THE EFFECT OF ALIEN PLANTS ON THE SURVIVAL OF LARVAL LEPIDOPTERA

by
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A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Honors Bachelor of Science in Biological Sciences with Distinction.

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ABSTRACT

The proliferation of alien plants and their widespread replacement of native plants is predicted to negatively affect the insect community. Conservation biocontrol seeks to protect natural enemies, such as predators and parasitoids, through methods such as habitat management, in which plants are used to provide necessary resources to natural enemies. Native plants may support a stronger population of natural enemies than exotic plants. Bagworm and polyphemus moth larvae were placed in alien and native plant plots, and their survival was tracked until pupation. It was predicted that plots planted with native plants would have enhanced natural enemy communities, resulting in increased mortality in caterpillar larvae. Thus, larval survival would serve as a relative measure of the natural enemy community in plots planted with alien plants versus plots planted with native plants. No difference was found between the survival of bagworm larvae between alien and native plots. Almost no difference was found in the survival of polyphemus larvae, though the polyphemus moth experiment may have been confounded by differing rates of growth based on food plant.
Chapter 1

INTRODUCTION

Conversion of land from natural habitat for residential, industrial, or agricultural purposes has a major impact on the environment (Dobson et al. 1997). With about 3-5% of the land in the United States left undisturbed, native animal species depend on coexistence on land with people to survive (Rosenzweig 2003). In human dominated ecosystems, native plants are being replaced by aliens (Tallamy 2007), which are defined by having their evolutionary history elsewhere (Tallamy 2004). There has been a long history of transporting alien plants into the United States, followed by their naturalization (Mack and Erneberg 2002). At least 500 alien plant species are seriously invasive in the United States (Blossey 1999). Most alien plants that have become established were deliberately released as part of ornamental horticulture (Mack and Erneberg 2002).

Alien plant species are a threat to North American ecosystems (Blossey 1999). Many studies show that invertebrate diversity decreases in habitats due to aliens (Tallamy 2004). High biodiversity is important in maintaining the stability and productivity of ecosystems (Strong 1992; Tilman 1999). Biodiversity builds redundancy – in which various species have the same role – which prevents food web collapse and increases environmental stability (Tallamy 2007). High biodiversity can also decrease an ecosystem’s susceptibility to invasions by exotic species (Tilman 1999). A decrease in biodiversity can cause a cascade of other negative ecological effects (Naeem et al. 1994).
Insects are the most important taxon in terms of transferring energy from plants to higher trophic levels (Tallamy 2007). Insects are important as a food source for many animals, including carnivorous insects, birds, bats, amphibians, some reptiles, and many larger mammals (Grissell 2001). Many studies have shown that insectivorous birds depend on the quantity and quality of their insect food supply (Tallamy 2004); 96% of birds feed insects to their young (Dickinson 1999). Without invertebrates such as insects, the earth would be devoid of higher life (Wilson 1987).

In insects, there are three main feeding guilds: scavengers, herbivores, and carnivores (Grissell 2001). There are three main types of carnivores, or “natural enemies” to herbivores: predators, parasites, and “parasitoids” (Price et al. 1980). Parasitoids are insects that lay their eggs on or in a host insect; the eggs hatch and the larvae develop, feeding on the host (Grissell 2001). Caterpillar parasitoids include tachinid flies and braconid and ichneumonid wasps (Janzen 1988). Specialist parasitoids tend to attack only specific instars (stages within the larval stage) of their host (Price et al. 1980).

Natural enemies depend on their prey. A diversity of alternate host species can increase longevity and fecundity in natural enemies (Frank et al. 2008). However, this diversity of herbivores depends upon a diversity of native plants. Most insect herbivores are specialists, only consuming a select few closely related plants (Bernays and Graham 1988; Novotny et al. 2002), while only about 10% of herbivorous insects are estimated to be generalists and able to grow and reproduce on unrelated plants (Bernays and Graham 1998). Lepidoptera have been observed to be the most specialized of herbivorous insects (Novotny et al. 2002). In the Costa Rican dry forest in Santa Rosa where there are over 3000 species of Lepidoptera, a plant species is used
by an average of only 4 to 8 caterpillar species (Janzen 1988). Congeneric trees (trees in the same genus) host similar communities of herbivorous insects because they tend to share many of the same phytochemicals (Kennedy and Southwood 1984). Some insects that feed on a variety of different foods over a large geographical range may be specialists in local communities (Fox and Morrow 1981). Insects overcome the chemistry of specific plants by specializing physiologically on digesting, storing, detoxifying, and excreting those chemicals. While this specialization enables them to utilize particular plant lineages, it also makes specialists more inefficient at using other plants (Ehrlich and Raven 1964). Studies have shown that some specialist insect herbivores can feed on alien congeners, but not necessarily to what degree (Keane and Crawley 2002). In biological control programs in which insects are introduced to feed on alien weed plants, if an alien plant to be controlled is closely related to a native, the introduced insects may pose a danger and feed on these native, non-target species of plants instead (Pemberton 2000).

The specificity in host plants by herbivorous insects is part of the enemy release hypothesis. The enemy release hypothesis attempts to explain the success of alien plants in new environments, making the following assumptions: 1) that most specialist herbivores will primarily feed on the native plants with which they share an evolutionary history and switch hosts to alien plants rarely, and 2) that generalist herbivores will also tend to feed more on native plants than they do on alien plants, as generalists also have host plant preferences. Thus, the enemy release hypothesis predicts that alien plants will support fewer insect herbivores than native plants (Keane and Crawley 2002; Tallamy 2004). However, there is still a controversy. Many studies that describe the small effect native insects have on alien plants are based on anecdotal
evidence. Other studies may incorrectly interpret their evidence in support of the hypothesis (Keane and Crawley 2002). Some studies have evidence supporting this hypothesis while others show evidence against it (Tallamy 2004). However, several studies show that alien plants support fewer herbivorous insects in their introduced range than in their native range; thus, native insects seem to utilize alien plants less as a food source than do insects in an alien plant’s ancestral range (Tallamy 2004).

While herbivorous insects are important, natural enemies are also directly affected by plants. Adult hymenopteran parasitoids feed on nectar and pollen (Ellis et al. 2005), which serve as significant attractants to these parasitoids, as well as raising longevity and fecundity (Price et al. 1980). Variation between plant species and within parts of the plants provides different refuges for herbivores from natural enemies, therefore affecting foraging efficiency. Herbivores may be outside of the area searched by natural enemies with a search pattern restricted to certain parts of plants. Certain plant traits may impede an enemy’s search for food such as hairs or secretions. Some plants may completely conceal the herbivores to enemies (Price et al. 1980). On the other hand, increased habitat complexity from a greater variety of plant species and structure is correlated with an increased natural enemy abundance (Tallamy 2007). Like herbivorous insects, natural enemies also share an evolutionary history with plants (Tallamy 2004). Natural enemies are another defense of plants against herbivores, and thus they have a mutualistic relationship (Price et al. 2004).

Gardeners often choose plants and maintain gardens in a way that excludes insects, increasing the risk of pest outbreaks (Grissell 2001). Exotic plants are traditionally chosen by gardeners over native plants for various reasons, such as aesthetic value and uniqueness, as well as unpalatability to insects (Tallamy 2004). In
a traditional garden with alien plants and low diversity of insect herbivores and carnivores, it is more likely for the ecosystem to become unstable and for an insect herbivore to reach pest levels (Grissell 2001).

Conservation biocontrol seeks to increase natural enemy diversity and abundance in the environment, which can lead to a reduction in pest populations, and thus a decrease in the need for pesticides. One form of conservation biocontrol is habitat management, in which plants are used to provide necessary resources to natural enemies, such as alternative foods and hosts, and refuges from disturbance. Although habitat management has recommended the use of exotic species, there are a number of advantages to using native plants, such as their local adaptation, a benefit to native plant communities and biodiversity, and a decreased likelihood of becoming invasive. (Fiedler and Landis 2007; Frank et al. 2008).

This study continues research in conservation biocontrol by comparing the effect of native plants in enhancing communities of natural enemies. Two species of Lepidoptera were chosen: bagworms, *Thyridopteryx ephemeraeformis*, and polyphemus moth, *Antheraea polyphemus*. The survival of their herbivorous larval stage (caterpillar) was measured in the experiment to quantify the effectiveness of natural enemy communities in two treatments: 1) in gardens consisting entirely of non-native plants, and 2) gardens built exclusively from native plants. If native plants provide a better habitat that promotes the efficacy of pest control in natural enemies, then the populations of caterpillar larvae will experience decreased survival in gardens with native plants than in gardens with exotic plants.
**Study Organisms**

Bagworms, *Thyridopteryx ephemeraeformis* (Figure 1), are in the family Psychidae. Members of this family are notable for living within a case created with silk and plant matter from their host plant, which they expand as they grow. Bagworms feed on a variety of plant species, including red cedar, *Juniperus virginiana*; in an outbreak, bagworms can cause serious defoliation. In most areas, there is only one generation of bagworms per season, and they pupate in late summer. Females remain in the case as wingless moths, while males emerge as moths and travel to fertilize females (Cranshaw 2004).

The polyphemus Moth, *Antheraea polyphemus* (Figure 2) is a member of the giant silk moths (family Saturniidae). The larvae grow relatively large, reaching 75 mm in length. These caterpillars occur through most of North America and feed on a variety of species of shrubs and trees, including maples. In the fall, they spin a tight cocoon with silk, either within a leaf on the host plant or in the leaf litter below a plant (Wagner 2005).

**Figure 1.** Bagworm, *Thyridopteryx ephemeraeformis*. Image Credit: D. Tallamy.

**Figure 2.** Polyphemus moth, *Antheraea polyphemus*. Image Credit: D. Tallamy.
Chapter 2
MATERIALS AND METHODS

The experiments were carried out in plots at three locations in Delaware, representing three replicates, one on the campus of the University of Delaware, one near White Clay Creek State Park, and one location near Middletown, DE. Each location had two circular plots 20 m in diameter, a plot planted with primarily alien plants, and a plot planted with native plants (Table 1). Thus, there were six plots. The alien and native plant species were planted in clusters of seven in each plot, and the clusters were planted in an approximate ring around the center. Two to four red cedars (*Juniperus virginiana*) were planted in clusters in the center of all plots (Figure 3). Six cabbages (*Brassica oleracea*) and six tomato plants (*Solanum lycopersicum*) were planted in a ring around the red cedar and within the ring formed by the other plants in all plots for separate experiments.

Bagworms and polyphemus moth adults were collected locally in Delaware and Maryland and then held until they laid eggs. Eggs were held until they hatched, and first instar larvae were placed within each plot.

Approximately 80 bagworms per plot were placed on red cedar in late June. Many died, and it is thought that mortality was not due to predation, but rather due to stress from transport. In July, the red cedar was repopulated with more locally-collected bagworms, resulting in approximately 40 bagworms per plot. Data for bagworm survival were only considered from this repopulation in July.
Approximately 15 polyphemus larvae per plot were placed on three trees per plot; there were 5 polyphemus larvae per plant. Polyphemus larvae in the native planted plots were placed on red maple, *Acer rubrum*, while larvae in the alien planted plots were placed on Norway maple, *Acer platanoides*. Two of the plants at one location (White Clay site) had only 2 polyphemus larvae, one plant on the alien side and one on the native side; thus, there were only 12 larvae in each plot at this location.

Numbers of larvae were recorded biweekly or weekly until pupation. Bagworm casings for bagworms that did not pupate were collected to observe if parasitoids emerged. The casings were stored in plastic containers in a refrigerator for several months.

Because certain plots started with differing numbers of larvae, percent survival is presented in the results. Total survival versus cumulative mortality in each plot was compared statistically at each time interval between alien and native plots with Cochran-Mantel-Haenzel’s (CMH) Test of Independence; because this test assumes continuity (while counts are discrete), the test was performed with continuity correction.
Table 1. List of native and alien plant species planted in experimental plots.

<table>
<thead>
<tr>
<th>Native</th>
<th>Alien</th>
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<tbody>
<tr>
<td><strong>Shrubs</strong></td>
<td></td>
</tr>
<tr>
<td>Choke cherry (<em>Aronia arbutifolia</em>)</td>
<td>Cotoneaster sp.</td>
</tr>
<tr>
<td>Buttonbush (<em>Cephalanthus occidentalis</em>)</td>
<td>Burning Bush (<em>Euonymus alatus</em>)</td>
</tr>
<tr>
<td>Alternate-leaved Dogwood (<em>Cornus alternifolia</em>)</td>
<td>Forsythia (<em>Forsythia x intermedia</em>)</td>
</tr>
<tr>
<td>Witch hazel (<em>Hamamelis virginiana mucronulatum</em>)</td>
<td>Privet (<em>Ligustrum obtusifolium</em>)</td>
</tr>
<tr>
<td>Winterberry (<em>Ilex verticillata</em>)</td>
<td>Andromeda (<em>Pieris japonica</em>)</td>
</tr>
<tr>
<td>Arrowwood (<em>Viburnum dentatum</em>)</td>
<td>Azalea (<em>Rhododendron sp.</em>)</td>
</tr>
<tr>
<td><strong>Trees</strong></td>
<td></td>
</tr>
<tr>
<td>Red maple (<em>Acer rubrum</em>)</td>
<td>Norway Maple (<em>Acer platanoides</em>)</td>
</tr>
<tr>
<td>Green Ash (<em>Fraxinus pennsylvanicus</em>)</td>
<td>Kousa Dogwood (<em>Cornus kousa</em>)</td>
</tr>
<tr>
<td>Sweetgum (<em>Liquidambar styracifolia</em>)</td>
<td>Autumn Olive (<em>Eleagnus umbellata</em>)</td>
</tr>
<tr>
<td>White Pine (<em>Pinus strobus</em>)</td>
<td>Golden Rain Tree (<em>Koelreuteria paniculata</em>)</td>
</tr>
<tr>
<td>Black cherry (<em>Prunus serotina</em>)</td>
<td>Norway Spruce (<em>Picea abies</em>)</td>
</tr>
<tr>
<td>Willow Oak (<em>Quercus phellos</em>)</td>
<td>Kwanzan Cherry (<em>Prunus serrulata</em>)</td>
</tr>
<tr>
<td>Basswood (<em>Tilia americana</em>)</td>
<td>European Linden (<em>Tilia chordata</em>)</td>
</tr>
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</table>

Figure 3. Design of experimental plots. The cluster in the center represents red cedars. Tomato and lettuce (not diagrammed) were planted around the red cedar. The trees and shrubs were planted in a circle around the red cedar. Outer clusters represents six plants planted around a single center plant.
Chapter 3

RESULTS

Populations of both bagworm and polyphemus larvae decreased over time, first rapidly and then slowly.

In the bagworms, the population of larvae in plots with alien plants was initially higher than the population of larvae in plots with native plants (Figure 4). However, in late-August, this relationship reverses; the population in native-planted plots becomes greater. The populations at each time point did not differ significantly (CMH Test, $P > .05$), though the August 7th time point was marginally significant ($P = .063$).

A large proportion of the bagworm casings that were stored to compare parasitization between plots molded over. No data were collected because of this.

In the polyphemus moth, the population of larvae in alien-planted plots was higher than the population of larvae in native-planted plots over the course of most of the experiment (Figure 5). The populations at each of the time points did not differ significantly, except for the last time point on September 23rd (CMH Test, $P = .034$).
**Figure 4.** Survival of bagworms from July to September in plots planted with alien plants (black diamonds) and plots planted with native plants (white squares). Error bars represent standard deviation.

**Figure 5.** Survival of polyphemus moth from August to pupation in September in plots planted with alien plants (black diamonds) and plots planted with native plants (white squares). Error bars represent standard deviation.
Chapter 4
DISCUSSION

Bagworm Discussion

The results suggest there is no difference in bagworm survival based on the evolutionary origin of the surrounding plant community. There are a number of possible explanations.

Perhaps the experimental gardens did not cause a difference in natural enemy populations. The predators and parasites controlling the bagworms in both experimental plots may have been equally high. Trees and shrubs are longer-lived species characteristic of late successional habitats, which have been shown to support more species of natural enemies (Price et al. 1980). Another reason natural enemy populations may be high is the nearby habitat; the plots may have been too close to large sources of natural enemies of undisturbed habitats with native plants, such as a woodlot for the University of Delaware site. Maintenance of late successional habitats such as woodlots may help to maintain parasitoid communities in nearby agricultural landscapes (Marino et al. 2006). On the other hand, natural enemy populations may have been equally low in both habitats. Ellis et al. (2005) studied the effect of flowering forbs on bagworms, and found that parasitization by wasps was significantly greater in bagworms that were on shrubs near flowers, showing that parasitoids may benefit from nectar and pollen from flowering plants (Fiedler and Landis 2007). It is possible that a greater variety of flowering plants would allow for more proliferation of
parasitoids. Despite the difference in origin of plant species, the plots may have provided similar resources to the natural enemies, resulting in similar natural enemy communities between treatments.

Also, it is possible that most of the natural enemy pressure on bagworm populations occurs at different times than measured. One possibility is that natural enemy pressure may occur most when the bagworms are smallest. Though I attempted to begin the experiment with first instar bagworms, a large number of these died in both alien-planted and native-planted plots, leaving almost no bagworms. Thus, the red cedar plants were restocked with bagworms in mid-July, but these bagworms were older and significantly larger. Because natural enemy selection of caterpillar prey can be dependent on the size of the larvae (Dyer 1997), it is possible that there is a difference in parasitization in the younger age group that could not be measured in this study. On the other hand, the parasitoids that affect bagworms may primarily attack the pupal stage, and data were not collected for survival after pupation (Ellis et al. 2005). The bagworm casings molding over introduced a confounding variable on pupal survival.

The reversal in survival between treatments in late-August suggests a possible temporal aspect to the natural enemies that prey upon bagworms that differs between alien- and native-planted plots, either seasonal or based on age of the bagworms, although again the differences between the plots are not significant.

Even if predator populations were affected, arthropods play a minor role in predation on bagworms (Ellis et al. 2005). It has been shown that birds and other vertebrates can be important in regulating bagworm populations (Ellis et al. 2005). At
the White Clay site, some bagworm casings were found that seemed to indicate bird predation.

Because of the loss of data due to the molding of the bagworm casings, it is unknown to what effect parasitization might have differed between treatments. A more controlled environment to prevent this would allow parasitization to be compared between plots.

In short, there is no difference between bagworm populations. This may be due to the lack of a difference in the natural enemy community that affect bagworms between the native and alien plots, possibly due to low populations because of the relative lack of flowers or to overwhelming contributions from nearby wooded habitats. These same plots were sampled to survey the native communities for a separate experiment, and the results of these surveys would help show if bagworm survival is an accurate reflection of natural enemy community health. However, based on the data, I reject the hypothesis that native plants provide more natural enemies, at least in the scope of those natural enemies that affect bagworms in the span of the larval stages tested.

**Polyphemus Discussion**

The polyphemus moths appear to survive better in alien-planted plots than in native-planted plots based on standard deviation, although not significantly so based on the CMH test. This is likely because the data for the CMH test was based on total survival per plot, while standard deviations were calculated from survival on each tree.

“Maple” is listed as a food plant for polyphemus (Wagner 2005), though it was observed that the larvae grew larger and more quickly on Norway maple than they did on red maple. This fits with studies that show that related plants, especially
congeners, are most likely to be accepted as alternative food sources by herbivores (Kennedy and Southwood 1984; Bernays and Graham 1988; Pemberton 2000; Keane and Crawley 2002; Novotny et al. 2002). However, slower development increases risk of predation for larvae, as well as decreasing resistance to pathogens (Price et al. 1980) and therefore there was greater mortality risk from predation and possibly pathogens for larvae on red maple. On the native-planted plots, no polyphemus moth pupae were found, and they may not even have reached pupation.

There are several possible explanations for this difference in growth rate. One reason may be that polyphemus moths tend to feed on other native species of maple rather than red maple. Polyphemus also accept a wide variety of other food plants and are not restricted to only feeding on species of maple (Wagner 2005); a few wild polyphemus moth were found on willow oak *Quercus phellos* during the study period. Species that are generalists over their geographical range specialize in different plants throughout their range (Fox and Morrow 1981), so it may be possible that polyphemus moths utilize red maple more, and grow faster, in some other part of its range. Norway maple has broader, thinner leaves, while red maple has thicker, waxier leaves; the leaves of Norway maple may be more similar to other native maple species, such as the silver maple *Acer saccharinum*. Alternatively, it is possible that the native red maple has defenses that prolong development in the polyphemus caterpillar, as found in other plants, such as tannins that reduce its digestibility, nutritional imbalance, or level of leaf water content (Price et al. 1980); on the other hand, the exotic Norway maple may not have this adaptation towards polyphemus caterpillars.

Because growth rate was not controlled for, it is questionable to interpret the results of this experiment as supporting the hypothesis that native plants generate
more natural enemies. If this experiment is repeated, the food plants between the native-planted and alien-planted plots should be chosen so that they result in more similar growth rates. If the polyphemus is used as an experimental subject again, growth rates need to be controlled for to eliminate this confounding variable. This may be possible by using the same food plant in both treatments, as in the bagworms, in which this problem did not arise.

I am not confident in attributing the difference in polyphemus survival to native plants attracting and supporting more natural enemies rather than increased risk to natural enemies for a longer duration. I reject the hypothesis based on the data from this experiment, but due to lack of control, further experimentation is necessary.

Currently, there is some evidence that native plants are as beneficial for conservation biocontrol as exotics. Studies to date comparing native and alien plants generally have analyzed forbs and grasses (Fiedler and Landis 2007) or perennials (Frank et al. 2008), while the plants used in this study consisted of trees and shrubs. Other studies focus on what specific resources are provided to the natural enemies, such as habitat complexity (Marino et al. 2006) or nectar and pollen (Ellis et al. 2005). Perhaps the experimental plots could be made more attractive to predators and parasitoids by utilizing a greater diversity of plants that provide a greater variety of resources. This may cause a greater effect on natural enemy communities, and possibly a greater difference between the plots on the caterpillar larvae survival. However, the experiments in this study do not support that native plant communities support more natural enemies than exotic plant communities.
REFERENCES


