant from a non-suitable plant (Nielsen 1988). Hawkes and Coaker (1979) established that the cabbage root fly (*Delia radicum*) oriented towards host plant odors even in the absence of visual or tactile cues. The production of plant volatiles can be positively correlated with the density of herbivores feeding on the plant, resulting in aggregated feeding behavior (Dicke and Vet 1999). Ameen and Story (1997b) did not compare the differences in

chemical attractants produced by their experimental host plants nor propose how differences in chemical profiles may have influenced feeding by *M. ochroloma*.

Finch and Collier (2000) summarize a number of prominent theories that attempt to explain how non-host plants interfere with host plant finding. These hypotheses include physical or visual disruption of the host plant architecture, chemical “masking” of host plant odors or production of chemical repellants, influencing host plant physiology, and Root’s (1973) resource concentration hypothesis and natural enemies hypothesis. Despite the plethora of attention devoted to the topic of host plant finding, no single theory has yet been able to explain the diversity of host plant finding behavior evidenced by phytophagous insects.

In choice experiments, Tahvanainen and Root (1972) showed that the flea beetle preferred the collard leaves alone to combinations of collard with tomato and collard with ragweed (*Ambrosia artemisiifolia*). They suggest this is because non-host plant chemical stimuli can dilute or mask chemical signals from host plants. Even when non-host plant leaves were buried, the olfactory cues alone were enough to repulse beetles, especially when the non-host plant was ragweed.

Non-host plant compounds in a more vegetationally complex environment may amplify the effect of distance, further masking or overpowering host plant finding cues. Non-olfactory components of a complex system may also factor into an insect’s host-finding efficacy. Insects seeking out a favorable microclimate will be further disoriented by the heterogeneous temperature, light and moisture gradients available among a non-cultivated plant community. In addition to the chemical defenses possessed by a single plant, plants in a complex environment benefit from the variability in these factors. The

additional protection afforded to a single plant by complex surroundings was termed “associational resistance” by Tahvanainen and Root (1972).

One of the most influential theories was the resource concentration hypothesis proposed by Root (1973). Root (1973) found that the herbivore load (defined as the biomass of herbivores per 100 g of dried foliage) was higher in pure stands than in perimeter rows, but that the perimeter rows had greater herbivore diversity and evenness than the pure stands. He proposed the resource hypothesis to explain the behaviors he observed in the field.

Root (1973) theorized that species will tend to stay in an area of suitable host plants. If a clump of host plants is favorable for the growth and development of a phytophagous insect, individuals of that species will tend to accumulate on or around that host plant. The more of the insect’s life cycle requirements that are met by this habitat, the more likely it is to remain there, and the longer the length of its stay will be. Generalist herbivores or those that have varying habitat or food requirement throughout their life cycle will tend to move among different host plants, rather than linger on one plant. The end result is that specialized herbivores tend to accumulate in pure stands of their host plants, and herbivores with generalized feeding patterns will move in and out of a stand. The accumulation of specialized herbivores may be enough to produce an overall higher herbivore load in pure stands (Root 1973). Root’s resource concentration hypothesis is complementary to the island biogeography model in predicting that herbivore abundance should be positively correlated with host plant patch size.

Additionally, Root (1973) found that crucifer-specialist herbivores with the narrowest host plant ranges (the flea beetle *Phyllotreta cruciferae* and the aphid

Brevicoryne brassicae) appeared at significantly higher densities in the pure stands. The other crucifer specialists in this community, including the diamondback moth, *Plutella maculipennis*, the flea beetle, *Phyllotreta striolata*, and the cabbage butterfly, *Pieris rapae*, were found on the perimeter rows and even feeding on wild crucifers around the perimeter. In both perimeter rows and in pure stands, herbivore load was positively correlated to the *P. cruciferae* population and species diversity was inversely correlated to *P. cruciferae* populations. Root's observation that other crucifer aphids emigrated from host plants that had been damaged by *P. cruciferae* suggests that interspecific competition reinforced the dominance of this flea beetle in pure stands.

Root (1973) offered the natural enemies hypothesis in addition to the resource concentration hypothesis in order to explain his results. Root theorized that because diverse vegetation provides more habitat niches and food resources for a greater number of herbivores, it also supports more predators and parasites. Habitats that support an abundance of natural enemies keep herbivore populations in check, so one or two species don't dominate the community structure.

Root (1973) found that the diversity of predators and parasitoids was higher in the pure stands than the perimeter on several occasions. Although the herbivore-to-predator ratio of the perimeter rows was generally higher than that of the pure stand, the predators' main prey were insects that made a small contribution to the herbivore load (early instar strip feeders and sap feeders). Adult flea beetles were the most prevalent component of this group, but are not predated upon and have only one specialized parasitoid. Thus, the natural enemies hypothesis could not completely account for the lower herbivore loads in the perimeter rows. According to Root, insects congregated in areas dominated by their

host plants and at the same time the wide variety of natural enemies which accumulated in diverse vegetation controlled and evened out herbivore populations outside the pure stands. Natural enemies and resource concentration work in a complementary fashion to produce the distribution of insects observed by Root (1973).

Within the crucifer-arthropod community characterized by Root (1973), each species preferred slightly different host plant dispersion characteristics. No single species dominated all plant densities or both cultivated and uncultivated treatments. Root (1973) concluded that while reduction of host plant density or intercropping may be effective in controlling some insect outbreaks, host plant resistance, predation, and parasitism and the timing of insect and host plant lifecycles were important factors in determining the severity of herbivore loads on vegetation.

Coll and Botrell (1994) found that tall varieties of corn (*Zea mays*) intercropped with beans (*Phaseolus vulgaris*) prevented colonization by adult Mexican bean beetles, *Epilachna varivestis*. These tall corn-bean intercrop plantings had lower overall beetle densities than bean monocultures or short corn-bean intercrops. Ostensibly, the tall corn physically disrupted the searching pattern of *E. varivestis*. Despite the adults' difficulty in locating the beans among the tall corn, *E. varivestis* larvae developed more quickly on tall corn-bean intercrop plots. In choice tests, *E. varivestis* preferred beans grown with tall corn over the other bean leaves (Coll and Botrell 1994). The overall *E. varivestis* density was higher in the monocropped plots, even taking into account the faster larval development in the tall corn intercropped plots. Coll and Botrell's (1994) finding (that *E. varivestis* preferred the beans grown with tall corn) does not fit with the associational resistance of Tahvanainen and Root (1972). However, the density of *E. varivestis* does

support Root's (1973) resource concentration hypothesis. At the same time, the authors observe that the population of natural enemies did not differ among the treatments and that the overall mortality due to predation was low and did not differ among the habitats (Coll and Botrell 1994).

Host Plant Finding Mechanisms

Taken together, the various theories of host plant finding explain the distribution of insects observed in the field but offer little insight into the how herbivores find their hosts. What are the mechanisms or behaviors involved in host plant finding?

Root (1973) predicted that altering the concentration of resources shifted the emigration-immigration balance, thus accounting for the variation in herbivore densities. As predicted by island biogeography and resource concentration hypotheses, Karevia (1983) found increasing flea beetle densities with larger patch sizes. Large patches had more beetles, regardless of the initial number of beetles placed in the patch, indicating that emigration was more sensitive to patch size than immigration (Karevia 1983). Garcia and Altieri (1992) observed that broccoli monocultures had more flea beetles than intercropped plots. They also demonstrated that even when *Phyllotreta cruciferae* were introduced into the monoculture and intercropped plots in equal numbers, the flea beetles left mixed croppings of broccoli and vetch in vast numbers. Within 24 hours, the flea beetle populations in the monoculture versus the vetch intercrop were similar to what they had been before the experiment (Garcia and Altieri 1992).

These findings support Andow's (1991) assertion that insects spend less time in patches of diverse vegetation and move more quickly than in monoculture plots.

Similarly, Hawkes and Coaker (1976) showed that although cabbage root flies (*Delia brassicae*) laid fewer eggs on host plants that were intercropped with clover than those in

monoculture, *D. brassicae* found the host plants in equal numbers in polyculture and monoculture. The clover did not hide the host plants. Instead the presence of the non-host plants increased *D. brassicae*'s movements within the plots, resulting in less time spent laying eggs and fewer eggs laid (Hawkes and Coaker 1979).

On the other hand, Stanton (1983) attributed herbivore concentrations to herbivore population growth within a colonized host plant patch as well as the emigration/immigration balance. A slightly different explanation was offered by Matter (1997) for the distribution of the red milkweed beetle *Tetraopes tetraophthalmus*. Matter (1997) observed that *T. tetraophthalmus*' density did increase with patch size, but not due to inter-patch migration. In fact, Matter (1997) found that female *T. tetraophthalmus* tended to migrate to smaller patches of host plants. Distribution and density patterns of *T. tetraophthalmus* were due to local reproduction and patch residence time. Matter (1997) points out that larger patches provide more suitable oviposition sites, more abundant food (which could produce larger and more fecund females) and decreased mate searching time in patches with large numbers of beetles.

Risch (1981) studied various species of chrysomelid beetles (*Acalyma thiemei* (Baly), *Ceratoma ruficornis rogersi*, *Diabrotica viridula* (Fab.), *Paranapiacaba waterhousei* (Jacoby), *Diabrotica balteata* (Le Conte) and *Diabrotica adelpha* (Harold) and examined their patterns of movement after landing on a potential host plant. As with other authors, Risch found that beetles left non-host plants more quickly than host plants, resulting in increased movement in polyculture plots. Emigration from plots as well as movement within plots were both higher in polyculture than in monoculture plots. Risch (1981) observed that these patterns were due to the presence of corn in the intercropped

plots. The beetles avoided host plants that were shaded by the corn and the corn also appeared to interfere with the beetle's flight patterns (Risch 1981).

Research Objectives and Hypotheses

There were three objectives of this research. The first objective was to determine if yellowmargined leaf beetles remained active into summer if crucifers are present under field conditions. Oliver and Chapin (1983) report that *M. ochroloma* enters aestivation from mid-June to October. The authors did not distinguish between aestivation (a diapause response) and quiescence caused directly by unfavorable resource or climatic conditions. I hypothesized that if the yellowmargined leaf beetle exhibited a pre-programmed diapause response, the beetles would not be apparent, even when food was available.

The second objective was to determine if initial infestations of *M. ochroloma* arise from within the field, or from field edges. Oliver and Chapin's (1983) observations that beetles can be found as early as 9 September in ground trash but not until a month later in the field implies that they may overwinter outside agricultural fields in the summer months and return during the autumn planting. I hypothesized that *M. ochroloma* infestations would arise first in areas closest to the overwintering location of the beetles. If beetles overwintered in field edges, then host plants on the borders of the field would be more rapidly infested than those host plants on the field interior.

The third objective was to determine if intercropping host plants with non-host plants would protect the host plants from beetle infestation. I hypothesized that host plants that were intercropped in low densities among non-host plants would be less "visible" to *M. ochroloma*, and thus less susceptible to infestations. The second part of this hypothesis was that locating host plants in experimental plots near non-experimental

host plants would create a larger island of host plants. *Microtheca ochroloma* would either already be present in the established non-experimental plots of host plants or more quickly find the areas with experimental and non-experimental plots in close proximity. Therefore, *Microtheca ochroloma* would be more abundant in the experimental plots close to other non-experimental host plots.

CHAPTER 3 METHODOLOGY

Border Versus Interior Experiment

I carried out this experiment on Rosie's Organic Farm, a certified organic farm located in southwest Gainesville, Florida. I chose this farm because it is a well-established certified organic farm that had experienced outbreaks of *M. ochroloma* and the farmer was willing to participate in the research. The farm consists of two non-contiguous fields; one of eight acres (3.2 ha) and the other of seven acres (2.8 ha). This experiment involved only the eight-acre (3.2-ha) field. The soils are Entisols; mineral, sandy soils with no obvious soil profile.

The field has been certified organic and managed organically since 1993. A typical season begins at the end of the summer, when the cover crop (a combination of cowpea and millet) is mowed and disked. Well-rotted chicken manure, the only fertility amendment, is applied to the fields at the rate of 2 tons/acre (1814 kg/ha). Vegetables and flowers are then seeded directly or transplanted from one of two greenhouses on the farm.

I seeded mizuna, *Brassica rapa*, var. Kyona (untreated seed, from Johnny's Seeds, Albion, ME) into four 72-cell transplant trays on 3 August 2001 and maintained the plants in a greenhouse until transplant. I used Scotts Metro-Mix, specially blended without starter fertilizer or wetting agents as the transplant media. No fertilizer was added to the transplants initially, which halted the seedlings' growth, and delayed transplanting by several weeks. I thinned the cells three weeks after planting, leaving only the largest

transplant in each cell. A single application of composted chicken manure was added one month after seeding (during the first week of September).

I had initially planned to use the entire field for this experiment, and surveyed it accordingly the last week of September. Because of the long growing season and diversified nature of the farm, beds are prepared, planted, and harvested on an as-needed basis. During the growing season at the farm, a single bed may be rotated through three different crops. The result is that the eight-acre area is heterogeneous; some areas are still in their summer cover crop while others are mowed and disked and ready to be planted and some have already been planted. After considering these factors, I decided to adjust the experimental design. The heterogeneity of the research site led me to divide the field and choose a single homogenous area for this experiment. The mizuna host plants were transplanted to into the experimental area on 2 October 2001.

I chose an experimental area in the northeast part of the field. The area consisted of 18 rows on 6 ft. (1.83 m.) centers, running north-south, approximately 250 ft. (76.2 m.) long. The rows had been planted in green beans and cucumbers during the first week of September 2001. The north border was the edge of the field, bordered by successional vegetation typical of this area of north Florida, including trees and shrubs and forbs. The south border was the irrigation lines and walkway dividing the north and south sections of the field. The east border was disked but unplanted. The west border was two rows of turnips that had been planted around the middle of July 2001. In August 2001, I surveyed the turnip rows and found several adult *M. ochroloma*, but no eggs or larvae and no evident plant damage.

Beginning with the second (easternmost) row of turnips, I measured out experimental plots of 3 ft. (0.914 m) long at either end (woods and interior) of every third row. In each experimental plot, I planted 12 host plants in a three by four block. I assigned interior plots the letters A through F and border plots the letters G through L (Figure 3-1). I recorded the number of beetles (adults, larvae and eggs) on each host plant in each plot at least twice a week beginning on 9 October 2001 and ending on 31 October 2001. By the end of October, many of the host plants had been completely eaten by yellowmargined leaf beetles and I was no longer able to sample.

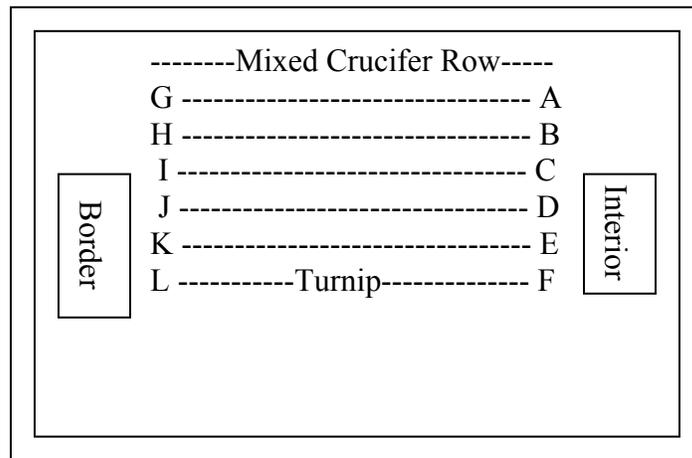


Figure 3-1. Field layout for border versus interior experiment. The dashed lines represent rows that were not part of the experiment, and the letters designate the experimental plots of host plants at both ends of the rows.

On two occasions (25 October and 29 October), I marked adult beetles using a water-based paint and small paintbrush. I assigned each of the interior plots a color and marked all the adults accordingly. The first time, I marked the beetles as I counted them. The second time I collected the beetles in a container and then marked and counted them. I then held the marked beetles in the container for 10 minutes, by which time the paint appear dry. I then released the beetles back into the middle of their respective plots. On

the two subsequent sampling dates (27 October and 31 October) I recorded the number and mark of all the beetles found in the experimental plots.

I used non-parametric methods to analyze the data. Graphing the untransformed data, I found that the mean and variance were highly correlated. Neither square root nor log transformations succeeded in diminishing this relationship to the point where the parametric measures would have been appropriate. I used the Wilcoxon rank sum test (Hollander and Wolfe 1999) to determine if there were differences between the numbers of beetles on the field borders versus in the field interior. I used Kruskal-Wallis multiple comparison test (Hollander and Wolfe 1999) to determine if there were differences among the plots which were nearby, far away or a medium distance from the non-experimental host plots. I used Wilcoxon comparisons *post-hoc* to test for differences between the three pairs of treatments (near-far, near-mid, and far-mid) (Hollander and Wolfe 1999).

I had three problems during this experiment. When I transplanted the host plants, I noticed that there was evidence of beetle activity in one of the transplant trays. There were several adults, a clutch of eggs and one newly hatched larva distributed among three of the plants in this tray. I removed and killed the beetles, since I did not want to introduce beetles to the field. Because the host plants were transplanted at a small size and the beetles are very evident, I don't believe there were any more beetles on previously transplanted trays and that this was an isolated incident.

A second problem was that each plot did not have a uniform host plant biomass, nor did I correct my calculations to take this into account. The differences were not

systematic, *i.e.* all the plants on the interior were smaller than the ones on the border, but nonetheless present.

Finally, my attempts to mark the yellowmargined leaf beetles failed. I did not recapture a single marked beetle in subsequent sampling. I believe that the paint either rubbed or washed off, or that I did not mark enough beetles relative to the total number of beetles in the field to recapture them.

Intercropping Experiment

I carried out this experiment on Rosie's Organic Farm, a certified organic farm located in southwest Gainesville, Florida. I seeded three 72-cell transplant tray of mizuna, *Brassica rapa*, var. Kyona (untreated seed, from Johnny's Seeds, Albion ME) and six trays of oak leaf lettuce, *Lactuca sativa* var. Berenice (untreated seed, Johnny's Seeds, Albion, ME.) during the second week of January 2002. I maintained the plants in a greenhouse until transplant. I used Scotts Metro-Mix, specially blended without starter fertilizer or wetting agents as the transplant media. Transplants were thinned at three weeks and fertilized every week after germination with fish emulsion fertilizer. On 15 March, I transplanted the seedlings to the field. The experimental design was a complete randomized block, consisting of four treatments replicated four times. Each block consisted of 32 plants.. The treatments were three densities of non-host plant (oak leaf lettuce) to host plants - 15:1, 7:1, and 3:1 plus a control plot that contained only mizuna. The resulting blocks had 30 non-host plants plus two host plants, 28 non-host plants plus four host plants, 24 non-host plants plus eight host plants and 32 host plants. The sixteen blocks were randomized between two adjacent rows. I left a border space of 6 ft. (1.82 m) between each treatment plot. The location of the host plants within the treatment block was selected using a random number table. There were no other host plants within

33 ft. (10 meters) of the experimental plots. Twice a week, from 16 March to 16 April, I recorded the number of beetles per host plant and the position of the host plant.

I encountered several problems during this experiment. No adult yellowmargined leaf beetles were present until the first week of April. I did not find any larvae or eggs during the entire course of the experiment. I stopped sampling after 16 April because the host plants were so badly damaged by other insects that I could not continue the experiment. The other factor was that the nutsedge and pigweed that had been controlled through hand weeding early in the season became completely out of control and took over several of the experimental plots.

Again I used non-parametric methods for data analysis because of the correlation between mean and variance. I used the Jockheere-Terpstra test for ordered alternatives (Hollander and Wolfe 1999) to determine if there were differences among the treatments. I used the multiple-comparison Hayter-Stone test (based on Wilcoxon ranks) *post hoc* to determine which plots were different.

CHAPTER 4 RESULTS

Border Versus Interior Experiment

There were significantly more adult yellowmargined leaf beetles in the interior plots than in those plots bordering the field edges ($W = 52, P = 0.04$). The border plots (G-L) had a mean \pm SE of 8.17 ± 3.67 adult beetles while the interior plots (A-F) had 54.5 ± 20.42 beetles (Figure 4-1). There were no differences between border versus interior location for either larvae or eggs ($P = 0.45$ and $P = 0.42$, respectively), although the oviposition locations reflected a pattern similar to that of the adult population (Fig. 4-2). The distribution of the yellowmargined leaf beetle larvae did not reflect the bimodal distribution of the adults and eggs.

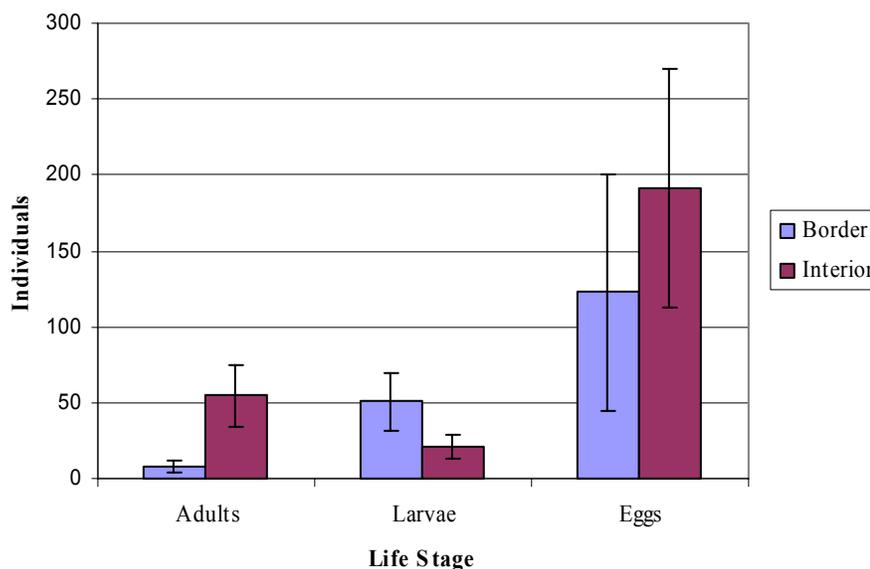


Figure 4-1 Mean number of yellowmargined leaf beetles in border versus interior plots according to life stage, Gainesville, FL 2001.

The data were highly variable for the beetles' location in the border versus the interior plots (Figure 4-2). Within the six experimental plots that comprised each of the variables "border" and "interior", the adults, larvae and eggs were highly aggregated into one or two plots. For example, I counted a total of 142 adult beetles in interior plot A, but no beetles in plot B. Similarly, there were two eggs in interior plot B, but 467 in interior plot A. I found the most larvae in the border plot 'I', which had 101 larvae but no larvae in border plot L.

The relationship between number of adults and number of offspring was inconsistent throughout the experimental plots. Plots with high larval populations and high egg counts did not always have the plots with high adult populations in previous weeks (Figure 4-3). Plot A had the most adult beetles, as well as the most beetle eggs but only the fourth highest larval count. For example, plots D, 'I', and J, had relatively few numbers of adult yellowmargined leaf beetles, but the second, third and fourth highest egg counts later that week. Plots C, D, and E all had moderate and comparable numbers of adults on 24 October, but subsequent oviposition varied as did their larval populations (Fig. 4-3).

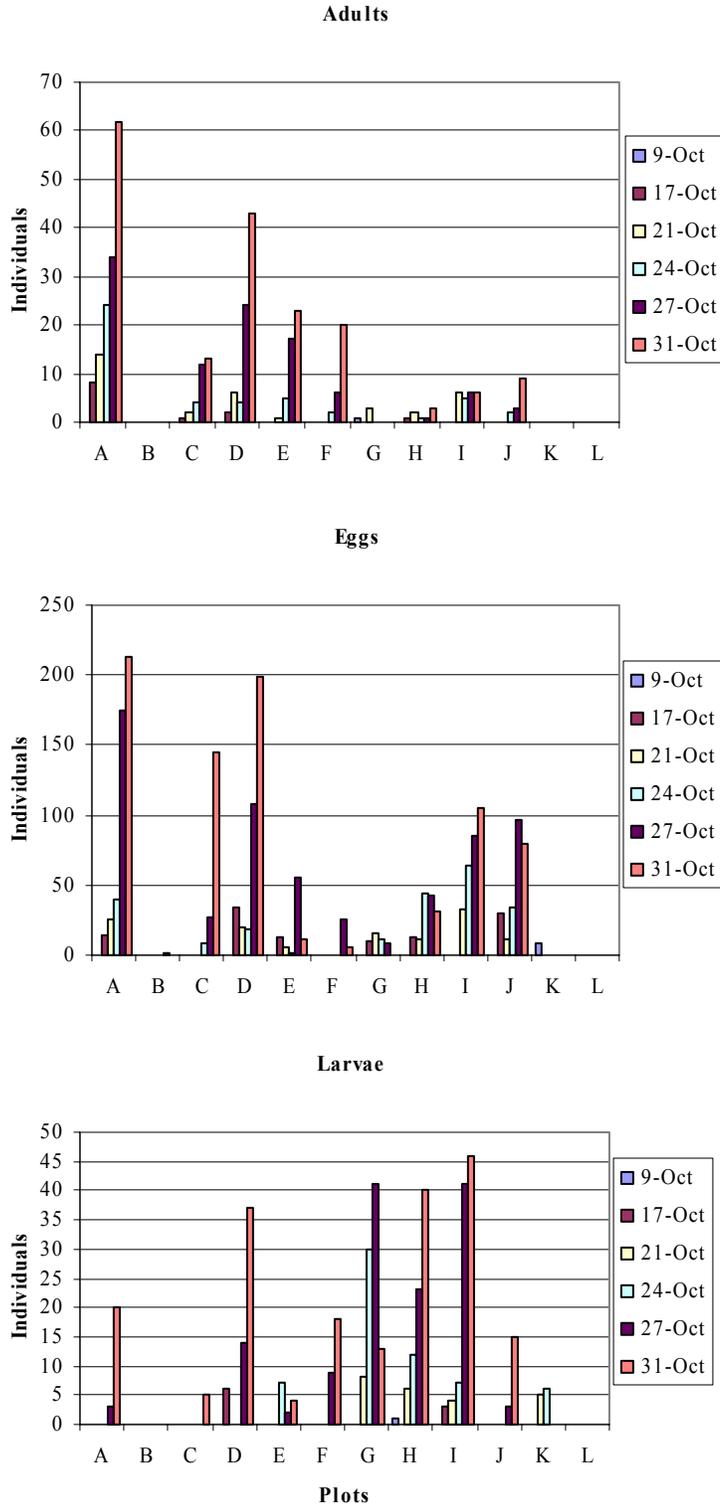


Figure 4-2 Total number of yellowmargined leaf beetles collected from host plants, Gainesville, FL 2001. Plots A-F are the interior plots; G-L are border plots. Note the different y-axis scales.

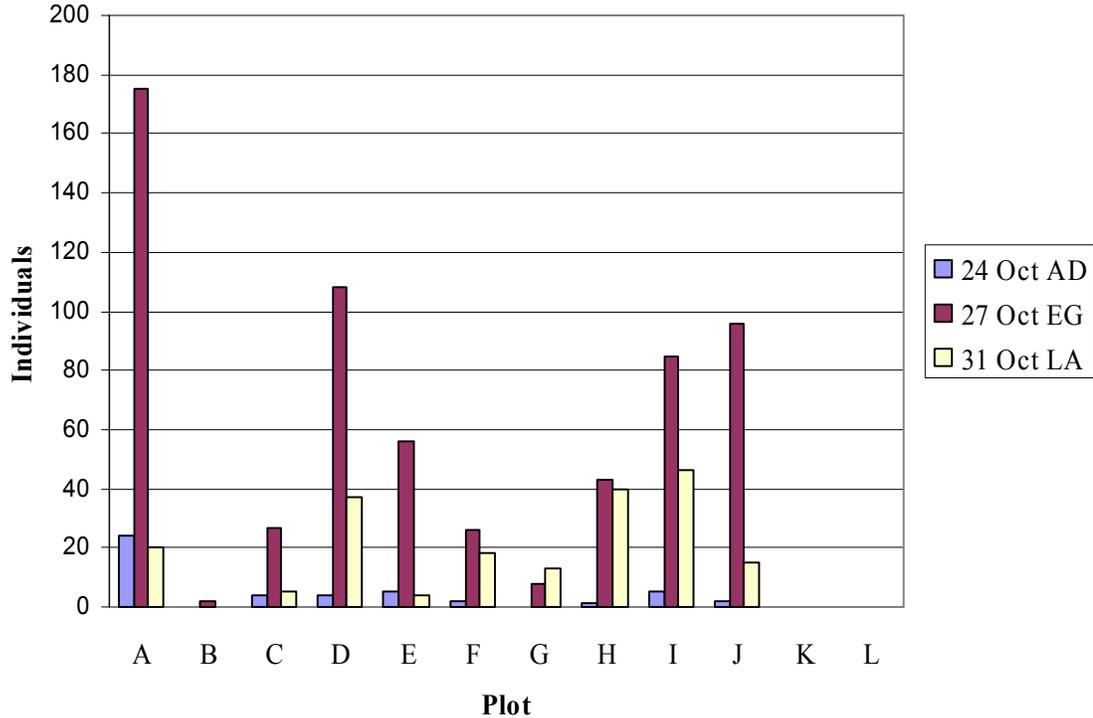


Figure 4-3 Yellowmargined leaf beetle adult (AD), egg (EG) and larval (LA) distributions during a one-week sampling period, Gainesville, FL 2001.

When I categorized the plots as nearby, medium distance or far away from other crucifer plantings, there was no difference in the number of adult ($X^2 = 1.91$, $P = 0.43$) or larval ($X^2 = 0.94$, $P = 0.66$) yellowmargined leaf beetles in the experimental plots. Three out of four of the plots categorized as near (plots F, G, and L) ranked towards the bottom of all the plots for number of adult beetles and eggs. Plot A had the highest number of adults overall, with 142. Plots A, F, and L ranked towards the bottom for number of larvae, but Plot G had the second highest number of larvae, with 82.

The quantity of eggs in a plot did correspond to its proximity to other crucifer plantings ($X^2 = 4.41$, $P = 0.11$). Multiple comparisons using Wilcoxon ranks revealed that the plots farthest away had more eggs than mid-distance plots ($W = 3.266$, $P = 0.0739$) but that there was no difference between the number of eggs in the nearest plot

and the farthest, or between the nearest and the mid-distance plot. The plots farthest from other crucifer plantings had a mean \pm SE of 274.75 ± 41.15 eggs, while the medium distance plots had 60.25 ± 33.51 eggs and the nearest plots had 135.75 ± 110.82 (Figure 4-4).

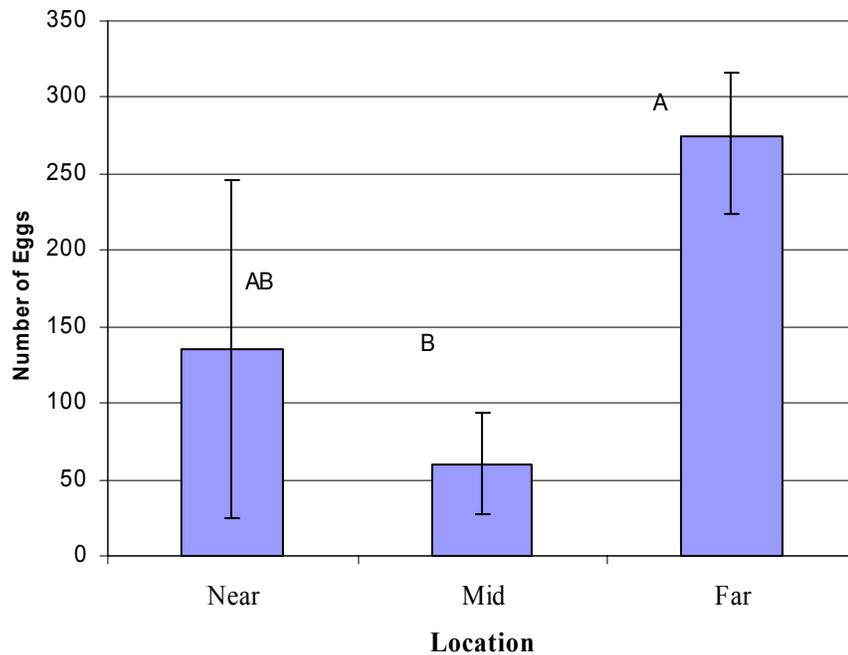


Figure 4-4 Mean number of yellowmargined leaf beetle eggs collected from experimental plots based on the proximity of the plots to non-experimental host plants, Gainesville, FL 2001.

Intercropping Experiment

I used the Jonckheere-Terpstra test for ordered alternatives to establish that there was an increasing treatment effect (*i.e.* plots with fewer plants had fewer beetles) ($J = 79$, $P < 0.0056$). (Figure 4-5) Multiple comparisons based on Wilcoxon ranks did not establish which plots were different¹. When plant density was taken into account, there were no treatment differences among the intercrop plots ($J = 48.5$, $P = 0.481$). There

¹ The critical value for the Hayter-Stone test at $\alpha = 0.10$ is $W = 2.873$. The highest statistic for these comparisons was for the monocrop to 1:15 treatment, which was $W = 1.4$.

were no more adult yellowmargined leaf beetles per plant in the monocropped (control) plots than in any of the intercropped (treatment) plots nor were there differences among yellowmargined leaf beetle populations per plant resulting from the various densities of intercropped plants in the treatment plots. I did not find any larvae or eggs in the control or treatment plots during the course of this experiment. However, there was a trend towards higher number of adult yellowmargined leaf beetles as the experiment progressed, indicating a seasonality effect (Figure 4-6).

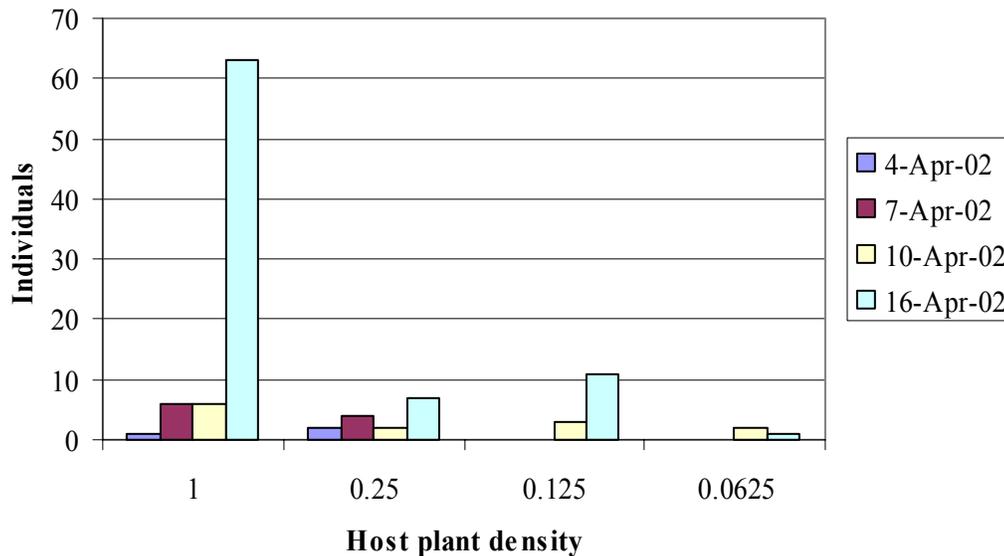


Figure 4-5 Mean number of yellowmargined leaf beetles collected on intercropped host plants by date and host plant density², Gainesville, FL 2002

² Host plant density is the ratio of non-host plants to host plants. The least dense plots of host plants (0.0625) had two host plants and 30 non-host plants (a ratio of 1:15 non-host plants to host plants). The other treatment ratios are 1:7(0.125), 1:3 (0.25) and a monocrop (control) plot containing all host plants, represented by 1.

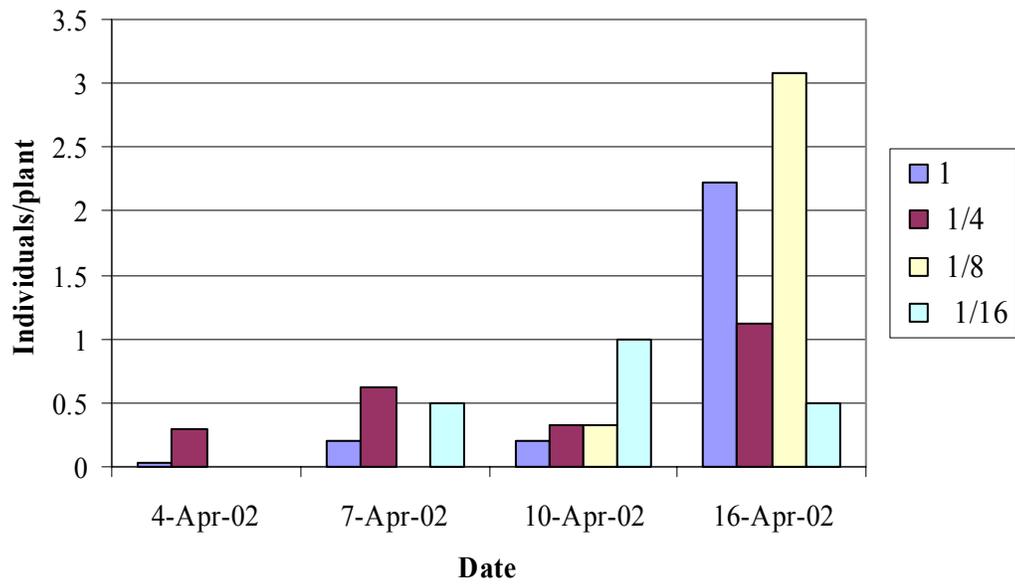


Figure 4-6 Mean number of yellowmargined leaf beetles found on host plants, Gainesville, FL 2002. Legend refers to the fraction of plants in a block that are host plants.

CHAPTER 5 DISCUSSION

Border Versus Interior Experiment

Whether or not *M. ochroloma* experiences a true aestivation or not remains unclear. While there does appear to be a pronounced summer dormancy, at least a limited number of beetles are active during the summer months. During sampling in July and August, I found a dozen adult yellowmargined leaf beetles on host plants. I did not observe *M. ochroloma* feeding in the field. The yellowmargined leaf beetles that I collected in the summer of 2001 mated and oviposited within 24 hours after I brought them into the lab. This is not an expected response from beetles in a pre-diapause state; but rather indicates that these beetles had not yet entered a preprogrammed diapause. I also discovered a few eggs and first instar larvae on transplants as I was setting them in the field on 2 October 2001. Finding beetles in the field during the summer and the rapidity with which these field collected beetles mated and oviposited under laboratory conditions suggests that *M. ochroloma* has one of three distinct dormancy strategies.

The first possibility is that they are not diapausing but are quiescent. Danks (1987) remarks that in insects whose lifecycle is directly controlled by temperature (i.e. non-diapausing insects), emergence tends to be more staggered than post-diapause emergence, due to variations among individual insects or differences in habitat microclimate. The second possibility is that *M. ochroloma* is aestivating. Masaki (1980) discusses five patterns of aestivation, one of which matches the apparent seasonal patterns of the yellowmargined leaf beetle. Based on my field observations during 2001

and 2002, I believe that the yellowmargined leaf is dormant during the warmest part of the year. The dormant period is both preceded and followed by periods of active feeding and reproduction in the spring and then again in the fall, continuing on into the next spring (Masaki 1980). It is not clear if an individual adult *M. ochroloma* can oviposit during both reproduction periods, or if mated beetles die off at the beginning of the summer, with their newly hatched offspring entering diapause directly without mating, and then emerging in the fall. If it is the latter, then what I collected in July and August of 2001 are what is left of the early generation adults who have mated and will continue to oviposit until death, without re-entering diapause. The rest of the population composed of non-parous adults is in fact diapausing.

The third alternative is that the yellowmargined leaf beetle has multiple overwintering strategies, as suggested by Masaki (1980) and similar those of the boll weevil in the tropics and sub-tropics (Palmer and Cate 1992). In this scenario, most of the population is in diapause, but a small percentage continue to feed and oviposit during the normal aestival period.

Boiteau et al. (1979a) observed pre-dormancy flight to nearby woods for bean leaf beetles, as did Voss and Ferro (1990) for Colorado potato beetles. Altieri (1994) summarized multiple incidences of diapause migration in insects. However, it is not evident that *M. ochroloma* seeks overwintering habitat outside agricultural fields. I found adult *M. ochroloma* in interior plots first and the number of adults increased more quickly in those plots. Most of these additional adults were recruited into interior plots (rather than oviposited there), since the 23-day lifecycle of *M. ochroloma* is too long for eggs to have hatched and be counted during the course of this study.

The higher populations of adult *M. ochroloma* in the field interior versus the field border suggest that a large number of adults overwinter in the field. My sampling indicates that large number of adults appear first in the autumn, followed in quick succession by eggs. A period of several weeks elapses before larval populations build up. Like other specialist herbivores, *M. ochroloma* likely overwinters near its feeding sites. When the yellowmargined leaf beetle emerges, it begins feeding on the first acceptable host plants it finds. No precise field records were available for the season previous to this field study, to confirm that overwintering locations were in fact close to the last season's feeding sites.

In addition to the higher adult populations in the field interior, there is a second reason to conclude that the population of yellowmargined leaf beetles on this farm overwinter within the field. While laying out the experimental plots on 26 September 2001, I surveyed the woody border along the northern border of the field. I looked specifically for any cruciferous plants that might have served as alternate hosts for *M. ochroloma* during the summer months. I did not find any plants that were likely to serve as suitable habitat for non-diapausing yellowmargined leaf beetles around the field edges.

Unlike the adult populations, egg and larval beetles of *M. ochroloma* were equally likely in border as well as interior sites. However, egg location showed a bimodal pattern, similar to the pattern of adult location. Since eggs are sessile, their distribution is the result of the adult female beetles' choice of oviposition sites. I believe that even though the adults emerged in the field interior, they did not limit their oviposition to those sites. This apparent dispersal by adult female beetles could be due to three different factors. Female beetles may disperse their eggs as a "bet-hedging" strategy in case of

disaster or to avoid intraspecific competition as found with red milkweed beetles, *T. tetraophthalmus* (Matter 1997). A single female *M. ochroloma* can oviposit between four to six eggs daily and is capable of a total fecundity of nearly 500 eggs (Ameen and Story 1997b). With a single beetle capable of producing that quantity of offspring, my data indicate that female beetles did not oviposit all their eggs in a single host plot.

Another other possibility is that adult beetles overwintered and emerged near old feeding sites, but through nonrandom searching, some females found other host sites more preferable and oviposited in those sites. Kareiva (1983) suggested that this type of movement frequently takes place and can account for the observed damage among treatments in an experimental field. It is also possible that the yellowmargined leaf beetle has multiple overwintering strategies. Just as there may be multiple types of dormancy in this population of *M. ochroloma*, there may be multiple dormancy locations as well. While the majority of beetles overwinter in the field, some beetles may be overwintering around field borders. The timing of dormancy induction and emergence may vary somewhat within this population, with a group of beetles entering and emerging together and the remainder emerging asynchronously both before and after the main group. If the field overwintering beetles emerge and oviposit first, that could account for their higher numbers in the interior plots initially. Beetles emerging later in the autumn or from field borders (or both) may find the experimental border plots and oviposit. If this second group happens to be smaller or oviposition takes place over a longer period of time, a pattern of their emergence and oviposition may be harder to detect than a larger group of beetles that emerges in a suitable field habitat

simultaneously and oviposits immediately. Tauber *et al.* (1988) described a similar scenario for the Colorado potato beetle.

The larval distribution was dissimilar from both adult and egg locations. While Nielsen (1988) indicates that adult chrysomelids do not move far during their lifespan, my data indicate that the larvae are mobile within the scale of a single, small (<10 acre) field. The lack of relationship between larval and adult locations is the evidence for larval dispersal. The border and interior plots were located at opposite ends of 250 ft (76.2 m) rows. On either given side of the field (border and interior) the experimental plots were located 15 ft (4.57 m) apart. The beetles were allowed to move freely about the field. In plot A, an interior plot with the most adults and highest number of eggs, I did not record any larvae until 27 October, three weeks after the study began. This indicates that once eggs hatched, the larvae likely moved to other feeding locations. The closest experimental plot was B, which had no beetles or larvae, and only two eggs during the duration of the study. However, the next closest plot of host plants was not B, but a non-experimental plot of host vegetation. This non-experimental vegetation consisted of a mixed row of kale and tat soi (*Brassica oleracea*, japonica group) on the east end of the experimental plots (Figure 3-1); in other words located on the opposite side of plot A than plot B. The beetles (adults or larvae) probably did not leave plot A, skip over or walk around plot B and then choose a subsequent experimental plot (C or D) to feed or oviposit. Instead, they moved to an area of non-experimental host plants.

Ameen and Story (1997) established that the food preferences of *M. ochroloma* vary with age, with adults preferring the largest variety of suitable hosts and first instars

preferring a single host. Narrower host preferences by earlier instars could also explain the difference between adult and larval distribution.

Based on MacArthur and Wilson's (1967) theory of island biogeography Janzen's (1968) subsequent interpretation and Root's (1973) resource concentration hypothesis, I expected to find more yellowmargined leaf beetles in the plots closest to alternative food sources (*i.e.* the biggest island, or in resource concentration terms, in the most resource rich area). The larger islands are easier for colonizing beetles to locate, and the abundance of food provides the incentive to remain in the area. The distribution of *M. ochroloma* in this experiment did not conform to this theory. I believe that two different processes occurred in the near plots. In plot A, which had the most adults, the adults found the larger island, but their progeny did not remain there. While the adult beetles emerging from dormancy or dispersing larvae may have found the larger islands (created by plot A and its adjacent non-experimental host vegetation) more easily, the concentration of resources did not keep the beetles within the experimental plots. The adjacent non-experimental host plants may have been more attractive than the host plants, in terms of architecture, or microclimate, host plant volatiles, or some other aspect of the field layout, or perhaps provided a refuge from intraspecific competition. The result was reduced larval populations in plot A. In effect, these non-experimental areas may have acted more as trap crops rather than serving to increase the attractiveness of the area overall. A similar result was obtained by Altieri and Schmidt (1986), who discovered that host collards which received the least flea beetle (*Phyllotreta cruciferae*) damage were located adjacent to wild mustard borders.

The other three near plots (F, G, and L) reflect two different situations. The high number of larvae in plot G (a border plot) did not come from high numbers of eggs in that plot, so the larvae clearly had moved to plot G from some other part of the field. In this case, the concentration of food resources attracted larvae from outside that plot. Finally, neither of the plots at the west end of the experimental area (plots F and L) attracted large numbers of beetles in any stage. The effect of concentrated resources here did not attract more beetles. I did not count the beetles in the alternative host plants to see if these alternative (non-experimental) hosts had served as a trap crop instead of creating a bigger island. While Ameen and Story (1997a) established that *M. ochroloma* could distinguish among several host plants and exhibits feeding preferences among these suitable hosts, the relative preferences of *M. ochroloma* for the food plants in this particular experiment have not been established.

In comparison, the experimental plots farthest away from the alternative host plants retained their populations of *M. ochroloma*. In effect, these far away plots served as isolated, distant islands, on which yellowmargined leaf beetles became stranded and concentrated in these plots. Altieri and Schmidt (1986) also found that *P. cruciferae* populations were positively correlated with distance from the preferred mustard host. There was no difference between the nearest and middle distance plots, indicating that the balance between dispersal and plot finding was equally likely from both types of plots.

The distribution of food resources is clearly not the only factor which influences beetle distribution. The high degree of variability within both treatments (border and interior) indicates that there is another underlying pattern to the distribution of the yellowmargined leaf beetles that was not captured by this experimental design. I believe

that the location of emergence of *M. ochroloma* and its initial feeding is likely to depend on the location of last year's feeding sites. Beetles emerge close to old feeding sites, or return to those sites first in search of suitable host plants. The differences between border and interior populations could reflect the fact that interior plots were closer to old feeding sites than border sites. The variation within the interior sites may reflect that those locations with high beetle populations are in the same place as last year's crucifer plantings, while those interior plots with low beetle populations are located farther away. Without an accurate map of previous plantings, I had no way of knowing where crucifers were planted the season before and the experimental plots were laid out without regard to this pattern.

The distribution of *M. ochroloma* within experimental plots was very uneven as well. Yellowmargined leaf beetles were not spread among the 12 host plants per plot, but clustered in just a few of the host plants. In a single plot, plants with only minor feeding damage grew along side plants that were completely defoliated. While this pattern was not captured in the data collection, it was evident when I examined the experimental plots. Host plant searching techniques may be just as important as the location of previous feeding sites in field distributions of *M. ochroloma*. Host plant searching by herbivores can be uniform or patch restricted (Stanton 1983). Insects that alter their searching strategy upon finding a suitable host plant are engaging in patch restricted searching. The result of patch restricted searching behavior is that insects remain in a patch longer and are less likely to leave the patch, *i.e.* they have a longer "residence time" in the patch.

Non-random insect distribution results indirectly from a heterogeneous environment and patch restricted searching. Additionally, Morris *et al.* (1996) remark that chrysomelid aggregations are formed directly over longer distances through aggregation or mating pheromones or short range by visual and tactile cues from conspecifics. Lewis (1994) used the term “herbivory-taxis” to describe the movement of herbivores towards less damaged plants. Building on the idea of herbivory-taxis, Morris *et al.* (1996) theorized that chrysomelid aggregations appear to move throughout an environment when the insects engage in both herbivory-taxis and congregation based on conspecific cues. Insects converge on a site, reduce the quantity and quality of the host plant, and then collectively move on to a better site. The mass movement of *M. ochroloma* from one host plant plot to another, and the aggregations of yellowmargined leaf beetles within a single plot exemplify how congregation and herbivory-taxis could act together under field conditions.

As mentioned previously, I did not correct for differing quantities of vegetation in the experimental plots, nor did I assess any chemical or qualitative differences among the host vegetation in the plots. Either or both of these factors may correlate with beetle distribution in the experimental plots.

Intercropping Experiment

In his study of the arthropod community of cabbage, Pimentel (1961) found more herbivores in dense plantings than sparse ones, but fewer herbivores per plant in dense plantings. Specialist chrysomelids were fewer in polyculture plots, but those polyphagous chrysomelids that consumed both squash and beans were more abundant in the squash/bean polycultures (Risch 1981). Bach (1980) found more striped cucumber beetles in monocropped systems. Like Pimentel (1961), Bach (1980) and Risch (1981), I found

more herbivores (in my case yellowmargined leaf beetles) in dense host plantings than sparse ones. I did not find any differences, however, in the number of beetles per plant, whereas Pimentel (1961) found fewer herbivores overall and Bach (1980) found more striped cucumber beetles in monocropped systems, as did Risch (1981). Stanton (1983) suggests that above a certain density of host plants, the environment becomes saturated with food, resulting in lower herbivore loads. The seasonality effect that I observed could have resulted from larger plants being easier for an herbivore to locate as the season progressed, as suggested by Pimentel (1961).

Intercropping host plants among non-host plants was not effective in preventing beetles from colonizing host plants. *Microtheca ochroloma* was able to find host plants equally well in sparse planting as in dense plantings of host plants. The presence of the non-host plants was not enough to diffuse the odor of the host plants, as Thiery and Visser (1986) found with when they used cabbage and tomato plants to mask the odor of potato host plants. In their study, Colorado potato beetles were disoriented by the presence of the non-host plants (although they were not repelled by them) and were unable to locate the potato plants Thiery and Visser (1986).

Coll and Botrell (1994) attributed the lower Mexican bean beetle densities in tall corn-bean intercropping systems to a multitude of factors, including decreased colonization by adults due to the tall corn impeding the flight of the beetles, and changes in the light regime in the intercropped plots, which prevented *E. varivestis* from finding its host. Neither of these factors affected the ability of *M. ochroloma* to find its host plants. Since the host and non-host plants were not of different heights and are of similar

architecture, the presence of the non-host plants did not discourage or confuse the yellowmargined leaf beetle.

There were more total yellowmargined leaf beetles in the monoculture plots than in the intercropped plots as predicted by Root's (1973) resource concentration hypothesis. While they did aggregate around their host plants, this aggregation behavior was not sufficient to produce a higher herbivore load (*i.e.* more beetles per plant). In contrast to the patch-restricted searching that took place in the border versus interior experiment, the beetles seem to engage in uniform searching when their population is low. Stanton (1983) comments that populations of insects that engage in a uniform searching strategy will be negatively correlated (or not correlated at all) with host plant density. This is because plants in a higher density habitat have a proportionately less chance of being selected than those plants which are sparsely planted.

The low population density in the intercropped plots failed to provoke the "herbivory-taxis" behavior (and resulting feedback loop) seen under higher densities of *M. ochroloma*. One or two adult yellowmargined leaf beetles may find a plant and feed on it, without producing the herbivory damage of a large group of adults or larvae. A congregation of *M. ochroloma* can quickly degrade its patch of food plants and the group will be forced to move on. A beetle searching and feeding singly will be able to feed off the same plant for much longer without degrading it, and thus has no incentive to keep searching for host plants.

The pure stands of host plants represented islands that were larger or more suitable for colonization than the individual plants interspersed among the non-host plants, as the theory of island biogeography suggests (MacArthur and Wilson 1967).

However the intercropping treatments probably did not act as smaller and smaller islands because in each of the three intercrop treatments, the host plants were distributed singly throughout the intercrop treatment, not clumped together to represent islands of various sizes. Similarly, Stanton (1983) suggests that herbivores do not recognize host plant patches as such, but instead are sensitive to the size of the “peripheral distance around the patch”. The non-host plants did not confer “associational resistance” (as described by Tahvanainen and Root 1972) to the host plants.

The role of competition and predation on *M. ochroloma* are still unclear. Both resource concentration hypothesis and natural enemies hypothesis work together in regulating phytophagous insect populations (Root 1973). Natural enemies of *M. ochroloma* have not been identified up to this point, either in *M. ochroloma*'s introduced or native range. I did not observe any predatory interactions during these experiments nor did field collected yellowmargined leaf beetles exhibit signs of parasitism (Bowers, unpublished). I do not believe natural enemies had any effect on these experiments.

Interspecific competition may have influenced the results of this intercropping experiment. During this experiment the most significant damage to the mizuna host plants was not due to *M. ochroloma*, but to various Lepidopteran larvae. Root (1973) suggested that interspecific competition decreased herbivore diversity in pure stands in collards. The presence of other crucifer specialists may have deterred *M. ochroloma* from colonizing the experimental plots. I did not survey overall herbivore populations in non-experimental areas of the field to compare with experimental areas, in order to see if *M. ochroloma* populations were lower overall, or only in this experimental plot due to other herbivores.

I was not able to assess the how intercropping may have influenced *M. ochroloma* mechanistically. While my results do not indicate differences in yellowmargined leaf beetle population per plant due to the treatments, there may be differences in frequency of host plant finding versus the duration of an insect's stay in a particular patch. As suggested by multiple authors, including Garcia and Altieri (1992), Finch and Kostal (1985), Finch and Collier (2000), Matter (1997) and Karevia (1983), insect populations within a stand of plants may have as much to do with how long each insect remains in a particular plot (*i.e.* how pleasing the plot is, or how many of the insects needs are met), not just how easy the plot is to locate. Garcia and Altieri (1992) suggest that a monoculture has chemical and physical qualities which “strongly attract, increase permanence, or even re-attract” departing herbivores. *Microtheca ochroloma* may have found the monoculture plots more easily than the intercrop plots, but the plots were not suitable for some other reasons, perhaps interspecific competition. In my first experiment (border versus interior experiment), I attempted to mark the beetles in order to establish how much movement between plots determined plot population. In the same experiment, the egg count gave some indication of how many adult beetles had visited a plot and remained long enough to oviposit. I did not count any eggs in the intercropping experiment, so it is difficult to know if there were any differences between plot finding and oviposition among the treatments.

It is interesting that the overall population of yellowmargined leaf beetles in the spring was much lower than in the fall. I did not find a single larva or egg in the spring plots, while counts of eggs during the fall reached over 30 eggs per plant in the most heavily infested plots. I contacted some of the same farmers I spoke with during the first

two seasons of my experiment and found that they had noted a marked decrease in populations of *M. ochroloma* during the autumn of 2002. Reports of lower field populations of yellowmargined leaf beetles in the fall 2002 season are anecdotal and have not been quantified.

CHAPTER 6 CONCLUSION

Research Implications

The long term goal of this research is to provide farmers with the basis for ecologically-based cultural control methods for *M. ochroloma*. Such methods are based on a fundamental knowledge of an insect's life cycle and behavior that is still lacking in this case. However, the results of this research have implications for current organic farming practices. Accurate field records of previous crucifer plantings and beetle outbreaks would be extremely useful in establishing a hypothesis on the source of beetle outbreaks. If a farmer (or farmers) could record the timing and a precise field location of host plants preferred by *M. ochroloma*, subsequent beetle infestations could be correlated with the location of the closest (or largest and closest) host plant patch. This type of record-keeping could yield valuable information about how *M. ochroloma* orients itself in the field and locates its host plants.

Although the results of the intercropping study presented here are not encouraging, I believe a longer term (multi-season) intercropping study might yield more useful results. Alternate intercropping patterns may prove more successful than the one tested in this study.

Directions for Future Study

I believe that establishing the source and timing of return of the yellowmargined leaf beetles to an agricultural field will first require the answers to some more fundamental questions. The focus for future research should establish the nature of

dormancy and emergence through controlled studies of *M. ochroloma* behavior under varying photoperiod and temperature regimes. Dissecting field-captured yellowmargined leaf beetles (in the spring, summer and fall) to determine the state of their reproductive organs and fat body is also essential in determining which stage of *M. ochroloma* is receptive to cues related to reproduction and dormancy.

Trap cropping may prove a useful control strategy for farmers who can afford the space and time. Since *M. ochroloma* can choose among host plants, a farmer might select a less valuable crop as a trap crop and establish it in the vicinity of a more valuable one, in order to draw *M. ochroloma* away.

In terms of behavioral studies, I think that research using mark-recapture methods and direction traps would be useful in a study of pre- and post- diapause movement of the yellowmargined leaf beetle. This type of study would be essential in establishing their overwintering habitat.

While many authors (Ehrlich and Raven 1964, Dicke and Vett 1999, Matsuda 1988) have stressed the importance of chemical interactions between plants and herbivores, a strict chemical co-evolutionary relationship is not universally accepted (Bernays and Graham 1988). The study of chemical interactions between plants and herbivores is still in its nascent stages; the chemical ecology of *M. ochroloma* is unexplored. The response of the yellowmargined leaf beetle to various host plant visual, chemical and tactile stimuli will certainly provide evidence about how *M. ochroloma* locates suitable host plants. The scale over which host plant attraction occurs is unknown, as is the nature of the attractants or stimulants (chemical or tactile or a combination of the two). Various responses have been observed in other insects.

Hawkes and Coaker (1979) found that *Delia radicum* oriented to host plant volatiles in the absence of tactile or visual cues. Finch and Collier (2000) propose that for *D. radicum* to oviposit, it must first locate a plant and then receive repeated tactile stimuli. How host plant allelochemicals and conspecific pheromones influence the behavior of *M. ochroloma* is unknown. The behavioral and chemical studies involving *Microtheca ochroloma* would be important in providing clues towards a general theory of host plant finding by herbivores.

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BIOGRAPHICAL SKETCH

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