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EVALUATION OF MICHIGAN NATIVE PLANTS TO PROVIDE
RESOURCES FOR NATURAL ENEMY ARTHROPODS

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EVALUATION OF MICHIGAN NATIVE PLANTS TO PROVIDE RESOURCES FOR NATURAL ENEMY ARTHROPODS

By

Anna Katherine Fiedler

A THESIS

Submitted to
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ABSTRACT

EVALUATION OF MICHIGAN NATIVE PLANTS TO PROVIDE RESOURCES FOR NATURAL ENEMY ARTHROPODS

By

Anna Katherine Fiedler

Biological control of pest insects may be enhanced by providing their natural enemies with plant resources including nectar and pollen, a practice known as habitat management. In the past, a limited set of annual plants, frequently not native to the area of study, has been used in habitat management. The goal of my research was to determine whether native plants could be effectively used in habitat management and whether natural enemy abundance was associated with particular plant characteristics. A comparison of the number of natural enemy arthropods at 43 native Michigan perennials and 5 non-native annuals revealed significant differences in attractiveness among plant species in early, mid, and late seasons in both 2004 and 2005 ($P<0.001$ in all cases). Within the native plants, a group of 24 native perennial plants attracted high numbers of natural enemies, including *Eupatorium perfoliatum*, *Monarda punctata*, *Silphium perfoliatum*, *Potentilla fruticosa*, *Coreopsis lanceolata*, *Spiraea alba*, *Agastache nepetoides*, *Anemone canadense*, and *Angelica atropurpurea.* I also considered whether specific plant characteristics played a role in natural enemy attraction to flowering plants. A multiple regression showed that in 2005 natural enemy numbers increased with peak bloom week and showed a significant positive linear and negative quadratic relationship with floral area. Subsets of the most attractive native Michigan plants can now be tested to develop a native plant community that provides nectar and pollen for beneficial insects throughout the growing season.

for Jake

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Chapter 1

THE USE OF NATIVE PLANTS IN HABITAT MANAGEMENT

Anna Katherine Fiedler

INTRODUCTION

Sustainable agriculture has been defined as the "production of food and fiber using a system that increases the inherent productive capacity of natural and biological resources" while farmers "earn adequate profits, provide consumers with wholesale, safe food, and minimize adverse impacts on the environment" (National Research Council (U.S.). 1991). The concept that agriculture should enhance its natural resource base is explicitly recognized in the USDA's current strategic plan, which lists "protect and enhance the nation's natural resource base and environment" as one of its five goals (www.usda.gov/ocfo/usdasp/usdasp.htm). This goal reflects a broad movement towards sustainability that recognizes agricultural systems as ecosystems that provide services to humans but also require stewardship.

The benefits that any ecosystem function provides to humans are known as ecosystem services. For example, population control of pest arthropods via the actions of natural enemy arthropods is one ecosystem service whose value to humans has been estimated at \$23 hectare^{-1} yr^{-1} on agricultural land (Costanza et al. 1997). A suite of other ecosystem services such as pollination and nutrient cycling may also be provided by agricultural ecosystems. This thesis is based on the premise that incorporation of native plants into agricultural landscapes has potential to enhance a suite of ecosystem services, including biological pest control.

Biological control has been defined as "the use of parasitoid, predator, pathogen, antagonist, or competitor populations to suppress a pest population, making it less abundant and thus less damaging than it would otherwise be" (Van Driesche and Bellows 1996). There are three primary approaches to insect biological control: introduction, augmentation, and conservation (DeBach 1964, Van Driesche and Bellows 1996, Ehler 1998). Introduction biological control involves the introduction of a nonnative natural enemy species to control a pest population. This is often referred to as "classical biological control," which specifically reunites a pest and a natural enemy from the native range. Augmentative biological control is the practice of periodically increasing natural enemy populations via inoculative or inundative releases (Van Lenteren 2000). Conservation biological control involves preserving or enhancing existing natural enemy populations (Ehler 1998).

CONSERVATION AND HABITAT MANAGEMENT

Conservation biological control is perhaps the least well studied of the approaches to insect biological control; however, this is changing rapidly (Barbosa 1998). The focus of conservation biological control is on conserving natural enemies that are already present in the landscape, via "actions that preserve or protect natural enemies" (Ehler 1998). This goal is achieved through decreasing natural enemy mortality or by providing resources that enhance their survival and efficacy. Pesticide-induced mortality of natural enemies is a major problem in many cropping systems. Mortality, however, can be reduced directly by altering the frequency, toxicity, or application method of the pesticide, or indirectly via provision of insect refuges near pesticide-treated areas (Johnson and Tabashnik 1999). Altering other types of disruptive practices, such as tillage, burning, chemical applications, etc., can also conserve natural enemies.

Habitat management is considered a subset of conservation biological control in which the focus is on providing natural enemy resources via managing plants and plant habitats (Landis et al. 2000). Natural enemies may be enhanced by plant-provided resources such as shelter, hosts, and non-host food. Frequently shelter and non-host food, including flower pollen and nectar, are absent in simplified agricultural systems and can be provided with either crop or non-crop plants (Wilkinson and Landis 2005). Consideration of these needs for natural enemies is one focus of conservation biological control.

NATURAL ENEMY REQUIREMENTS

All insect predators and parasitoids have requirements, beyond access to hosts or prey, for their optimal survival and fecundity and consequent effectiveness as biocontrol agents. These may include the presence of alternate hosts or prey, shelter from unfavorable weather conditions, and non-host food resources.

ALTERNATE HOST/PREY

Many parasitoids and predators require alternate hosts or prey either to complete their life cycle or to sustain them while the primary host is not present (van Emden 2003). In the latter case, they need food resources to survive until the main host or prey is available (DeBach and Rosen 1991, Menalled et al. 1999). In agricultural landscapes, such alternate hosts or prey often occur in uncultivated land (van Edmen 1965). When absent, such "refuges" can be constructed to provide alternate host or prey to the primary natural enemy (DeBach and Rosen 1991).

SHELTER

Natural enemies require shelter from adverse conditions, including extreme temperatures, low relative humidity, pesticides, and dust, for maximum longevity and reproductive success. Moderated microclimates, in-season refuges, and overwintering sites are examples of resource types that provide shelter (Powell 1986, Gurr et al. 1998, Nentwig et al. 1998). In a study on the effect of microhabitat, Dyer and Landis (1996) found that longevity of the parasitoid *Eriborus terebrans* (Hymenoptera: Ichneumonidae) was increased at temperatures of 25°C versus 35°C and at high versus low relative humidity. In a second study, more *E. terebrans* were found in corn field edges near woody refuges that provided moderated microclimate than in the center of the field early in the growing season, before canopy closure of corn (Dyer and Landis 1997). Refuges may also be important when pesticides are applied to a field. These refuges may be within a host (if an endoparasitoid), under stones or leaf litter, on nearby vegetation, or in surrounding forest (Croft 1990). Microhabitat physical factors, such as temperature, relative humidity, and light, can alter the effects of pesticides on insects (Croft 1990). Lee et al. (2001) found evidence that within-field refuges buffer negative effects of pesticide applications on carabid beetles. When refuges were present, beetle communities rebounded from pesticide application more rapidly than when refuges were absent.

Dust is known to be detrimental to many natural enemies, particularly parasitoids. Negative impacts include insect desiccation, increased preening interfering with mobility, and possibly increased leaf temperature (Letourneau and Altieri 1999). Ground covers can reduce dust in fields and orchards and thereby increase natural enemy effectiveness.

Overwintering sites are crucial to all natural enemies and may be particularly limited in annual crop fields where dormant season vegetation is absent. Varchola and Dunn (2001) found that, early in the growing season, hedgerow corn field margins supported higher carabid beetle populations than fields bordered by grass. Natural enemy populations benefit in a variety of ways from shelter provided by non-crop areas.

FOOD SOURCES

Parasitoids require only one insect host to develop to an adult, but some feed on hemolymph of multiple hosts as an adult, known as host-feeding (Gordh et al. 1999). Even parasitoids that engage in host-feeding are unlikely to be solely dependent on host-derived nutrients (Kidd and Jervis 1989). Many parasitoids, in fact, require a source of non-host food for maximum fecundity and longevity (Doutt 1964, Stapel et al. 1997). Adult parasitoids that use hosts exclusively for oviposition and not for a food source are completely dependent on other food sources for their nutrition (Wäckers 1999). Similarly, many predators are functional omnivores and obtain essential water and nutrients from plants (Eubanks and Denno 1999). Non-host food types include direct plant resources such as floral and extrafloral nectar and pollen, or plant sap, and indirect plant resources, such as honeydew produced by plant-feeding Homoptera (Jervis et al. 1993).

Access to floral nectar or honeydew provides a source of carbohydrate to fuel parasitoid function. Dyer and Landis (1996) found in lab olfactory and greenhouse studies that the presence of a sugar source increased longevity of *E. terebrans* more than water alone. Similarly, Costamagna and Landis (2004) found that *Glyptapanteles* *militaris* (Hymenoptera: Braconidae) parasitoids lived significantly longer when provided with 50% honey and 50% distilled water than water alone. Various other studies have found increased fecundity rates and longevity of several parasitoid species when they have access to floral or extrafloral nectar (Idris and Grafius 1995, Stapel et al. 1997, Baggen and Gurr 1998, Engel et al. 2001, Wäckers et al. 2005).

Parasitoids may be time- or energy-limited in the field. If a parasitoid population is occupied with finding food resources, its energy is not allocated to host finding and it will not be as effective in decreasing pest populations (Lewis et al. 1998). Hunger is likely the most important internal factor driving parasitoid foraging decisions. Food availability and the parasitoid's physiological state affect adult parasitoid effectiveness and time investment in finding hosts. Sugar availability also changes parasitoid time resource allocation. Stapel et al. (1997) found increased retention time in a patch and rate of parasitism in *M. croceipes* females in the presence of extrafloral nectar and sucrose. Parasitoids minimize food foraging time so that maximum time and energy can be allocated to host finding (Lewis et al. 1998).

There is some evidence that, at points in some parasitoids' life cycle, access to sugars is more important than host availability. Baggen and Gurr (1998) showed that *Copidosoma koehleri* (Hymenoptera: Encyrtidae) females deprived of hosts for the first 5 days of development showed no change in number of eggs laid or longevity, while *C. koehleri* longevity was significantly increased when adults were caged with flowering plants of dill (*Anethum graveolens* L.), coriander (*Coriandrum sativum* L.), and borage (*Borago officinalis* L.).

Predators use prey resources directly, but often are able to supplement their diets with plant resources, especially pollen. Higher *Colemegilla maculata* (Coleoptera: Coccinellidae) population densities have been found near dandelions, presumably because they were feeding on pollen (Harmon et al. 2000). Predators also use plants as direct food resources when prey is scarce. Eubanks and Denno (1999) found increased longevity in big-eyed bug *Geocoris punctipes* (Hemiptera: Geocoridae) when they had access to lima bean pods versus only lima bean leaves. Similarly, Legaspi and O'Neil (1993) found that longevity of the spined soldier bug *Podisus maculiventris* (Hempitera: Pentatomidae) with access to green bean (*Phaseolus vulgaris*) slices was four times that found when plant food was not available. In addition, Yong (2003) found that the ambush bug *Phymata pennsylvanica* (Hemiptera: Reduviidae) lived longer in the absence of prey if provided with a sucrose solution than with water or nothing. The bug, however, was unable to molt when provided with a diet of sucrose alone. Patt et al. (2003) studied green lacewing *Chrysoperla carnea* (Neroptera: Chrysopidae) and found those with access to prey, pollen, and sucrose exhibited shortened second instar times versus lacewings fed only on prey. These studies indicate that many predators function as omnivores in cases of low or poor quality prey availability. This means that predator use of nectar or pollen resources allows them to survive until prey are again available or to improve their development if available prey are not optimal.

Food Source Finding and Utilization

When insects are searching for resources they respond to a set of sensory stimuli from their external environment. These stimuli may be chemosensory (tactile, gustatory and air-mediated) or visual (Bell 1990). Herbivore feeding may induce a variety of plant defenses, including the release of volatile chemicals (Takabayashi and Dicke 1996). Natural enemies have been shown to respond to these volatiles by using them as cues for host-finding (Turlings and Wackers 2004). These herbivore-induced plant volatiles have been isolated, and synthetic volatiles have been shown to be effective at attracting natural enemies in field situations (James 2003). The consistent natural enemy response to volatile chemicals with or without the plant that initially produced them indicates that these could be applied in field settings to attract natural enemies to areas in which herbivore populations are still low. However, this approach may encourage natural enemies to concentrate in areas where there is not a large enough prey population to maintain natural enemies, so may be a short-term solution.

While natural enemies have been found to use plant allelochemicals to locate hosts (Vinson 1976, van Alphen and Vet 1986, Barbosa and Benrey 1998, Barbosa and Wratten 1998), little research has been performed on their use of plant semio-chemicals to locate plant food sources. Natural enemies may use similar searching strategies to locate plant resources and insect prey or hosts. Insect-pollinated flowers, unlike insect prey and hosts, are structured to be highly detectable (Wäckers 1994). Therefore, natural enemies may rely more on visual cues for location of nectar and pollen than they do for location of insect prey or hosts.

The relationship between suites of floral characteristics and insects is best known for pollinators. Insects and flowers have relationships that are considered to be specialized, but recent greater understanding of the generalized relationships between flowers and insects indicates that several pollinator groups may visit individual plant species, and in turn insect species often visit more than one plant species (Waser et al. 1996, Memmott 1999, Fenster et al. 2004). Plant species also have been shown to vary significantly in their attractiveness to pollinators (Memmott 1999). Insect color perception ranges from 300-650mn, from ultraviolet to yellow-orange, with peaks of receptivity in the ultraviolet, green-blue, and yellow ranges (Kevan and Baker 1984, Endler 1990, Chittka and Menzel 1992, Kevan et al. 1996). Insect groups may be attracted to specific colors: flies and beetles to white, large bees and butterflies to purple, pink, and blue flowers (Waser et al. 1996). A number of hymenopteran pollinators have been tested for their response to visual cues in the form of hue (what humans perceive as color), brightness, and intensity (saturation or purity of color). Hymenoptera respond to wavelength and in many cases cannot distinguish between colors of different brightness and intensity (Lunau 1990, Wardle 1990, Chittka et al. 1992, Gumbert 2000). Studies have shown that pollinator abundance increases with flower number (Conner and Rush 1996, Ohashi and Yahara 1998), individual flower size (McCall and Primack 1992, Conner and Rush 1996, Hegland and Totland 2005), and visual display (Thomson 1981, Ohashi and Yahara 1998, Hegland and Totland 2005). In addition to floral characteristics, pollinators respond to abiotic conditions (Kevan and Baker 1984) including weather, time of day and temperature (McCall and Primack 1992), as well as season (McCall and Primack 1992, Totland 1993, Hegland and Totland 2005).

The response of natural enemies to flowers is not as well understood as that for pollinators, but several studies have been conducted on individual species, primarily on their response to color. The predators *Chrysoperla carnea* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) show a greater response to yellow traps versus red, orange, black, white, blue, or green, while *Hippodamia convergens* (Coleoptera: Coccinellidae) does not show an affinity for any of these colors (Maredia et al. 1992). The parasitoid wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae) is able to distinguish between yellow and blue, and prefers yellow over blue when yellow is associated with an inconsistent host or sugar reward, but the reverse is not the case (Oliai and King 2000). Wäckers (1994) found that the parasitoid *Cotesia rubecula* (Hymenoptera:Braconidae) displayed an innate visual preference for yellow versus grey during food foraging, and those that were food-deprived were more attracted to yellow than those that were not. Begum et al. (2004) tested the response of the parasitoid *Trichogramma carverae* Oatman and Pinto to alyssum (*Lobularia maritima* L.) flowers of different colors. They found that with both cultivars of different colors and flowers that were dyed, parasitoids that had access to white flowers lived longer than parasitoids that were confined with colored flowers (pink, blue, or purple). These studies indicate that natural enemies may have species-specific innate and/or learned responses to color in relation to plant-provided food.

The response of specific natural enemies is also known for volatiles and plant food location, as well as plant height. Lewis and Takasu (1990) tested the effect of odors associated with food and host on the parasitoid *Microplitis croceipes* (Hymenoptera: Braconidae). They found that females trained to two odors separately with plant food and host would select the odor corresponding with their needs, i.e. if they were hungry they chose the food-associated odor, while if they were well fed they chose the host-associated odor. Food-deprived *C. rubecula* showed an innate preference for rape-seed flowers over rape-seed leaves (Wäckers 1994), indicating that insects may also be able to determine the difference between flower and leaf odors when locating plant food resources. Coll and Bottrell (1996) found that maize height was the primary factor causing lower immigration rates of the parasitoid *Pediobius foveolatus* in plots with tall maize compared to those with short maize. The type and height of field border may affect natural enemy movement, as well. Wratten et al. (2003) found that while three syrphid species traveled 200 m from a plant source of pollen with either no barriers or with a post-and-wire fence barrier, fly movement was significantly limited in areas bordered with poplar trees. Both studies indicate that natural enemy movement may be halted by tall plants, which could concentrate natural enemy numbers on tall plants on field edges, but decrease movement within and between clumps of tall plants.

Nectar Resources

While provision of plant nectar is commonly cited as a basic part of any habitat management program, not all nectars are universally accepted. Wäckers (1999) tested the gustatory response of *Cotesia glomerata* to 14 naturally occurring saccharides. Sugar solutions were accepted at varying concentrations; only eight of 14 evoked a feeding response in food-deprived individuals. *Cotesia glomerata* were most sensitive to fructose, and several sugars (galactose, lactose, mannose, melibiose, raffinose, and rhamnose) did not evoke any feeding response at any concentration. Sugar acceptance varies not only between species, but also between insect orders. While *C. glomerata* accepts a broad range of sugars, adult herbivore host species (*Pieris* spp.) show no consistent response to any sugars besides sucrose and fructose (Romeis and Wackers 2000). This presents the potential for "selective food plants" that benefit natural enemies but not their herbivore hosts/prey. Meiners et al. (2003) found that when the parasitoid *Microplitis croceipes* is exposed only to odor mixtures, it responds to single compounds within those mixtures and does show an innate preference for some plant compounds. These findings indicate that, at least for some insects, there are both learned and innate preferences for food from specific plants.

Although nectar or pollen may be present on a plant, it may not be available to natural enemies. Wasps have differing abilities to "manipulate floral parts to obtain nectar or pollen" due to their behaviors and size (Patt et al. 1997a). Given this variation, specific parasitoid species are able to feed on certain flower types and unable to feed on others (Jervis et al. 1993, Idris and Grafius 1995, Orr and Pleasants 1996). Exposed nectaries on an umbel, which occur in Apiaceae, have been shown to have good nectar accesibility (Jervis et al. 1993, Patt et al. 1997a). In some cases nectar foraging is not limited by floral structure. Some natural enemies engage in "nectar robbing" by chewing a hole in the base of the flower to access nectar, rather than entering through the corolla and pollinating a plant (Idris and Grafius 1995). In addition, some insects are small enough to fit entirely inside the plant corolla (Gilbert and Jervis 1998, Jervis 1998), while others feed on extrafloral nectar (Stapel et al. 1997).

There is evidence that insects not only respond to the morphology of flowers, they also respond to the nectar chemistry. The most common nectar sugars are sucrose, a disaccharide, and fructose and glucose, both monosacccharides, (Baker and Baker 1983), but various other sugars, as well as amino acids, are also found in nectar in small amounts (Table 1). Different sugars have different sweetnesses to humans, and have been shown to have varying attractiveness to birds and bees, so it is probable that nectars taste different to different natural enemies (Baker and Baker 1983). Some plant families consistently have sucrose-rich or hexose-rich nectars, while others have diverse nectar components within the family (Baker and Baker 1983). The sucrose:hexose ratios have been analyzed for flowers that specific insect types frequently visit. There were not enough beetle attractive flowers to elucidate any trends of preference, but wasp attractive flowers tend to be sucrose-rich, while fly attractive flowers have more hexose than sucrose sugars (Baker and Baker 1983). Southwick (1981), however, found that flowers with short corollas tend to have hexose-dominated nectar, while flowers with long corollas are more likely to have sucrose-dominated nectar, so floral morphology and nectar chemistry may be related factors in the attractiveness to potential pollinators. In addition to nectar sugars, natural enemies may be attracted to or repelled by other nectar components, especially amino acids (Baker and Baker 1983).

Table 1. Sugars found in nectar and their frequency of occurrence in nectar.

Monosaccharides	Disaccharides	Other
Fructose* (most common)	Sucrose (most common)	Stachyose (rare)
Glucose* (most common)	Maltose (occasional)	Gentiobiose (very rare)
Galactose (occasional)	Melibiose (occasional)	Mannitriose (very rare)
Arabinose (occasional)	Cellobiose (rare)	
Mannose (occasional)	Melezitose (occasional)	
Rhamnose (occasional)	Raffinose (occasional)	*: Hexose sugars

Source: Baker and Baker 1983

Finally, even after a natural enemy is attracted to, accesses, and consumes nectar or pollen, the sugars or proteins may have different levels of digestibility and energy convertibility. When fed a variety of plant pollens, the predatory mite *Iphiseius degenerans* exhibited differing longevity in a laboratory study (Vantornhout et al. 2004). Developmental times on almond, apple, castor bean and plum pollen were significantly shorter than those on sweet pepper pollen, indicating that sweet pepper pollen was less suitable for development. Lundgren and Wiedenmann (2004) performed a study of the nutritional suitability of corn pollen for the predatory lady beetle *Coleomagilla maculata.* Their results indicated percent organic matter in the pollen was negatively correlated with adult mortality rate, while percent ash was positively correlated with *C. maculata* death rates. These studies indicate that certain pollen components may be more or less suitable for predator arthropod development and alternative food sources.

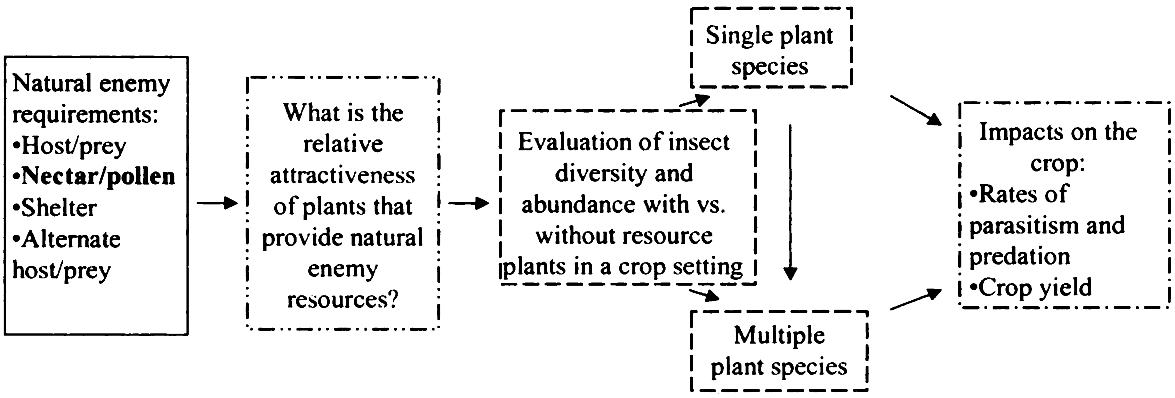
Parasitoids respond differently to different nectar sugars. Wäckers (2001) tested the longevity of the parasitoid *Cotesia glomerata* when exposed to individual sugars or water only (control). Sugars differed greatly in their effect on parasitoid longevity. Parasitoids lived longest (15-16 times the control) when fed glucose, fructose, or sucrose. Several other sugars that occur occasionally in nectar (erlose, maltose, melibiose, melezitose, mannose and stachyose) increased longevity by a factor of 6.9-11.2 compared to water. Trehalose and galactose slightly raised *C. glomerata* lifespan, while lactose and raffinose did not significantly increase longevity. Rhamnose lowered parasitoid lifespan in the experiment. Because all nectars are composed of more than one sugar, such dramatically different results are unlikely in the field. Wäckers (2001) did find, however, that rhamnose significantly decreased *C. glomerata* longevity even at a 4:1 ratio of glucuse:rhamnose, indicating that rhamnose in combination with other nectars still has potential to impact insect longevity. This experiment illustrates the importance of testing nectar content in plants used for habitat management to assure that it is actually beneficial to natural enemies.

Developing Habitat Management Programs

Framework

While scientists and farmers may have an understanding that specific plants attract and provide resources to beneficial insects, and that these natural enemy populations may in turn help control pest populations, there are many steps in developing such a program successfully. The first step in this process is to determine which plants best provide resources to beneficial insects (Fig. 1). This has been addressed in lab studies of specific plant-insect interactions, observational studies of what set of insects utilize plants already growing in an area, and experimental field tests that examine individual plants and all of the natural enemy insects that utilize specific plant resources. Next, resource plants placed in crop settings allow evaluation of either single or multiple plant species for their impact on natural enemy abundance and diversity (Fig. 1). Finally, once the impact of single or multiple resource plants in a crop on natural enemy abundance and diversity is measured, the ultimate goal is that biocontrol organisms have impacts on the nearby crop itself. Specifically, rates of parasitism and predation, as well as which specific natural enemies are impacting pest populations, indicate whether and how plant resource presence ultimately affects crop yield in agricultural systems (Fig. 1).

Figure 1. A conceptual model illustrating the necessary components for development of a habitat management program.



Recommended Plants

There are many sources of information suggesting plant species to provide natural enemy resources. In fact, the concept that plant-provided resources can enhance biological control is somewhat of a dogma in many gardening and farming interest groups. A web search using the terms "beneficial insect" and "plant" resulted in over 7000 hits (Google 12/15/2003). Web sources that contained recommendations for specific plants varied from Cooperative Extension, research reports, and municipal websites to commercial, personal, and general interest websites. The first eight sites located in the search were examined in detail (Appendix A).

Many of the website resources did not cite any information on how or why the author believed these plants attract beneficials, rather, this information was simply presented as fact. The plant species recommended at some sites (especially commercial sites) were very specific (Appendix A). The Extension webpages were better documented and frequently cited more than one information source for their plant recommendations. The number of plant species recommended at these sites was quite extensive.

Two well-documented sources (each citing greater than five references) were used for additional documentation regarding which plants are frequently recommended to encourage beneficial insects. They were: 1) a publication from Midwest Biological Control News (Steffan and Whitaker 1996) and 2) Appropriate Technology Transfer for Rural Areas (ATTRA) (Dufour 2000) (Appendix A). Both sources went beyond recommending specific plant species and included information regarding which plants provide resources for specific insect types. Temporal availability of nectar and pollen was also considered. It is commonly assumed that one flowering plant species cannot provide these resources through an entire season (Steffan and Whitaker 1996, Long et al. 1998).

The majority of resources recommended the Apiaceae and Asteraceae plant families. Several plants were commonly recommended, including: angelica, coriander, dill, fennel, Queen Anne's lace, coneflower, cosmos, "daisy", yarrow, thyme, alfalfa, clover species, sweet alyssum, and buckwheat (Appendix A). Data supporting these recommendations, however, was rarely cited.

The same search was again performed two years later (Google 11/01/2005), resulting in 54,600 hits. Several of the webpages that were top hits in 2003 remained top hits, and in general the information is similar, with websites from agency, commercial, and personal websites. One notable new site with different information was the third website shown: a site from the Minnesota department of agriculture (www.mda.state.mn.us/biocon/biogarden). This site lists whether plants in a beneficial insect garden are native or not, but does not list the origin of the recommendation.

Plant evaluation

Personal observation is a frequently cited method used to determine which plants provide resources for beneficial insects. In a review by Bugg and Waddington (1994), a table listing several California weeds "that harbor alternate hosts or prey of beneficial insects" uses "personal observation" or "personal communication" for the information source of a majority of species.

Alternately, some type of formal survey or evaluation may be used to determine which plants provide beneficial insect resources. These are performed: 1) in a laboratory setting, with a small set of plants and natural enemies, 2) in a field cage, or 3) in an open field setting. Several studies used laboratory trials with specific plants and insects to determine which plants would provide natural enemy resources (Patt et al. 1997a, Baggen and Gurr 1998, Baggen et al. 1999). Baggen and Gurr (1998) used the flowering plants coriander (*Coriandrum sativum*), dill, borage (*Borago officinalis*), and faba bean to assess longevity of the parasitoid *C. koehleri* in a laboratory setting. Greater longevity was found in the dill, borage, and coriander plant treatments with flowers than in plots without flowers. Baggen et al. (1999) performed a similar study with dill, faba bean (*Vicia faba*), phacelia (*Phacelia tanacetifolia*), nasturtium (*Tropaeoleum majus*), and buckwheat. They found increased lifetime fecundity in the potato crop pest insect

Pthorimea operculella, (Lepidoptera:Gelichiidae) with access to buckwheat, dill, or faba bean extrafloral nectaries, while increased longevity of *C. koehleri* was found with access to any of these species. This study outlines the possibility that plants provide food resources not only to beneficial insects, but to pests as well. On the other hand, nasturtium and Phacelia increased fecundity of *C. koehleribut* but not *P. operculella*, indicating the potential for "selective food plants" (Baggen and Gurr 1998) that benefit natural enemies and not pest insects.

Field studies

Several single plant evaluations in field studies have evaluated natural enemy visitation at flowering plants. Plant attractiveness to natural enemies is often quantified via timed observation periods and vacuum sampling. Chaney (1998) observed and vacuum sampled insects found at 22 plant species in beds spaced 1m center to center and intercropped with lettuce. He plotted the mean number of pest and beneficial insects on each plant and found that some of the tested plants had potential to be used as insectary plants, which provide resources to insects. The study layout, however, is difficult to understand; no statistical analyses were performed on the data, and no sampling dates were given (other than "weekly") for the data. Due to these factors, the study, as presented, shows trends but there is no way to determine significant differences between plants.

In another plant evaluation, Nentwig (1998) observed and vacuum sampled flower-visiting insects at about 80 plant species planted in random plots in a 8 ha wheat field in Switzerland. He found differing levels of plant attractiveness to different insect species as measured by number of insects in a taxon (e.g. Carabidae, Cantharidae) found on different plant species. High numbers of arthropods were found on poppy (*Papaver rhoeas*), rape (*Brassica napus*), buckwheat (*Fagopyrum esculentum*), and tansy (*Tanacetum vulgare*). No mention is made regarding whether plants were randomly assigned locations, and no statistical tests were performed on these data. Again, trends for attraction of certain insect types to specific plants were reported; however, it is unclear whether the differences are statistically significant.

Hamilton et al. (2003, 2004) conducted a three-year plant evaluation study with thirty plant species in New Jersey USA. The layout is difficult to interpret, but it appears that the experiment was laid out in two locations with one replicate at each in 2000 and a second replicate at each location was added in 2001 and 2002. Flowering plant attractiveness to Hymenoptera and adult syrphids was examined. An LSD mean separation indicates that fennel (*Foeniculum vulgare*) drew significantly more Hymenoptera than all other plants in all three years, and yarrow (*Achillia mellefolium*), coreopsis (*Coreopsis tinctoria*), coriander, and buckwheat attracted the most adult syrphids, although not significantly more than other plant species in all three years. This study again provides trends, but due to the low replicate number and study design, results may not be reliable.

Beneficial insectary plantings were also tested by Colley and Luna in Oregon USA (2000). Eleven plant species in 1.5 m^2 plots with four replicates in a complete randomized-block design were planted alongside a field of corn. Timed observations of syrphid fly visits were performed at eight dates from June–Sept. Syrphids exhibited a high degree of feeding selectivity, but the number observed at each plant species was influenced by which other plants were in bloom at the same time.

Only a handful of evaluations has been performed on what individual plant species provide to insects. Several of these were performed in no-choice laboratory studies, several more were structured as preliminary studies, with inadequate replication or statistical analysis, and the final study outlined (Colley and Luna 2000) focused on syrphid fly presence only. I was unable to find any studies that have examined all visiting insects at single plant species in an outdoor setting with adequate replication over an entire growing season.

Observational studies

Several observational field studies rating level of natural enemy insect visitation to flowering plants have been published. Bugg et al. (1987) carried out a field survey of all flower-visiting insects associated with common knotweed (*Polygonum aviculare*) and found 36 insect taxa using common knotweed flower resources. Van Emden (1963) performed a study of parasitic Hymenoptera in different field settings. He found increased activity of parasitic Hymenoptera in the presence of flowering plants. Harmon et al. (2000) found a significantly positive correlation between the presence of *Coleomegilla maculata* and that of dandelion flowers, indicating that *C. maculata* could be feeding on dandelion flower resources. Shole (1984) studied insect presence and location on two species of goldenrod, *Solidago juncea* and *S. altissima*, over two growing seasons. He found increased numbers of flower feeders, parasitoids (some of which appeared to be flower feeding), and predators when the respective *Solidago* species were in bloom. Tooker and Hanks (2000) tabulated data from a previous study on insects found on 112 species of flowering plants of central Illinois. Their focus was on hymenopteran families that contain primarily parasitic insects. They found the highest species diversity of wasps on plants in the family Apiaceae. Jervis et al. (1993) studied parasitic hymenoptera visiting inflorescences of 53 plant species in a variety of habitats. They found most species at Apiaceae, and some at plants of Convolvulaceae and Compositae. These numbers did not reflect a fixed sampling period, however, and are likely to be biased towards more intense sampling on Apiaceae. These studies, much like many of the single species experimental plant observations, are useful for examination of general trends. However, they were not designed as scientific experiments with randomization and replication (with the exception of Harmon et al. (2000)), and several studies are very limited in the insects or plants examined.

Field evaluation studies of individual plant species

Once a flowering plant has been determined as attractive to and a potential food plant for natural enemies, the next step is to test the impact of that species at the field level. Klinger (1987) examined the effect of margin strips of *Sinapis alba* L. and *Phaceliea tanacetifolia* Benth. on natural enemy presence in winter wheat crops. They found significantly higher numbers of both predator species in and near the margin strips, as well as an "attractive effect" of syrphids to the margin strips. A similar study by Hickman and Wratten (1996) examined the effect of *Phaceliea tanacetifolia* Benth. strips on syrphid populations in winter wheat fields. They also found higher syrphid numbers in fields with *P. tanacetifolia* boundaries on two sides of the field than in control fields, but no significant season-long difference in syrphid numbers in fields with versus without phacelia. Chaney (1998) established strips of sweet alyssum (*Lobularia maritima* L.) on one side of lettuce fields in both commercial and organic production to examine beneficial insect populations. He found more beneficial insects near the alyssum planting and a trend of fewer aphids near the alyssum, but no statistical analyses were performed on the data. Stephens et al. (1998) collected parasitoids in areas of stone-fruit orchard with and without buckwheat (*Fagopyrum esculentum* Moench) sown in the understory, and suction sampled buckwheat foliage. They found that *Anacharis* sp. parasitoids were attracted by floral resources to orchard areas with buckwheat. Baggen and Gurr (1998) used 1x8 m plots of coriander (*Coriandrum sativum*) and faba bean (*Vicia faba*) in potato (*Solanum tuberosum*) plantings to examine nectar plant effects on a crop pest (*P. opurculella*) and its parasitoid (*C. koehleri*). They observed the greatest parasitism rates in *P. opurculella* on potatoes closer to the flowering plants. Winkler (2005) compared the number of the parasitoid *Diadegma semiclausen* (Hymenoptera: Ichneumonidae) in fields bordered by either a flowering species: *Centaurea jacea, Anethum graveolens, Fagopyrum esculentum*, *Lobularia maritima*, or grass. More parasitoids were found in fields bordered by *A. graveolens* but not *F. esculentum*, despite the fact that *D. semiclausen* showed increased longevity with access to *F. esculentum* in laboratory studies. These studies examine the effect of one pre-determined plant species on a specific class of natural enemies, so none address whether the plants used to provide plant resources are more attractive to natural enemies than others in the field and examine a broad insect group.

Field evaluation of plant species mixtures

Single species evaluations can lead either to studies on individual plant species effects on field crops or to plant species mixture effects on field crops. Plant mixtures have been examined in numerous experiments. Nentwig (1988) examined the effect of a mown meadow versus a strip-managed meadow that always contained unmown strips on arthropod predator populations. Density of most arthropods was found to be greater in strip-managed than mown areas. Spider densities were evaluated by Jmhasly and Nentwig (1995) in wheat fields that had sown weed strips placed in them. They found a trend towards higher spider density close to the strips (which was significantly higher on one of five testing dates). Long et al. (1998) studied the effect of insectary border or strip plantings on beneficial insect presence and dispersal at three farm sites. They labeled insectary planting strips with rubidium, and measured the occurrence of rubidium-labeled insects (which had fed on the labeled plant resources) from 0 to 250 feet from the strips. The study indicated that beneficial insects did visit the mixed species plantings, and that they move into nearby crops. The effect of a vegetation corridor composed of 65 flowering plant species on natural enemy presence in a monocrop was studied by Nicholls et al. (2001). They found that the corridor provided long-term natural enemy populations that dispersed into the crop field when pest populations increased. Lee et al. (2001) examined the effect of refuge insect strips containing orchard grass (*Dactylus glomerata*), white clover (*Trifolium repens*), and a mixture of perennial flowering plants on beetle populations in a corn crop. They compared effects of refuge vs. crop vegetation on carabids and found evidence that refuges impacted community composition, as well as evidence "that refuges can contribute to greater carabid populations in the field" (Lee et al. 2001). Varchola and Dunn (2001) studied the effect of vegetation diversity (either complex prairie vegetation or simple communities that were brome grass dominated) on carabid abundance and species richness in an agricultural system. They found significantly greater carabid species richness in complex than simple agricultural systems before canopy closure. All of these studies illustrate examples of increased natural enemy numbers in areas with increased habitat diversity or heterogeneity.

The volume of studies on plantings of species mixtures at the field level is great, but there is no discussion of whether the plant species for these mixtures were evaluated separately for their use by pest or natural enemy insects. Therefore, many of these plant mixtures could contain plants that increase pest populations or do not actually provide key natural enemies with accessible or beneficial resources. The focus of published mixed plant species evaluations is primarily on which insects are found on the plant and utilize the resources it provides, with an assumption that all plants in the group are providing resources to natural enemies.

Crop impact evaluation

The final step in introduction of resource plants for beneficials is to determine what effect the presence of the plants has on crop damage or yield. As previously illustrated, quite a few studies have examined the abundance of parasitoids and predators in relation to habitat management. Another group of studies have gone one step further and examined changes in rates of parasitism and predation (usually measured via a change in number of pest insects) in crop fields as a result of habitat management changes. Klinger (1987) performed a study using margin strips of two flowering species in conjunction with a winter wheat field. He found that the areas near strips contained more predators and a reduced cereal aphid population near strips than areas far from strips, but the decrease was not significant. Hickman and Wratten (1996) examined syrphid populations and impacts on aphid populations in fields with border strips of *Phacelia tanacetifolia*. Although they found trends for increased syrphids and decreased aphid populations near borders, no significant differences in either were found. In fields with flowering strips, Thies and Tscharntke (1999) found increased levels of parasitism on *Meligethes aeneus*, an oilseed rape pest, that extended to decreased rape damage. The results of these studies did not show consistent impacts on herbivore populations in crops, and the differences did not transfer to crop yield.

Given that it has proven difficult to accurately measure the impact of natural enemies on pest populations in areas with habitat management versus monocrops, it is extremely difficult to translate the presence of non-crop plantings and increased natural enemy abundance into effects on crop yield, although this is the ultimate goal of habitat management. There is a set of studies, however, that indicates that landscape context plays a role in the success or failure of habitat manipulation (Thies and Tscharntke 1999, With et al. 2002, Menalled et al. 2003, Thies et al. 2003). Gurr et al. (2003) encourage consideration of habitat management impacts at the crop level, as well as impacts that extend to the farm and landscape.

PLANT SELECTION FOR HABITAT MANIPULATION

There is extensive literature that lists or recommends plant species to provide natural enemies with non-host resources. There is, however, a startling lack of information about exactly why specific plants were initially chosen for further study. Likely, this is often due to an initial observation of a large number of insects visiting a specific plant. However, this decision-making process is rarely documented. Patt et al. (1997a) and Baggen et al. (1999) made plant choices with specific consideration of flower morphology and selective access for beneficial insects. Chaney (1998) eliminated plants that "were unsuitable for one or more reasons" in his individual plant observation study, but failed to enumerate those reasons. Plants were selected for their ornamental value and previous success in attracting natural enemies by Frank and Shrewsbury (2004). Rebek et al. (2005) chose plants that would bloom throughout the growing season. The most complete criteria for plant selection are enumerated by Winkler (2005), including: "the amount of pollen and nectar production, presence of extrafloral nectaries, flowering period, overall attractiveness for flower visiting insects and possible effects as alternative hostplant for cabbage pests." Many studies, however, appear to have a more haphazard selection criteria.

Another group of studies examined "weeds" surrounding crops for floral resources (Foster and Ruesink 1984, Idris and Grafius 1995, Nentwig 1998, Nentwig et al. 1998). Weeds are resources already available near the crop, and the weeds may provide resources to natural enemies. Weeds are, however, invasive by definition in the cropping system and may present farmers with added problems. In fact, many of the approximately 80 plants Nentwig (1998) tested are plants that are native in Europe, where the study was carried out, but are weedy species in other locales. This group of plants was narrowed down to a seed mixture of 29 plant species (Nentwig et al. 1998) which is recommended for use in strips along crop fields in Europe. The mix contains the biennials greater burrdock (*Arctium lappa*), Fuller's teasel (*Dipsacus fullonum*), wild parsnip (*Pastinaca sativa*), and bladder campeon (*Silene alba*), which are all considered weeds in the United States. In fact, Fuller's teasel and wild parsnip are such a severe problem that they are listed as prohibited noxious weeds (USDA plant database). Although not considered invasive in Europe, these plant species would not be candidates for weedy borders in other locales. While inexpensive, the approach of augmenting weedy species populations in crop areas to provide resources to natural enemies may have difficulty gaining wide acceptance.

Absence of native plants in habitat management

The plant species most frequently tested for habitat management are exotic to the locale of their use. While observational studies included some native plants, the most frequently recommended plants utilized in the single plant species evaluations include: phacelia (*Phacelia tenacetefolia*), buckwheat (*Fagopyron esculentum*), dill (*Anethum graveolens*), fennel (*Foeniculum vulgare*), coriander (*Coriandrum sativa*), faba bean (*Vicia faba*), and alyssum (*Lobularia maritima*). All except phacelia are nonnative to the U.S. The vast majority of the list compiled from web sources on "beneficial plant" and "insect" are also species not native to the U.S. Plants used for habitat management may be classified as introduced or native to the study area, and annual or perennial (Table 2). Eight of 14 studies examined focused on introduced, annual plants, but again, the greatest exception is Nentwig's (1998) study that includes weedy species.

Table 2. Study type and plant type used in habitat management studies to provide nectar and pollen to natural enemies.

Study	Study type	Number of plant species: Introduced	Native	Annual	Perennial*
Baggen and Gurr (1998)	Lab, field	4	-	4	-
Baggen et al. (1999)	Lab	6	-	6	-
Chaney (1998)	Field	12	10	21	1
Colley and Luna (2000)	Field	10	1	7	4
Foster and Ruesink (1984)	Lab	5	-	2	3
Frank and Shrewsbury (2004)	Field	1	2	1	2
Hickman and Wratten (1996)	Field	1	-	1	-
Idris and Grafius (1995)	Field	13	-	2	11
Long et al. (1998)	Field	2	12	13	1
Nentwig et al. (1998)	Field	6	23	9	20
Orr and Pleasants (1996)	Lab	-	11	-	11
Patt et al. (1997b)	Lab, field	2	-	2	-
Patt et al. (1997a)	Field	20	3	11-13	10-12
Rebek et al. (2005)	Field	2	2	-	4
	Total	**84**	**64**	**79-81**	**67-69**

*Includes biennials and perennials.

The result of repeated recommendations for non-native plants is that habitat management, a discipline focused on increasing plant diversity and providing habitat for natural enemy arthoropods, frequently proposes introduction or augmentation of non-native plant species. These non-natives are being added in agricultural systems that have already been drastically modified and are composed primarily of non-native plants. An estimated 5000 non-native plant species have been introduced into the U.S., while a total of about 17,000 native plant species exist (Pimentel et al. 2000). Non-native plants often have greater potential for invasion than natives (Blossey and Nötzold 1995) and may serve as pre-adapted overwintering hosts for nonnative pathogens.

There are sound reasons that the currently recommended non-native plants became commonly used in habitat management. These plants are easy to establish, adaptable to varied locations, and there are adequate seed sources of them. In addition, they may have been bred or selected to have prolific flower displays that are more likely to be apparent to natural enemies. However, native plants could also be selectively bred to exhibit many of these traits.

There is no *a priori* reason to suspect that native plants cannot perform the same function as current nonnatives that are recommended. Use of native plants for habitat management has several benefits. Native plants are pre-adapted to the local environment and its natural enemies. Their use adds to native biodiversity, increases demand and future availability of native plants, and may be a catalyst for restoration of native communities.

Predominance of annual plants

The most widely used plants for habitat management are annual plants. Several factors make annual species attractive for use in habitat management experiments. Seed and plant material of cultivated plants are easy to access and reliably available (Colley and Luna 2000). Annuals lend themselves better than perennials to laboratory experiments, as time of flowering is more easily controlled (Baggen et al. 1999). In many cases annual, cultivated plants are also very adaptable (Colley and Luna 2000). For example, phacelia will grow on any soil, has a long flowering period, good flower cover, and is resistant to frost (Hickman and Wratten 1996). This set of characteristics makes the plant and the research results transferable to many different situations.

It is also recognized that plant resources must be available in phenological synchrony with natural enemies, preferably throughout the cropping period (Patt et al. 1997b, Nentwig et al. 1998, Rebek et al. 2005). As annuals have only one year to produce flowers, they frequently have a prolific floral display in the first year. The extended and reliable bloom period of the frequently used cultivated annuals makes them excellent plants to provide resources to natural enemies in areas planted with one to several plant species that neighbor crop fields (Baggen and Gurr 1998). Non-native annuals may have marketable plant parts or flowers (i.e. dill or coriander), providing farmers with additional income (Patt et al. 1997b, Gurr et al. 1998). Many of the cultivated annuals have also been planted extensively in different countries and continents, so there is reliable information on their propagation and establishment. The fact that there is published information on specific plants leads researchers to perform further studies on the same plants. Several studies have specifically focused on plants that are already known to be attractive to natural enemies (Hickman and Wratten 1996, Patt et al. 1997a, Colley and Luna 2000, Frank and Shrewsbury 2004). Given the early established success of several annual, cultivated plants in surviving in a variety of areas, providing long bloom periods, and record of attractiveness to natural enemies, it is no wonder that many of the same plants are used time after time in habitat management studies.

Annual plants, however, have several drawbacks in a habitat management system. First, they must be re-planted annually in order to maintain plant resource availability. If the plant re-seeds itself, replanting is not necessary, but the plant is then more likely to become an invasive weed in a cropping system, mixing with the crop and requiring additional control. One goal of habitat management is to provide natural enemies with overwintering sites and refuges from the frequent disturbance in annual cropping systems (Corbett and Rosenheim 1996, Lee et al. 2001). If the non-crop resource plants are annuals, the area planted with resource plants must be frequently disturbed and may no longer function as an overwintering site or in-season refuge for natural enemies, nor will a resident natural enemy population be able to establish in the area (Landis et al. 2000). This set of drawbacks indicates that perennial, native plants should also be examined for use in habitat management.

In summary, with more careful selection criteria for plants in habitat management, plants may be chosen that address a variety of goals in habitat management that benefit natural enemies and improve landscape biodiversity. These include: plants that best provide natural enemies with plant resources, bloom throughout the season, are not invasive, and provide natural enemies with overwintering habitat.

The overall goal of my research is to improve the effectiveness of habitat management to increase natural enemy abundance and decrease the need for chemical pesticide use in agriculture while maintaining native plant species in the landscape. My specific objectives to meet this goal are to: 1) screen native Michigan plants to find a subset of those most attractive to natural enemies that bloom during the entire growing season, and 2) facilitate native plant selection for habitat management in other locales by determining whether natural enemies respond to certain plant characteristics.

Chapter 2

For Environmental Entomology

ATTRACTIVENESS OF MICHIGAN NATIVE AND NON-NATIVE PLANTS TO ARTHROPOD NATURAL ENEMIES AND HERBIVORES

Anna Katherine Fiedler

ABSTRACT

The use of plants to provide nectar and pollen resources to natural enemies via habitat management is a growing focus of conservation biological control. Current guidelines frequently recommend use of annual plants not native to the management area, but Michigan native perennial plants are likely to provide similar resources and may have several advantages over non-natives. I compared a set of 43 native Michigan, USA perennial plants and five frequently recommended non-native annual plants for their attractiveness to natural enemies and herbivores for two years. Plant species differed significantly in their attractiveness to natural enemies. In year one, non-native annual plants outperformed many of the native Michigan plants. In year two, however, many native perennial plants attracted higher numbers of natural enemies than non-native plants. In year two, we compared each flowering plant against the background vegetation (grass) for their attractiveness to natural enemies and herbivores. Screening individual plant species allowed rapid assessment of attractiveness to natural enemies. I identified 24 native perennial plants that attracted high numbers of natural enemies, with promise for habitat management. Among these are *Eupatorium perfoliatum*, *Monarda punctata*, *Silphium perfoliatum*, *Potentilla fruticosa*, *Coreopsis lanceolata*, *Spiraea alba*, *Agastache nepetoides*, *Anemone canadense*, and *Angelica atropurpurea*. Subsets of these plants can now be tested to develop a community of native plant species that attracts diverse natural enemy taxa and provides nectar and pollen throughout the growing season.

INTRODUCTION

Conservation biological control involves practices which protect and enhance natural enemies already present in the landscape by decreasing natural enemy mortality or providing resources that enhance natural enemy survival and efficacy (Ehler 1998). Using plants to provide needed resources to natural enemies, termed habitat management, is a growing focus of conservation biological control (Landis et al. 2000). Habitat management can provide natural enemies with alternate hosts (DeBach and Rosen 1991, Menalled et al. 1999, van Emden 2003), shelter (Powell 1986, Gurr et al. 1998, Nentwig et al. 1998), and non-host food (Baggen et al. 1999, Wilkinson and Landis 2004) in ways that enhance biological control (Gurr et al. 2003).

Both parasitoids and predators benefit from access to non-host food, especially nectar and pollen. For parasitoids, access to nectar may be crucial for adult survival in species that do not host feed (Jervis and Kidd 1986). Several laboratory studies have shown increased longevity and/or fecundity of adult parasitoids with access to nectar or sugars (Dyer and Landis 1996, McDougall and Mills 1997, Baggen et al. 1999, Wäckers 1999, Jacob and Evans 2000, Romeis and Wackers 2002). At points in some parasitoid life cycles, access to sugars may be more important than host availability (Baggen and Gurr 1998). While predators frequently use prey resources as adults, they often supplement their diets with plant resources including phloem fluids (Legaspi and O'Neil 1993, Eubanks and Denno 1999) and pollen (Harmon et al. 2000). In some cases, predators may require protein garnered from flower pollen to mature eggs, or access to pollen may increase fecundity (Hickman and Wratten 1996).

Despite the potential benefits of plant resources to natural enemies, plant species must be carefully selected to ensure natural enemies can take advantage of the resources. Many natural enemies have mouthparts that are not specialized for flower-feeding and may be unable to access to nectar in flowers with deep, narrow corollas (Jervis et al. 1993, Orr and Pleasants 1996, Wäckers et al. 1996). Nectar and pollen availability may increase pest insect populations as well as natural enemy populations. Screening plants to select those which provide resources to natural enemies and not herbivorous pests is an important consideration (Baggen and Gurr 1998, Baggen et al. 1999, Winkler 2005). In addition, plant and insect phenology must coincide so that insects garner benefits of access to nectar and pollen at the correct time to increase their populations (Jervis et al. 1993, Orr and Pleasants 1996, Colley and Luna 2000, Siekmann et al. 2001).

When the goal of a habitat management program is to increase plant resource availability to beneficial insects, several methods have been used to test which plants are most attractive to natural enemies. The most controlled are laboratory studies of specific plant-insect interactions which consider whether specific natural enemies can access and feed on plant nectar or pollen of specific flowering plants (Patt et al. 1997a, Baggen and Gurr 1998, Baggen et al. 1999). Another tactic is the use of observational studies of insects using plants already growing in an area to determine which are most frequently visited by natural enemies (van Emden 1963, Shole 1984, Bugg et al. 1987, Jervis et al. 1993, Bugg and Waddington 1994, Idris and Grafius 1995, Tooker and Hanks 2000). A third is to select a group of plants based on previous success and establish them individually (White et al. 1995, Hickman and Wratten 1996) or in plant groupings (Chaney 1998, Nentwig et al. 1998, Nicholls et al. 2001, Frank and Shrewsbury 2004, Rebek et al. 2005, Pontin et al. 2006) and assess the number and type of natural enemies in the planting or nearby field. None of these studies, however, have established replicated groups of plant species and compared their individual attractiveness to natural enemies.

Non-indigenous plants have often been the focus of habitat management. In part, this is because a small group of effective plants have been repeatedly used worldwide. These include: alyssum (*Lobularia maritima* (L.) Desv.), borage (*Borago officinalis* L.) and coriander (*Coriandrum sativum* L.), native to the Mediterranean and Southern Europe, dill (*Anethum graveolens* L.) and buckwheat (*Fagopyrum esculentum* Moench), native to Asia, faba bean (*Vicia faba* L.), native origin unknown, possibly the Mediterranean, and phacelia (*Phacelia tanacetifolia* Benth), native to California, USA. Many of these plants are also annual, which provides planting and flowering flexibility but precludes potential benefits of establishing more permanent habitats.

Non-native invasive plants have large impacts on landscapes in the United States, displacing native plant species and sometimes dominating ecosystems (Pimentel et al. 2000). In addition, the use of non-natives may increase the risk of non-native pest problems including non-native pathogens (Blossey and Nötzold 1995). The current emphasis on non-native species in habitat management could exacerbate these problems.

While most guidelines recommend annual plants not native to the management area, there is no reason to suspect that perennial native plants cannot perform as well as annual non-natives. Use of native perennial plants for habitat management has several benefits. These species are adapted to the local environment. They add to native biodiversity and may be used to restore imperiled habitats. Finally, they are less likely to be invasive than non-native annuals. In addition, their perennial habit provides natural enemy overwintering sites and results in a one-time seed or plant purchase and establishment of plants, as compared to yearly establishment of annual species.

Despite the extensive literature on habitat management, there is a lack of studies using a screening process that examines the entire natural enemy and herbivore community visiting single plant species with adequate replication. In this study, I tested 43 native perennial species for their attractiveness to natural enemies over two growing seasons, making this the most extensive study of its kind.

My objective was to compare the attractiveness to natural enemy and herbivore arthropods of 43 Michigan native perennial plants and five of the most widely recommended annual resource plants not native to Michigan. I determined attractiveness by examining arthropod abundance at plants when they were in full bloom. The goal of this process was to select of a subset of plants for further consideration in a successful habitat management program. My hypotheses were that: 1) plant species would vary in attractiveness to natural enemy arthropods, 2) some native plants would be as or more attractive to natural enemy arthropods as frequently recommended non-natives, 3) plant species would attract different numbers and types of natural enemy and herbivore taxa, and 4) attractiveness would increase as perennial plants matured.

METHODS

Plant Selection Criteria

I selected 43 species of Michigan native plants for study using the following criteria: 1) native Michigan perennials, 2) adapted to non-irrigated agricultural field conditions (full sun, moderate drought periods likely), 3) represent a diversity of bloom periods from early through late season, 4) from a variety of plant families, 5) varied floral color and morphology, 6) forb or shrub species formerly common in Michigan prairie and oak savanna habitats, and 7) commercially available Michigan genotypes. Native plants were selected in consultation with a Michigan native plant nursery owner (William Schneider, pers. comm.). Five plant species not native to Michigan were also selected for study based on the following criteria: 1) commonly recommended to enhance beneficial insects and 2) fit criteria 2-4 above. All of the frequently used non-natives were annuals.

STUDY SITE

The study site was a former agricultural field on the Michigan State University Entomology Farm in Ingham County, MI. Soil consisted of a Marlette fine sandy loam (Soil Conservation Service 1979) and was previously farmed in a corn-soybean rotation. Plants were established in 1 m^2 blocks spaced 6 m apart within a matrix of orchardgrass (*Dactylis glomerata* L.) that was regularly mowed to prevent flowering. The experiment was conducted in a randomized complete block design with five replicates of each of the 43 native Michigan perennial plants and the five non-native plant species (Table 3). Native plants were obtained as rooted plugs (Wildtype Design Native Plants & Seeds, Ltd., Mason MI) and planted in September 2003. Plant densities of three, five, or eight plants per plot were selected based on individual species characteristics such that the plot would be densely filled with plant material at maturity. Non-native annual species were planted for comparison to native species, as follows. *V. faba* (cv. Windsor) (Johnny's Seeds, Winslow, ME) was seeded on 20 May 2004 and on 9 May 2005. Sixteen plugs per

m^2 of *L. maritima* cv. Snow Crystals (Ball seed company, Chicago, IL) were planted on 20 May 2004 and 16 June 2005. On 29 May 2004 and 9 May 2005, *A. graveolens* cv. Mammoth island, *C. sativum* (Spice Coriander), (Richters Herb Specialists, Goodwood, Ontario), and *F. esculentum* cv. Mancan, (Simmons Family Farms, North Branch, MI) were seeded. Vouchers of all plant species were deposited in the Michigan State University (MSU) herbarium in May 2006 (Appendix B).

Table 3. Plant species established at the MSU Entomology Research Farm, E. Lansing, MI. Bloom period is indicated by letters: e = early (May-June), m = middle (July-mid-August), and l = late season (mid-August on). All plants are native Michigan plants except the last five that are annuals.

Family	Genus and species	Common Name	Plants / m^2	Plant Type
Native species				
Laminaceae	*Agastache nepetoides*	Yellow giant hyssop	8	forb
Liliaceae	*Allium cernuum*	Nodding wild onion	8	forb
Fabaceae	*Amorpha canescens*	Leadplant	8	shrub
Ranunculaceae	*Anemone canadensis*	Canada anemone	8	forb
Apiaceae	*Angelica atropurpurea*	Angelica	5	forb
Apocynaceae	*Apocynum cannabinum*	Indian hemp	5	forb
Ranunculaceae	*Aquilegia canadensis*	Columbine	8	forb
Asclepiadaceae	*Asclepias incarnata*	Swamp milkweed	8	forb
Asclepiadaceae	*Asclepias tuberosa*	Butterfly weed	8	forb
Asteraceae	*Aster laevis*	Smooth aster	8	forb
Asteraceae	*Aster novae-angliae*	New England aster	8	forb
Asteraceae	*Cacalia atriplicifolia*	Pale Indian plantain	5	forb
Rhamnaceae	*Ceanothus americanus*	New Jersey tea	5	shrub
Rubiaceae	*Cephalanthus occidentalis*	Buttonbush	3	shrub
Asteraceae	*Coreopsis lanceolata*	Sand coreopsis	8	forb
Fabaceae	*Desmodium canadense*	Showy tick trefoil	8	forb
Poaceae	*Elymus canadensis*	Canada wild rye	8	grass
Asteraceae	*Eupatorium perfoliatum*	Boneset	8	forb
Rosaceae	*Fragaria virginiana*	Wild strawberry	8	forb
Geraniaceae	*Geranium maculatum*	Wild geranium	8	forb
Asteraceae	*Helianthus strumosis*	Pale-leaved sunflower	5	forb
Apiaceae	*Heracleum maximum*	Cow parsnip	5	forb
Saxifragaceae	*Heuchera americana*	Alum root	8	forb
Hydrophyllaceae	*Hydrophyllum virginianum*	Virginia waterleaf	8	forb
Fabaceae	*Lespedeza hirta*	Hairy bush-clover	8	forb
Asteraceae	*Liatris aspera*	Rough blazing star	8	forb
Campanulaceae	*Lobelia siphilitica*	Blue lobelia	8	forb
Lamiaceae	*Monarda punctata*	Horsemint	8	forb
Onagraceae	*Oenothera biennis*	Evening primrose	8	forb
Poaceae	*Panicum virgatum*	Switch grass	5	grass
Scrophulariaceae	*Penstemon hirsutus*	Penstemon	8	forb
Rosaceae	*Potentilla fruticosa*	Shrubby cinquefoil	8	shrub
Asteraceae	*Ratibida pinnata*	Yellow coneflower	8	forb
Rosaceae	*Rosa setigera*	Michigan rose	3	shrub
Caprifolaceae	*Sambucus racemosa*	Red-berried elder	5	shrub
Poaceae	*Schizachyrium scoparius*	Little bluestem	8	grass
Scrophulariaceae	*Scrophularia marilandica*	Late figwort	8	forb

Table 3. Cont'd.

Family	Genus and species	Common Name	Plants / m^2	Plant Type
Asteraceae	*Senecio obovatus*	Round-leaved ragwort	5	forb
Asteraceae	*Silphium perfoliatum*	Cup plant	5	forb
Asteraceae	*Solidago riddellii*	Riddell's goldenrod	8	forb
Asteraceae	*Solidago speciosa*	Showy goldenrod	8	forb
Rosaceae	*Spiraea alba*	Meadowsweet	5	shrub
Verbenaceae	*Verbena stricta*	Hoary vervain	8	forb
Asteraceae	*Vernonia missurica*	Ironweed	8	Forb
Scrophulariaceae	*Veronicastrum virginicum*	Culver's-Root	8	forb
Apiaceae	*Zizia aurea*	Golden alexanders	8	forb
Non-native species				
Apiaceae	*Anethum graveolens*	Dill	Broadcast	annual
Apiaceae	*Coriandrum sativum*	Coriander/ Cilantro	Broadcast	annual
Polygonaceae	*Fagopyrum esculentum*	Buckwheat	Broadcast	annual
Brassicaceae	*Lobularia maritima*	Alyssum	16	annual
Fabaceae	*Vicia (vigna) faba*	Faba (Fava) bean	16-24	annual

To maintain background fertility for the orchardgrass, granular nitrogen (urea or ammonium nitrate, 33.6 kg N/hectare) was applied to the entire field on 23 June 2004 and 14 April 2005. In response to apparent nutrient deficiencies in particular plant species, I applied liquid fertilizer (5.7 L of 20-20-20: Peters professional all-purpose plant food) on 23 June 2004 to *Ceanothus americanus* L., *Monarda punctata* L., *Sambucus racemosa* L., *Hydrophyllum virginianum* L., *Amorpha canescens* (Pursh), and *Aquilegia canadensis* L.

FLOWER PHENOLOGY

I observed all plants weekly for occurrence of open flowers with dates of first, last, and peak bloom, as well as full bloom period, recorded for each species. Hereafter, I use "peak bloom" to refer to the specific week of maximum floral display for each species.

ARTHROPOD COLLECTION

From May through September 2004 and 2005, I sampled arthropods weekly from flowering plants between the hours of 0930-1330 EST on sunny, calm days. For insect sampling "full bloom period" refers to samples collected the week of peak bloom from a particular plant species plus one week on either side. A three week period was chosen to reduce the influence of week-to-week variability in insect catch due to weather and plant phenology. To collect insects, a fine mesh white no-see-um netting bag (Kaplan Simon Co., Braintree, MA) was placed over the intake on a gas-powered leaf blower modified into a vacuum (Stihl BG55 Norfolk, VA). Each plot was vacuumed until all flowers were sampled (limited to 30 sec in 2004). To compare the number of insects in flowering plants versus nonflowering plants, we placed a $1 m^2$ PVC quadrat in the mown orchardgrass matrix in each of 5 blocks and vacuum sampled the quadrat weekly from 21 June through September 2005. These samples will be referred to as the "grass control."

Insects were frozen, identified to family, separated into natural enemies, herbivores, and "other," and counted. Insects from any predaceous or parasitic family, or genus or species within a family known to be predaceous or parasitic, were included as natural enemies. Insects from any family known to be broadly herbivorous were counted as herbivorous insects. Arthropod vouchers representative of each taxon were deposited in the MSU entomology museum in May 2006 (Appendix C). Attractiveness here is based on the number of arthropods collected per sample and as such it is a measurement of attraction to, arrestment at, and tenure time on the plant species once the arthropod has arrived.

Taxonomy

Insect taxonomic classification follows Triplehorn and Johnson (2005) and plant nomenclature follows Voss (1972, 1985, 1996).

Statistical Analysis

Plant species were divided into three categories according to timing of the peak bloom date: early season (May – June), mid season (July – 20 August 2004 and July – 9 August 2005) or late season (21 August 2004 and 10 August 2005 – September). Numbers of natural enemies per flowering plant and block were natural log (x+1) transformed to better fit assumptions of normality and homogeneity of variance. A simple regression was conducted between the log (x+1) number of natural enemies and the week of peak bloom for each plant in 2004 and 2005 (SAS Institute 2003, PROC REG). Due to a non-linear relationship between natural enemy number and week of peak bloom, a polynomial term was included in the regression for both years, but this term was significant only in 2004. A two-way ANOVA with block and plant species as factors was conducted on the mean insect counts over three dates (SAS Institute 2003, PROC GLM). Due to lack of homogeneity of variance between treatments, data for early season 2004 and mid and late season 2005 were analyzed using a weighted least squares approach based on a separate variance estimate for each treatment (Kutner et al. 2005). Least squares means with separations were performed based on Tukey adjustment and Satterthwaite's adjustment for degrees of freedom (α=0.05) (Satterthwaite 1946).

RESULTS

A total of 41 and 48 of the 48 flowering plant species bloomed in 2004 and 2005, respectively. Individual species bloomed from early May through September in 2004 and May through 4 October in 2005 and had similar bloom periods from year to year except where noted (Tables 4, 5). In both years, natural enemy numbers at most species increased significantly throughout the season (Fig. 2, Table 6). In 2004, the most attractive plant in the early season averaged 11.5 natural enemies per sample during full bloom period, while mid and late season plants exceeded 30 and 80 natural enemies per sample, respectively.

During full bloom period in 2005, the most attractive plants contained over 30, 33, and 199 insects per sample in the early, mid, and late seasons, respectively. Overall natural enemy numbers were smaller in 2004 than in 2005, with season-long averages of 13.8 and 20.5 per plant species per sample, respectively.

Table 4. Flowering phenology 2004. Plants are listed in order of bloom. Non-native plant names are underlined. ■=peak bloom date, ▪=full bloom,— =in bloom.

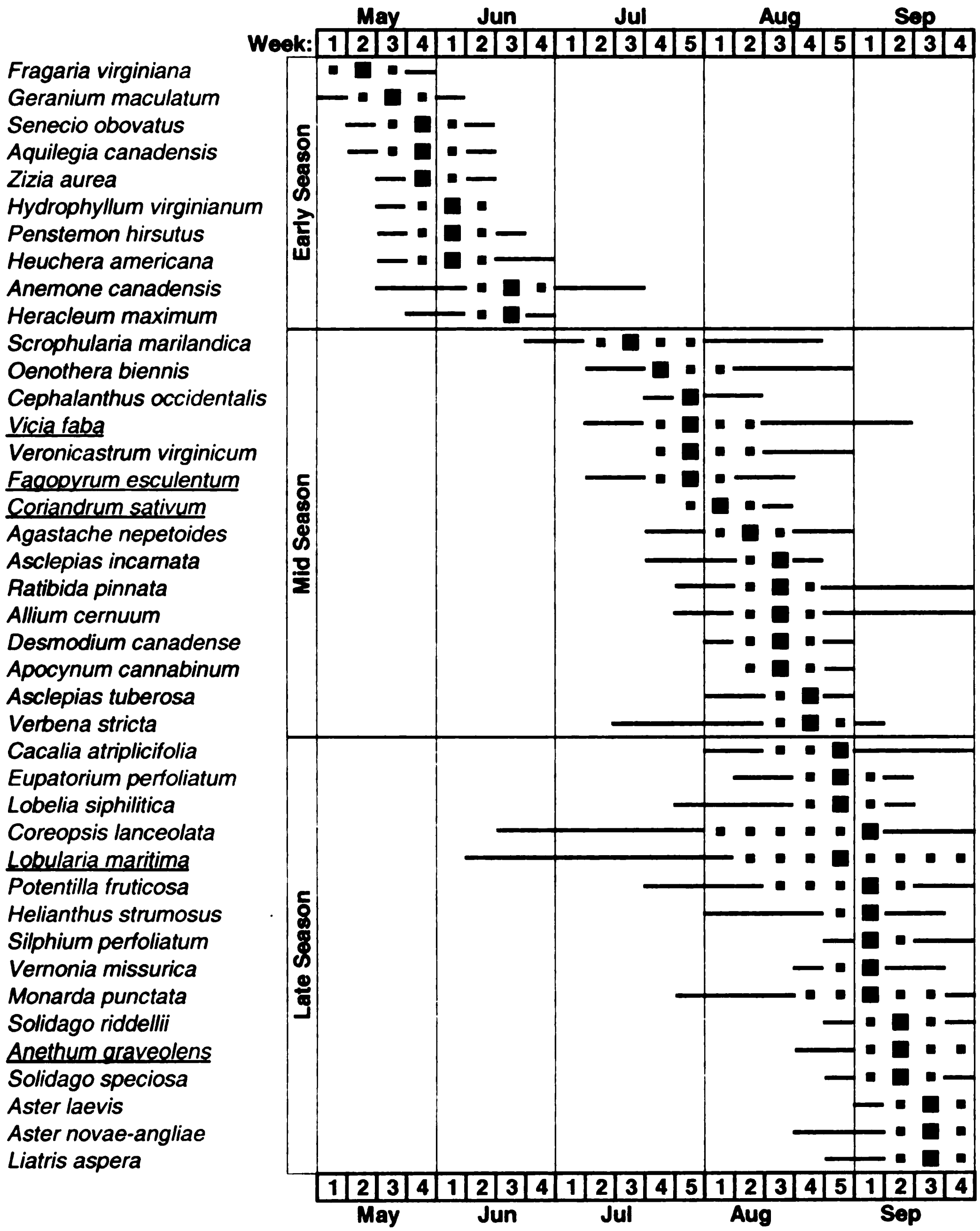
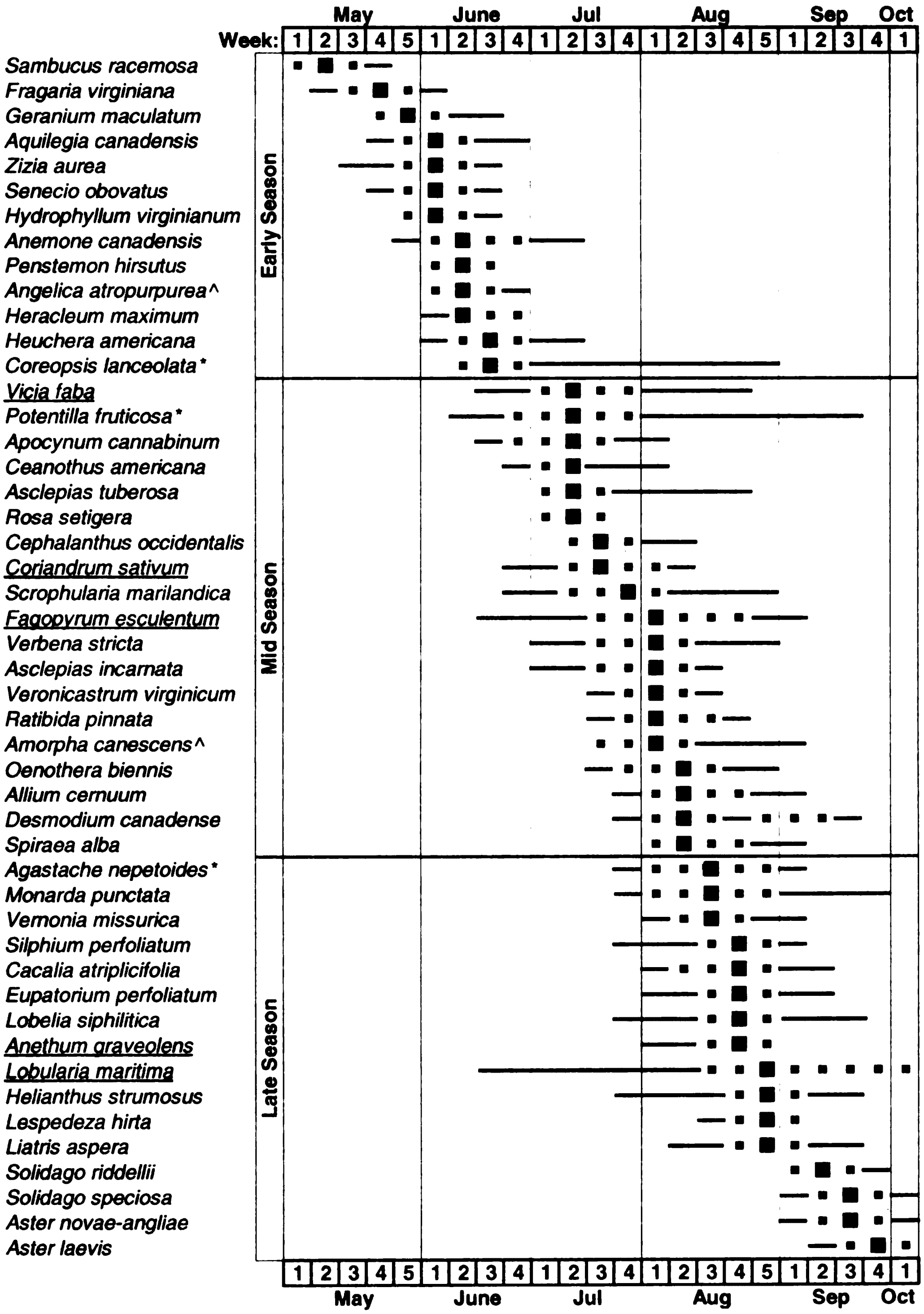


Table 5. Flowering phenology 2005. Plants are listed in order of bloom. Non-native plant names are underlined. ■=peak bloom date, ▪=full bloom,— =in bloom. *Plants had similar phenologies in 2004 and 2005 except where noted. Observed 2004 peak bloom dates were Aug. 31 for *C. lanceolata* and *P. fruticosa*, and Aug. 13 for *A. nepetoides*. ^= Did not bloom in 2004.



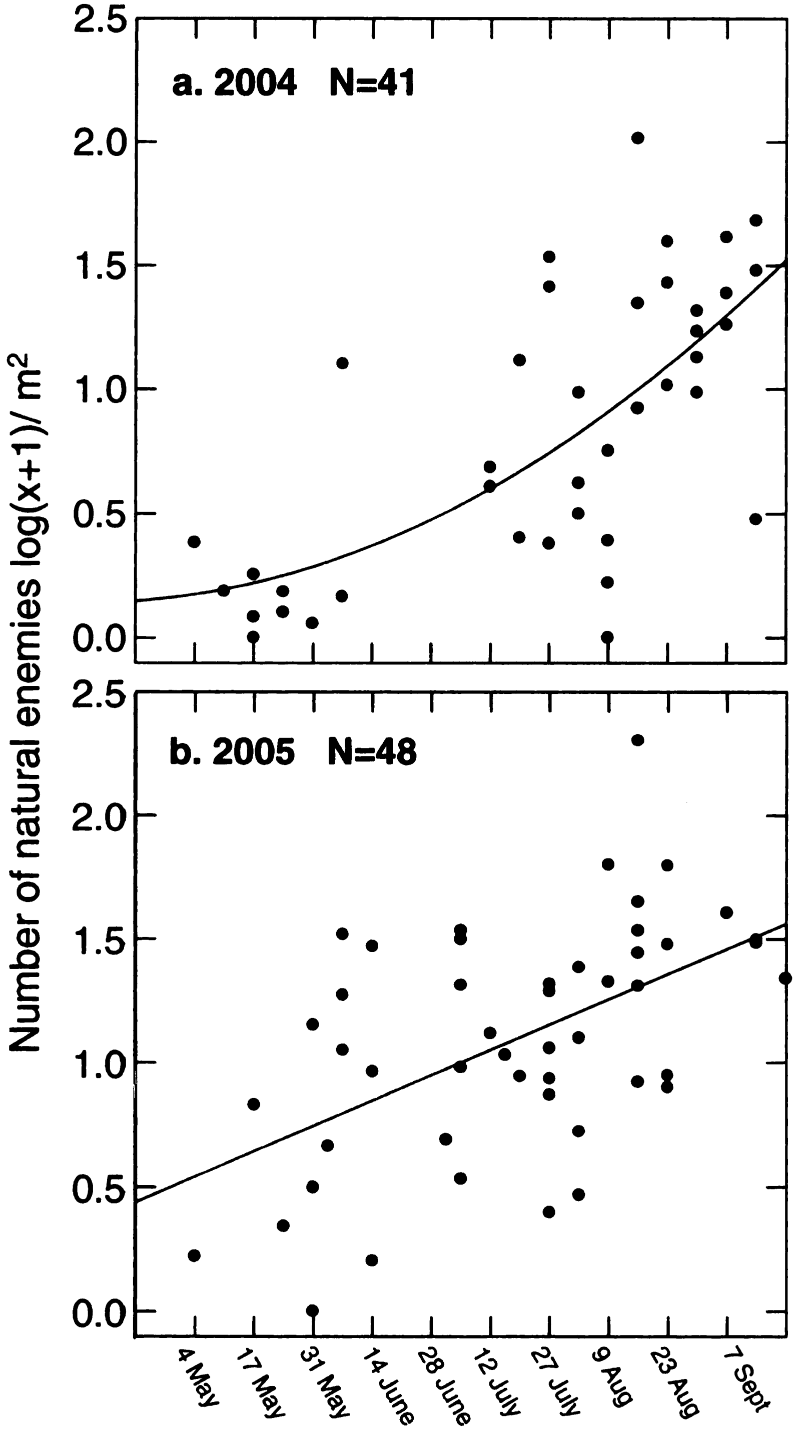


Figure 2. Simple regression between mean number of natural enemies [log(x+1)] per plant species during full bloom versus week of peak bloom per species.

Table 6. Simple regression of log(x+1) number of natural enemies versus week of peak bloom.

Variable	Estimate ±SEM	F	P	R^2
2004*				
Intercept	0.19 ± 0.13	2.24	0.14	—
$Week^2$	0.0028 ± 0.00047	35.46	<.001	0.47
2005				
Intercept	0.440 ± 0.16	7.64	0.008	—
Week	0.051 ± 0.011	19.96	<.001	0.30

*P>0.5 for week

In both 2004 and 2005, there was a significant (P<0.001) species effect on the mean number of natural enemies collected during full bloom period, indicating that species differed significantly in their attractiveness to natural enemies (2004: early season df=10, F=23.16 P<0. 001; mid season df=14, F=29.26, P<0.001; late season df=15, F=8.78, P<0.001; 2005: early season df=13, F=23.59, P<0.001, mid season df=18, F=53.67, P<0.001, late season df=15, F=32.27, P=0<.001). Within the native plants alone, significant effects on natural enemy attractiveness were also found in both years (2004: early season df=9, F=21.52, P<0.001; mid season df=11, F=9.74, P<0. 001; late season df=13, F=7.82, P<0.001; 2005: early season df=12, F=20.14, P<0.001; mid season df=15, F=44.02, P<0.001; late season df=14, F=33.04, P<.001), indicating that native plants varied significantly in their attractiveness. There was no significant effect of block (P<0.05) except in late season 2005, when plants in block 4 attracted significantly fewer insects (df=4, F=3.18, P=0.020). Block 4 was on a slight elevation and plants there may have experienced more moisture stress during the particularly dry 2005 growing season.

EARLY SEASON

In 2004, the native *Heracleum maximum* (Bartr.) was significantly more attractive than other plants (Fig. 3a) Note: *Coreopsis lanceolata* bloomed in late season 2004 and is statistically compared to species in Figure 5a. Non-native *L. maritima* and natives *Fragaria virginiana* Duchesne (listed from most to least natural enemies per sample) formed the next most attractive group of species. In 2005, *Angelica atropurpurea* L., which did not bloom in 2004, and *Coreopsis lanceolata* L., which bloomed during the late season in 2004, were the most attractive plants to natural enemies. *Anemone canadensis*, *Zizia aurea* (L.) Koch, *Penstemon hirsutus* (L.) Willd., *H. maximum* and *F. virginiana* were the next most attractive plants but overlapped in significance with the least attractive species (Fig. 3b). Samples taken from 21 June 2005 onward illustrate that *A. atropurpurea, C. lanceolata, A. canadensis, P. hirsutus* and *H. maximum* attracted more natural enemies than a neutral grass background (grass control) during the same period. Although no grass samples were taken when *Z. aurea* and *F. virginiana* were blooming, these species attracted more natural enemies than other plants blooming in May and early June. In both 2004 and 2005, no natural enemies were collected at *Aquilegia canadensis* L. even though abundant blossoms were observed. *Lobularia maritima* and *H. maximum* were relatively less attractive in 2005 than in 2004. Overall, however, plants attracted more natural enemies in 2005 than in 2004 during the early season, with several plants averaging 4 to 60 times more natural enemies in 2005 than in 2004, i.e. *Z. aurea, A. canadensis, P. hirsutus*, *H. virginiana* and *F. virginiana*.

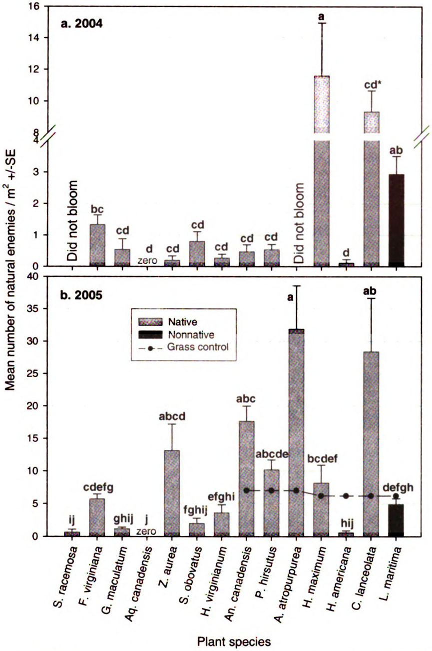


Figure 3. Early season mean number of natural enemies collected per 1 m^2 plot the week during the full bloom period for each species (peak bloom date 1 May – 21 June) 2004 and 2005. Plants listed in 2005 bloom order from left to right. 2004 samples were limited to 30s, in 2005 plots were sampled until all flowers were sampled. Grass control was sampled from 21 June 2005 onward only. *A. canadensis*, *P. hirsutus*, and *A. atropurpurea* grass control points represent the mean of 1 date, remaining points represent the mean of 2 dates. Although not in full bloom in early season, *Lobularia maritima* is included as the only non-native comparison plant blooming in early season. Bars with different letters within a figure are significantly different using Tukey-adjusted means comparisons ($p<0.05$). * *Coreopsis lanceolata* bloomed in late season in 2004 and is statistically compared to species in Fig. 5a.

Mid Season

In 2004, the non-natives *F. esculentum*, *C. sativum* and *V. faba* were far more attractive than most of the native plants, with *Agastache nepetoides* (L.) Kuntze (which bloomed in late season 2005 and is statistically compared to species in Fig. 5a) the only native plant that attracted greater than 5 natural enemies per sample on average (Fig. 4a). However, in 2005, *Apocynum cannabinum* L., *Potentilla fruticosa* auct. non L. (which bloomed in the late season in 2004 and is statistically compared to species in Fig. 5a), *Spiraea alba* Duroi, the non-native *V. faba, Ratibida pinnata* (Vent.) Barnh., non-native *F. esculentum* and *Oenothera biennis* L. and *Verbena stricta* Vent. were the most attractive plants (Fig. 4b). The remaining plant species were not significantly more attractive than the least attractive plants and did not attract more natural enemies than grass controls from the same period. All mid season native plants attracted more natural enemies in 2005 than in 2004, including *P. fruticosa* (a late blooming plant in 2004). Overall, many of the plants were far more attractive in 2005 than in 2004, except the annual non-natives *F. esculentum* and *C. sativum,* which had fewer natural enemies in 2005 than in 2004.

Late Season

In 2004, several native species attracted as many or more natural enemies as one or more of the non-natives (Fig. 5a). *Eupatorium perfoliatum* L. and *L. maritima* attracted significantly more insects than many other species. *Aster novae-angliae* L., *Solidago riddellii* Frank ex Riddell, *Aster laevis* L., *Anethum graveolens* L., *Lobelia siphilitica* L., and *Helianthus strumosus* L. formed the next most attractive group but

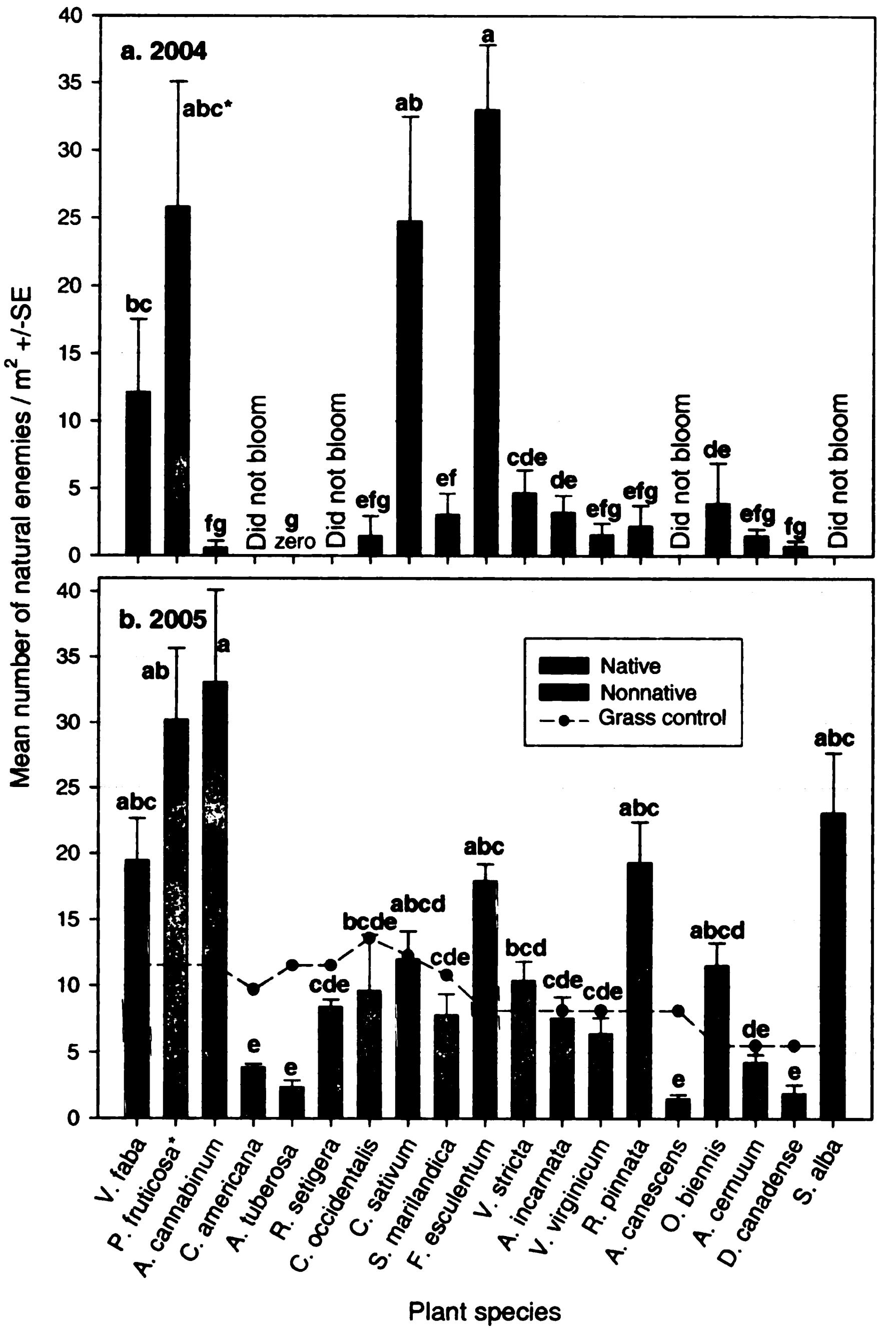


Figure 4. Mid season mean number of natural enemies collected per m^2 plot during the full bloom period for each species in 2004 and 2005 (peak bloom date 1 July – 20 Aug. 2004 and 1 July – 9 Aug. 2005. Plants listed in 2005 bloom order from left to right. 2004 samples were limited to 30s, in 2005 plots were sampled until all flowers were sampled. Grass controls are a mean from the 3 week full bloom period for each flowering species. Bars with different letters within a figure are significantly different using Tukey-adjusted means comparisons ($p<0.05$). **Potentilla fruticosa* bloomed in late season 2004 and is statistically compared to species in Fig. 5a.

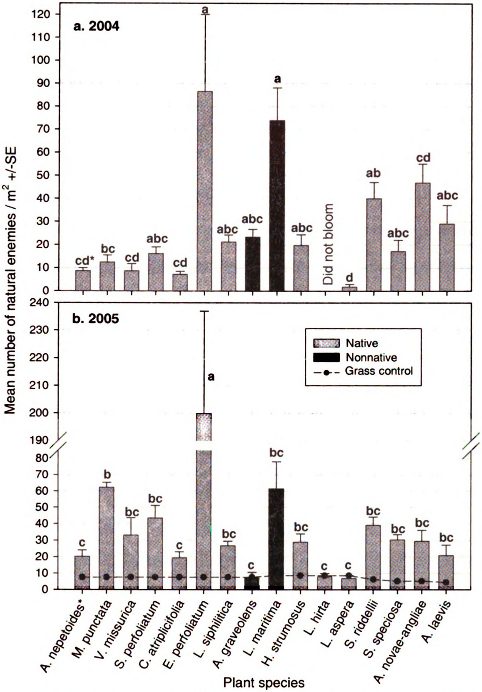


Figure 5. Late season mean number of natural enemies collected per m^2 during the full bloom period for each species in 2004 and 2005 (peak bloom date 21 Aug. – 21 Sept. 2004 and 10 Aug. – 27 Sept. 2005). Plants listed in 2005 bloom order from left to right. 2004 samples were limited to 30s, in 2005 plots were sampled until all flowers were sampled. Grass controls are a mean from the 3 week full bloom period for each flowering species. Bars with different letters within a figure are significantly different using Tukey-adjusted means comparisons ($p<0.05$). Note change in Y axis scale from Figures 3 and 4. ******Agastache nepetoides* bloomed in mid season in 2004 and is statistically compared to species in Fig. 4a.

overlapped broadly with the least attractive plants. In 2005, most natives performed better than non-native *A. graveolens*, which was decimated by Papilionidae larvae (Fig. 5b). Native *E. perfoliatum* was significantly more attractive than any other plant species, and *Monarda punctata* L., non-native *L. maritima*, natives *Silphium perfoliatum* L., *S. riddellii*, *Vernonia missurica* Raf., *Solidago speciosa* Nutt., *A. novae-angliae,* and *H. strumosus* all attracted more than 25 natural enemies on average. All but 3 plant species were more attractive to natural enemies than the grass control, while species listed above attracted more than twice as many natural enemies as the grass control. Overall, native plants blooming before September performed better in 2005 than in 2004, including *E. perfoliatum, M. punctata*, *V. missurica*, and *Cacalia atriplicifolia* L., which were over twice as attractive to natural enemies in 2005 as in 2004. A group of species blooming from mid-September on performed similarly and quite well in both years, while non-natives *A. graveolens* and *L. maritima* had fewer natural enemies in 2005 than in 2004.

NATURAL ENEMY TAXA

The relative proportions of natural enemy taxa collected were similar in 2004 and 2005. The major difference between years was that more Coleoptera and fewer Hemiptera were collected in 2005 (Fig. 6). At the family level, the overall patterns were also similar between years except Cantharidae, Miridae and Empididae were relatively more abundant and Anthocoridae less abundant in 2005 versus 2004 (Fig. 7).

In 2004, the most numerous taxon was Anthocoridae (entirely *Orius insidiosus* (Say)), followed by Chalcidoidea, Arachnida, Cantharidae, and Empididae (Fig. 7a). In 2005, Anthocoridae and Chalcidoidea were again the most common natural enemy groups, followed by Cantharidae, Arachnida, and Miridae (*Plagiognathus politus* Uhler) (Fig. 7b). The most numerous beetles in both years were Cantharidae. Arachnida were composed of Thomisidae, Salticidae, Tetragonathidae, Aranaeidae, and Lycosidae. Many Arachnida, however, were immatures unidentifiable to family so all are grouped into Arachnida. The most numerous Hemiptera in both years were Anthocoridae. Thysanoptera were not identified to family in 2004, but 14% of total thrips in 2005 were predatory Aeolothripidae (Fig. 7b). The most common Hymenoptera in both years were Chalcidoidea. The most numerous Diptera in both years were Empididae.

All natural enemy taxa except Syrphidae were more numerous on plants in 2005 than in 2004 (Table 7). Spiders were collected at all blooming plants from mid-July on in both 2004 and 2005, demonstrating the ubiquity of this taxon. Anthocoridae had the highest seasonal totals of any natural enemies and were present from June-September 2004 and May-September 2005. I collected an average of 5 Aeolothripidae per sample at *C. lanceolata*, more than at any other plant. All beetle groups were present throughout the season in low numbers, and Coccinellid and Cantharid numbers were greatest at the end of the growing season. Chrysopidae was the only Neuropteran family collected in both seasons, except for 1 Hemerobiid at *F. esculentum* in 2005. Chalcidoidea were collected from plants during the entire growing season during 2004 and 2005, and most numerous in August. Other Hymenopteran groups included Cynipoidea and Braconidae, which were present during the entire growing season in 2005, and Bethylinidae, which were collected from mid-August through September in 2005 only (Appendix D). Empididae had highest numbers from June through August. Syrphidae were present in both years from June through August. Other Dipteran groups included Dolichopodidae, which were

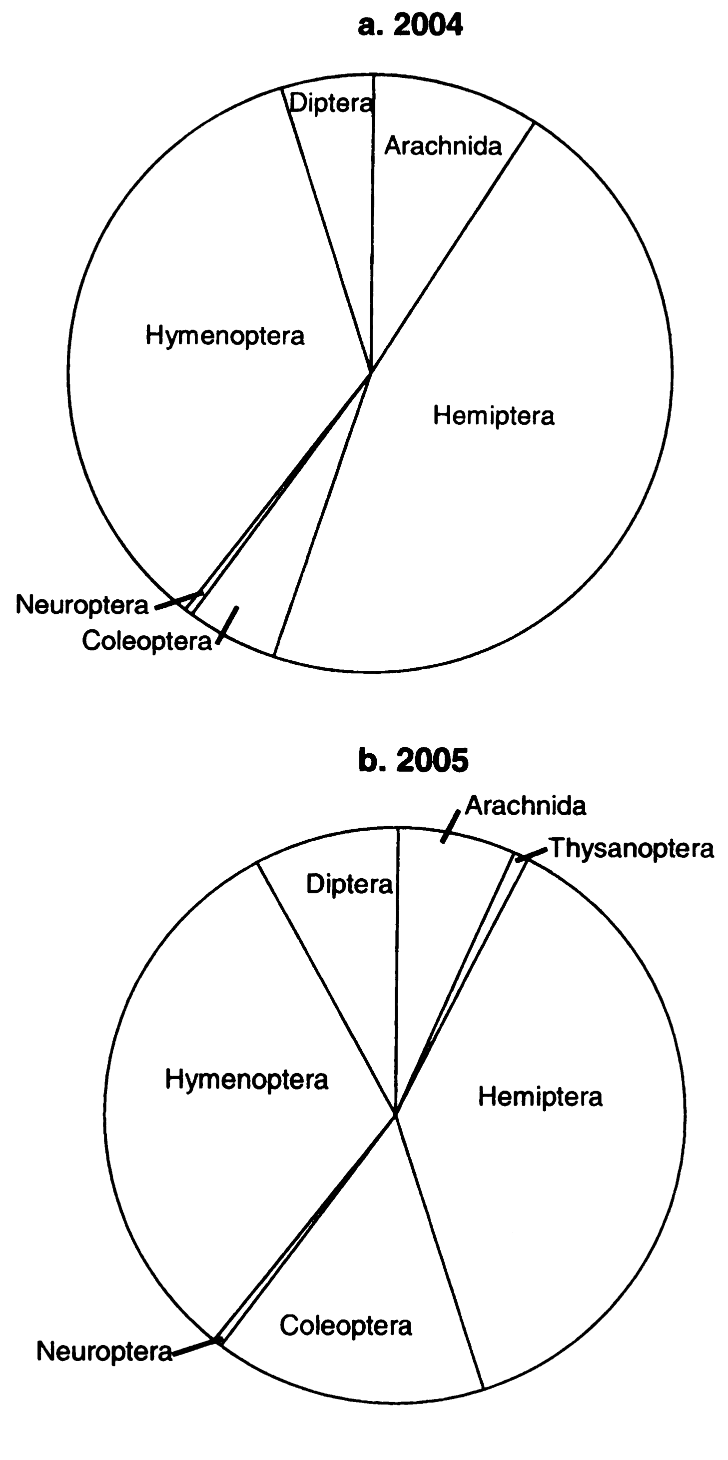
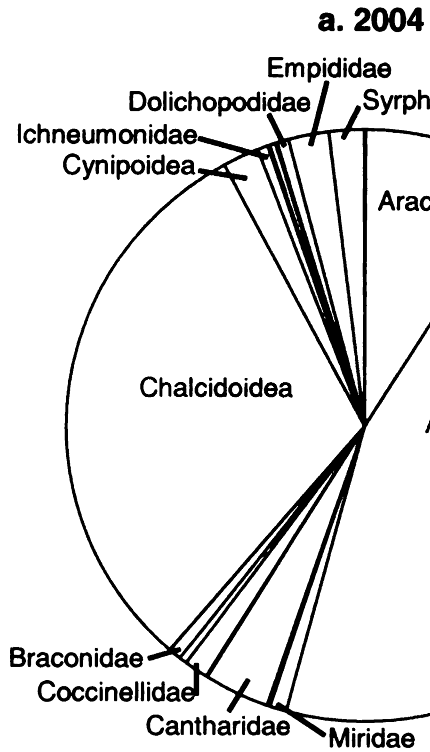


Figure 6. Proportion of total natural enemies collected at all flowering plants by order.



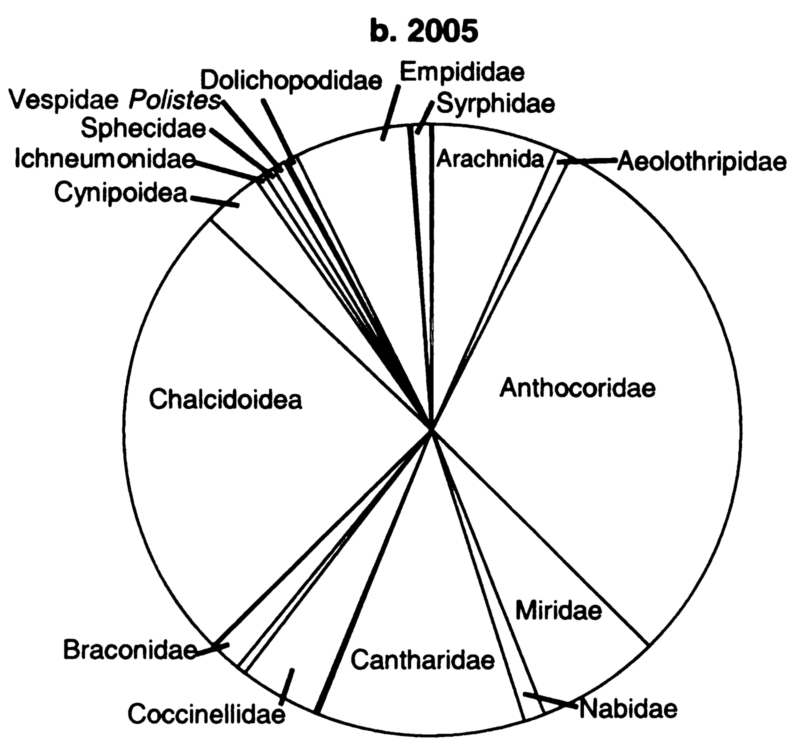


Figure 7. Proportion of total natural enemies collected at all flowering plants by family. Taxa comprising less than 0.5% of the total are not labeled. Aeolothripidae were not counted separately in 2004.

Table 7. Natural enemy taxa collected at plants during full bloom period in 2004 and 2005. The nine most numerous groups of natural enemies are shown here. Numbers represent the total of included natural enemies collected in the number of samples listed. ^*Plagiognathus politus* Uhler and *Chlamydatus associatus* Uhler were counted as natural enemies. "." indicates plant did not flower in 2004, so could not be sampled.

Season	Plant Species	Number of samples 2004	Number of samples 2005	Arachnida: Arachnida 2004	Arachnida: Arachnida 2005	Hemiptera: Anthocoridae 2004	Hemiptera: Anthocoridae 2005	Hemiptera: Miridae 2004	Hemiptera: Miridae 2005	Coleoptera: Cantharidae 2004	Coleoptera: Cantharidae 2005	Coleoptera: Coccinellidae 2004	Coleoptera: Coccinellidae 2005
Early Season	*S. racemosa*	0	15	.	5	.	0	.	0	.	0	.	0
	F. virginiana	12	15	6	12	0	0	0	0	0	0	1	0
	G. maculatum	13	15	3	4	0	2	0	0	0	0	0	1
	Aq. canadensis	10	15	0	0	0	0	0	0	0	0	0	0
	Z. aurea	14	15	1	3	0	20	0	1	0	0	1	10
	S. obovatus	15	14	5	0	0	10	0	0	0	1	0	5
	H. virginianum	15	10	1	7	0	1	0	2	0	0	0	0
	An. canadensis	15	15	1	7	0	112	0	4	0	1	0	0
	P. hirsutus	15	15	3	2	1	30	0	0	0	0	0	1
	A. atropurpurea	0	15	.	2	.	77	.	0	.	4	.	7
	H. maximum	15	12	0	2	11	32	0	0	7	3	2	0
	H. americana	7	15	0	0	0	0	0	1	0	0	0	1
	C. lanceolata	15	15	20	3	30	180	1	34	9	6	1	0
Mid Season	*V. faba*	14	15	11	6	80	46	0	8	0	0	14	90
	P. fruticosa	15	15	40	45	150	190	4	5	14	20	0	11
	A. cannabinum	6	15	1	45	0	22	0	5	0	12	0	38
	C. americana	0	8	.	8	.	2	.	0	.	0	.	0
	A. tuberosa	3	15	0	8	0	4	0	0	0	0	0	0
	R. setigera	0	13	.	27	.	27	.	2	.	0	.	0
	C. occidentalis	5	10	3	10	2	24	0	0	0	0	0	1
	C. sativum	15	14	18	13	123	16	0	3	56	0	0	5
	S. marilandica	15	15	11	13	4	3	0	0	0	0	2	3
	F. esculentum	15	15	14	29	315	87	0	0	3	1	5	13
	V. stricta	15	15	15	15	16	62	0	8	0	0	2	2
	A. incarnata	15	15	7	21	13	18	0	1	0	1	8	4
	V. virginicum	15	15	2	11	11	59	0	0	0	0	0	2
	R. pinnata	12	15	6	53	1	60	0	11	0	2	0	1
	A. canescens	0	15	.	3	.	5	.	1	.	0	.	1
	O. biennis	15	15	7	12	20	39	0	87	0	0	1	7
	A. cernuum	15	15	7	11	2	28	0	9	0	2	1	3
	D. canadense	15	15	6	8	1	1	0	1	0	0	0	0
	S. alba	0	15	.	28	.	164	.	17	.	23	.	10
Late season	*A. nepetoides*	15	15	13	42	54	60	0	69	0	5	1	7
	M. punctata	15	6	66	22	44	40	33	81	3	190	2	4
	V. missurica	15	15	16	36	6	24	0	21	1	1	2	17
	S. perfoliatum	15	15	20	31	23	142	1	72	19	94	1	10
	C. atriplicifolia	14	15	14	17	15	92	0	20	4	48	0	7
	E. perfoliatum	12	15	38	55	863	1249	3	336	92	949	3	14
	L. siphilitica	15	15	26	30	147	102	2	34	9	62	1	47
	A. graveolens	15	15	24	10	22	2	0	19	1	12	41	14
	L. maritima	15	15	74	36	515	263	6	40	4	22	2	7
	H. strumosus	15	15	36	37	39	42	0	10	7	70	0	10
	L. hirta	0	15	.	11	.	28	.	7	.	0	.	51
	L. aspera	7	15	3	16	4	26	0	4	0	9	2	18
	S. riddellii	15	15	53	24	276	272	6	4	44	2	3	46
	S. speciosa	15	15	20	49	101	180	13	1	16	2	7	79
	A. novae-angliae	15	15	95	58	497	227	3	0	0	0	2	21
	A. laevis	15	15	54	41	339	189	3	0	0	0	2	19
Total per taxa				740	928	3725	4259	75	918	289	1542	107	587

	Taxa	Hymenoptera				Diptera					
		Chalcidoidea		Cynipoidea		Syrphidae		Empididae		Total per plant species	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	.	1	.	0	.	0	.	3	.	9
	F. virginiana	5	41	4	3	0	0	0	11	16	67
	G. maculatum	3	5	0	3	0	0	0	1	6	16
	Aq. canadensis	0	0	0	0	0	0	0	0	0	0
	Z. aurea	1	85	0	15	0	0	0	60	3	194
	S. obovatus	1	8	0	1	5	1	0	2	11	28
	H. virginianum	3	15	0	1	0	0	0	6	4	32
	An. canadensis	2	57	0	7	1	1	0	59	4	248
	P. hirsutus	4	70	0	10	0	1	0	4	8	118
	A. atropurpurea	.	261	.	22	.	0	.	96	.	469
	H. maximum	52	38	45	12	13	3	23	4	153	94
	H. americana	0	5	0	0	1	0	0	0	1	7
	C. lanceolata	68	48	0	2	2	12	2	43	133	328
Mid Season	*V. faba*	38	20	3	2	1	4	11	91	158	267
	P. fruticosa	160	77	8	16	1	16	1	30	378	410
	A. cannabinum	3	126	0	25	0	7	0	184	4	464
	C. americana	.	7	.	2	.	5	.	3	.	27
	A. tuberosa	0	7	0	0	0	1	0	10	0	30
	R. setigera	.	15	.	5	.	6	.	15	.	97
	C. occidentalis	1	33	0	0	0	0	0	25	6	93
	C. sativum	57	74	8	2	86	33	6	3	354	149
	S. marilandica	9	29	0	0	5	5	6	41	37	94
	F. esculentum	67	57	10	13	12	7	55	8	481	215
	V. stricta	22	36	0	0	0	1	6	16	61	140
	A. incarnata	7	23	0	5	0	2	0	22	35	97
	V. virginicum	4	6	2	0	1	4	0	4	20	86
	R. pinnata	18	89	0	4	1	15	0	20	26	255
	A. canescens	.	1	.	1	.	1	.	0	.	13
	O. biennis	10	14	2	0	2	1	6	1	48	161
	A. cernuum	11	5	0	0	0	0	0	1	21	59
	D. canadense	0	8	0	2	0	1	1	2	8	23
	S. alba	.	45	.	12	.	2	.	10	.	311
Late season	*A. nepetoides*	34	70	1	0	0	2	24	30	127	285
	M. punctata	32	14	2	9	0	0	0	1	182	361
	V. missurica	103	377	0	4	0	2	0	9	128	491
	S. perfoliatum	172	280	0	1	0	2	2	3	238	635
	C. atriplicifolia	68	83	0	4	0	3	1	5	102	279
	E. perfoliatum	195	288	8	54	1	1	16	16	1219	2962
	L. siphilitica	117	94	5	7	0	0	1	3	308	379
	A. graveolens	230	37	2	1	2	0	6	0	328	95
	L. maritima	454	278	52	168	11	3	1	1	1119	818
	H. strumosus	192	229	1	0	1	1	8	2	284	401
	L. hirta	.	16	.	0	.	0	.	1	0	114
	L. aspera	4	29	0	0	0	1	0	0	13	103
	S. riddellii	184	146	4	17	2	0	4	3	576	514
	S. speciosa	91	93	2	6	2	0	0	1	252	411
	A. novae-angliae	96	104	2	5	2	0	2	4	699	419
	A. laevis	26	41	0	0	6	0	0	3	430	293
	Total per taxa	2544	3485	161	441	158	144	182	857	7981	13161

most common mid season in both years, and Bombyliidae, which, although present in low numbers, showed particular attraction in both years to *H. strumosus* in early September, and were also collected at *C. lanceolata* from 24 Aug to 8 Sept in 2004, which bloomed earlier in 2005 (Appendix D).

The most common natural enemy arthropods in grass controls were Chalcidoidea (especially Mymaridae), Nabidae, Thomisidae, Staphylinidae, and Cynipoidea. Mymaridae, Nabidae, and Staphylinidae were more common in grass than in flowering plant samples.

Plant Attractiveness to Herbivores

In both 2004 and 2005, plants that were more attractive to natural enemies were also generally more attractive to herbivorous insects (Figs. 8, 9, 10) although exceptions occur. For example, *H. maximum* was attractive to natural enemies but not herbivores in 2004 (Fig. 8a), while the opposite was true for *Heuchera americana* L. Species that attracted greater numbers of natural enemies than herbivores in early season 2004 included *F. virginiana*, *S. obovatus*, *H. maximum*, and *C. lanceolata*. In 2005, *A. canadensis* and *A. atropurpurea* were the species with greater numbers of natural enemies than herbivores (Fig. 8b).

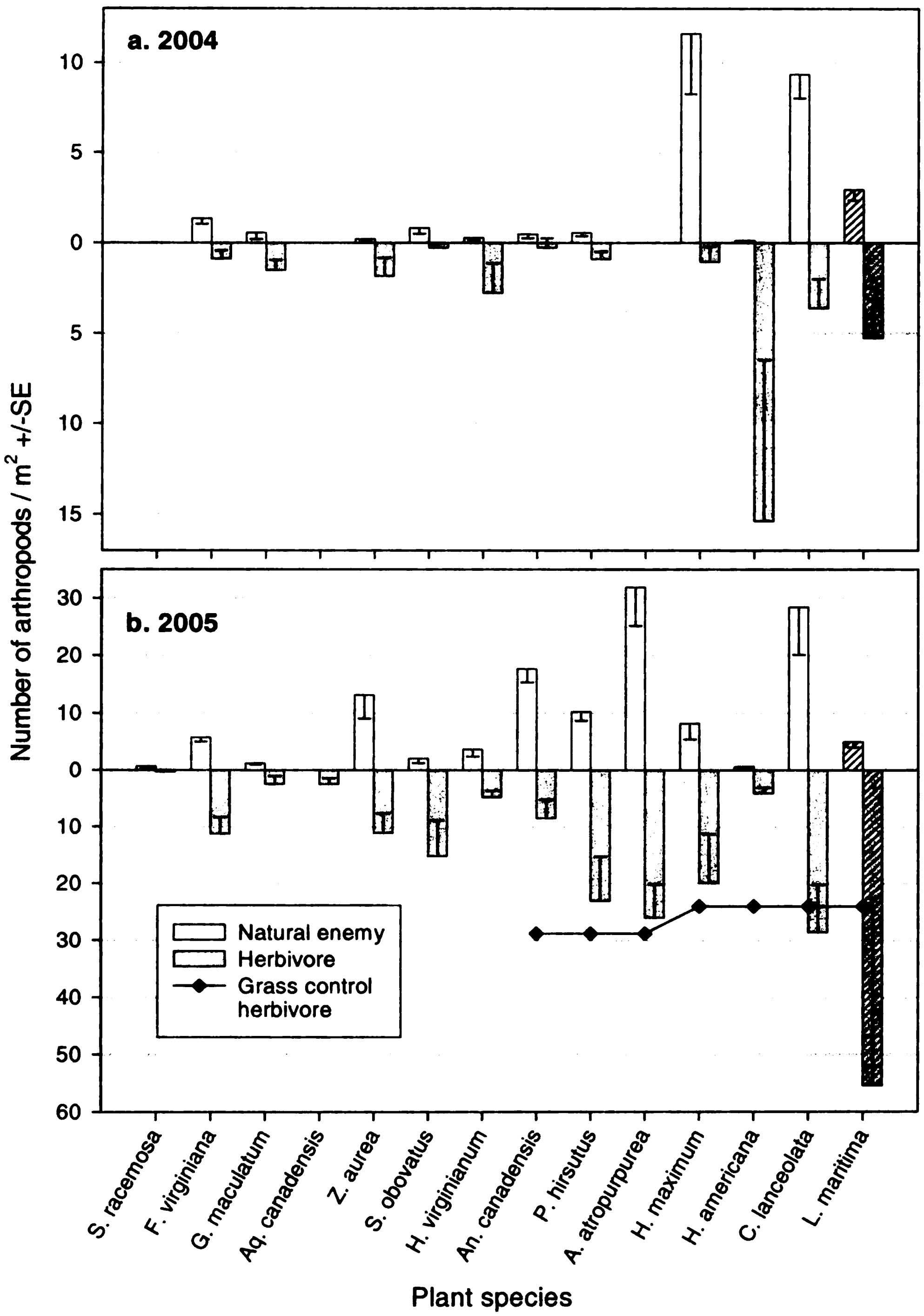


Figure 8. Early season mean number of natural enemies and herbivores collected per m^2 plot the week before, during, and after peak bloom in 2004 and 2005. Plants listed in bloom order. Grass control samples were collected in 2005 from 21 June onward. Cross-hatched bars are non-native plant species.

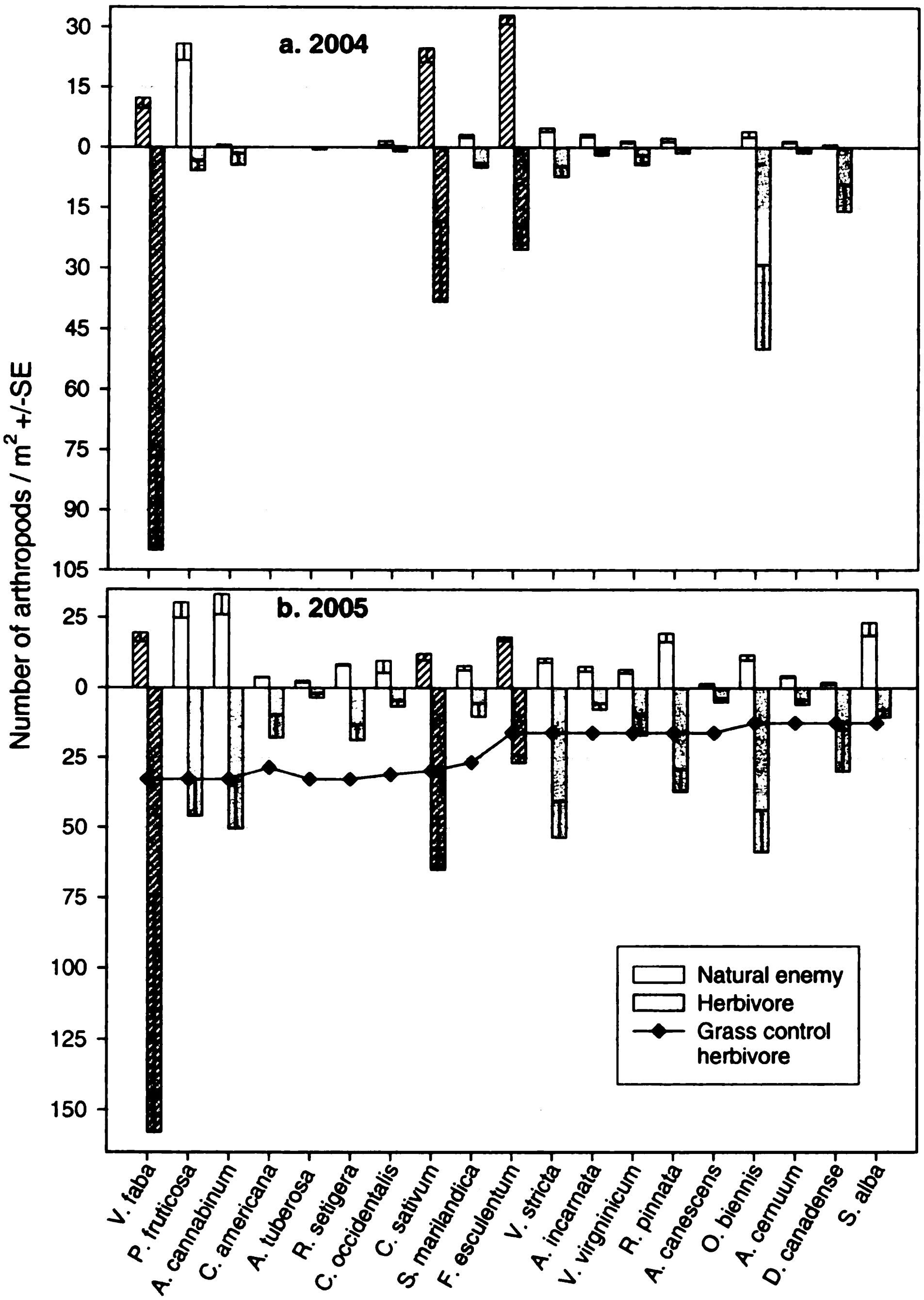


Figure 9. Mid season mean number of natural enemies and herbivores collected per m^2 plot the week before, during, and after peak bloom in 2004 and 2005. Plants listed in bloom order. Grass control samples were collected in 2005 only. Cross-hatched bars are non-native plant species.

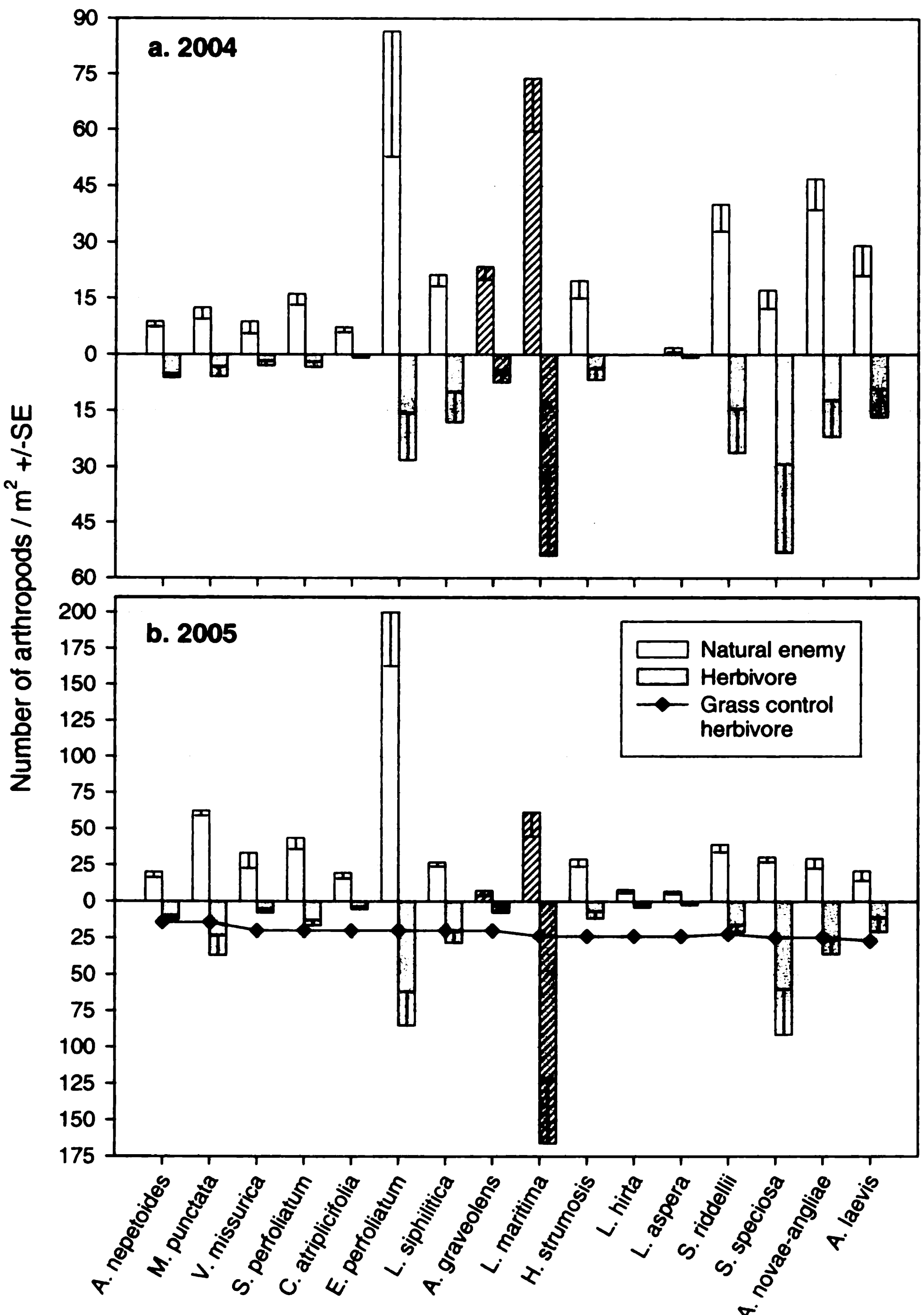


Figure 10. Late season mean number of natural enemies and herbivores collected per m^2 plot the week before, during, and after peak bloom in 2004 and 2005. Plants listed in bloom order. Grass control samples were collected in 2005 only. Cross-hatched bars are non-native plant species.

During mid season the non-native plants, notably *V. faba*, attracted more herbivores than the background grass controls. In 2004, the native *P. fruticosa* was the one plant notably more attractive to natural enemies than herbivores (Fig. 9a). In 2005, the most attractive mid season native plants all were more attractive to herbivores than natural enemies (Fig.9b). Specifically, *P. fruticosa*, *A. cannabinum*, *V. stricta*, *R. pinnata*, and *O. biennis* all had greater numbers of herbivores than natural enemies.

In the late season, herbivore numbers for many species were relatively less than in the early and mid season. In 2004, *E. perfoliatum*, *L. siphilitica*, *S. perfoliatum,* and *H. strumosus* all were more attractive to natural enemies than herbivores, while the opposite was true for *S. speciosa* (Fig. 10a). In 2005, *M. punctata*, *V. missurica*, *S. perfoliatum*, *C. atriplicifolia, E. perfoliatum, H. strumosus,* and *S. riddellii* all were more attractive to natural enemies than herbivores, while the opposite was true for *L. maritima* (Fig. 10b).

The most common herbivores collected in grass controls differed somewhat from those at flowering plants, and included (in order of decreasing total number) Lepidoptera, Cicadellidae, Chrysomelidae, Cercopidae, and Aphididae.

Herbivore Taxa

At the order level, the relative composition of the herbivore taxa were very similar in 2004 and 2005 (Fig. 11). Coleoptera were relatively more abundant in 2005, with a corresponding decrease in Diptera, Lepidoptera, Thysanoptera, and Hemiptera. Miridae were the most numerous herbivorous insect family in both years (Fig. 12), with many composed of *Lygus* sp. Cicadellidae and Aphididae were also common in both years, with aphid numbers increasing relative to Cicadellid numbers in 2005 (Fig. 12).

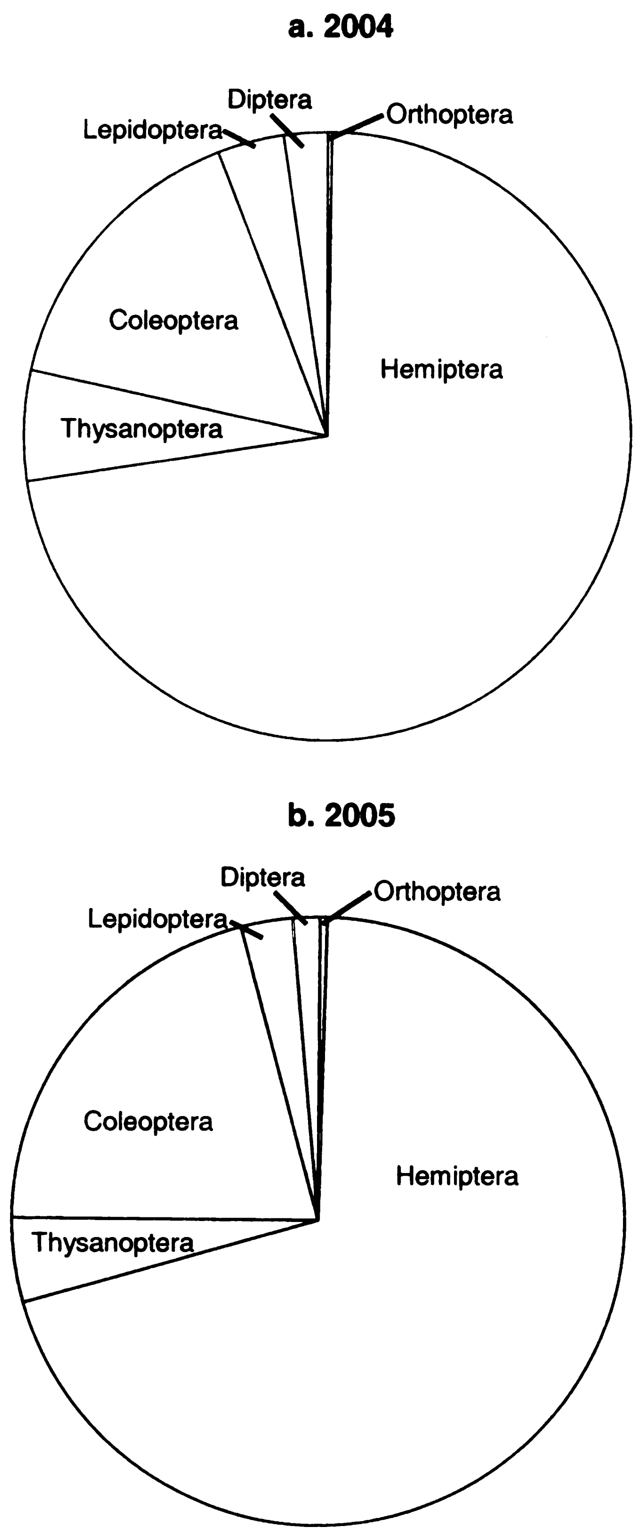


Figure 11. Proportion of total herbivore hexapods collected at flowering plants by order.

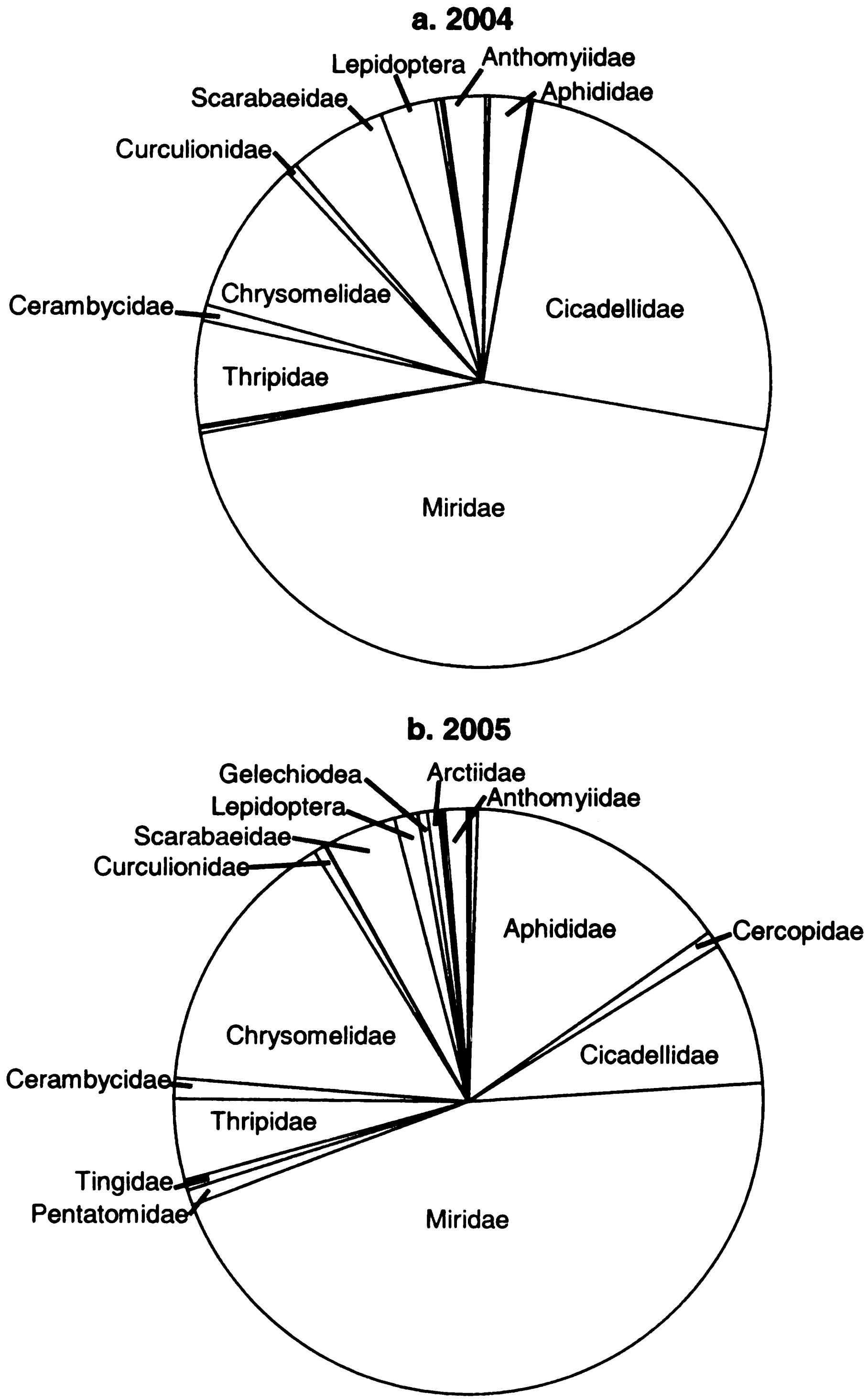


Figure 12. Proportion of total herbivore hexapods collected at flowering plants by family, except in the case of Lepidoptera, which are composed of larva and unidentifiable adults. Taxa comprising less than 0.5% of the total are not labeled.

The most numerous Coleopteran herbivores in both years were Chrysomelidae, and Cerambycidae and Curculionidae were collected in small numbers in both years (Fig. 12). Scarabaeidae were almost entirely composed of Japanese beetle (*Popillia japonica* Newman). Lepidopteran adults were not frequently collected in samples (Fig. 11). Only adult Lepidoptera of families known to be pest species on plants of agricultural importance were counted separately as herbivores. Larvae and any unidentifiable adults were identified to order, and are listed as Lepidoptera (Fig. 12, Table 8). Low numbers of dipteran herbivores were collected at plants (Fig. 11).

In both 2004 and 2005, more herbivorous insects were collected than natural enemy insects (Tables 7, 8). All herbivore taxa except Cicadellidae were more numerous in 2005 than in 2004 (Table 8). In 2005, Miridae, Cicadellidae, Aphididae, and Thripidae were collected at nearly all plant species (Table 8). Miridae were present through the entire growing season in both 2004 and 2005, with numbers increasing throughout the season. Mirids were most numerous in 2005 at *C. sativum, V. stricta, E. perfoliatum*, and *S. speciosa*. Cicadellid numbers were greatest at *V. faba* and *Oenothera biennis* L. in both 2004 and 2005, and aphids were very numerous at *V. faba* and *A. cannabinum* in 2005. Several Hemipterans that occurred in low numbers overall were found at several plant species in large numbers (Appendix E).

Table 8. Herbivore taxa collected at plants during full bloom period in 2004 and 2005. The eight most numerous groups of herbivores are shown here. Numbers represent the total of included herbivores collected in the number of samples listed. *2004 Thysanoptera include herbivorous and predatory species; 2005 numbers include only herbivorous Thysanoptera, many of which were Thripidae. "." indicates plant did not flower in 2004, so could not be sampled.

	Taxa	Number of samples		Hemiptera						Thysanoptera	
				Aphididae		Cicadellidae		Miridae		Thripidae*	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	0	15	.	0	.	1	.	3	.	0
	F. virginiana	12	15	0	3	6	68	1	41	1	25
	G. maculatum	13	15	1	3	1	4	5	12	6	12
	Aq. canadensis	10	15	0	9	0	1	0	18	0	6
	Z. aurea	14	15	0	30	0	10	0	47	0	64
	S. obovatus	15	14	0	50	9	13	2	59	9	85
	H. virginianum	15	10	0	1	2	3	3	23	0	2
	An. canadensis	15	15	2	4	6	17	2	39	3	24
	P. hirsutus	15	15	1	16	2	9	4	216	5	54
	A. atropurpurea	0	15	.	57	.	19	.	180	.	85
	H. maximum	15	12	1	33	4	1	12	48	10	101
	H. americana	7	15	0	14	0	0	0	4	2	6
	C. lanceolata	15	15	2	5	74	92	46	170	0	118
Mid Season	*V. faba*	14	15	15	1580	1234	562	94	189	37	3
	P. fruticosa	15	15	1	10	67	51	84	491	3	29
	A. cannabinum	6	15	26	660	0	2	0	17	0	9
	C. americana	0	8	.	2	.	7	.	118	.	9
	A. tuberosa	3	15	0	9	2	4	0	24	0	2
	R. setigera	0	13	.	4	.	27	.	117	.	25
	C. occidentalis	5	10	0	3	4	5	0	40	0	4
	C. sativum	15	14	40	70	93	66	188	756	228	10
	S. marilandica	15	15	2	3	35	28	18	109	17	4
	F. esculentum	15	15	6	13	25	17	165	289	12	12
	V. stricta	15	15	5	33	8	15	73	656	5	7
	A. incarnata	15	15	2	22	4	9	3	22	11	6
	V. virginicum	15	15	3	12	4	4	31	213	21	4
	R. pinnata	12	15	0	10	7	57	10	357	0	23
	A. canescens	0	15	.	15	.	18	.	18	.	1
	O. biennis	15	15	4	10	357	178	166	491	85	13
	A. cernuum	15	15	5	5	4	0	1	29	3	9
	D. canadense	15	15	9	121	16	5	8	11	6	40
	S. alba	0	15	.	12	.	7	.	16	.	6
Late season	*A. nepetoides*	15	15	1	2	20	11	42	96	9	10
	M. punctata	15	6	8	1	6	14	114	111	9	6
	V. missurica	15	15	1	1	22	14	47	40	2	2
	S. perfoliatum	15	15	0	1	14	9	19	84	5	4
	C. atriplicifolia	14	15	0	1	1	18	2	44	1	2
	E. perfoliatum	12	15	0	4	40	7	296	957	7	8
	L. siphilitica	15	15	5	4	10	6	204	349	3	3
	A. graveolens	15	15	61	3	7	11	63	86	1	2
	L. maritima	15	15	3	10	61	21	595	303	6	1
	H. strumosus	15	15	1	0	22	5	32	26	27	6
	L. hirta	0	15	.	0	.	11	.	14	.	4
	L. aspera	7	15	1	2	2	5	2	14	1	0
	S. riddellii	15	15	3	6	42	36	494	161	6	12
	S. speciosa	15	15	0	0	21	36	744	1101	0	2
	A. novae-angliae	15	15	1	2	89	29	394	383	7	7
	A. laevis	15	15	0	0	21	12	213	258	3	0
	Total per taxa			210	2856	2342	1545	4177	8850	551	867

		Coleoptera				Lepidoptera		Diptera			
	Taxa	Chrysomelidae		Scarabaeidae		Lepidoptera^		Anthomyiidae		Total per plant species	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	S. racemosa	.	0	.	0	.	0	.	0	.	4
	F. virginiana	0	2	0	0	2	1	1	3	11	143
	G. maculatum	0	1	1	0	0	0	5	1	19	33
	Aq. canadensis	0	0	0	0	0	0	0	0	0	34
	Z. aurea	0	2	0	0	0	0	3	4	3	157
	S. obovatus	1	0	0	0	1	0	3	1	25	208
	H. virginianum	0	0	0	0	0	4	37	12	42	45
	An. canadensis	2	0	0	0	0	2	1	13	16	99
	P. hirsutus	0	0	0	0	0	3	0	28	12	326
	A. atropurpurea	.	0	.	0	.	0	.	45	.	386
	H. maximum	0	0	0	0	143	1	60	73	230	257
	H. americana	0	0	0	0	0	0	0	1	2	25
	C. lanceolata	16	0	0	0	2	16	0	14	140	415
Mid Season	V. faba	5	0	9	1	1	2	1	17	1396	2354
	P. fruticosa	2	0	0	38	5	13	2	2	164	634
	A. cannabinum	0	19	1	17	0	16	0	11	27	751
	C. americana	.	0	.	0	.	0	.	5	.	141
	A. tuberosa	0	1	0	0	0	4	0	3	2	47
	R. setigera	.	2	.	41	.	3	.	2	.	221
	C. occidentalis	0	2	1	4	0	1	0	0	5	59
	C. sativum	5	1	9	0	3	1	6	2	572	906
	S. marilandica	0	4	0	2	0	1	1	0	73	151
	F. esculentum	4	5	165	50	0	1	0	0	377	387
	V. stricta	1	16	0	7	15	47	0	2	107	783
	A. incarnata	1	20	3	5	4	6	0	0	28	90
	V. virginicum	0	7	0	4	0	0	1	0	60	244
	R. pinnata	0	21	0	15	0	14	0	0	17	497
	A. canescens	.	2	.	14	.	1	.	0	.	69
	O. biennis	2	10	129	159	0	2	1	0	744	863
	A. cernuum	4	24	0	0	2	0	0	0	19	67
	D. canadense	5	5	191	258	3	2	0	0	238	442
	S. alba	.	10	.	72	.	0	.	0	.	123
Late season	A. nepetoides	6	33	4	17	12	4	0	0	94	173
	M. punctata	6	62	0	1	6	8	1	0	150	203
	V. missurica	2	28	0	13	2	3	0	0	76	101
	S. perfoliatum	10	108	0	21	2	0	0	0	50	227
	C. atriplicifolia	4	6	1	0	1	2	0	0	10	73
	E. perfoliatum	93	111	0	2	19	36	1	0	456	1125
	L. siphilitica	5	11	1	2	20	4	1	0	249	379
	A. graveolens	12	9	1	0	0	1	0	0	145	112
	L. maritima	347	2073	0	1	20	15	91	2	1123	2426
	H. strumosus	11	114	0	0	4	7	0	0	97	158
	L. hirta	.	4	.	26	.	1	.	0	.	60
	L. aspera	0	6	0	0	1	2	0	0	7	29
	S. riddellii	13	38	0	0	8	0	0	0	566	253
	S. speciosa	66	82	1	1	5	5	0	1	837	1228
	A. novae-angliae	78	39	1	5	5	17	2	0	577	482
	A. laevis	110	12	0	1	5	2	0	0	352	285
	Total per taxa	811	2890	518	777	291	248	218	242	9118	18275

The most common Thysanoptera were identified as herbivorous Thripidae, which were counted separately from predatory Aeolothripidae in 2005. Thripidae were most common in the early season, and especially numerous at *C. lanceolata* and *H. maximum* (Table 8). A large proportion of Chrysomelidae were collected at *L. maritima*; these were almost entirely *Phyllotreta striolata* F. and *Phyllotreta* spp. (Table 8). Japanese beetle (Coleoptera: Scarabaeidae) were present from July through August in both years and most numerous at *Desmodium canadense* (L.) DC., *O. biennis*, *F. esculentum*, and *Rosa setigera* Michx. Anthomyiid numbers were highest in June, and a large number were collected at *L. maritima* in 2004 (Table 8).

DISCUSSION

From the full set of 48 flower species, floral resources were available to insects from 1 May through 30 September 2004 and 4 May through 4 October 2005. The overlap in plant phenology suggests that a subset of the most attractive species can be selected for further testing for insect habitat manipulation. The native plants tested showed differing attractiveness to natural enemies, which has also been found with non-native plants in other studies (Baggen et al. 1999, Colley and Luna 2000).

Three widely used non-natives (*L. maritima, F. esculentum*, and *V. faba*) were very attractive to natural enemies, indicating that recommendations for their use are well founded. However, many Michigan native plants were as, or more, attractive as these frequently recommended non-natives. The native perennials became more attractive to natural enemies as they matured and were more likely to attract more natural enemies than non-native annuals in year two. This suggests that as perennial natives establish they have potential to be more attractive to natural enemies than previously tested annuals for habitat management (Orr and Pleasants 1996, Nentwig et al. 1998). In addition, the perennial plants tested have the potential to provide plant resources over a greater part of the growing season than annuals. Perennial natives began blooming in early May; the attractive plant *F. virginiana* bloomed in mid-May, followed by *Z. aurea* in early June. Both provide floral resources before seeded annual plants bloomed in our study, and *F. virginiana* provided floral resources before the danger of frost damage to annual plugs had passed. Other perennial species also bloomed through September in both 2004 and 2005, during which time the only blooming non-native was *L. maritima*.

In addition to nectar and pollen, perennial plants may provide a moderated microclimate and shelter from disturbance in highly disturbed agricultural areas, characteristics which have been shown to increase natural enemy effectiveness (Dyer and Landis 1996). Rebek et al. (2005) found that plants with flowers intact did not attract significantly different numbers of natural enemies than plants with flowers excised. Likewise, we collected natural enemies in grass alone, indicating that it may provide some environmental benefit, such as moderated microclimate, shelter, and alternate prey. However, I did have a set of native plants that were more attractive to natural enemies than the background grass matrix, and which could provide additional sugar and protein sources to natural enemies. I did not see alternate prey in large numbers on any plants with the exception of *V. faba*, which was infested with aphids in 2005, leading to a high density of lady beetle larvae, pupae, and adults on this species.

Considering bloom period and attractiveness to natural enemies, I propose a set of plants most suitable for further study (Table 9). In agricultural settings, these plants could be established in strips in or along crop fields to provide nectar and pollen to natural enemies and evaluate the effect of strips on crop yield. In addition to attractiveness to natural enemies, the number and type of herbivore collected at a plant must be evaluated. If an herbivore occurs in higher numbers at a flowering plant than in grass alone, its pest potential in crops surrounding the flowering plant strip must be considered (Winkler 2005). For example, Japanese beetle attraction by resource plants may be of great concern in fruit crops. The native *O. biennis* and non-native *F. esculentum* attracted large numbers of Japanese beetle in both 2004 and 2005. The presence of *Lygus* and Cicadellidae will be of concern to farmers of crops susceptible to direct damage or viruses transmitted by these insects. The natives *V. stricta* and *R. pinnata* attracted large numbers of *Lygus* in 2005. Surprisingly, samples from the previously recommended non-natives *C. sativum* and *F. esculentum* also contained *Lygus* in relatively large numbers. In addition, the Chrysomelidae common at *L. maritima* included *Phyllotreta striolata* (F.), a known herbivore of cabbage and mustard, and *Phyllotreta* spp., a potential herbivore on brassicas. This indicates that frequently recommended non-native *L. maritima* attracts a known canola pest and potential pest on other Brassicas, which may increase herbivory if planted near brassicaceous crops (Burgess 1981, Lamb and Palaniswamy 1990).

Table 9. Michigan native plant species best suited to attract natural enemy insects based on both 2004 and 2005 data. Plants listed in 2005 bloom order. 2005 bloom period is indicated by letters: e = early (May-June), m = middle (July-mid-August), and l = late season (mid-August on). Tolerance indicates plant suitable for wet-dry environments.

Bloom	2005 Peak Bloom Date	Common Name	Genus and species	Plant Type	Tolerance
e	24 May	Wild strawberry	*Fragaria virginiana* Duchesne[1]	Forb	Average
e	6 June	Golden alexanders	*Zizia aurea* (L.) Koch	Forb	Wet
e	14 June	Canada anemone	*Anemone canadensis* L.[1]	Forb	Average
e	14 June	Penstemon	*Penstemon hirsutus* (L.) Willd.	Forb	Average
e	14 June	Angelica	*Angelica atropurpurea* L.[1]	Forb	Average
e	21 June	Cow parsnip	*Heracleum maximum* Bartr.[1]	Forb	Average
e	21 June	Sand coreopsis	*Coreopsis lanceolata* L.	Forb	Dry
m	12 July	Shrubby cinquefoil	*Potentilla fruticosa* auct. non L.	Shrub	Average
m	12 July	Indian hemp	*Apocynum cannabinum* L.[2]	Forb	Average
m	2 Aug.	Hoary vervain	*Verbena stricta* Vent.	Forb	Dry
m	2 Aug.	Swamp milkweed	*Asclepias incarnata* L.	Forb	Wet
m	2 Aug.	Yellow coneflower	*Ratibida pinnata* (Vent.) Barnh.	Forb	Average
m	9 Aug.	Evening primrose	*Oenothera biennis* L.[3]	Forb	Average
m	9 Aug.	Meadowsweet	*Spiraea alba* Duroi	Shrub	Wet
l	16 Aug.	Yellow giant hyssop	*Agastache nepetoides* (L.) Kuntze	Forb	Average
l	16 Aug	Horsemint	*Monarda punctata* L.	Forb	Dry
l	23 Aug.	Ironweed	*Vernonia missurica* Raf.	Forb	Average
l	23 Aug.	Cup plant	*Silphium perfoliatum* L.	Forb	Average
l	23 Aug.	Boneset	*Eupatorium perfoliatum* L.	Forb	Wet
l	23 Aug.	Blue lobelia	*Lobelia siphilitica* L.	Forb	Average
l	30 Aug.	Pale-leaved sunflower	*Helianthus strumosus* L.	Forb	Dry
l	13 Sept.	Riddell's goldenrod	*Solidago riddellii* Frank ex Riddell[4]	Forb	Wet
l	20 Sept.	New England aster	*Aster novae-angliae* L.	Forb	Average
l	27 Sept.	Smooth aster	*Aster laevis* L.	Forb	Average

[1]Although attractive to natural enemies, these species are difficult to establish from seed.
[2]*Apocynum cannabinum* is considered an agricultural weed, and should be used with caution.
[3]*Oenothera biennis* attracted large numbers of Japanese beetle in both 2004 and 2005.
[4]*Solidago speciosa* may be substituted in dry environments but was slightly less attractive to natural enemies and attracted more pests.

In native prairie and savanna habitats, grasses were a component of the plant matrix and may be vital components of habitat strips. Although not tested in our study for attractiveness to natural enemies, I planted *Panicum virganum* L., *Elymus canadensis* L., and *Schizachyrium scoparium* (Michx.) Nash to test survivorship and growth in our field plots. The grasses survived and filled the 1 m^2 test plots after 2 years of growth. These species, as well as *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash, are all relatively easy to establish native grasses for potential inclusion with forbs in a planted strip. In addition to providing structural support, grasses have been shown to support ground beetle populations in previous studies (Varchola and Dunn 1999, Lee et al. 2001, Varchola and Dunn 2001). We collected higher numbers of Nabidae and Staphylinidae in the non-native grass control than in many flowering plant samples, indicating that these groups may also benefit from the inclusion of grass in plant mixtures.

The natural enemy groups most frequently collected at plants for habitat management in this study could impact a variety of crop pest populations. The most common natural enemy, *Orius insidiosus*, has been shown to be a predator on a variety of small, soft-bodied insects, including: soybean aphid (Rutledge and O'Neil 2005), spiraea aphid (Brown 2004), cotton aphid (Rondon et al. 2004), sweet potato whitefly (Hagler et al. 2004), cotton bollworm eggs (Parajulee et al. 2006), western flower thrips (Xu et al. 2006), two-spotted spider mite (Rondon et al. 2004, Xu et al. 2006), and striped and spotted cucumber beetle (Platt et al. 1999). The two Cantharidae species collected were *Chauliognathus marginatus* Fabricius and *C. pennsylvanicus* Deg. In their larval stage, both species are voracious predators on soil-dwelling soft-bodied insects and have been seen feeding on adult Chrysomelidae and cicindelinae carabids (Balduf 1935). Both species feed exclusively on pollen and nectar as adults (Ramsdale 2001). The coccinellid species collected in this study included *Harmonia axyridis* Pallas, *Coccinella septempunctata* L., *Coleomegilla maculata* DeG., and *Hippodamia variegata* Goeze. All of these species are known predators on aphids and other small soft-bodied insects as larvae and adults (Hoffmann and Frodsham 1993). The most numerous Chalcidoidea collected at resource plants was Encrytidae C*opidosoma*. This genus is known to contain polyembryonic parasitoids of Lepidoptera, and *C. floridanum* is a known parasitoid of cabbage looper (*Pieris rapae* L.). The Miridae collected were *Plagiognathus politus* Uhler and *Chlamydatus associatus* Uhler; both species were seen preying on soybean aphid in Michigan (Alejandro Costamanga, pers. comm.. 2005). In addition, *P. politus* was documented as a predator on the Chrysomelid *Galerucella calamariensis* L. (Hunt-Joshi et al. 2005). Although *G. calamariensis* is an herbivore for weed biocontrol, *P. politus* may feed on other Chrysomelids that are crop pests. The natural enemy community at these native plant species, therefore, has potential to control a range of pest species, including a variety of Aphididae, thrips, herbivorous mites, Lepidoptera and Chrysomelidae.

In 2004, arthropod sampling time was limited to 30s/1 m^2 plot, while in 2005 sampling was continued in each plot until all flowers were sampled. Sample duration in 79% percent of samples taken in 2005, however, was less than 30s. Most samples of greater than 30s were taken from August on. While the increased sampling time was unlikely to affect results from small plants with few flowers, it may have increased the number of natural enemies at the largest, late blooming plants in late season 2005.

Therefore, it is likely that results from 2005 indicate closer to a true estimate of insect numbers at flowers in late 2005 than they would have had we limited sampling to 30s.

Arthropods in this study were collected via vacuum sampling, which may have biased samples towards more sedentary groups, such as arachnids. In contrast, the vacuum sampling method may have been less likely to collect more vagile natural enemy groups such as Syrphidae, as well as herbivore groups such as Lepidoptera. Rebek et al. (2005) performed arthropod sampling with both sticky cards and vacuum sampling, and observed lower numbers of arachnids and higher numbers of syrphids in sticky card samples than in vacuum samples.

In this study, I did not assess whether natural enemy insects were feeding on plant nectar and pollen or using the plant for other resources, such as alternate prey or favorable microclimate. Future research could determine which natural enemy and herbivore species benefit from plant resources provided by each plant species. Additional future questions to be addressed are how to select plants for soil moisture, strip planting, and how to manage for weed control and plant succession over time.

Out of practicality, this study was limited to 43 of nearly 1000 flowering forbs and shrubs native to Michigan (Voss 1985). Although we selected from species that were readily available, as well as plants with a variety of bloom periods, statures, and plant families, other plants such as *Rudbeckia hirta* L. and *Eupatorium maculatus* L. are readily available and similar to other species I tested. These species would be good candidates for broadening future native plant selection for habitat management.

The establishment time of perennial plants greatly increases time before flowering and therefore time before insect abundance at plants can be measured. Although perennials outperformed annual non-natives that were previously recommended for habitat management in their third growing season, the perennial planting approach requires project duration of multiple years. This difficulty is likely one if the primary factors that perennial plants have not been frequently considered in habitat management studies in the past.

Overall, the frequently recommended non-native plants used in this study were highly attractive to natural enemies, but our results indicate that equal or greater numbers of natural enemies are found at some native plant species compared with the non-native plants. Not only did plants differ in the total number and type of natural enemies attracted to them, they also differed in the number and type of herbivore attracted to them. These differences indicate the potential to grow specific plant species in agriculture to attract natural enemies of the pests that are most common in surrounding crops, while not providing resources to crop pests themselves. The process of screening individual plant species for their attractiveness to natural enemies allows rapid plant screening to maximize resource plant effectiveness before in-field trials with multiple species are performed. With this information a community of native plant species can be developed to attract insects across taxa and provide nectar and pollen throughout the season.

Results from plant screening as outlined here, however, have limited usefulness in areas with different native plant communities than those in Michigan prairie and savanna habitats. Therefore, a consideration of the plant characteristics of the most attractive native plants could streamline future selection of both Michigan native plants and plants native to other locales (Chapter 3).

Chapter 3

PLANT CHARACTERISTICS ASSOCIATED WITH NATURAL ENEMY ATTRACTIVENESS TO MICHIGAN NATIVE PLANTS

Anna Katherine Fiedler

ABSTRACT

Insects are known to respond to plant characteristics in their search for plant-provided resources. I used 43 native Michigan and 5 non-native plant species to test whether the number and type of natural enemies and herbivores attracted to a plant were predicted by plant characteristics including; floral area per m^2 plot, week of peak bloom, maximum flower height, hue, chroma, corolla depth, and corolla width. Similar patterns between natural enemy abundance and plant characteristics were found in both the 2004 and 2005 growing seasons. A multiple regression on log transformed natural enemy numbers versus plant characteristics indicated a positive linear relationship between week and number of natural enemies that explained the largest proportion of variation in 2005 (R^2=0.30). In 2005, natural enemy abundance also increased significantly with floral area (partial R^2=0.13) and floral area^2 (partial R^2=0.07). A comparison of native and non-native species in 2005 indicated that natural enemies respond more strongly to floral area at non-native than native plants. The first principal component from a PCA of plant characteristics explained 30.1% of plant characteristic variability. A simple regression using PCA factor-1 showed an increase in natural enemy number with increasing floral area, week of peak bloom, and maximum flower height and decreasing corolla width (R^2=0.37). Herbivore abundance also increased significantly with PCA factor-1, but the relationship was much weaker (R^2=0.090). Results indicate that consideration of floral area for a given week of peak bloom has potential to streamline plant selection for habitat management and increase the attractiveness of habitat management plantings to natural enemies.

INTRODUCTION

One branch of conservation biological control, habitat management, focuses on increasing natural enemy populations by providing them with plant resources (Landis et al. 2000). Plant-provided resources may include alternate hosts (DeBach and Rosen 1991, Menalled et al. 1999, van Emden 2003), shelter (Powell 1986, Gurr et al. 1998, Nentwig et al. 1998), and non-host food (Baggen et al. 1999, Wilkinson and Landis 2004). Natural enemies may benefit from access to plant-provided nectar and pollen. Adult parasitoids show increased longevity and/or fecundity with access to nectar or sugars (Dyer and Landis 1996, McDougall and Mills 1997, Baggen et al. 1999, Wäckers 1999, Jacob and Evans 2000, Romeis and Wackers 2002). Predators use prey resources as adults but may show increased longevity or fecundity if their diet is supplemented with plant resources, including phloem fluids (Legaspi and O'Neil 1993, Eubanks and Denno 1999) and pollen (Harmon et al. 2000). These resources are often scarce in agricultural systems, but may be provided by flowering plants as part of cropping systems.

A relatively small group of annual plants has been widely tested and recommended to provide plant resources for habitat management. These include: alyssum (*Lobularia maritima* (L.) Desv.), buckwheat (*Fagopyron esculentum* Moench), coriander (*Coriandrum sativum* L.), dill (*Anethum graveolens* L.), and faba bean (*Vicia faba* L.). These plants are easily established in new locations and their bloom period can be controlled by altering planting time. However, with few exceptions they are not native to the areas in which they are currently used. In contrast, native plants may have advantages over exotics in that they are adapted to the local environment, increase native biodiversity, and may help restore degraded habitats. Nevertheless, recommendations for use of native plants in habitat management requires an extensive screening process (see Chapter 2) to determine which native plants best attract natural enemies in specific habitats. Armed with available information on natural enemy attractiveness to 43 native and five non-native species, I evaluated patterns in natural enemy response to various plant characteristics. If present, strongly predictive characters could inform plant selection in other regions and help maximize the effectiveness of habitat management for biological control.

As insects search for resources they respond to a set of sensory stimuli from their external environment. These stimuli may be chemosensory (tactile, gustatory and air-mediated) or visual (Bell 1990). Herbivore feeding may induce a variety of plant defenses, including the release of volatile chemicals that natural enemies use as cues for host or prey location (Takabayashi and Dicke 1996, Turlings and Wackers 2004). While natural enemies have been found to respond to plant allelochemicals to locate hosts (Vinson 1976, van Alphen and Vet 1986, Barbosa and Benrey 1998, Barbosa and Wratten 1998), little research has been performed on their use of plant-produced allelochemicals to locate plant food sources. However, some parasitoids do show preference for odors associated with either plant food or host, depending on their physiological needs (Lewis and Takasu 1990, Wäckers 1994). Natural enemies may use similar searching strategies to locate plant resources as to locate insect prey or hosts. Insect-pollinated flowers, unlike insect prey and hosts, are structured to be highly detectable (Wäckers 1994), so that they are easily found and pollinated by insects. Therefore, natural enemies may rely more on visual cues for location of nectar and pollen than they do for location of insect prey or hosts.

Various visual signals indicate the presence of plant resources for insects. These include: plant height (Coll and Bottrell 1996, Wratten et al. 2003), flower size (Conner and Rush 1996, Hegland and Totland 2005), number of open flowers (Conner and Rush 1996, Hegland and Totland 2005), and flower color (Wardle 1990, Chittka and Menzel 1992, McCall and Primack 1992, Wäckers 1994, Waser et al. 1996, Begum et al. 2004). After an insect locates a floral resource, resource accessibility may be limited by flower morphology; corolla depth and width either prevent or allow insect access to nectar (Jervis et al. 1993, Patt et al. 1997, Fenster et al. 2004).

The relationship between suites of floral characteristics and insects is best known for pollinators. Insects and flowers have relationships that are considered to be specialized, but recently a greater understanding of the relationships between flowers and insects indicates that several pollinator groups may visit an individual plant species, and in turn insect species often visit more than one plant species (Waser et al. 1996, Memmott 1999, Fenster et al. 2004). Plant species also have been shown to vary significantly in their attractiveness to pollinators (Memmott 1999). Insect groups may be attracted to specific colors: flies and beetles to white, large bees and butterflies to purple, pink, and blue flowers (Waser et al. 1996). Insect color perception ranges from wavelengths of 300-650 nm (ultraviolet to yellow-orange). Peaks of receptivity occur in the ultraviolet, green-blue, and yellow ranges (Kevan and Baker 1984, Endler 1990, Chittka and Menzel 1992, Kevan et al. 1996). Many hymenopteran pollinators have been tested for their response to visual cues in the form of hue (what humans perceive as color), brightness, and intensity (saturation or purity of color). Hymenoptera respond to wavelength and in many cases cannot distinguish between colors of different brightness and intensity (Lunau 1990, Wardle 1990, Chittka et al. 1992, Gumbert 2000). Pollinator numbers increase with flower number (Conner and Rush 1996, Ohashi and Yahara 1998), individual flower size (McCall and Primack 1992, Conner and Rush 1996, Hegland and Totland 2005), and visual display (Thomson 1981, Ohashi and Yahara 1998, Hegland and Totland 2005). In addition to floral characteristics, pollinators respond to abiotic conditions (Kevan and Baker 1984). These include weather, time of day and temperature (McCall and Primack 1992), as well as season (McCall and Primack 1992, Totland 1993, Hegland and Totland 2005).

The response of natural enemies to flowers is not as well understood as that for pollinators, but several studies have been performed on individual species, primarily on their response to color. The predators *Chrysoperla carnea* (Neuroptera: Chrosopidae) and *Coccinella septempunctata* (Coleoptera: Coccinellidae) show greater responses to yellow traps versus red, orange, black, white, blue, or green, while *Hippodamia convergens* (Coleoptera: Coccinellidae) does not show an affinity for any of these colors (Maredia et al. 1992). The parasitoid wasp *Nasonia vitripennis* (Hymenoptera: Pteromalidae) is able to distinguish between yellow and blue and prefers yellow over blue when yellow is associated with an inconsistent host or sugar reward, but the reverse is not the case (Oliai and King 2000). The parasitoid *Cotesia rubecula* (Hymenoptera: Braconidae) is more attracted to flower odor than leaf odor and when offered both a yellow target and a leaf, lands preferentially on the yellow target (Wäckers 1994). The response of several natural enemy species to color is known but the natural enemy response to plant characteristic groupings is not.

The objectives of the current study were to 1) determine whether natural enemy abundance at flowers was associated with floral characteristics including: peak bloom week, floral area, maximum flower height, chroma, hue, and corolla depth and width, 2) determine whether the response changes as perennial plants mature, 3) assess whether natural enemy taxa respond differentially to floral characteristics, and 4) assess whether natural enemies respond differently to floral characteristics of native perennial than non-native annual plants.

METHODS

I selected 43 Michigan native plant species for study in consultation with a Michigan native plant nursery owner (William Schneider, pers. comm.). Five plant species not native to Michigan that are frequently recommended to enhance natural enemy insects were also included in this study for comparison (Table 10, see Chapter 2).

STUDY SITE

The study site was an agricultural field on the Michigan State University Entomology Farm in Ingham County, MI that was previously farmed in a corn-soybean rotation. The soil type was a Marlette fine sandy loam (Soil Conservation Service 1979). The experiment was conducted in a randomized complete block design with one replicate of each plant species in each of 5 blocks. Plants were established in 1 m^2 plots spaced 6 m apart with mown orchardgrass (*Dactylis glomerata* L.) between plots. Rooted native plant plugs (Wildtype Design Native Plants & Seeds, Ltd., Mason MI) were planted in September 2003. In May of 2004 and 2005, non-native annual species were seeded or planted for comparison to native species (Chapter 2).

Table 10. Plant species established at the MSU Entomology Research Farm, E. Lansing, MI. Plant code is the shortened plant name that appears in figures. All plants are native Michigan plants except the last five that are annuals.

Family	Genus and species	Plant Code	Common Name	Plant Type
Native species				
Laminaceae	*Agastache nepetoides*	1	yellow giant hyssop	forb
Liliaceae	*Allium cernuum*	2	nodding wild onion	forb
Fabaceae	*Amorpha canescens*	3	leadplant	shrub
Ranunculaceae	*Anemone canadensis*	4	Canada anemone	forb
Apiaceae	*Angelica atropurpurea*	5	angelica	forb
Apocynaceae	*Apocynum cannabinum*	6	Indian hemp	forb
Ranunculaceae	*Aquilegia canadensis*	7	columbine	forb
Asclepiadaceae	*Asclepias incarnata*	8	swamp milkweed	forb
Asclepiadaceae	*Asclepias tuberosa*	9	butterfly weed	forb
Asteraceae	*Aster laevis*	10	smooth aster	forb
Asteraceae	*Aster novae-angliae*	11/12*	New England aster	forb
Asteraceae	*Cacalia atriplicifolia*	13	pale Indian plantain	forb
Rhamnaceae	*Ceanothus americanus*	14	New Jersey tea	shrub
Rubiaceae	*Cephalanthus occidentalis*	15	buttonbush	shrub
Asteraceae	*Coreopsis lanceolata*	16	sand coreopsis	forb
Fabaceae	*Desmodium canadense*	17	showy tick trefoil	forb
Asteraceae	*Eupatorium perfoliatum*	18	boneset	forb
Rosaceae	*Fragaria virginiana*	19	wild strawberry	forb
Geraniaceae	*Geranium maculatum*	20	wild geranium	forb
Asteraceae	*Helianthus strumosis*	21	pale-leaved sunflower	forb
Apiaceae	*Heracleum maximum*	22	cow parsnip	forb
Saxifragaceae	*Heuchera americana*	23	alum root	forb
Hydrophyllaceae	*Hydrophyllum virginianum*	24	Virginia waterleaf	forb
Fabaceae	*Lespedeza hirta*	25	hairy bush-clover	forb
Asteraceae	*Liatris aspera*	26	rough blazing star	forb
Campanulaceae	*Lobelia siphilitica*	27	blue lobelia	forb
Lamiaceae	*Monarda punctata*	28	horsemint	forb
Onagraceae	*Oenothera biennis*	29	evening primrose	forb
Scrophulariaceae	*Penstemon hirsutus*	30	penstemon	forb
Rosaceae	*Potentilla fruticosa*	31	shrubby cinquefoil	shrub
Asteraceae	*Ratibida pinnata*	32	yellow coneflower	forb
Rosaceae	*Rosa setigera*	33	Michigan rose	shrub
Caprifolaceae	*Sambucus racemosa*	34	red-berried elder	shrub
Scrophulariaceae	*Scrophularia marilandica*	35	late figwort	forb
Asteraceae	*Senecio obovatus*	36	round-leaved ragwort	forb
Asteraceae	*Silphium perfoliatum*	37	cup plant	forb
Asteraceae	*Solidago riddellii*	38	Riddell's goldenrod	forb
Asteraceae	*Solidago speciosa*	39	showy goldenrod	forb
Rosaceae	*Spiraea alba*	40	meadowsweet	shrub
Verbenaceae	*Verbena stricta*	41	hoary vervain	forb
Asteraceae	*Vernonia missurica*	42	ironweed	forb

Table 10. Cont'd.

Family	Genus and species	Plant Code	Common Name	Plant Type
Scrophulariaceae	*Veronicastrum virginicum*	43	Culver's-Root	forb
Apiaceae	*Zizia aurea*	44	golden alexanders	forb
Non-native species				
Apiaceae	*Anethum graveolens*	45	dill	annual
Apiaceae	*Coriandrum sativum*	46	coriander/ cilantro	annual
Polygonaceae	*Fagopyrum esculentum*	47	buckwheat	annual
Brassicaceae	*Lobularia maritima*	48	alyssum	annual
Fabaceae	*Vicia (vigna) faba*	49	faba (fava) bean	annual

*Aster novae-angliae had white and purple color morphs, considered separately in analysis. Total N=49 although there are 48 species.

ARTHROPOD COLLECTION

From May through September 2004 and 2005, arthropods were sampled weekly from flowering plants between the hours of 0930-1330 EST on calm, sunny days. Statistical analyses were conducted on insect samples collected the week before, week of, and week after the peak bloom date for each plant species. This three week period was chosen to reflect the plants' general attractiveness over time and to reduce the influence of week-to-week variability in insect catch due to plant phenology or weather. Insects were collected into a fine mesh white no-see-um netting bag (Kaplan Simon Co., Braintree, MA) placed over the intake on a gas-powered leaf blower that was modified into a vacuum (Stihl BG55 Norfolk, VA). Each plot was vacuumed until all flowers were sampled (up to 30 sec in 2004). Insects were frozen, separated into natural enemies, herbivores, and "other," identified to family, and counted. Insects from any parasitic or predaceous family, or genus or species within a family known to be parasitic or predaceous, were included as natural enemies (see Chapter 2). Insects were counted as herbivores if they were a member of a family known to be broadly herbivorous (see Chapter 2). Attractiveness here is based on the number of natural enemy arthropods collected per sample; therefore, it includes both arthropod attraction to the plant and subsequent retention on it.

TAXONOMY

Plant nomenclature follows Voss (1972, 1985, 1996), plant taxonomy follows Judd (2002), and insect taxonomic classification follows Triplehorn and Johnson (2005).

PLANT CHARACTERISTICS

I measured maximum flowering height during bloom period. Three flowering plants per plot were randomly selected and measured to the nearest 0.5 cm at the highest part of the tallest open flower. To estimate flower apparency, or the area within the plot composed of flowers when a plant was in bloom, we counted the number of open flowers per plot weekly. For plant species with flowers containing multiple florets, natural flower clusters were counted and measured. We took digital photos of ten representative flowers or flower clusters per species with a ruler included for reference in each photo (Coolpix 4800, Nikon, Melville NY). Floral area was selected using the magic wand tool and filled in with white (Knoll 2000, Adobe photoshop 6.0). Images were then converted to black and white and resized to a lower resolution. We calculated floral area using ScionImage freeware (Alpha 4.0.3.2, www.scioncorp.com). The average area per flower was then multiplied by the number of flowers or clusters to determine total floral area per plot.

Flower color was measured in all cases on young open flowers with intact stamens. Color was measured in both 2004 and 2005 with an S2000 fiber optic spectrophotometer (Ocean Optics, Inc., Dunedin Forida. PX2 pulsed xenon light source

23 mm from sample platform) to determine floral reflectance from wavelengths of 400-700 nanometers. Five flowers of each species were clipped, placed on ice, and percent reflectance of flowering material was measured within five hours of collection. In most cases, the top, center of a petal (or ray flower) was measured. If an individual floret was too small to fill the sample area (as in *Sambucus racemosa*), a flower cluster was placed in the sample area and measured. If a flower had petals or ray flowers too narrow to fill the opening, (as in *Aster laevis*) several were aligned across the sample area. Chroma, the intensity of color, and hue, a measurement of color, were calculated using a formula modified from Endler (1990), in which numbers for chroma indicate the percent color saturation and numbers for hue indicate the color, measured on a 360° scale, with red at 0°, yellow at 90°, green at 180°, and blue at 270°.

Floral morphology was measured on young, open flowers with intact stamens using a Spot Imaging System (v.3.5.9 Diagnostic Instruments, Inc., Sterling Heights, Michigan) attached to an Olympus SZX12 stereoscope. Corolla depth and width were measured to the nearest 0.01cm for five flowers per species. For species with florets, one floret was measured; in Asteraceae, one young, open disc flower was measured per flower head. Width was measured at the point where the corolla fused and depth was measured from that point to the floral nectaries. In species with nectaries located at the point where petals attach to the gynoecium, corolla depth was measured as zero. A set of species, *Amorpha canescens*, *Desmodium canadense*, *Lespedeza hirta*, *Vicia faba*, *Lobelia siphilitica*, *Asclepias incarnata* and *Asclepias tuberosa*, had neither a completely open floral structure nor fused corollas. In these cases corolla width and depth measurements as described above would not have related to functional nectar accessibility for insects. Therefore, a functional corolla width of a slit between flower petals and functional corolla depth from this slit to the base of fused anthers were measured on these flowers. In the case of *Asclepias* spp., with five hood-shaped staminal appendages radiating from the center, I used width of the slit in one hood-shaped appendage and depth from the slit in the hood-shaped appendage to the base of each hood-shaped appendage.

STATISTICAL ANALYSIS

I calculated the mean of flower area, flower height, week of peak bloom, and number of natural enemies collected the week before, week of, and week after peak bloom within each block and then calculated the means of each of these across blocks, yielding one mean for each plant species per year. Arthropod counts were natural log (x+1) transformed to homogenize variances. The relationship between natural enemy abundance and set of plant characteristics per species was examined for each year of the study, first on all natural enemies, and then on the three most frequently collected natural enemy groups: Anthocoridae, Chalcidoidea, and Arachnida (Chapter 2).

I conducted a multiple linear regression on the log (x+1) transformed natural enemy and herbivore counts versus a set of plant characteristics: flower area, maximum flower height, week of peak bloom, chroma, hue, corolla width, and corolla depth (PROC REG, SAS Institute 2003). A multiple regression tests for a relationship between each predictor and the response after removing the variance in the response explained by all of the predictors already added to the model. The regression also determines the percent of variance in one continuous response variable (here, number of natural enemies) explained by a set of continuous predictor variables. Natural enemy counts were log transformed to homogenize variances. After data transformation, data were normally distributed based on normal probability plots. Plant characteristics were not highly correlated, indicating that no variables were redundant in the final model (PROC CORR, SAS Institute 2003).

Table 11. Flower characteristic variables included in multiple regression.

Flower characteristic
Week of peak bloom
Week of peak bloom^2
Maximum flower height
Floral area
Floral area^2
Corolla width
Corolla depth
Chroma
Hue

A set of plant characteristics were included in multiple regressions (Table 11). A nonlinear relationship between (log+1) number of natural enemies and both floral area and week was evident in some cases when data from 2004 and 2005 were graphed. In an analysis of biological patterns such as these, it is appropriate to include nonlinear terms for variables when there is a visible nonlinear relationship (Quinn and Keough 2002). Indeed, the polynomial terms for week and floral area increased the model explanatory power in some cases, indicating they more accurately fit the data than a linear term alone. Therefore, I included floral area^2 and week^2 in the variables used to construct the model (Table 11) and these variables are reported where they add significantly to the model explanatory power ($P \leq 0.05$). I used forward stepwise selection, in which the model is built with variables added sequentially in each case. Although this method tends to underestimate p-values because the data are used to construct the model (Neter et al.

1996), it was appropriate to use here, where patterns between insect abundance and plant characteristics were not yet known.

Eupatorium perfoliatum L., with three times more natural enemies collected at it than at any other plant species, was an influential point in the multiple regressions. The order of variable selection changed without this plant species included in the model, indicating that the effect of this plant species, rather than a set of plant characteristics, was being tested in multiple regressions including plant characteristics from 48 species. Therefore *E. perfoliatum* was eliminated from multiple regressions shown in tables, is included in all graphs except where noted, and the differences with and without the species are noted in the text.

In order to evaluate whether the natural enemy natural enemy response to plant characteristics was different for native and non-native species in 2005, I performed an ANCOVA with plant origin as a categorical variable. Due to the limited number of non-natives (5 species), I calculated values across the three sample dates, used data from each block separately, and included block in the model (Natives: N= 210, Non-natives: N=25). Predictor variables included variables that were significant in the multiple regression: week, floral area, and floral area^2. Interaction terms were removed from the model when $P>0.1$.

Although none of the variables were so strongly correlated that the assumption of independence was violated in the multiple regression, the Pearson correlation coefficients between variables were as great as 0.49, indicating some collinearity between variables (an absolute value of 1 indicates completely correlated variables). Because a Principal Components Analysis (PCA) creates independent variables, and a PCA allows the relationship between all plant characteristics to be graphed on one plot, I performed a PCA on the plant characteristics for 2004 and 2005. This resulted in a set of new, non-correlated principal components calculated with eigenvectors based on a set of loadings for each year, the magnitude and direction of which explain the relative importance in the principal component. I used the first Principal Component vs. (log+1) number of natural enemies and herbivores to perform linear regressions by year in order to examine the relationship between plant characteristics, natural enemies, and herbivores in a nonparametric fashion (Wilkinson 2004).

RESULTS

In the multiple regression model with forward selection, there was a significant relationship between log (x+1) natural enemy number and week and floral area in both 2004 and 2005 (Table 12). With *E. perfoliatum*, chroma and natural enemy number had a marginally significant negative relationship in 2004 ($P=0.053$), and in 2005 floral area was the first variable selected in the model ($P<0.001$), followed by week ($P<0.001$) and chroma ($P=0.053$).

In 2004 the positive curvilinear relationship between week of peak bloom and number of natural enemies explained 49.5% of the variation in number of natural enemies, indicating the number of natural enemies increased throughout the growing season, with a greater increase from weeks 12-22 than earlier in the season (Table 12, Fig. 13a). When the variability due to week was removed, a positive linear relationship between number of natural enemy and floral area explained 16.6% of the variability in number of natural enemies, and when this variation was removed an additional 12.4% of the variability was explained by a negative curvilinear relationship (Table 12, Fig. 14a). This relationship indicates a positive response of natural enemies to floral area up to a point, after which increased numbers of natural enemies were not collected at flowering plants even as floral area increased. There was a marginally significant positive relationship between corolla width and number of natural enemies. With *E. perfoliatum* included, there was a marginally significant (P=0.082, partial R^2=0.018) negative relationship between chroma and number of natural enemies, indicating that more insects were collected at flowers with low color saturation, i.e. light colored or white. In 2004, native plants were immature and still becoming established; 37 of 43 native plant species bloomed in 2004, while all 43 bloomed in 2005. As a result, 2005 is likely a more representative year for insect and plant characteristic patterns seen at mature perennial plants; therefore I will focus on results from 2005.

In the 2005 growing season, the first variable selected in the model was week, and a positive linear relationship with week explained 30% of the variation in natural enemy abundance (Table 12, Fig. 13b). The next model variable was a positive linear relationship with floral area, followed by a negative quadratic relationship with floral area. (Table 12, Fig. 14b). With *E. perfoliatum* included, floral area was selected first in the model ($p<0.001$), followed by week ($P<0.001$) and chroma ($P<0.053$).

Table 12. Multiple regression of log(x+1) number of natural enemies versus plant characteristics of 42 native and 5 non-native Michigan plant species. *Eupatorium perfoliatum* is excluded. Results reported in forward selection order.

Variable	Estimate ±SEM	F	P	Partial R^2
2004				
Intercept	-0.0570 ± 0.135	0.18	0.675	—
$Week^2$	$1.39x10^{-3} \pm 3.73x10^{-4}$	13.86	<.001	0.495
Floral area	$1.08x10^{-3} \pm 1.64x10^{-4}$	42.83	<.001	0.166
Floral $area^2$	$-2.62x10^{-7} \pm 5.30x10^{-8}$	24.44	<.001	0.124
Corolla width*	0.0751 ± 0.0411	3.35	0.076	0.018
		Overall model R^2		0.803
2005				
Intercept	0.263 ± 0.147	3.21	0.080	—
Week	$0.0383 \pm 3.94x10^{-5}$	15.47	<.001	0.298
Floral area	$5.71x10^{-4} \pm 1.72x10^{-4}$	11.08	0.002	0.134
Floral $area^2$	$-1.12x10^{-7} \pm 4.48x10^{-8}$	6.23	0.016	0.071
		Overall model R^2		0.502

*P-values ≤0.10 are reported.

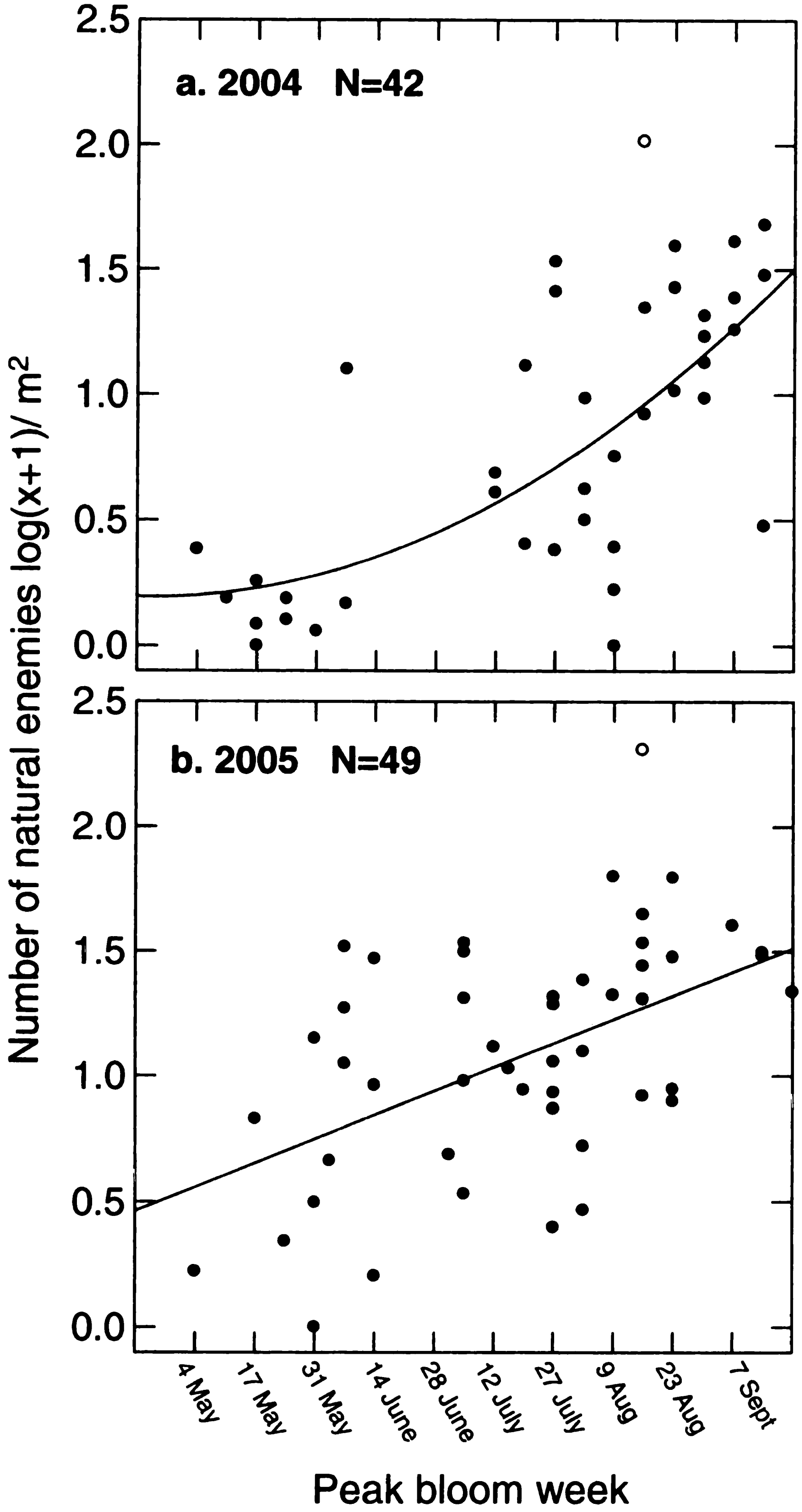


Figure 13. Mean number of natural enemies (log [x +1] transformed) per plant species vs. peak bloom week, 2004 and 2005. Curve fit is polynomial if week^2 is significant in the multiple regression model. Fits do not include *E. perfoliatum*, the open dot.

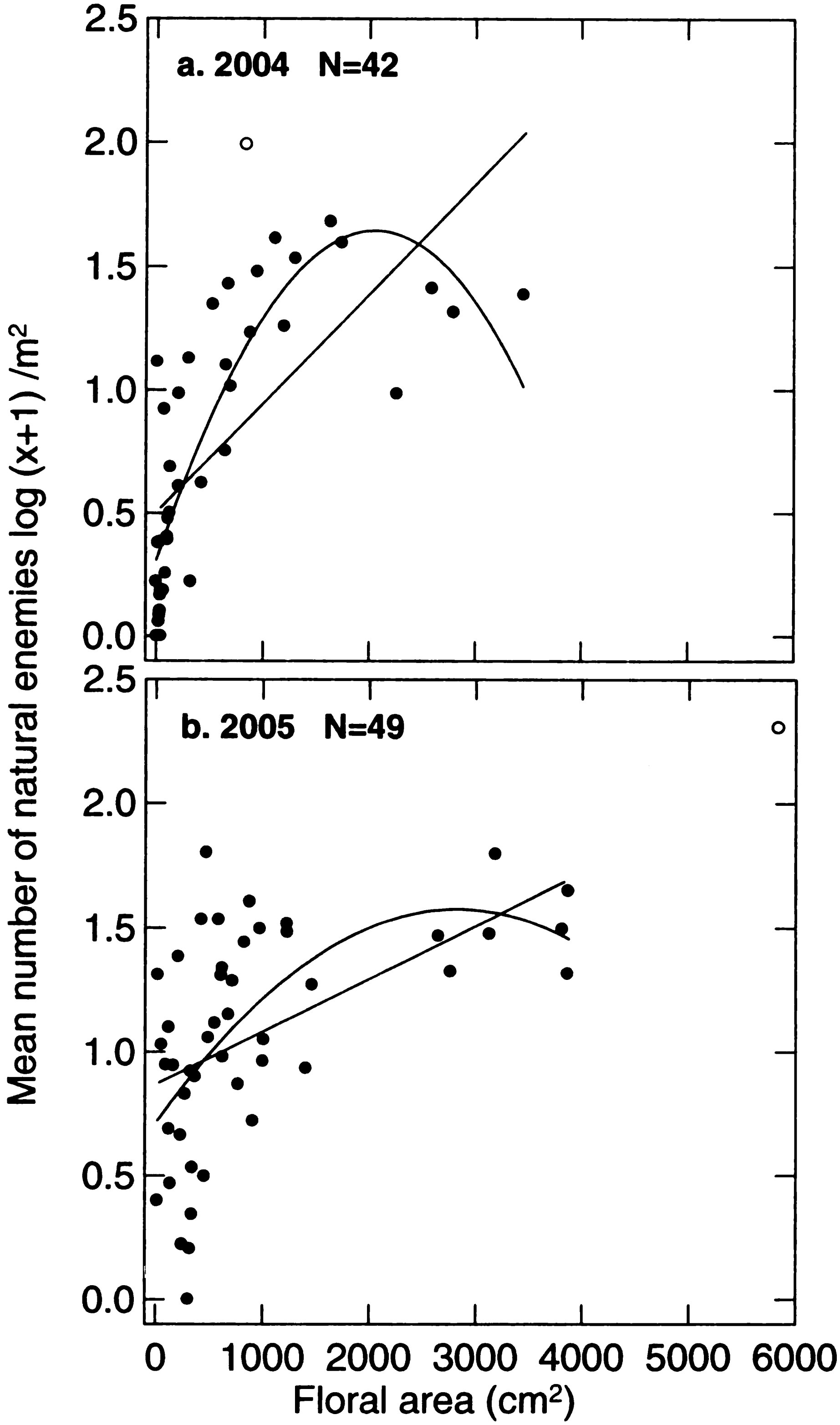


Figure 14. Mean number of natural enemies (log [x +1] transformed) per plant species vs. floral area. Curve fit is polynomial if floral area^2 is significant in the multiple regression model. Fits do not include *E. perfoliatum*, the open dot.

NATURAL ENEMY TAXA

I also used multiple regressions to examine the response of the three most abundant natural enemies in 2005 to plant characteristics. These groups included: Anthocoridae (entirely composed of *Orius insidiosus* (Say)), Chalcidoidea, and Arachnida (see Chapter 2). In all three cases, numbers of each natural enemy group showed a positive relationship with week and floral area (Table 13).

A positive curvilinear relationship between anthocorid number and week^2 indicates that numbers decreased midseason and again increased late in the growing season, possibly in response to larger floral displays (Table 12, Fig. 15). There was also a significant positive linear relationship and negative quadratic relationship between anthocorid number and floral area. With *E. perfoliatum* included, floral area was the first model variable ($P<0.001$, partial $R^2=0.40$), followed by week^2 ($P<0.001$, partial $R^2=0.039$).

Chalcidoidea also showed a positive linear and negative curvilinear relationship with floral area; in this model floral area was selected before week (Table 13). With *E. perfoliatum* included, there was no significant relationship with week but was a significant positive relationship between maximum flower height and number of chalcids ($P=0.047$, partial $R^2=0.053$).

A positive relationship between week and number of arachnids was selected first in the model, followed by floral area, corolla width, and a marginally significant negative relationship with chroma (Table 13). With *E. perfoliatum* included, only the response to floral area was significant ($P<0.001$, $R^2=0.23$).

Table 13. Natural enemy response to floral characteristics in 2005. Multiple regression of log(x+1) number of three most numerous natural enemy groups vs. plant characteristics by season, reported in forward selection order. *Eupatorium perfoliatum* is not included in this analysis.

Taxon	Variable	Estimate ±SEM	F	P	Partial R^2
Anthocoridae~					
	Intercept	-0.053 ± 0.092	0.32	0.572	—
	$Week^2$	$1.48 \times 10^{-3} \pm 3.22 \times 10^{-4}$	21.23	<.001	0.343
	Floral area	$6.32 \times 10^{-4} \pm 1.44 \times 10^{-4}$	19.35	<.001	0.125
	Floral $area^2$	$-1.33 \times 10^{-7} \pm 3.75 \times 10^{-8}$	12.61	0.001	0.119
			Overall model R^2		0.586
Chalcidoidea					
	Intercept	0.074 ± 0.130	0.32	0.574	—
	Floral area	$4.85 \times 10^{-4} \pm 1.52 \times 10^{-4}$	10.22	0.003	0.324
	Floral $area^2$	$-8.50 \times 10^{-8} \pm 3.96 \times 10^{-8}$	4.61	0.037	0.057
	Week	0.018 ± 0.009	4.25	0.045	0.055
			Overall model R^2		0.436
Arachnida					
	Intercept	-0.121 ± 0.083	2.14	0.151	—
	Week	0.030 ± 0.004	45.00	<.001	0.495
	Floral area	$6.26 \times 10^{-5} \pm 2.01 \times 10^{-5}$	9.67	0.003	0.057
	Corolla width	0.038 ± 0.019	4.17	0.047	0.032
	Chroma*	-0.233 ± 0.126	3.42	0.072	0.031
			Overall model R^2		0.615

~Anthocoridae were entirely composed of *Orius insidiosus* (Say). *P-values ≤0.10 are reported.

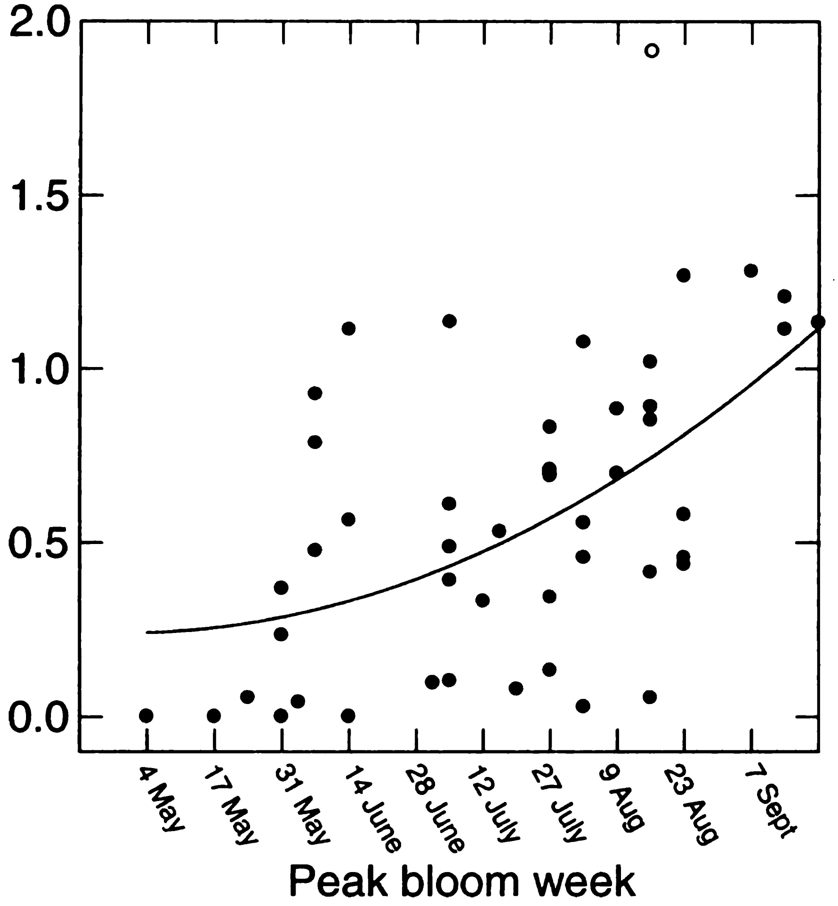


Figure 15. Mean number of Anthocoridae (log [x +1] transformed) per plant species vs. peak bloom week, 2005. Curve fit is polynomial, as week^2 is significant in the multiple regression model. Fit does not include *E. perfoliatum*, the open dot.

PLANT ORIGIN

In 2005 the slope of natural enemy response to plant characteristics between native and non-native species was significantly different for week and floral area, although the primary effect of week was marginally significant when the difference in plant origin was accounted for (Table 14). Natives reached peak bloom in a narrower timeframe than non-natives (Fig. 16). At both native and non-native plant species, the natural enemy response to floral area began to level off at greater than $2000cm^2$. At native plant species, however, natural enemies appeared to have a maximum attractiveness to floral area, while at non-natives natural enemy numbers still continued to increase (Fig. 17). With *E. perfoliatum*, week was no longer significant, and the interaction between floral area and origin decreased in significance.

Table 14. ANCOVA of log(x+1) number of natural enemies versus plant characteristics, with plant origin included as a categorical variable. Each of 5 blocks is included in the analysis. Data are from 2005. *Eupatorium perfoliatum* excluded.

Variable	Estimate ±SEM	F	P
Intercept	0.173 ± 0.065	—	0.001
Origin	1.783 ± 0.411	18.87	<.001
Week	0.036 ± 0.005	2.77	0.097
Week*origin	-0.123 ± 0.030	16.31	<.001
Floral area	$5.43 \times 10^{-4} \pm 6.70 \times 10^{-5}$	73.73	<.001
Floral area*origin	$2.03 \times 10^{-4} \pm 6.60 \times 10^{-5}$	9.40	0.002
Floral area^2	$-9.51 \times 10^{-8} \pm 0$	34.50	<.001

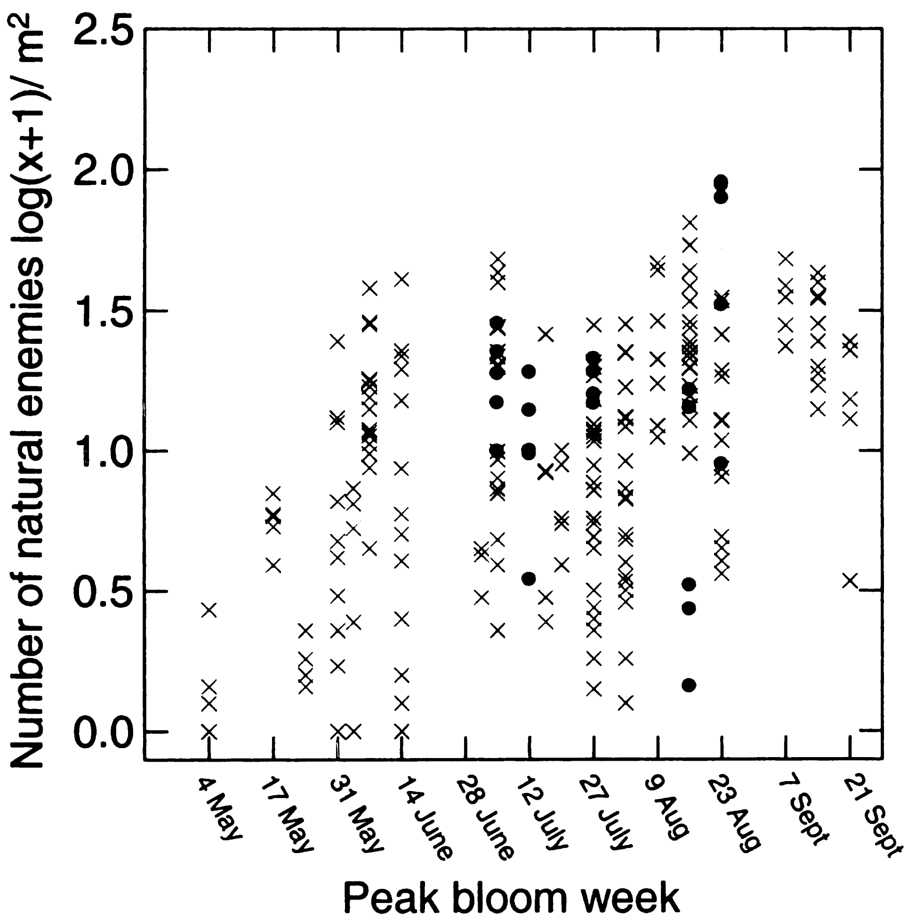


Fig. 16. Difference in week of peak bloom between native and non-native plant species in 2005. × native •:non-native. *Eupatorium perfoliatum* not shown.

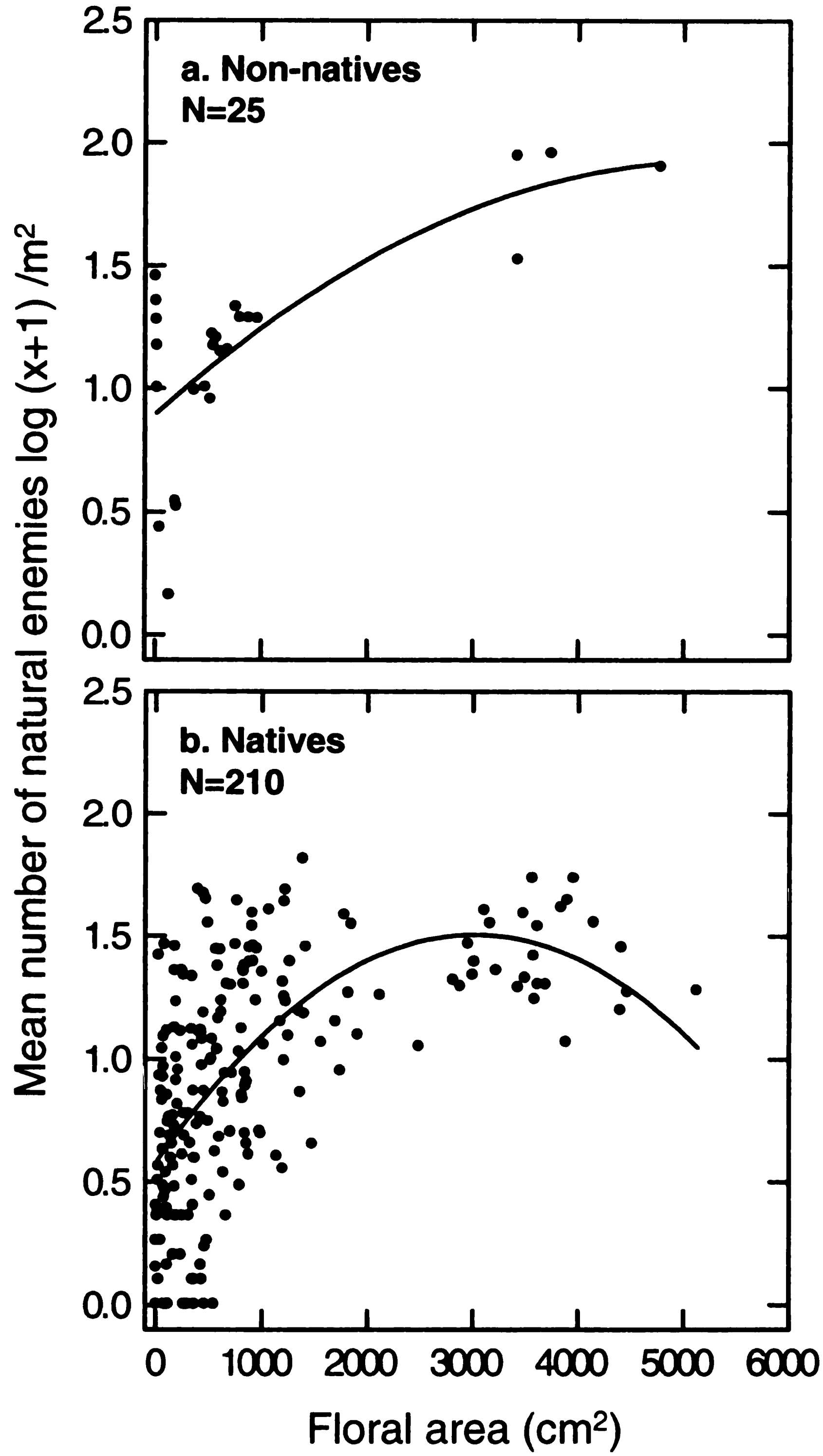


Figure 17. Mean number of natural enemies (log [x +1] transformed) vs. floral area, native and non-native species separate. All five replicates from each species are shown here. Data are from 2005. *Eupatorium perfoliatum* not shown.

PRINCIPAL COMPONENTS ANALYSIS

Natural enemies

The first principal component resulting from the PCA explained 35.1% and 30.1% of the variability in plant characteristics in 2004 and 2005, respectively. Loading values indicate the magnitude and direction a plant characteristic plays in the PCA, and values near 1 or -1 play the greatest role in the PCA. Loadings from both 2004 and 2005 (Table 15) indicate that larger PCA values are associated with week of peak bloom i.e. plants that bloomed later in the season, with taller maximum flower height, greater floral area, and decreased corolla width. The natural enemy response to the first principal component was significant and positive in each 2004 and 2005 (Fig. 18), which mirrors the positive relationship between natural enemy numbers over the season and with increased floral area in multiple regressions. The PCA also indicates that tall plants blooming late in the season with prolific flowering area are likely to have small corolla widths (Table 15).

Table 15. Principal component loadings for flower characteristics by year. Magnitude and sign of the number indicate the strength and direction of the relationship between the PCA value and set of flower characteristics.

	PCA loading	
Flower characteristic	**2004**	**2005**
Week of peak bloom	0.756	0.760
Maximum flower height	0.759	0.703
Chroma	0.318	0.284
Hue	-0.138	-0.045
Flower area	0.755	0.679
Corolla width	-0.736	-0.688
Corolla depth	-0.279	-0.148

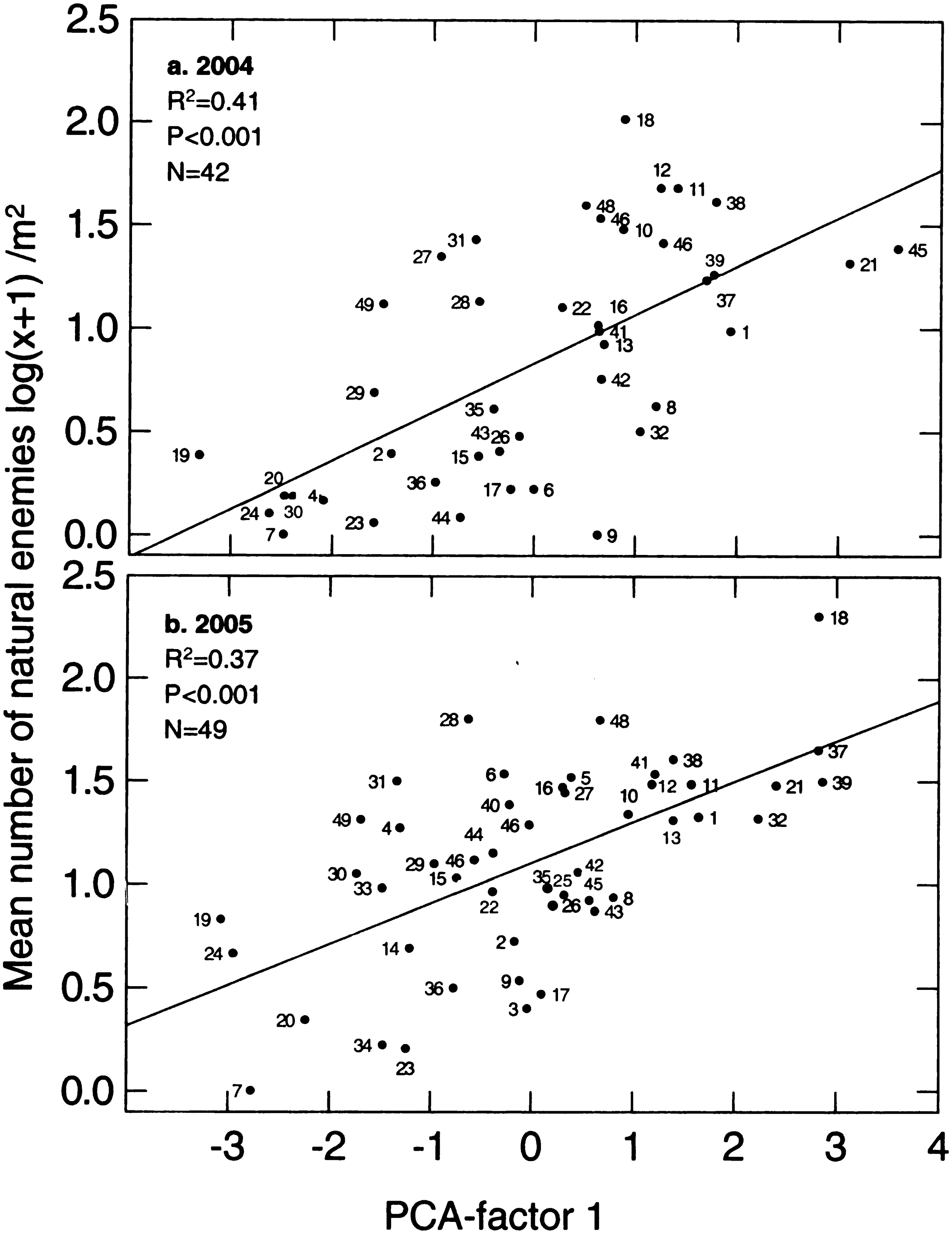


Figure 18. Linear regression by year showing a significant positive relationship between the first principal component from flower characteristics and the mean number of natural enemies per sample. Multiple coefficients of determination (R^2), probability values (P) and number of samples (N) are shown for each year. Numbers match species names as listed in Table 10.

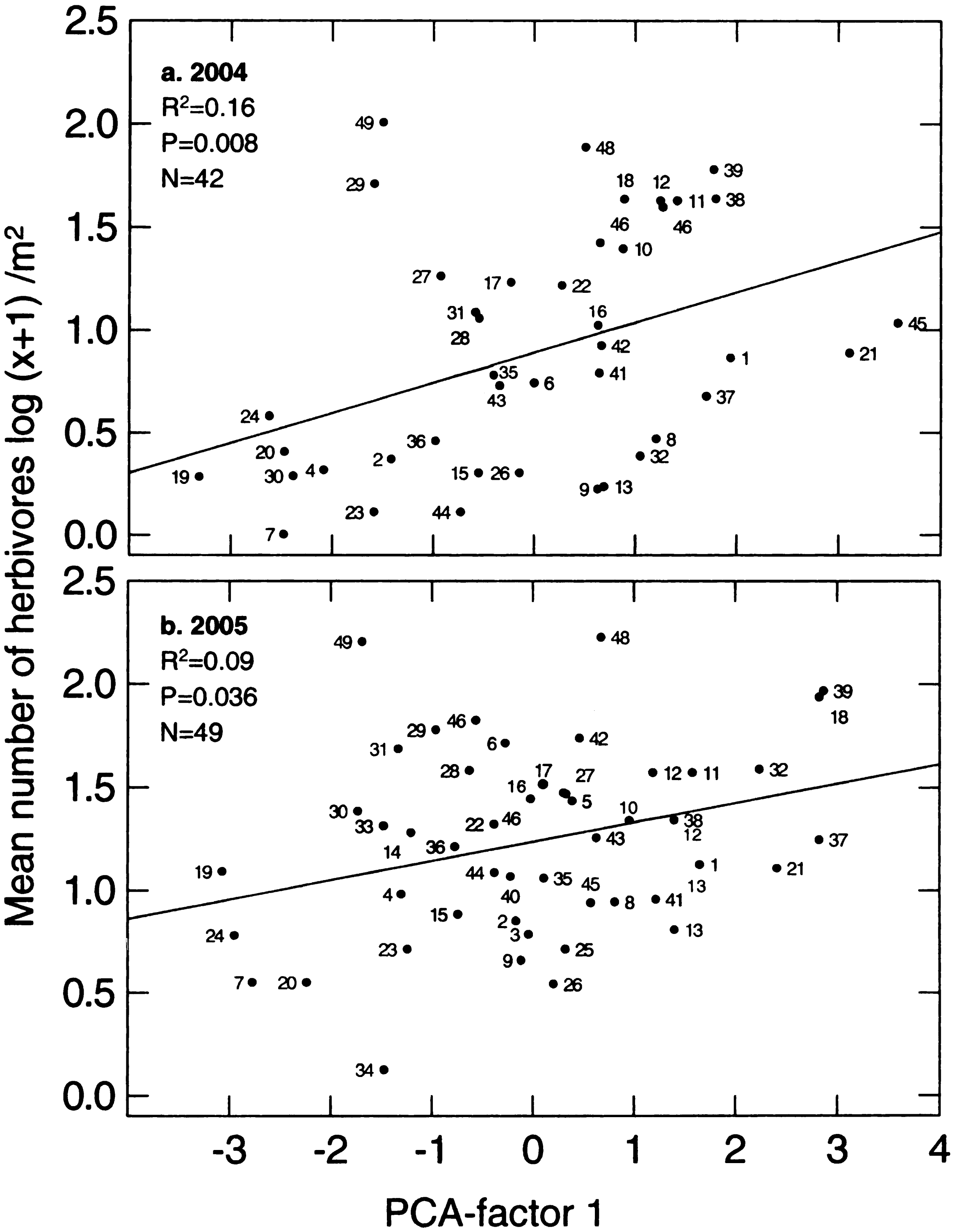


Figure 19. Linear regression by year showing a positive relationship between the first principal component from flower characteristics and the mean number of herbivores per sample. Numbers match species names as listed in Table 10.

Herbivores

The relationship between PCA-factor 1 and number of natural enemies explained 40.8% and 36.8% of the variation in number of natural enemies in 2004 and 2005, respectively. The relationship between herbivore number and PCA-factor 1 was also positive and significant in both years; 16.2% and 9% of the variability in number of herbivores was explained by this relationship (Fig. 19). This indicates that herbivores responded more weakly to grouped floral characteristics measured here than did natural enemies.

DISCUSSION

The perennial plants used in this study were planted in fall 2003 and were maturing during 2004. During this establishment year some plants did not bloom at all or much later than in 2005. In contrast, most native perennials were fully established in 2005, filling in the $1m^2$ plots, and with bloom periods that more closely match their natural phenology. Therefore, 2005 is likely a year that represents phenology and insect attraction more typical of this system, and discussion will focus on 2005 data. Plant characteristics, including maximum flower height, week of peak bloom, floral area, chroma, hue, corolla depth, and corolla width, were measured on 48 plant species to determine whether any were associated with increased natural enemy visitation during full bloom period.

The number of insects increased significantly throughout the season in both 2004 and 2005. The first season of growth in the field for native perennials was 2004, allowing plants blooming late in the season more time to establish than those blooming early.

Therefore, the linear increase in natural enemy number by week that was observed in 2005 is more likely the pattern for insect numbers at established native perennials than the positive quadratic relationship in 2004. Floral area and floral area^2 were the variables next selected in stepwise multiple regression, indicating that floral area plays a large role in resource plant attractiveness to natural enemies. When *E. perfoliatum*, the native plant with far more natural enemies than any other species, was included in multiple regressions, floral area was the first model variable included in forward selection. Whether or not *E. perfoliatum* is included in the model, the recommendation is consistent: for a given bloom period, select plants with the greatest floral area possible.

In 2004, the relationship between floral area and number of natural enemies indicated a point at which natural enemy response leveled off. This point was at about 2000 cm^2 of floral area/m^2 (Fig. 14a). In 2005, floral area predicted a linear increase in natural enemy visitation, and again all flowers with greater than 2000 cm^2/m^2 were attractive to natural enemies. Overall, these patterns indicate that at low floral areas, the natural enemy abundance increased rapidly with floral area, and at greater than 2000 cm^2/m^2, the natural enemy response leveled off, with an average of 20 or greater natural enemies/m^2 collected per sample at peak bloom.

Flower-visiting insects have previously been shown to respond to floral area and number of open flowers per plant, but not necessarily in a consistent fashion. Ohashi et al. (1998) found that the number of bumblebee (*Bombus diversus*) visits increased with the number of flowering heads per plant, up to a saturation point. The number of flower heads per plant that were visited was linearly related to display size. However, the bumblebee visitation rate increased with number of flower heads, independent of the size of floral display. Conner and Rush (1996) similarly found that the number of flowers probed by pollinators increased as the number of open flowers per plant increased, and pollinators were more likely to visit plants with more open flowers. However, the number of open flowers did not change the amount of time pollinators spent per flower. Hegland and Totland (2005) found that insect visitation frequency to plants increased significantly with the size of visual display but not with the number of flowers per plot. This suggests that insects searching for floral resources are more likely to visit plants with increased floral area, but allocate the same amount of time per flower. Because foraging rates once they locate a plant is constant per flower, insects are more likely to be retained at plants with more open flowers. There is also evidence that insects are more likely to forage in dense flowering patches (Thomson 1981). In this study, I measured the natural enemy response per floral area and not per number of flowers. The natural enemy response to floral area in this case indicates that natural enemies are responding in either a linear or curvilinear manner to floral area. This response could be due to greater retention at plants with more flowers and/or greater attraction to plants with greater floral area.

Natural enemy numbers were greater at plants that bloomed later in the season. Studies indicate that insect seasonal response to flowering plants is not consistent in all ecosystems. McCall and Primack (1992) examined pollinators in tundra, fynbos (a fire-dependent scrubland with very high plant diversity and plants that are primarily hard-leaved evergreens), and deciduous woodland-meadow. They found that insect abundance peaked early in the season in tundra, overall insect numbers were lowest in the fynbos, and insect numbers were greatest and peaked late in the season in the deciduous woodland-meadow. This finding indicates that insect abundance does not increase throughout the season in all ecosystems. Crop systems, however, are most often located in areas with a longer growing season than tundra and more regular moisture regime than fynbos. Therefore, the positive relationship between week of peak bloom and number of natural enemies is likely similar in agricultural systems in many geographic regions, although it would be strengthened if tested with a different set of native plants in another region.

An inclusion of native perennial and non-native annual as categorical variables in an ANCOVA indicated that the week of peak bloom for non-natives was earlier than for natives, and occurred in a compressed time period between 5 July and 23 August in 2005. The ANCOVA also showed a significant interaction between floral area and plant origin; natural enemies responded more strongly to floral area at the non-native annual species previously noted for their success in habitat management than at the native perennials in this study. Nectar quantity or quality may limit natural enemies at high densities at the native species. The non-native annual plants have been selected previously as prolific nectar providers or the nectar provided by the annuals may contain more concentrated sugars or sugars that natural enemies are able to ingest (Wäckers 1999).

Despite the strong patterns of natural enemy increase with week of peak bloom and floral area, results indicate that natural enemies are not responding strongly to other plant characteristics measured, including chroma, hue, corolla depth, and corolla width.

Other studies indicate that insects respond to color saturation (chroma) and to hue. Color is an important cue for recognition and detection of flowers from a distance (Kevan et al. 1996). Vegetation, soil, and stone all have similar and weak reflectances in the insect visual spectrum, so appear "dull" to insects, and flowers with UV absorbance stand out against this background (Kevan et al. 1996). Bees respond to color contrast versus a background color, but not to flower color intensity or wavelength (Lunau 1990). Begum et al. (2004) found a greater response of the parasitoid *Trichogramma carvarae* to white than purple, light pink, or dark pink flowers of the same plant species. In my study a multiple regression by natural enemy group indicated a marginally significant negative relationship between arachnid number and chroma, indicating arachnids were more likely to be found at pale or white flowers. Previous findings indicate that natural enemies show a greater response to pale or white flowers, which they are likely seeing as contrasting with the background, rather than those with saturated colors. Insect vision sensitivity ranges from 300-650 nm, and insects are sensitive to wavelengths into the ultraviolet range, as opposed to humans (400-700 nm). I measured flower reflectance from 400-700 nm and used these reflectances to calculate chroma and hue. With reflectances beginning at 330 nm, a comparison of reflectance in the UV spectrum may have explained a greater percentage of natural enemy number variation at flowers.

A simple linear regression between number of natural enemies and the first principal component from a PCA on floral characteristics indicates that natural enemies are responding significantly to an interrelated set of floral characteristics. Principal component loadings indicate that this response is to increasing floral area, peak bloom week, maximum flower height, and decreasing corolla width. Maximum flower height, floral area, date of peak bloom, and corolla width are plant characteristics that are interrelated: taller plants have more three-dimensional area that may be occupied by flowers, plants blooming later in the growing season are more likely to be taller, as they have more time to store resources before blooming, and Asteraceae (which frequently have narrow corollas) dominated the species blooming in the late season.

Natural enemies may be limited by inability to physically access floral resources at plants (Wäckers et al. 1996, Patt et al. 1997, Jervis 1998). In 2005, Arachnida were more common at plants with greater corolla width. The plant characteristic groupings of the principal components, however, indicated that natural enemies were more likely to be at plants with narrow corollas. The plants in this group were prolific late blooming tall plants, and nearly exclusively Asteraceae. In these species disc flowers of the composite flowering structure, although narrow, were shallow and allowed nectar to pool, therefore increasing nectar accessibility for natural enemies. Several earlier blooming flower species with deep corollas also had large enough openings that the most common natural enemies likely could enter the flower and access nectar. These data indicate that although floral morphology was not a key component of natural enemy attractiveness in this study, it may play a role in retention of insects at a plant species.

The response by natural enemies indicated that the taxa most frequently collected at flowers, Anthocoridae (entirely composed of *Orius insidiosus* (Say)), Chalcidoidea, and Arachnida, primarily responded to week of peak bloom and floral area. This indicates that selecting plants for specific plant characteristics is not a method for attracting specific natural enemy groups, although arachnids were likely at flowers not to feed on floral resources but to feed on insect resources that may have been more common at pale or white flowers with large corolla openings.

A linear regression of the log (x+1) number of herbivores and the first principal component explained four times less variability than the natural enemy response in 2005.

This indicates that herbivores are responding less strongly to floral characteristics than natural enemies. Although herbivores and natural enemies do increase at plants with a set of similar floral characteristics, the relationship between floral characteristics chosen for their attractiveness to natural enemies is much stronger. This suggests that the benefit of selecting plants for natural enemy attractiveness may outweigh the potential costs of increased herbivore populations.

The set of three floral characteristics included in the model explained 50% of the variability in natural enemy number when perennial plants were fully established (i.e. 2005). Natural enemies may have responded to other additional factors that were not measured in this study. Natural enemies have been shown to respond to non-visual plant characteristics such as floral volatiles or plant volatiles triggered by herbivore feeding on the plant (Bell 1990, Wackers and Lewis 1994), and natural enemy retention at plants may have been driven by nectar or pollen quantity or quality (Wackers and Lewis 1994, Fenster et al. 2004). In addition, intraguild predation may have occurred on plants with many insects present at them, or interspecific competition for nectar and pollen between bees and natural enemies may have decreased survival and resource availability of natural enemies.

Pollinating insects also have been found to respond to weather factors such as light levels, temperature, and time of day (McCall and Primack 1992). While abiotic factors were not measured in this study, insects were collected during the same time period each day, on sunny days when possible and never during rainy weather. In addition, the insect samples were taken over a 3-week period, to smooth any week by week weather variation. Despite these factors, it is possible that natural enemy visitation at plants was affected by weather in a way that was not accounted for in this study.

In this study system, natural enemy numbers increased significantly over the growing season and with floral area at a plant species. This result indicates selecting plants that are the most prolific bloomers at a specific time will yield the greatest natural enemy numbers at plants. Herbivorous insect numbers showed a weaker response to the plant characteristics measured than natural enemies, so fewer herbivores than natural enemies are likely to be attracted to flowers of plants selected to optimize the success of conservation biological control via habitat management. A consideration of plant selection for large floral area would simplify selection of highly attractive plants and could increase the use and ultimate effectiveness of habitat management worldwide.

APPENDIX A

Recommended natural enemy resource plants based on top ten applicable hits in a Google internet search (http://www.google.com) for "beneficial insect" and "plant". Search performed 12/15/2003.

Reference:	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Apiaceae (Carrot Family)	x	x						x	x	
anise *(Pimpinella anisum)*		x	x					x		
angelica *(Angelica archangelica)*			x	x		x				x
caraway (*Carum carvi)*	x	x	x							
celery *(Apium* spp.*)*									x	
chervil *(Anthriscus* spp.*)*		x		x					x	
coriander (cilantro) (*Coriandrum sativum)*	x			x		x		x	x	
dill (*Anethum graveolens)*	x	x		x		x		x	x	
fennel (*Foeniculum vulgare*)	x			x		x		x	x	
flowering ammi/(*Ammi majus)*	x	x								
ivy *(Hedera* spp.*)*			x							
lovage (*Levisticum* spp.)				x						
parsley (*Petroselinum*)		x		x						
sweet cicely (*Ossmorhiza* spp.)				x						
toothpick ammi (*Ammi visnaga)*	x									
wild parsnip (*Pastinaca sativa)*	x									
Compositae (Aster Family)		x	x					x		
ageratum *(Ageratum housonianum)*			x							
aster (wild romance)							x			
aster (wonder of Staffa)							x			
black-eyed susan (*Rudbeckia* spp.)			x							
blanketflower (*Gaillardia* spp.)	x		x				x			
calendula (*Calendula* spp.)				x						
coneflower (*Echinacea* spp.)	x		x				x	x		
coreopsis (*Coreopsis* spp.)	x	x	x							
cosmos (*Cosmos* spp.)	x	x	x					x		
daisy			x	x	x	x		x		
dandelion (*Tanaxacum* spp.)		x								
erigeron				x						
goldenrod (*Solidago* spp.)	x	x	x	x	x					x
golden marguerite *(Anthemis tincoria)*		x	x				x			
Joe-Pye weed *(Eupatorium maculatum)*			x							
lettuce (*Lactuca* spp.)										x
ragweed (*Ambrosia* spp.)										x
tansy (*Tanacetum vulgare)*	x									
yarrow (*Achillea* spp.)	x	x	x	x	x	x		x		x
Labiatae/lamiacae (Mint familiy)						x				
bee balm *(Monarda* spp.*)*			x	x				x		
catnip *(Nepeta cataria)*			x			x				
lavender *(Lavandula* spp.*)*			x					x		
lemon balm *(Melissa officinalis)*			x							
rosemary *(Rosmarinus* spp.*)*			x			x				
russian sage *(Perovskia atriplicifolia)*			x					x		
sage *(Salvia* spp.)			x							
spearmint *(Mentha spicata)*		x	x			x				
sweet marjoram *(Origanum vulgare)*			x							
thyme *(Thymus* spp.*)*		x	x	x		x				

	Reference:	1	2	3	4	5	6	7	8	9	10
Fabaceae (Legume/pea family)											
	alfalfa (*Medicago sativa*)	x	x			x					x
	big flower vetch (*Vicia* spp.)	x				x					
	clover *(Trifolium spp.)*		x								
	cowpea (*Vigna* spp.)		x								
	fava or faba bean (*Vicia faba)*	x									
	hairy vetch (*Vicia villosa)*	x	x			x					
	lupine *(Lupinus* spp.)							x			
	soybeans *(Glycines max)*					x					
	sweet clover (*Melilotus* spp.)	x	x	x	x	x	x				
	white clover (*Trifolium* spp.)		x								
Brassicaceae (Mustard family)			x								
	basket-of-gold alyssum (*Aurinium saxatilis)*	x									
	candytuft (*Iberis* spp.)		x		x						
	hoary alyssum (*Berteroa incana)*	x									
	mustards (*Brassica* spp.)	x									
	sweet alyssum (*Lobularia* spp.)	x	x		x	x			x	x	
	yellow rocket (*Barbarea vulgaris)*	x									
	wild mustard (*Brassica kaber)*	x	x								
Other plant families											
Apocynaceae	oleander (*Nerium* spp.)										x
Asclepidaceae	milkweeds (*Asclepias* spp.)	x	x								
Asclepidaceae	butterfly milkweed (*Asclepias tuberosa*)			x							
Boraginaceae	borage *(Borago officinalis)*			x							
Caprifoliaceae	blue elderberry (*Sambucus caerulea*)		x								
Caprifoliaceae	snowberry (*Symphoricarpos*)				x						
Caryophyllaceae	gypsophila (*Gypsophila* spp.)				x						
Celastraceae	euonymus *(Euonymus spp.)*			x							
Convolvulaceae	morning-glory (*Ipomoea* spp.)										x
Crassulaceae	sedum *(Sedum spp.)*			x							
Graminaceae	corn (*Zea* spp.)		x								
Hydrophyllaceae	baby blue eyes *(Nemophila spp.)*		x								
Hydrophyllaceae	phacelia (*Phacelia* spp.)	x									
Iridaceae	crocuses (*Crocus* spp.)		x								
Liliaceae	allium spp.			x							
Loganiaceae	butterfly bush *(Buddleia davidii)*			x							
Onagraceae	evening primrose (*Oenethera bienni* s)				x						
Polygonaceae	buckwheat (*Fagopyrum* spp.)	x	x	x	x						
Polygonaceae	common knotweed *(Polygonum aviculare)*		x								
Rhamnaceae	ceanothus (*Ceanothus* spp.)		x		x						
Rosaceae	cinquefoil (*Potentilla* spp.)	x									
Rosaceae	raspberries, other brambles *(Rubus spp.)*			x							
Rutaceae	rue				x		x				
Valerianaceae	valerian (*Valeriana* spp.)				x						
Verbenaceae	blue mist caryopteris *(C. x clandonensis)*										
	tihonia *(Tanacetum rotundifolia)*			x							
Trees											
Fabaceae	black locust		x								
Rosaceae	hollyleaf cherry (P*runus ilicifolia*)		x								
Rosaceae	soapbark tree (Q*uillaja saponaria*)		x								
Salicaceae	willows		x								
Sterculiaceae	flowering bottle tree (*Brachychiton* spp.)		x								

References

1[c]:Steffan, Shawn, Whitaker, Paul. Guarding the Garden: Habitat Manipulation to Favor Natural Enemies. Midwest Biological Control News, Vol. III #4, April 1996

2[c]: http://attra.ncat.org/attra-pub/farmscape.html Dec. 2000

3[c]:http://www.princetonol.com/groups/mg/attracting.html ATTRACTING BENEFICIALS. Barbara J. Bromley, Mercer Co. Horticulturist '97

4[b]:http://www.charmeck.org/Departments/LUESA/Solid+Waste/PLANT+Program/Beneficial+Insect+Information.htm © 2003

5[a]:http://www.abirdshome.com/beneficialinsect.html Attracting and Keeping Beneficial Insects in the Yard and Garden © 1997-2003 (Last updated 12/15/2003)

6[a]:http://www.mastergardenproducts.com/gardenerscorner/attrcting_beneficial_insect.htm © 2001 (Updated12/2/03)

7[a]:http://www.gardensalive.com/idis.asp?PN=04892&SID=100406&EID=0508wm&prd=y#more Beneficial Insect Garden: A Garden Designed to Attract Beautiful and Beneficial Insects! ©2003

8[a]:http://users.ms11.net/~habitat/index.htm Plants That Attract Beneficial Insects (Last updated 2/6/2003)

9[a]:http://www.greenhome.com/learn/garden/Bugging.shtml Bugging out in the Garden: Put Beneficial Insects to Work Defending Your Plants, Chris Clarke © 2001

10[a]:http://www.suite101.com/article.cfm/garden_pests/42960 suite101.com Three Beneficial Insect Types. Carla Goodloe June 23, 2000

[a]: zero references cited

[b]: one reference cited

[c]: greater than one reference cited

APPENDIX B
PLANT VOUCHER DATA

Family	Genus and species	Collection Date	Accession number
Lamiaceae	*Agastache nepetoides (L.) Kuntze*	9-Sep	47
Liliaceae	*Allium cernuum Roth*	9-Sep	27
Fabaceae	*Amorpha canescens Pursh*	9-Sep	28
Poaceae	*Andropogon scoparius (Michx.) Nash*	9-Sep	41
Ranunculaceae	*Anemone canadensisL.*	30-Jun	9
Apiaceae	*Anethum graveolens L.*	5-Aug	22
Apiaceae	*Angelica atropurpurea L.*	30-Jun	10
Apocynaceae	*Apocynum cannabinum L.*	5-Aug	25
Ranunculaceae	*Aquilegia canadensis L.*	23-Jun	1
Asclepiadaceae	*Asclepias incarnata L.*	9-Sep	29
Asclepiadaceae	*Asclepias tuberosa L.*	5-Aug	12
Asteraceae	*Aster laevis L.*	29-Sep	46
Asteraceae	*Aster novae-angliae L.*	29-Sep	51/52
Asteraceae	*Cacalia atriplicifolia L.*	9-Sep	37
Rhamnaceae	*Ceanothus americanus L.*	5-Aug	13
Rubiaceae	*Cephalanthus occidentalis L.*	5-Aug	14
Asteraceae	*Coreopsis lanceolata L.*	5-Aug	15
Apiaceae	*Coriandrum sativum L.*	5-Aug	23
Fabaceae	*Desmodium canadense (L.) DC.*	5-Aug	16
Poaceae	*Elymus canadensis L.*	5-Aug	17
Asteraceae	*Eupatorium perfoliatum L.*	9-Sep	38
Polygonaceae	*Fagopyrum esculentum Moench*	5-Aug	26
Rosaceae	*Fragaria virginiana Duchesne*	23-Jun	2
Geraniaceae	*Geranium maculatum L.*	23-Jun	3
Asteraceae	*Helianthus strumosus L.*	9-Sep	39
Apiaceae	*Heracleum maximum Bartr.*	30-Jun	11
Saxifragaceae	*Heuchera americana L.*	30-Jun	50
Hydrophyllaceae	*Hydrophyllum virginianum L.*	23-Jun	4
Fabaceae	*Lespedeza hirta (L.) Hornem.*	9-Sep	30
Asteraceae	*Liatris aspera Michx.*	9-Sep	31
Campanulaceae	*Lobelia siphilitica L.*	9-Sep	40
Brassicaceae	*Lobularia maritima (L.) Desv.*	9-Sep	45
Lamiaceae	*Monarda punctata L.*	9-Sep	32
Onagraceae	*Oenothera biennis L.*	9-Sep	33
Poaceae	*Panicum virgatum L.*	5-Aug	18
Scrophulariaceae	*Penstemon hirsutus (L.) Willd.*	23-Jun	5
Rosaceae	*Potentilla fruticosa auct. non L.*	5-Aug	19
Asteraceae	*Ratibida pinnata (Vent.) Barnh.*	9-Sep	34
Rosaceae	*Rosa setigera Michx.*	5-Aug	20
Caprifolaceae	*Sambucus racemosa L.*	23-Jun	6
Scrophulariaceae	*Scrophularia marilandica L.*	5-Aug	21

APPENDIX B
PLANT VOUCHER DATA
Page 2 of 2 pages

Family	Genus and species	Collection Date	Accession number
Asteraceae	*Senecio obovatus Muhl. ex Willd.*	23-Jun	7
Asteraceae	*Silphium perfoliatum L.*	9-Sep	42
Asteraceae	*Solidago riddellii Frank ex Riddell*	29-Sep	48
Asteraceae	*Solidago speciosa Nutt.*	29-Sep	49
Rosaceae	*Spiraea alba Duroi*	9-Sep	43
Verbenaceae	*Verbena stricta Vent.*	9-Sep	35
Asteraceae	*Vernonia missurica Raf.*	9-Sep	44
Scrophulariaceae	*Veronicastrum virginicum (L.) Farw.*	9-Sep	36
Fabaceae	*Vicia (vigna) faba L.*	5-Aug	24
Apiaceae	*Zizia aurea (L.) Koch*	23-Jun	8

All specimens collected in 2006. **Michigan, Ingham County,** Michigan State University Campus. 42° 41'31N 84 °29'24W. Elevation 265 m. Michigan genotype plants grown for study of natural enemy insects at native plants by Anna Fiedler. Planted in full sun in a previously plowed agricultural field. All native plants acquired from a commercial source: Wildtype Native Plant Nursery, Mason, Michigan.

Investigator's Name:
Anna K. Fiedler

Date: 23 May, 2006

Received the above listed specimens for deposit in the Michigan State University Herbarium.

14 July 2006

Curator Date

APPENDIX C.1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2006-04

Title of thesis or dissertation (or other research projects):
Evaluation of Michigan Native Plants to Provide Resources for Natural Enemy Arthropods

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s) (typed)
Anna Katherine Fiedler

Date 17 July 2006

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America.
Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:
Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX C
INSECT SPECIMEN VOUCHER DATA
Page 1 of 9 Pages

Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Coleoptera				
Anobiidae	June 6 2005, ANGATR			1
Anthicidae	June 15 2004, LOBMAR			1
Anthicidae	July 12 2005, ROSSET			1
Anthicidae	August 16 2005, LOBSIP			1
Cantharidae *Chauliognathus marginatus* (Fabricius)	June 15 2004, HERMAX			1
Cantharidae *Chauliognathus marginatus* (Fabricius)	June 22 2004, LOBMAR			1
Cantharidae *Chauliognathus marginatus* (Fabricius)	July 6 2005, POTFRU			3
Cantharidae *Chauliognathus marginatus* (Fabricius)	July 27 2005, FAGESC			1
Cantharidae *Chauliognathus pennsylvanicus* (DeG.)	August 3 2004, CORSAT			1
Cantharidae *Chauliognathus pennsylvanicus* (DeG.)	August 23 2005, LOBMAR			2
Cantharidae *Chauliognathus pennsylvanicus* (DeG.)	August 30 2005, LOBSIP			1
Carabidae	May 25 2004, SENOBO			1
Carabidae	August 3 2004, CORSAT			1
Carabidae	Sept. 15 2004, MONPUN			1
Carabidae	May 12 2005, FRAVIR			1
Cerambycidae *Megacyllene robiniae* (Forster)	Sept. 1 2004, EUPPER			2
Cerambycidae *Tetraopes* sp.	August 3 2004, ASCINC			1
Chrysomelidae	May 25 2004, SENOBO			1
Chrysomelidae	August 3 2004, CORSAT			1
Chrysomelidae	July 12 2005, ASCINC			1
Chrysomelidae	May 15 2004, ANECAN			1
Chrysomelidae Diabrotica *undecimpunctata* sp.	August 17 2004, EUPPER			1
Chrysomelidae *Phyllotreta striolata* (Fabricius)	August 24 2004, LOBMAR			4
Chrysomelidae *Phyllotreta* sp. 1	August 23 2005, LOBMAR			1
Chrysomelidae *Phyllotreta* sp. 2	August 23 2005, LOBMAR			2
Coccinellidae	August 2 2005, FAGESC			1
Coccinellidae *Coccinella septempunctata* L.	June 15 2004, HERMAX			1
Coccinellidae *Coccinella septempunctata* L.	August 24, 2004, VERSTR			1
Coccinellidae *Coccinella septempunctata* L.	Sept. 15 2004, ANEGRA			1
Coccinellidae *Coleomegilla maculata* (DeG.)	May 5 2004, FRAVIR			1
Coccinellidae *Coleomegilla maculata* (DeG.)	May 19 2004, ZIZAUR			1
Coccinellidae *Cycloneda* sp.	Sept 15 2004, ASTNOV			1
Coccinellidae *Cycloneda* sp.	Sept 22 2004, SOLSPE			1
Coccinellidae *Cycloneda munda* (Say)	July 12 2005, VICFAB			1

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. See Table 10 for full plant names. CONTROL indicates sample taken from Orchardgrass.

Investigator: Anna K. Fiedler

Date

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator Date 7/17/2006

Voucher number **2006-04**

Appendix C

Insect Voucher Specimen Data

Page 2 of 9 Pages

Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Coleoptera cont.				
Coccinellidae *Harmonia axyridis* (Pallas)	June 14 2004, HERMAX			1
Coccinellidae *Harmonia axyridis* (Pallas)	August 3 2004, ASCINC			1
Coccinellidae *Harmonia axyridis* (Pallas)	June 28 2005, APOCAN			1
Coccinellidae *Hippodamia variegata* (Goeze)	Sept. 1 2004, LOBSIP			1
Coccinellidae *Hippodamia variegata* (Goeze)	Sept. 8 2004, CORLAN			1
Coccinellidae *Hippodamia parenthesis* (Say)	Sept. 22 2004, ANEGRA			1
Corylophidae	August 3 2004, ASCINC			1
Corylophidae	August 17 2004, AGANEP			1
Corylophidae *Orthoperus glaber* (LeConte)	August 16 2005, SPIALB			2
Curculionidae	May 25 2004, SENOBO			1
Cryptophagidae	August 17 2004, AGANEP			2
Cryptophagidae	July 6 2005, CONTROL			1
Dermestidae	June 28 2005, APOCAN			1
Erotylidae	July 6 2005, CONTROL			1
Histeridae	June 15 2004, ANECAN			1
Lampyridae	July 6 2005, CEAAME			1
Lampyridae *Photinus pyralis* L.	August 3 2004, EUPPER			1
Mordellidae	June 14 2005, SENOBO			1
Nitidulidae	August 24 2004, EUPPER			1
Nitidulidae	Sept. 15 2004, MONPUN			1
Nitidulidae	May 11 2005, SAMRAC			1
Nitidulidae	June 14 2005, PENHIR			1
Phalacridae	August 10 2004, RATPIN			1
Phalacridae	August 10 2004, APOCAN			1
Phalacridae	August 17 2004, VERSTR			1
Phalacridae	July 6 2005, CONTROL			1
Phalacridae *Olibrus semistriatus* (LeConte)	August 2 2005, RATPIN			2
Phalacridae *Stilbus apicalis* (Melsheimer)	July 6 2005, CONTROL			1
Ripiphoridae	Sept. 1 2004, MONPUN			1
Scarabaeidae	June 3 2004, HERMAX			1
Scarabaeidae *Popillia japonica* Newman	July 28 2004, CORSAT			1
Staphylinidae	June 15 2004, LOBMAR			1
Staphylinidae	August 3 2004, AGANEP			1

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. Anna K. Fiedler. Voucher number 2006-04

Appendix C

Insect Voucher Specimen Data

Page 3 of 9 Pages

Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Diptera				
Anthomyiidae	May 11 2004, SAMRAC			1
Anthomyiidae	May 19 2004, GERMAC			1
Anthomyiidae	May 25 2004, HYDVIR			2
Bibionidae	May 31 2004, ZIZAUR			1
Bombyliidae	August 24 2004, CORLAN			1
Calliphoridae	June 8 2004, HERMAX			1
Calliphoridae	August 24 2004, CACATR			1
Calliphoridae	June 15 2004, HERMAX			1
Cecidomyiidae	May 19 2004, SENOBO			1
Cecidomyiidae	May 19 2004, GERMAC			1
Chamaemyiidae	August 23 2005, VERMIS			1
Chironomidae	May 4 2005, SAMRAC			2
Chironomidae	May 19 2004, GERMAC			1
Chironomidae	May 25 2004, SENOBO			1
Chloropidae	June 21 2005, CONTROL			1
Chloropidae	June 3 2004, ANECAN			2
Chloropidae	June 3 2004, PENHIR			1
Chloropidae	June 8 2004, HERMAX			2
Culicidae	June 15 2004, CORLAN			1
Dolichopodidae	June 15 2004, LOBMAR			1
Dolichopodidae	June 15 2004, CORLAN			1
Dolichopodidae	June 22 2004, ANECAN			1
Dolichopodidae	July 27 2005, VERVIR			1
Dolichopodidae	June 28 2005, APOCAN			1
Drosophilidae	August 24 2004, DESCAD			1
Ephydridae	May 25 2004, SENOBO			1
Ephydridae	June 8 2004, LOBMAR			3
Ephydridae	June 15 2004, LOBMAR			1
Ephydridae	June 15 2004, ANECAN			2
Ephydridae	July 27 2005, FAGESC			2
Empididae *Platypalpus* sp.	June 8 2004, HERMAX			1
Empididae *Platypalpus* sp.	August 3 2004, CORSAT			1
Empididae *Platypalpus* sp.	August 17 2004, EUPPER			1
Empididae *Platypalpus* sp.	May 17 2005, FRAVIR			2
Empididae *Platypalpus* sp.	July 6 2005, POTFRU			4
Empididae *Platypalpus* sp.	August 2 2005, RATPIN			2
Lonchopteridae	August 3 2004, AGANEP			1
Milichiidae *Eusiphona mira* (Coquillett)	August 2 2005, RATPIN			2
Muscidae	August 17 2004, ASCINC			1
Phoridae	May 25 2004, HEUAME			1
Sarcophagidae	May 25 2004, AQUCAN			1

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. Anna K. Fiedler. Voucher number 2006-04

Appendix C

Insect Voucher Specimen Data

Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Diptera cont.				
Scathophagidae	Sept. 15 2004, SOLSPE			1
Scathophagidae	June 14 2005, SENOBO			1
Scathophagidae	August 24 2004, LOBMAR			2
Sciaridae	May 5 2004, FRAVIR			1
Sciomyzidae	Sept. 22 2004, ASTLAE			1
Sciomyzidae	Sept. 29 2004, ASTNOV			1
Sepsidae	June 15 2004, HERMAX			2
Sepsidae	Sept. 22 2004, ASTLAE			2
Sphaeroceridae	August 17 2004, VERSTR			2
Sphaeroceridae	August 24 2004, LOBMAR			2
Sphaeroceridae	June 28 2005, APOCAN			1
Stratiomyidae	June 15 2994, CORLAN			1
Stratiomyidae	June 21 2005, CORLAN			2
Syrphidae	June 8 2004, HERMAX			1
Syrphidae	June 15 2004, HERMAX			1
Syrphidae	June 29 2004, LOBMAR			1
Syrphidae	Sept. 15 2004, SOLSPE			1
Syrphidae	Sept. 22 2004, ANEGRA			1
Syrphidae *Allograpta obliqua* (Say)	May 25 2004, SENOBO			2
Syrphidae *Allograpta obliqua* (Say)	July 25 2005, RATPIN			1
Syrphidae *Eristalis arbustorum* (L.)	June 8 2004, HERMAX			2
Syrphidae *Eristalis arbustorum* (L.)	June 15 2004, HERMAX			1
Syrphidae *Eristalis arbustorum* (L.)	June 15 2004, CORLAN			1
Syrphidae *Eristalis arbustorum* (L.)	June 22 2004, HERMAX			1
Syrphidae *Eristalis arbustorum* (L.)	June 22 2004, CORLAN			1
Syrphidae *Eristalis arbustorum* (L.)	Sept. 1 2004, HELSTR			1
Syrphidae *Eristalis arbustorum* (L.)	Sept. 15 2004, ASTLAE			2
Syrphidae *Eristalis arbustorum* (L.)	Sept. 22 2004, SOLSPE			1
Syrpidae *Sphaerophoria* sp.	May 25 2004, SENOBO			1
Syrpidae *Sphaerophoria* sp.	June 15 2004, ANECAN			1
Syrpidae *Sphaerophoria robusta* (Curr.)	May 25 2004, SENOBO			1
Syrpidae *Sphaerophoria robusta* (Curr.)	July 12 2005, POTFRU			1
Syrphidae *Toxomerus* sp.	May 25 2004, SENOBO			1
Syrphidae *Toxomerus* sp.	June 3 2004, HEUAME			1
Syrphidae *Toxomerus* sp.	June 8 2004, LOBMAR			1
Syrphidae *Toxomerus* sp.	June 15 2004, LOBMAR			1
Syrphidae *Toxomerus* sp.	June 22 2004, CORLAN			2
Syrphidae *Toxomerus* sp.	June 22 2004, HERMAX			1
Syrphidae *Toxomerus* sp.	June 22 2004, LOBMAR			1
Syrphidae *Toxomerus* sp.	June 22 2004, POTFRU			2
Syrphidae *Toxomerus* sp.	Sept. 8 2004, ASTNOV			1
Tachinidae	June 15 2004, HERMAX			1

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. Anna K. Fiedler. Voucher number 2006-04

Appendix C

Insect Voucher Specimen Data

Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Diptera cont.				
Tachinidae	August 3 2004, AGANEP			1
Tachinidae	August 3 2004, CORSAT			1
Tachinidae	August 17 2004, APOCAN			1
Tachinidae	June 28 2005, CORLAN			1
Tephritidae	July 28 2004, CORSAT			1
Tephritidae	August 10 2004, CORSAT			2
Tipulidae	May 31 2004, ZIZAUR			1
Tipulidae	Sept. 1 2004, LOBSIP			1
Hemiptera				
Fulgoroidea	August 10 2004, CORSAT			2
Aphididae	August 3 2004, CORSAT			1
Anthocoridae *Orius insidiosus* (Say)	June 3 2004, PENHIR			1
Anthocoridae *Orius insidiosus* (Say)	June 8 2004, HERMAX			2
Anthocoridae *Orius insidiosus* (Say)	July 12 2005, POTFRU			2
Aradidae	Sept. 22 2004, SOLRID		1	
Cicadellidae	May 11 2004, SENOBO			2
Cicadellidae	August 2 2005, SCRMAR			1
Coreidae	June 21 2005, CORLAN			1
Lygaeidae	August 17 2004, ASCINC			1
Lygaeidae	Sept. 1 2004, CORLAN			1
Membracidae	Sept. 1 2004, VERMIS			2
Miridae	May 19 2004, GERMAC			2
Miridae	May 25 2004, HYDVIR			2
Miridae *Chlamydatus associatus* (Uhler)	July 19 2005, CONTROL			1
Miridae *Chlamydatus associatus* (Uhler)	August 2 2005, OENBIE			1
Miridae *Chlamydatus associatus* (Uhler)	August 2 2005, RATPIN			1
Miridae *Chlamydatus associatus* (Uhler)	August 9 2005, MONPUN			3
Miridae *Chlamydatus associatus* (Uhler)	August 16 2005, SILPER			1
Miridae *Lygus* sp.	June 6 2005, AQUCAN			1
Miridae *Plagiognathus politus* (Uhler)	July 12 2005, CORSAT			1
Miridae *Plagiognathus politus* (Uhler)	July 12 2005, VICFAB			1
Miridae *Plagiognathus politus* (Uhler)	August 16 2005, SILPER			5
Nabidae	August 3 2004, CORSAT			1
Pentatomidae *Perillus bioculatus* (L.)	June 22 2004, LOBMAR		1	
Pentatomidae *Perillus bioculatus* (L.)	Sept. 22 2004, SOLRID		1	
Pentatomidae *Podisus maculiventris* (L.)	August 10 2004, ASCINC			1
Pentatomidae *Podisus maculiventris* (L.)	August 17 2004, VERSTR		1	
Pentatomidae *Podisus maculiventris* (L.)	August 16 2005, HELSTR			1
Piesmatidae	June 15 2004, HERMAX			1
Rhopalidae	June 15 2004, CORLAN			1
Thyreocoridae	July 12 2005, CEAAME			1
Tingidae	August 3 2004, ASCINC			1

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. Anna K. Fiedler. Voucher number 2006-04

Appendix C

Insect Voucher Specimen Data

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Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Hymenoptera				
Chalcidoidea	May 5 2004, FRAVIR			1
Chalcidoidea	May 11 2004, FRAVIR			1
Chalcidoidea	May 19 2004, GERMAC			1
Chalcidoidea	May 25 2004, PENHIR			1
Chalcidoidea	June 3 2004, HYDVIR			1
Chalcidoidea	June 8 2004, ANECAN			1
Chalcidoidea	June 8 2004, LOBMAR			3
Chalcidoidea	June 8 2004, HERMAX			7
Chalcidoidea	June 15 2004, HERMAX			3
Chalcidoidea	June 15 2004, LOBMAR			4
Chalcidoidea	June 22 2004, CORLAN			1
Chalcidoidea	June 22 2004, HERMAX			1
Chalcidoidea	June 22 2004, LOBMAR			1
Chalcidoidea	June 29 2004, FAGESC			2
Chalcidoidea	Sept. 1 2004, SILPER			2
Chalcidoidea	August 30 2005, LOBSIP			1
Chalcidoidea	August 30 2005, LOBMAR			1
Encyrtidae	Sept. 8 2004, ASTNOV			1
Encyrtidae	August 23 2005, SILPER			4
Encyrtidae *Copidosoma* sp.	Sept. 8 2004, ASTNOV			2
Encyrtidae *Copidosoma* sp.	August 30 2005, VERMIS			3
Eurytomidae	July 27 2005, CORSAT			1
Eurytomidae *Bruchophagous* sp.	August 23 2005, LOBMAR			3
Eurytomidae *Systole* sp. var albipennis	July 27 2005, CORSAT			1
Mymaridae	May 25 2004, SENOBO			1
Mymaridae	June 8 2004, HERMAX			1
Mymaridae	June 8 2004, LOBMAR			1
Perilampidae	July 19 2005, CORSAT			1
Pteromalidae *Halticoptera* sp.	August 30 2005, LOBMAR			2
Pteromalidae *Pteromalus* sp.	August 30 2005, LOBSIP			2
Pteromalidae Pteromalinae	August 30 2005, LOBSIP			1
Cynipoidea	May 5 2004, FRAVIR			1
Cynipoidea	June 8 2004, HERMAX			1
Cynipoidea	June 8 2004, LOBMAR			1
Cynipoidea	June 15 2004, HERMAX			3
Cynipoidea	June 15 2004, LOBMAR			4
Cynipoidea	June 22 2004, LOBMAR			2
Cynipoidea	June 29 2004, FAGESC			1
Cynipoidea	August 23 2005, LOBMAR			3
Cynipoidea Figitidae Eucoilinae	August 23 2005, LOBMAR			3

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. Anna K. Fiedler. Voucher number 2006-04

Appendix C

Insect Voucher Specimen Data

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Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Hymenoptera cont.				
Apidae *Apis mellifera* L.	August 3 2004, CORSAT			1
Apidae *Apis mellifera* L.	August 24 2004, CACATR			1
Bethylidae	July 12 2005, ASCINC			1
Bethylidae	August 9 2005, SPIALB			1
Bethylidae	August 23 2005, MONPUN			1
Braconidae	May 11 2004, GERMAC			1
Braconidae	June 8 2004, HERMAX			3
Braconidae	June 8 2004, LOBMAR			1
Braconidae	June 15 2004, ANECAN			1
Braconidae	June 15 2004, HERMAX			1
Braconidae	June 22 2004, LOBMAR			2
Braconidae	Sept. 15 2004, SOLRID			1
Cephidae	June 15 2004, HERMAX			1
Conopidae	August 2 2005, OENBIE			1
Conopidae	Sept. 27 2005, SOLSPE			1
Formicidae	May 19 2004, GERMAC			1
Formicidae	Sept. 7 2005, HELSTR			3
Ichneumonidae	June 8 2004, HERMAX			1
Ichneumonidae	June 15 2004, PENHIR			1
Ichneumonidae	June 15 2004, HERMAX			2
Ichneumonidae	June 22 2004, HERMAX			1
Ichneumonidae	Sept. 1 2004, CACATR			1
Ichneumonidae	May 17 2005, ZIZAUR			1
Ichneumonidae	May 17 2005, FRAVIR			1
Ichneumonidae	July 12 2005, VICFAB			1
Sphecidae	June 8 2004, HERMAX			2
Sphecidae	June 15 2004, HERMAX			2
Sphecidae	June 15 2004, CORLAN			1
Sphecidae	June 22 2004, HERMAX			2
Sphecidae	August 3 2004, CORSAT			1
Sphecidae	August 10 2004, ASCINC			1
Sphecidae	Sept. 15 2004, ANEGRA			2
Sphecidae	June 14 2005, ZUZAUR			1
Sphecidae	August 16 2005, CACATR			1
Pompilidae	August 24 2004, CACATR			1
Pompilidae	August 16 2005, CACATR			1
Tiphiidae	Sept. 8 2004, HELSTR			1
Tiphiidae	Sept. 15 2004, SILPER			1
Vespidae	June 15 2004, HERMAX			1
Vespidae *Polistes* sp.	June 8 2004, HERMAX			1
Vespidae *Polistes* sp.	June 15 2004, HERMAX			1
Vespidae *Polistes* sp.	Sept. 15 2004, ANEGRA			1
Vespidae *Polistes* sp.	Sept. 22 2004, SOLRID			2

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. Anna K. Fiedler. Voucher number 2006-04

Appendix C

Insect Voucher Specimen Data

Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Number of: Nymphs	Number of: Adults
Lepidoptera				
Arctiidae	Sept. 15 2004, ANEGRA			1
Arctiidae	August 9 2005, SPIALB			1
Danaeidae *Danaus Plexippus* (L.)	Sept. 15 2004, SOLSPE			1
Noctuidae	Ausust 2 2005, OENBIE			1
Nymphalidae	June 14 2005, SENOBO			1
Pieridae	Sept. 15 2004, ASTNOV			2
Sphingidae	August 16 2005, LOBSIP			1
Acari	August 17 2004, LOBMAR			1
Arachnida Araneae Aranaeidae	Sept. 8 2004, ASTNOV			1
Arachnida	May 11 2004, SENOBO			1
Chilopoda	Sept. 8 2004, POTFRU			1
Collembola	May 11 2004, SENOBO			2
Dermaptera Forficulidae	Sept. 8 2004, MONPUN			1
Ephemeroptera	August 24 2004, VERSTR			1
Neuroptera				
Chrysopidae	June 14 2005, CORLAN			1
Chrysopidae	July 27 2005, RATPIN			1
Chrysopidae	August 16 2005, SILPER			2
Hemerobiidae	July 27 2005, FAGESC			1
Odonata	Sept. 8 2004, ANEGRA			1
Orthoptera Acrididae	Sept. 1 2004, LOBSIP			1
Orthoptera Gryllidae	August 24 2004, VERSTR			1
Psocoptera	Sept 22 2004, ANEGRA			1
Thysanoptera	May 5 2004, FRAVIR			1
Thysanoptera	August 17 2004, LOBMAR			1
Trichoptera	Sept. 15 2004, ASTNOV			1

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Insect Voucher Specimen Data

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Species or other taxon	Date collected, Plant collected from*	Number of: Larvae	Nymphs	Adults
Slide mounted specimens				
Thysanoptera				
Aeolothripidae *Aeolothrips fasciatus* L.	June 21 2005, CORLAN			4
Thripidae	June 21 2005, CORLAN			3
Specimens in ethanol				
Hymenoptera				
Encyrtidae *Copidosoma*	Sept. 9 2005, HELSTR			4
Figitidae Eucoilinae	August 23 2005, LOBMAR			6
Eurytomidae *Bruchophagus*	August 23 2005, LOBMAR			5
Eupelmidae (5 males in 1 vial):				
Halticoptera	August 23 2005, LOBMAR			1
Pteromalus	August 23 2005, LOBMAR			2
? (no antennae)	August 23 2005, LOBMAR			1
Arachnida Araneae				
Salticidae	July 20 2004, SCRMAR			1
Salticidae	August 24, 2004, HELSTR			2
Tetragnathidae	August 10 2004, DESCAD			1
Thomisidae	July 13 2004, SCRMAR			1
Thomisidae	August 3 2004, VERSTR			1
Thomisidae	August 3 2004, FAGESC			2
Homoptera Aphididae	June 8 2004, LOBMAR			1
Neuroptera Chrysopidae	July 28 2004, SCRMAR	1		

*All specimens collected: USA Michigan, Ingham County, Michigan State University Campus, Ent. Farm. 42º 41'31N 84 º29'24W. Elevation 265 m. Date noted above. Anna K. Fiedler. Voucher number 2006-04

APPENDIX D

Natural enemy taxa collected at plants during full bloom period in 2004 and 2005. Groups of natural enemies with fewer than 10 total in 2005 are excluded. These include: Staphylinidae, Pentatomidae, Reduviidae, Conopidae, Hemerobiidae, and Mantidae. Numbers represent the total of included natural enemies collected in the number of samples listed. ^*Plagiognathus politus* Uhler and *Chlamydatus associatus* Uhler were counted as natural enemies. *Aeolothripidae were identified as *Aeolothrips fasciatus* (L.), and counted as natural enemies. Aeolothripidae were not counted separately from herbivorous thrips in 2004; in 2005, 119 of 986 total thrips were Aeolothripidae.

	Taxa	Number of samples		Arachnida: Arachnida		Thysanoptera: Aeolothripidae*		Hemiptera: Anthocoridae		Hemiptera: Miridae^		Hemiptera: Nabidae	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	0	15	.	5		0	.	0	.	0	.	0
	F. virginiana	12	15	6	12		0	0	0	0	0	0	1
	G. maculatum	13	15	3	4		0	0	2	0	0	0	0
	Aq. canadensis	10	15	0	0		0	0	0	0	0	0	0
	Z. aurea	14	15	1	3		0	0	20	0	1	0	0
	S. obovatus	15	14	5	0		0	0	10	0	0	0	1
	H. virginianum	15	10	1	7		0	0	1	0	2	0	0
	An. canadensis	15	15	1	7		1	0	112	0	4	0	0
	P. hirsutus	15	15	3	2		10	1	30	0	0	0	0
	A. atropurpurea	0	15	.	2		2	.	77	.	0	.	0
	H. maximum	15	12	0	2		1	11	32	0	0	0	0
	H. americana	7	15	0	0		0	0	0	0	1	0	1
	C. lanceolata	15	15	20	3		74	30	180	1	34	0	0
Mid Season	*V. faba*	14	15	11	6		0	80	46	0	8	1	1
	P. fruticosa	15	15	40	45		3	150	190	4	5	2	22
	A. cannabinum	6	15	1	45		1	0	22	0	5	0	0
	C. americana	0	8	.	8		0	.	2	.	0	.	1
	A. tuberosa	3	15	0	8		0	0	4	0	0	0	2
	R. setigera	0	13	.	27		2	.	27	.	2	.	2
	C. occidentalis	5	10	3	10		1	2	24	0	0	0	0
	C. sativum	15	14	18	13		1	123	16	0	3	1	2
	S. marilandica	15	15	11	13		0	4	3	0	0	0	0
	F. esculentum	15	15	14	29		6	315	87	0	0	0	30
	V. stricta	15	15	15	15		0	16	62	0	8	0	5
	A. incarnata	15	15	7	21		1	13	18	0	1	0	1
	V. virginicum	15	15	2	11		0	11	59	0	0	1	0
	R. pinnata	12	15	6	53		6	1	60	0	11	0	13
	A. canescens	0	15	.	3		0	.	5	.	1	.	8
	O. biennis	15	15	7	12		0	20	39	0	87	2	4
	A. cernuum	15	15	7	11		0	2	28	0	9	0	4
	D. canadense	15	15	6	8		0	1	1	0	1	0	2
	S. alba	0	15	.	28		1	.	164	.	17	.	10
Late season	*A. nepetoides*	15	15	13	42		3	54	60	0	69	0	5
	M. punctata	15	6	66	22		0	44	40	33	81	1	1
	V. missurica	15	15	16	36		0	6	24	0	21	0	0
	S. perfoliatum	15	15	20	31		1	23	142	1	72	0	0
	C. atriplicifolia	14	15	14	17		0	15	92	0	20	0	0
	E. perfoliatum	12	15	38	55		0	863	1249	3	336	0	3
	L. siphilitica	15	15	26	30		0	147	102	2	34	2	4
	A. graveolens	15	15	24	10		0	22	2	0	19	2	1
	L. maritima	15	15	74	36		2	515	263	6	40	1	23
	H. strumosus	15	15	36	37		0	39	42	0	10	0	0
	L. hirta	0	15	.	11		1	.	28	.	7	.	0
	L. aspera	7	15	3	16		0	4	26	0	4	0	0
	S. riddellii	15	15	53	24		1	276	272	6	4	1	0
	S. speciosa	15	15	20	49		0	101	180	13	1	0	3
	A. novae-angliae	15	15	95	58		0	497	227	3	0	0	0
	A. laevis	15	15	54	41		1	339	189	3	0	0	3
	Total per taxa			740	928		119	3725	4259	75	918	14	153

	Taxa	Coleoptera						Neuroptera		Hymenoptera			
		Cantharidae		Carabidae		Coccinellidae		Chrysopidae		Braconidae		Chalcidoidea	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	.	0	.	0	.	0	.	0	.	1	.	1
	F. virginiana	0	0	0	1	1	0	0	0	0	11	5	41
	G. maculatum	0	0	0	0	0	1	0	0	0	2	3	5
	Aq. canadensis	0	0	0	0	0	0	0	0	0	0	0	0
	Z. aurea	0	0	0	0	1	10	0	1	0	2	1	85
	S. obovatus	0	1	1	0	0	5	0	0	0	0	1	8
	H. virginianum	0	0	0	0	0	0	0	0	0	4	3	15
	An. canadensis	0	1	0	0	0	0	0	1	1	14	2	57
	P. hirsutus	0	0	0	0	0	1	0	0	0	14	4	70
	A. atropurpurea	.	4	.	0	.	7	.	0	.	4	.	261
	H. maximum	7	3	0	0	2	0	1	0	4	1	52	38
	H. americana	0	0	0	0	0	1	0	0	0	0	0	5
	C. lanceolata	9	6	1	1	1	0	0	3	2	13	68	48
Mid Season	*V. faba*	0	0	0	0	14	90	3	5	2	1	38	20
	P. fruticosa	14	20	0	0	0	11	1	5	3	5	160	77
	A. cannabinum	0	12	0	0	0	38	0	13	0	1	3	126
	C. americana	.	0	.	0	.	0	.	0	.	2	.	7
	A. tuberosa	0	0	0	0	0	0	0	0	0	2	0	7
	R. setigera	.	0	.	0	.	0	.	0	.	2	.	15
	C. occidentalis	0	0	0	0	0	1	1	0	0	1	1	33
	C. sativum	56	0	1	1	0	5	2	1	3	1	57	74
	S. marilandica	0	0	0	0	2	3	3	3	0	0	9	29
	F. esculentum	3	1	0	1	5	13	7	3	1	6	67	57
	V. stricta	0	0	0	1	2	2	1	6	2	2	22	36
	A. incarnata	0	1	0	0	8	4	2	3	0	0	7	23
	V. virginicum	0	0	0	1	0	2	0	0	1	3	4	6
	R. pinnata	0	2	0	1	0	1	0	4	0	4	18	89
	A. canescens	.	0	.	0	.	1	.	0	.	0	.	1
	O. biennis	0	0	0	0	1	7	7	0	0	5	10	14
	A. cernuum	0	2	0	0	1	3	0	1	0	0	11	5
	D. canadense	0	0	0	0	0	0	0	1	0	0	0	8
	S. alba	.	23	.	6	.	10	.	2	.	6	.	45
Late season	*A. nepetoides*	0	5	0	0	1	7	0	5	0	2	34	70
	M. punctata	3	190	2	6	2	4	0	0	0	2	32	14
	V. missurica	1	1	0	0	2	17	0	0	1	3	103	377
	S. perfoliatum	19	94	0	0	1	10	0	5	0	2	172	280
	C. atriplicifolia	4	48	0	0	0	7	0	0	0	1	68	83
	E. perfoliatum	92	949	0	0	3	14	0	0	2	6	195	288
	L. siphilitica	9	62	0	0	1	47	1	1	3	6	117	94
	A. graveolens	1	12	0	0	41	14	1	5	5	1	230	37
	L. maritima	4	22	0	3	2	7	0	0	10	62	454	278
	H. strumosus	7	70	0	0	0	10	0	1	2	5	192	229
	L. hirta	.	0	.	0	.	51	.	0	.	2	.	16
	L. aspera	0	9	0	0	2	18	1	0	0	1	4	29
	S. riddellii	44	2	1	2	3	46	1	0	10	4	184	146
	S. speciosa	16	2	0	4	7	79	1	0	3	6	91	93
	A. novae-angliae	0	0	0	0	2	21	1	0	1	8	96	104
	A. laevis	0	0	0	0	2	19	0	0	1	7	26	41
	Total per taxa	289	1542	6	28	107	587	34	69	57	225	2544	3485

		Hymenoptera										Diptera	
	Taxa	Cynipoidea		Bethylinidae		Ichneumonidae		Sphecidae		Vespidae polistes		Syrphidae	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	.	0	0	0	.	0	.	0	.	0	.	0
	F. virginiana	4	3	0	0	1	5	0	0	0	0	0	0
	G. maculatum	0	3	0	0	1	0	0	0	0	0	0	0
	Aq. canadensis	0	0	0	0	0	0	0	0	0	0	0	0
	Z. aurea	0	15	0	0	0	0	0	0	0	0	0	0
	S. obovatus	0	1	0	0	0	1	0	0	0	0	5	1
	H. virginianum	0	1	0	0	0	0	0	0	0	0	0	0
	An. canadensis	0	7	0	0	0	1	0	0	0	0	1	1
	P. hirsutus	0	10	0	0	0	2	0	0	0	0	0	1
	A. atropurpurea	.	22	0	0	.	0	.	1	.	1	.	0
	H. maximum	45	12	0	0	9	0	4	0	3	0	13	3
	H. americana	0	0	0	0	0	0	0	0	0	0	1	0
	C. lanceolata	0	2	0	0	0	1	0	0	0	1	2	12
Mid Season	*V. faba*	3	2	0	0	2	7	0	2	0	1	1	4
	P. fruticosa	8	16	0	0	1	2	0	0	0	0	1	16
	A. cannabinum	0	25	0	0	0	3	0	1	0	0	0	7
	C. americana	.	2	0	0	.	1	.	0	.	0	.	5
	A. tuberosa	0	0	0	0	0	0	0	2	0	0	0	1
	R. setigera	.	5	0	0	.	2	.	0	.	0	.	6
	C. occidentalis	0	0	0	0	0	0	0	0	0	0	0	0
	C. sativum	8	2	0	0	3	0	1	10	2	0	86	33
	S. marilandica	0	0	0	0	0	1	0	1	5	12	5	5
	F. esculentum	10	13	0	0	3	2	0	3	1	1	12	7
	V. stricta	0	0	0	0	2	2	0	0	0	0	0	1
	A. incarnata	0	5	0	0	0	0	0	8	0	0	0	2
	V. virginicum	2	0	0	0	1	0	0	0	0	0	1	4
	R. pinnata	0	4	0	0	0	0	0	0	0	0	1	15
	A. canescens	.	1	0	0	.	0	.	0	.	0	.	1
	O. biennis	2	0	0	0	0	0	0	0	0	0	2	1
	A. cernuum	0	0	0	0	1	0	0	0	0	0	0	0
	D. canadense	0	2	0	0	0	1	0	0	0	0	0	1
	S. alba	.	12	0	0	.	3	.	5	.	1	.	2
Late season	*A. nepetoides*	1	0	0	1	0	0	0	0	0	0	0	2
	M. punctata	2	9	0	2	1	0	0	0	0	0	0	0
	V. missurica	0	4	0	0	1	1	0	0	0	0	0	2
	S. perfoliatum	0	1	0	0	0	0	0	5	1	0	0	2
	C. atriplicifolia	0	4	0	0	1	1	0	6	0	1	0	3
	E. perfoliatum	8	54	0	2	3	0	0	18	0	1	1	1
	L. siphilitica	5	7	0	2	3	0	0	7	0	0	0	0
	A. graveolens	2	1	0	0	1	2	1	4	10	2	2	0
	L. maritima	52	168	0	2	4	4	0	3	0	0	11	3
	H. strumosus	1	0	0	0	0	0	0	0	0	0	1	1
	L. hirta	.	0	0	1	.	0	.	0	.	0	.	0
	L. aspera	0	0	0	0	0	0	0	0	0	0	0	1
	S. riddellii	4	17	0	0	2	4	3	0	4	58	2	0
	S. speciosa	2	6	0	0	0	11	1	2	0	14	2	0
	A. novae-angliae	2	5	0	2	2	12	0	0	0	1	2	0
	A. laevis	0	0	0	1	5	5	0	0	0	1	6	0
	Total per taxa	161	441	0	13	47	74	10	78	26	95	158	144

	Taxa	Diptera										Total per plant species	
		Stratiomyidae		Empididae		Tachinidae		Bombyliidae		Dolichopodidae			
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	0	0	.	3	.	0	.	0	.	0	.	10
	F. virginiana	0	0	0	11	0	0	0	0	0	1	17	86
	G. maculatum	0	0	0	1	0	0	0	0	0	0	7	18
	Aq. canadensis	0	0	0	0	0	0	0	0	0	0	0	0
	Z. aurea	0	0	0	60	0	0	0	0	0	0	3	197
	S. obovatus	0	0	0	2	0	0	0	0	0	0	12	30
	H. virginianum	0	0	0	6	0	0	0	0	0	0	4	36
	An. canadensis	0	0	0	59	0	0	0	0	2	0	7	265
	P. hirsutus	0	0	0	4	0	0	0	0	0	0	8	144
	A. atropurpurea	0	0	.	96	.	0	.	0	.	0	.	477
	H. maximum	0	0	23	4	0	0	0	0	0	1	174	97
	H. americana	0	0	0	0	0	0	0	0	0	0	1	8
	C. lanceolata	0	4	2	43	0	1	4	0	0	0	139	426
Mid Season	*V. faba*	0	0	11	91	0	0	0	0	1	6	167	290
	P. fruticosa	0	6	1	30	0	0	0	0	2	2	383	455
	A. cannabinum	0	4	0	184	0	1	0	0	0	9	4	497
	C. americana	0	0	.	3	.	0	.	0	.	0	.	31
	A. tuberosa	0	0	0	10	0	0	0	0	0	0	0	36
	R. setigera	0	0	.	15	.	0	.	0	.	4	.	109
	C. occidentalis	0	0	0	25	0	0	0	0	0	2	7	97
	C. sativum	0	1	6	3	1	0	0	0	4	3	372	169
	S. marilandica	0	0	6	41	0	0	0	0	1	4	46	115
	F. esculentum	0	0	55	8	0	1	0	0	2	5	495	273
	V. stricta	0	0	6	16	0	0	0	0	2	0	68	156
	A. incarnata	0	0	0	22	0	1	0	0	10	3	47	114
	V. virginicum	0	0	0	4	0	0	0	0	0	5	23	95
	R. pinnata	0	1	0	20	0	1	0	0	0	11	26	296
	A. canescens	0	0	.	0	.	0	.	0	.	0	.	21
	O. biennis	0	0	6	1	0	0	0	0	1	1	58	171
	A. cernuum	0	0	0	1	0	0	0	0	0	0	22	64
	D. canadense	0	0	1	2	0	0	0	0	2	2	10	29
	S. alba	0	1	.	10	.	0	.	0	.	2	.	348
Late season	*A. nepetoides*	0	0	24	30	1	0	0	0	1	1	129	302
	M. punctata	0	1	0	1	0	0	0	0	0	0	153	373
	V. missurica	0	0	0	9	0	0	0	0	0	2	130	497
	S. perfoliatum	0	0	2	3	0	0	1	0	0	5	239	653
	C. atriplicifolia	0	0	1	5	0	0	0	0	0	2	103	290
	E. perfoliatum	0	2	16	16	0	1	0	0	3	1	1224	2996
	L. siphilitica	0	0	1	3	0	0	0	0	1	1	315	400
	A. graveolens	0	0	6	0	2	0	0	0	0	0	350	110
	L. maritima	0	0	1	1	0	1	0	1	14	2	1101	921
	H. strumosus	0	0	8	2	0	0	3	21	6	0	295	428
	L. hirta	0	0	.	1	.	0	.	0	.	0	.	118
	L. aspera	0	0	0	0	0	0	0	0	0	0	14	104
	S. riddellii	0	0	4	3	0	4	0	0	0	0	589	587
	S. speciosa	0	0	0	1	0	1	0	0	0	0	244	452
	A. novae-angliae	0	0	2	4	0	0	0	0	0	0	699	442
	A. laevis	0	0	0	3	0	0	0	0	0	0	433	311
	Total per taxa	0	20	182	857	4	12	8	22	52	75	8160	14144

APPENDIX E

Herbivore taxa collected at plants during full bloom period in 2004 and 2005. Groups of herbivores with fewer than 10 total in 2005 are excluded. These include: Psyllidae, Tenthredinidae, Pieridae, and Yponomeutidae. Numbers represent the total of included herbivores collected in the number of samples listed. *2004 Thysanoptera include herbivorous and predatory species; 2005 numbers include only herbivorous Thysanoptera, many of which were Thripidae. ^^Tephritidae and Otitidae were counted separately in 2005 only, In 2005 32 total Tephritids and 109 Otitidae were collected; in 2004, 92 Tephritidae and Otitidae were collected.

	Taxa	Number of samples		Orthoptera		Hemiptera							
					**	Aphididae		Cercopidae		Cicadellidae		Miridae	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	S. racemosa	0	15	.	0	.	0	.	0	.	1	.	3
	F. virginiana	12	15	0	0	0	3	0	10	6	68	1	41
	G. maculatum	13	15	0	0	1	3	0	5	1	4	5	12
	Aq. canadensis	10	15	0	0	0	9	0	4	0	1	0	18
	Z. aurea	14	15	0	0	0	30	1	3	0	10	0	47
	S. obovatus	15	14	0	0	0	50	2	2	9	13	2	59
	H. virginianum	15	10	0	2	0	1	0	1	2	3	3	23
	An. canadensis	15	15	0	0	2	4	0	20	6	17	2	39
	P. hirsutus	15	15	0	1	1	16	1	18	2	9	4	216
	A. atropurpurea	0	15	.	0	.	57	.	1	.	19	.	180
	H. maximum	15	12	0	0	1	33	1	1	4	1	12	48
	H. americana	7	15	0	0	0	14	0	0	0	0	0	4
	C. lanceolata	15	15	0	0	2	5	0	7	74	92	46	170
Mid Season	V. faba	14	15	1	5	15	1580	2	4	1234	562	94	189
	P. fruticosa	15	15	2	23	1	10	0	22	67	51	84	491
	A. cannabinum	6	15	0	2	26	660	0	0	0	2	0	17
	C. americana	0	8	.	0	.	2	.	1	.	7	.	118
	A. tuberosa	3	15	0	2	0	9	0	3	2	4	0	24
	R. setigera	0	13	.	9	.	4	.	12	.	27	.	117
	C. occidentalis	5	10	0	0	0	3	0	0	4	5	0	40
	C. sativum	15	14	0	6	40	70	0	0	93	66	188	756
	S. marilandica	15	15	0	0	2	3	0	1	35	28	18	109
	F. esculentum	15	15	0	3	6	13	1	7	25	17	165	289
	V. stricta	15	15	2	1	5	33	1	6	8	15	73	656
	A. incarnata	15	15	0	1	2	22	0	0	4	9	3	22
	V. virginicum	15	15	2	0	3	12	0	0	4	4	31	213
	R. pinnata	12	15	0	13	0	10	0	5	7	57	10	357
	A. canescens	0	15	.	0	.	15	.	0	.	18	.	18
	O. biennis	15	15	1	1	4	10	1	2	357	178	166	491
	A. cernuum	15	15	0	1	5	5	0	0	4	0	1	29
	D. canadense	15	15	1	0	9	121	0	1	16	5	8	11
	S. alba	0	15	.	2	.	12	.	8	.	7	.	16
Late season	A. nepetoides	15	15	0	0	1	2	0	0	20	11	42	96
	M. punctata	15	6	1	0	8	1	0	0	6	14	114	111
	V. missurica	15	15	0	0	1	1	0	5	22	14	47	40
	S. perfoliatum	15	15	0	0	0	1	2	1	14	9	19	84
	C. atriplicifolia	14	15	0	0	0	1	0	0	1	18	2	44
	E. perfoliatum	12	15	1	0	0	4	0	0	40	7	296	957
	L. siphilitica	15	15	4	0	5	4	2	1	10	6	204	349
	A. graveolens	15	15	0	0	61	3	0	1	7	11	63	86
	L. maritima	15	15	0	3	3	10	0	4	61	21	595	303
	H. strumosus	15	15	1	0	1	0	0	2	22	5	32	26
	L. hirta	0	15	.	0	.	0	.	1	.	11	.	14
	L. aspera	7	15	0	0	1	2	0	2	2	5	2	14
	S. riddellii	15	15	2	1	3	6	1	6	42	36	494	161
	S. speciosa	15	15	1	0	0	0	0	5	21	36	744	1101
	A. novae-angliae	15	15	3	0	1	2	0	2	89	29	394	383
	A. laevis	15	15	1	0	0	0	0	0	21	12	213	258
	Total per taxa			23	76	210	2856	15	174	2342	1545	4177	8850

	Taxa	Hemiptera				Thysanoptera		Coleoptera					
		Pentatomidae		Tingidae		Thripidae*		Cerambycidae		Chrysomelidae		Curculionidae	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	S. racemosa	.	0	.	0	.	0	.	0	.	0	.	0
	F. virginiana	0	2	0	0	1	25	0	0	0	2	0	10
	G. maculatum	0	0	0	0	6	12	0	0	0	1	1	0
	Aq. canadensis	0	0	0	0	0	6	0	0	0	0	0	0
	Z. aurea	0	0	0	0	0	64	0	0	0	2	0	4
	S. obovatus	0	1	0	0	9	85	0	0	1	0	1	0
	H. virginianum	0	1	0	0	0	2	0	0	0	0	0	1
	An. canadensis	0	1	0	0	3	24	0	0	2	0	0	1
	P. hirsutus	1	1	0	0	5	54	0	0	0	0	0	0
	A. atropurpurea	.	0	.	0	.	85	.	0	.	0	.	3
	H. maximum	0	1	0	0	10	101	0	0	0	0	0	0
	H. americana	0	37	0	0	2	6	0	0	0	0	0	0
	C. lanceolata	2	1	0	0	0	118	0	0	16	0	0	4
Mid Season	V. faba	0	3	0	0	37	3	0	0	5	0	0	0
	P. fruticosa	0	13	0	0	3	29	0	0	2	0	0	3
	A. cannabinum	0	0	0	0	0	9	0	0	0	19	0	3
	C. americana	.	0	.	0	.	9	.	0	.	0	.	1
	A. tuberosa	0	0	0	0	0	2	0	0	0	1	0	0
	R. setigera	.	0	.	0	.	25	.	0	.	2	.	3
	C. occidentalis	0	0	0	0	0	4	0	0	0	2	0	0
	C. sativum	3	2	0	0	228	10	0	0	5	1	0	1
	S. marilandica	2	3	0	0	17	4	0	0	0	4	0	0
	F. esculentum	3	4	0	0	12	12	0	0	4	5	0	0
	V. stricta	0	2	0	0	5	7	0	0	1	16	0	0
	A. incarnata	0	1	1	0	11	6	0	13	1	20	0	1
	V. virginicum	2	1	0	0	21	4	0	0	0	7	0	0
	R. pinnata	0	1	0	38	0	23	0	0	0	21	0	0
	A. canescens	.	2	.	0	.	1	.	0	.	2	.	0
	O. biennis	1	3	0	0	85	13	0	0	2	10	2	4
	A. cernuum	0	6	0	0	3	9	0	0	4	24	0	0
	D. canadense	0	4	0	0	6	40	0	0	5	5	0	0
	S. alba	.	0	.	0	.	6	.	9	.	10	.	4
Late season	A. nepetoides	0	1	0	0	9	10	0	1	6	33	0	0
	M. punctata	0	11	0	0	9	6	0	0	6	62	4	5
	V. missurica	1	2	0	1	2	2	0	1	2	28	0	0
	S. perfoliatum	0	1	0	0	5	4	0	5	10	108	0	0
	C. atriplicifolia	0	0	0	0	1	2	0	2	4	6	0	4
	E. perfoliatum	0	0	0	0	7	8	9	64	93	111	38	42
	L. siphilitica	1	3	0	0	3	3	0	0	5	11	2	12
	A. graveolens	0	2	0	0	1	2	0	0	12	9	0	0
	L. maritima	6	37	0	0	6	1	0	0	347	2073	6	1
	H. strumosus	0	0	0	10	27	6	1	0	11	114	0	0
	L. hirta	.	0	.	0	.	4	.	1	.	4	.	0
	L. aspera	0	1	0	0	1	0	0	0	0	6	0	0
	S. riddellii	0	1	0	0	6	12	54	34	13	38	2	2
	S. speciosa	0	2	0	8	0	2	20	87	66	82	2	10
	A. novae-angliae	6	3	12	42	7	7	0	0	78	39	0	3
	A. laevis	0	9	0	12	3	0	0	0	110	12	0	1
	Total per taxa	28	163	13	111	551	867	84	217	811	2890	58	123

		Coleoptera				Lepidoptera							
	Taxa	*Elateridae*		*Scarabaeidae*		*Lepidoptera^*		*Arctiidae*		*Gelechiodea*		*Noctuidae*	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	.	1	.	0	.	0	.	0	.	0	.	0
	F. virginiana	0	0	0	0	2	1	0	0	0	2	0	0
	G. maculatum	0	0	1	0	0	0	0	0	0	0	0	0
	Aq. canadensis	0	0	0	0	0	0	0	0	0	0	0	0
	Z. aurea	0	1	0	0	0	0	0	0	0	2	0	0
	S. obovatus	0	0	0	0	1	0	0	0	0	1	0	0
	H. virginianum	0	0	0	0	0	4	0	0	0	0	0	0
	An. canadensis	0	0	0	0	0	2	0	0	0	7	0	0
	P. hirsutus	0	0	0	0	0	3	0	0	0	1	0	0
	A. atropurpurea	.	1	.	0	.	0	.	0	.	0	.	0
	H. maximum	0	0	0	0	143	1	0	0	0	0	0	0
	H. americana	0	0	0	0	0	0	0	0	0	0	0	0
	C. lanceolata	0	0	0	0	2	16	0	0	0	0	0	0
Mid Season	*V. faba*	0	0	9	1	1	2	0	0	0	2	0	0
	P. fruticosa	0	0	0	38	5	13	0	1	0	13	0	0
	A. cannabinum	0	0	1	17	0	16	0	0	0	3	0	0
	C. americana	.	0	.	0	.	0	.	0	.	0	.	0
	A. tuberosa	0	0	0	0	0	4	0	0	0	0	0	0
	R. setigera	.	0	.	41	.	3	.	0	.	2	.	0
	C. occidentalis	0	0	1	4	0	1	0	6	0	1	0	0
	C. sativum	0	0	9	0	3	1	0	0	0	2	0	0
	S. marilandica	0	0	0	2	0	1	0	0	0	0	0	0
	F. esculentum	0	0	165	50	0	1	0	0	0	0	0	0
	V. stricta	0	0	0	7	15	47	0	0	0	4	0	0
	A. incarnata	0	0	3	5	4	6	0	1	0	0	0	0
	V. virginicum	0	0	0	4	0	0	0	5	0	1	0	0
	R. pinnata	0	0	0	15	0	14	0	2	0	2	0	0
	A. canescens	.	0	.	14	.	1	.	0	.	0	.	0
	O. biennis	0	0	129	159	0	2	0	0	0	6	0	3
	A. cernuum	0	0	0	0	2	0	0	1	0	11	0	0
	D. canadense	0	0	191	258	3	2	0	0	0	0	0	0
	S. alba	.	0	.	72	.	0	.	6	.	2	.	1
Late season	*A. nepetoides*	0	0	4	17	12	4	0	6	0	2	0	0
	M. punctata	0	0	0	1	6	8	0	0	0	1	0	0
	V. missurica	0	0	0	13	2	3	0	1	0	2	0	2
	S. perfoliatum	0	0	0	21	2	0	2	6	0	4	1	0
	C. atriplicifolia	0	0	1	0	1	2	0	1	0	0	0	0
	E. perfoliatum	0	0	0	2	19	36	0	15	0	26	0	0
	L. siphilitica	0	11	1	2	20	4	0	4	0	3	0	3
	A. graveolens	0	0	1	0	0	1	1	0	0	0	0	0
	L. maritima	0	0	0	1	20	15	0	4	0	7	0	0
	H. strumosus	0	0	0	0	4	7	1	2	0	3	0	1
	L. hirta	.	0	.	26	.	1	.	0	.	0	.	0
	L. aspera	0	0	0	0	1	2	0	1	0	0	0	1
	S. riddellii	0	0	0	0	8	0	4	3	0	0	1	0
	S. speciosa	0	0	1	1	5	5	19	29	0	1	1	1
	A. novae-angliae	0	0	1	5	5	17	2	4	0	6	2	0
	A. laevis	0	0	0	1	5	2	0	3	0	2	0	0
	Total per taxa	0	14	518	777	291	248	29	101	0	119	5	12

		Lepidoptera				Diptera					
	Taxa	*Nymphalidae*		*Pyralidae*		*Anthomyiidae*		*Tephritidae*		**Total per plant species**	
	Plant Species	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Early Season	*S. racemosa*	.	0	.	0	.	0		0	.	5
	F. virginiana	0	0	0	0	1	3		0	11	167
	G. maculatum	0	0	0	0	5	1		0	20	38
	Aq. canadensis	0	0	0	0	0	0		0	0	38
	Z. aurea	0	0	0	0	3	4		0	4	167
	S. obovatus	0	1	0	0	3	1		0	28	213
	H. virginianum	0	0	0	0	37	12		0	42	50
	An. canadensis	0	0	0	0	1	13		0	16	128
	P. hirsutus	0	0	0	0	0	28		0	14	347
	A. atropurpurea	.	0	.	0	.	45		0	.	391
	H. maximum	0	0	0	0	60	73		0	231	259
	H. americana	0	0	0	0	0	1		0	2	62
	C. lanceolata	0	0	0	0	0	14		0	142	427
Mid Season	*V. faba*	0	0	1	0	1	17		3	1400	2371
	P. fruticosa	1	0	0	0	2	2		0	167	709
	A. cannabinum	0	0	0	0	0	11		0	27	759
	C. americana	.	0	.	0	.	5		1	.	144
	A. tuberosa	0	1	0	0	0	3		0	2	53
	R. setigera	.	0	.	0	.	2		5	.	252
	C. occidentalis	0	0	0	0	0	0		0	5	66
	C. sativum	0	0	0	0	6	2		0	575	917
	S. marilandica	0	0	0	0	1	0		1	75	156
	F. esculentum	0	0	0	0	0	0		0	381	401
	V. stricta	0	0	0	0	0	2		7	110	803
	A. incarnata	0	6	0	0	0	0		3	29	116
	V. virginicum	0	2	0	0	1	0		1	64	254
	R. pinnata	0	0	0	1	0	0		4	17	563
	A. canescens	.	0	.	0	.	0		0	.	71
	O. biennis	0	0	1	0	1	0		0	750	882
	A. cernuum	0	0	1	5	0	0		0	20	91
	D. canadense	0	0	0	0	0	0		1	239	448
	S. alba	.	0	.	0	.	0		0	.	155
Late season	*A. nepetoides*	0	0	0	1	0	0		0	94	184
	M. punctata	0	0	0	0	1	0		0	155	220
	V. missurica	0	0	0	1	0	0		4	77	120
	S. perfoliatum	0	2	0	0	0	0		0	55	246
	C. atriplicifolia	0	0	0	1	0	0		0	10	81
	E. perfoliatum	0	0	0	0	1	0		1	504	1273
	L. siphilitica	0	0	0	8	1	0		0	258	424
	A. graveolens	0	0	0	0	0	0		0	146	115
	L. maritima	0	0	0	15	91	2		0	1135	2497
	H. strumosus	0	0	0	0	0	0		0	100	176
	L. hirta	.	0	.	0	.	0		0	.	62
	L. aspera	0	0	0	1	0	0		1	7	36
	S. riddellii	0	3	0	3	0	0		0	630	306
	S. speciosa	0	0	1	0	0	1		0	881	1371
	A. novae-angliae	2	0	0	0	2	0		0	604	542
	A. laevis	0	0	0	0	0	0		0	353	312
	Total per taxa	3	15	4	36	218	242		32	9380	19468

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