Powdery Mildew (Erysiphe cruciferarum) Affects the Allelopathic and Competitive Abilities of Invasive Garlic Mustard (Alliaria petiolata)

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Wright State University

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POWDERY MILDEW (*Erysiphe cruciferarum*) AFFECTS THE ALLELOPATHIC AND COMPETITIVE ABILITIES OF INVASIVE GARLIC MUSTARD (*Alliaria petiolata*)

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

By

ANDREW RUSSELL OFFICER
B.S., Wright State University, 2008
I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Andrew Russell Officer ENTITLED Powdery mildew (*Erysiphe cruciferarum*) affects the allelopathic and competitive abilities of invasive garlic mustard (*Alliaria petiolata*) BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

Don Cipollini, Ph.D.
Thesis Director

David Goldstein, Ph.D., Chair
Department of Biological Sciences

Committee on Final Examination

Don Cipollini, Ph.D.

Thomas Rooney, Ph.D.

James Amon, Ph.D.

Andrew Hsu, Ph.D.
Dean, Graduate School
ABSTRACT

Officer, Andrew Russell. M.S. Department of Biological Sciences. Wright State University. 2012. Powdery mildew (*Erysiphe cruciferarum*) affects the allelopathic and competitive abilities of invasive garlic mustard (*Alliaria petiolata*).

Garlic mustard (*Alliaria petiolata*) has been previously found to be significantly affected negatively by powdery mildew (*Erysiphe cruciferarum*). While we could not significantly corroborate those findings we did find evidence that *E. cruciferarum* does inhibit *A. petiolata*’s allelopathic and competitive effects which benefits some target neighbor species such as *Impatiens capensis* and *Elymus canadensis*. We also found that the inhibition of *A. petiolata* by *E. cruciferarum* had negative consequences on another neighboring invasive species (*Lonicera maackii*) compared to those grown next to uninfected *A. petiolata*. *Acer saccharum*, a slow-growing species had no effect between neighbors. Sterilization treatments had variable effects on target plants, many of which mirror the effects which allelopathic plants (*A. petiolata*) that disrupt soil microbes seem to have. Sterilization inhibited growth of *E. canadensis* through the destruction of beneficial effects from microbes, while increasing the growth of *L. maackii* by inhibiting the pathogenic effects of microbes.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>SECTION</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>NON-NATIVE INVASIVE SPECIES</td>
<td>1</td>
</tr>
<tr>
<td>PLANT INTERACTIONS</td>
<td>3</td>
</tr>
<tr>
<td>GARLIC MUSTARD AS A MODEL INVASIVE PLANT</td>
<td>5</td>
</tr>
<tr>
<td>ALLELOPATHY</td>
<td>6</td>
</tr>
<tr>
<td>POWDERY MILDEW</td>
<td>8</td>
</tr>
<tr>
<td>HYPOTHESES AND PREDICTED RESULTS</td>
<td>9</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>12</td>
</tr>
<tr>
<td>SOIL AND CONDITIONS</td>
<td>12</td>
</tr>
<tr>
<td>EXPERIMENT 1: <em>Impatiens capensis</em></td>
<td>13</td>
</tr>
<tr>
<td>EXPERIMENT 2: <em>Acer saccharum</em></td>
<td>14</td>
</tr>
<tr>
<td>EXPERIMENT 3: <em>Elymus canadensis</em></td>
<td>15</td>
</tr>
<tr>
<td>EXPERIMENT 4: <em>Lonicera maackii</em></td>
<td>16</td>
</tr>
<tr>
<td>STATISTICS</td>
<td>16</td>
</tr>
<tr>
<td>RESULTS</td>
<td>18</td>
</tr>
<tr>
<td>EFFECTS OF SOIL TYPE, NEIGHBOR AND FUNGICIDE TREATMENTS ON <em>Impatiens capensis</em></td>
<td>18</td>
</tr>
<tr>
<td>EFFECTS OF NEIGHBOR TREATMENT ON <em>Acer saccharum</em></td>
<td>19</td>
</tr>
</tbody>
</table>
# TABLE OF CONTENTS (continued)

<table>
<thead>
<tr>
<th>SECTION</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>EFFECTS OF SOIL TYPE AND NEIGHBOR TREATMENT</td>
<td></td>
</tr>
<tr>
<td>ON <em>Elymus canadensis</em></td>
<td>20</td>
</tr>
<tr>
<td>EFFECTS OF SOIL TYPE AND NEIGHBOR TREATMENT</td>
<td></td>
</tr>
<tr>
<td>ON <em>Lonicera maackii</em></td>
<td>21</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>23</td>
</tr>
<tr>
<td>ALLELOPATHIC EFFECTS VS. COMPETITIVE EFFECTS</td>
<td>23</td>
</tr>
<tr>
<td>COMPETITIVE EFFECTS</td>
<td>24</td>
</tr>
<tr>
<td>POWDERY MILDEW</td>
<td>25</td>
</tr>
<tr>
<td><em>Impatiens capensis</em></td>
<td>25</td>
</tr>
<tr>
<td><em>Acer saccharum</em></td>
<td>27</td>
</tr>
<tr>
<td><em>Elymus canadensis</em></td>
<td>29</td>
</tr>
<tr>
<td><em>Lonicera maackii</em></td>
<td>30</td>
</tr>
<tr>
<td>CONCLUSIONS</td>
<td>32</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>34</td>
</tr>
</tbody>
</table>
LIST OF FIGURES

FIGURE 1. Experimental design layout for the *Impatiens capensis* experiment utilizing the neighbor, sterilization and fungicide treatments……….43

FIGURE 2. Experimental design layout for the *Acer saccharum* experiment utilizing the neighbor treatment…………………………44

FIGURE 3. Experimental design layout for the *Elymus canadensis* and *Lonicera maackii* experiments utilizing the neighbor and sterilization treatments……….45

FIGURE 4. Mean final height, final basal stem diameter (BSD) and final number of seed pods of *Impatiens capensis* in response to soil sterilization, fungicide and neighbor treatments…………………………….46

FIGURE 5. Mean change in height and basal stem diameter (BSD) in *Impatiens capensis* over time in response to sterilization, fungicide and neighbor treatments……………………………………………………47

FIGURE 6. Mean final height, final basal stem diameter (BSD), total number of leaves and final biomass of *Acer saccharum* in response to the neighbor treatment………………………………………………48

FIGURE 7. Mean change in height and basal stem diameter (BSD) in *Acer saccharum* over time in response to the neighbor treatment…………………………….49

FIGURE 8. Mean final height, number of tillers, and total leaf weight of *Elymus canadensis* in response to soil sterilization and neighbor treatment…………….50
LIST OF FIGURES (continued)

FIGURE 9. Mean change in height and number of tillers in *Elymus canadensis* over time in response to sterilization and neighbor treatments..........................51

FIGURE 10. Mean final height, final basal stem diameter (BSD), total number of leaves and total biomass of *Lonicera maackii* in response to soil sterilization and neighbor treatments..................................................52

FIGURE 11. Mean change in height and basal stem diameter (BSD) in *Lonicera maackii* in response to sterilization and neighbor treatments...............................53
LIST OF TABLES

TABLE 1. Results of two-way ANOVA of neighbor, sterilization and fungicide treatments on height, basal stem diameter and total number of seed pods on Impatiens capensis……………………………………………………………….39

TABLE 2. Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with neighbor, sterilization and fungicide treatments on height and basal stem diameter on Impatiens capensis……………………………………………………………….39

TABLE 3. Results of one-way ANOVA of neighbor treatment on height, basal stem diameter, and total biomass on Acer saccharum……………………………40

TABLE 4. Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with the neighbor treatment on height and basal stem diameter on Acer saccharum…………………………….40

TABLE 5. Results of two-way ANOVA of neighbor and sterilization on height, above-ground biomass and number of tillers on Elymus canadensis………………40

TABLE 6. Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with neighbor and sterilization treatments on height and number of tillers on Elymus canadensis……………………………………………………………….41
LIST OF TABLES (continued)

TABLE 7. Results of two-way ANOVA of neighbor and sterilization on branch length, total leaves, basal stem diameter, height and total biomass on *Lonicera maackii* .................................................................41

TABLE 8. Correlation matrix of *Lonicera maackii* end of season measures...........42

TABLE 9. Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with neighbor and sterilization treatments on height and basal stem diameter on *Lonicera maackii* .................................................................42
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INTRODUCTION

Non-Native Invasive Species

Non-native invasive species cause economic and environmental harm wherever they are spread (Mack et al. 2000; Pimentel et al. 2000). They affect more than just the seasoned naturalist, but also the average tax payer. Approximately 137 billion dollars have been spent on non-native invasive species annually since the year 2000. Over 34 billion dollars of this total is spent towards non-native invasive plants annually, falling only behind non-native invasive mammals at 37 billion annually for the most costly invaders (Pimentel et al. 2000). Additionally non-native invasive species cause immeasurable loss by pushing some native species to the point of extinction, something which does not have a monetary value attached to it, but has a great ecological value.

The mechanisms of invasion can be so complex that they are only understood after an invasion has been able to reach massive proportions. Only when we look at biogeographic differences within the species do we really begin to understand these mechanisms of invasion (Hallett 2006; Hierro et al. 2005). How can these species function as a normal, undisruptive neighbor in its native range while it wreaks havoc on neighbors in its introduced range? There is not a single answer to this question. Many of the answers have been put forth as hypotheses such as the enemy release hypothesis, novel weapons hypothesis, propagule pressure hypothesis, and the evolution of invasiveness hypothesis. The enemy release hypothesis states that when a species is introduced to a new range in which there are no specialized enemies, this species will be
released from the predation it would normally encounter in its native range and it will be
given an advantage over new neighbors (Mack et al. 2000). The novel weapons
hypothesis states that a species in its introduced range may contain specific biochemical
weapons (allelochemicals) which inhibit neighbors directly or by disturbing other
interactions vital to the neighbor, giving this species some advantage. These same
allelochemicals are ineffective against neighbors in the species native range (Callaway
and Ridenour 2004). Propagule pressure hypothesis states that a species will be a
successful invader if it has a higher propagule pressure which is influenced by the
number of invasions, the size of these invasions, and the pathway of invasion (Colautti et
al. 2006). Finally the evolution of invasiveness hypothesis states that when a species is
introduced to a new environment it will evolve quickly to adapt and will benefit from
increased growth, increased seed production, and better defense from herbivores (Blossey
& Notzold 1995; Bossdorf et al. 2005). Each of these hypotheses shows that invaders
have special ways of obtaining an edge over native species. Many times species have
invasive traits from more than one of these hypotheses, making each invader unique.

Natural invasions are fairly rare considering what a species must go through in
order to become invasive. Most invasive species have been introduced either
intentionally or accidentally by humans, so this is a more recent type of problem with the
current increase in globalization (Meyerson and Mooney 2007). Invasion can occur from
simply owning an exotic species and releasing it into the wild causing an unintentional
invasion. This is part of a major problem in the Everglades of South Florida where over
1810 Burmese pythons have been removed from the park in the past decade (US Natural
Park Service Website 2012). Some of these pythons were released by owners who could
no longer care for the large snakes and eventually they became a breeding population. Others were released by natural disaster when Hurricane Andrew destroyed a breeding facility nearby, releasing thousands of snakes. Alternatively, invasions can occur from species that have been purposely introduced for various reasons only to attain invasive status many years later. *Pueraria lobata* (Kudzu) is an invasive vine which was purposely introduced from Japan for soil erosion control and livestock feed in the late 1800s. The U.S. government even paid farmers to grow the plant until it became known as a noxious plant in 1953 (Winberry and Jones, 1973). In both cases, humans are facilitating many more invasions much faster than ever before.

**Plant Interactions**

Plants have many different interactions with their environment. Plants depend on light, water, and minerals as basic elements needed to survive. There are many interactions that plants utilize to give them an edge at gaining these crucial necessities. The most common of all plant interactions is the symbiosis between a plant and mycorrhizal fungi (Schubler *et al.* 2001; Simon *et al.* 1993). Eighty percent of all land plant species, 92% of all land plant families, are mycorrhizal (Wang and Qui 2006). Dating back 462-353 million years ago makes this type of interaction one of the oldest plant mutualisms and leads many to believe that it was influential in the colonization of land by ancient plants (Simon *et al.* 1993). Mycorrhizae benefit plants in many ways by increasing their absorptive root area belowground. This provides the host plant with increased uptake of water and minerals; most prevalent is the phosphorus ion. In return for these minerals mycorrhizae receive carbohydrates translocated from the plants leaves.
which complete the mutualistic relationship. Each species of plant differs in its dependency on mycorrhizal associations (Klironomos 2002), but many species are highly dependent for normal growth. Deficiencies in mycorrhizal colonization can therefore be observed as slower or stunted growth in species with increased dependency (Stinson et al. 2006).

There are multiple ways mycorrhizae colonize host plants. The two most common associations are ectomycorrhizae and endomycorrhizae. Ectomycorrhizae colonize the roots extracellularly by covering the root tips and then forming a net of hyphae around the root cortex. Endomycorrhizae colonize the roots intracellularly in a variety of ways which create further classifications. Arbuscular mycorrhizae, the most common of all endomycorrhizae, enter the plants cells and form either vesicles or arbuscules. Arbuscular mycorrhizal symbiosis is formed by more than 80% of all land plant families making it instrumental in many plant life cycles (Schubler et al. 2001).

Plants interact with nature in a multitude of ways. In addition to interacting with mycorrhizal fungi, plants interact with other plants, pathogens, herbivores, and the elements. Plants interact with other plants most generally through competition. They compete with each other for belowground resources such as those found in soil as well as aboveground resources, mainly light and space. These interactions can easily be unbalanced from the normal interaction in many ways. A change in the diversity or amount of mycorrhizal fungi within the soil may cause increased antagonistic effects in plant-plant interactions (Hoeksema 2005). Some interactions may have beneficial effects on other neighboring plants such as protecting it from other herbivores or harmful elements. A simple example of this would be a small herbaceous plant being protected
from trampling by a larger neighbor with thorns. So by simply changing another relationship that plants form, other interactions may be altered. Plants also have interactions with pathogens which can cause beneficial or negative effects on the plant. Again though, this plant-pathogen interaction may also have direct effects on the plant’s other routine interactions with nature such as the plant-plant described before. If you change one aspect of any normal interaction, then it may affect another interaction which can in turn have effects on others, making this a very complex system.

**Garlic mustard as a model invasive plant**

*Alliaria petiolata* (M. Bieb.) Cavara and Grande (garlic mustard), is a Eurasian native which is invasive in North America. It was introduced as a culinary and medicinal herb in 1868 in Long Island, New York along with many more undocumented introductions in following years. Garlic Mustard (*A. petiolata*) arrived in Ohio sometime shortly before 1934 as it occurs in only two reported counties at that time (Schaffner 1934). Currently it is found throughout Ohio, 36 other states and 3 Canadian provinces (USDA 2010). It began being noticed as an invasive non-native around the 1990s when seed dispersal rates and advancing fronts of *A. petiolata* were noticed to be much higher than expected (Nuzzo 1999).

*A. petiolata* possesses many qualities that contribute to successful invasions of plant species. It may produce a vast range of seed amounts from hundreds to even thousands produced per plant. These seeds can disperse up to 40 meters away (Nuzzo 1999) by wind, water, animals or humans and are viable in soil for up to five years. *A. petiolata* is also a self-fertilizing plant which gives it a generalist quality in not having to
depend on pollinators. *A. petiolata*’s growth is another typical invasive plant quality. As a shade-tolerant biennial, *A. petiolata* grows as a small rosette cluster in its first year, only growing a few inches from the ground. Over winter this rosette remains green where it is given an extra advantage over other species which must start from seed. This rosette quickly grows into a mature flowering plant reaching up to 100cm by mid-spring, growing up to 1.9 centimeters per day. Additionally, *A. petiolata* lacks significant herbivory in its invasive range in contrast to its native range where it is a food plant for almost 70 species of Lepidoptera (Hinz and Gerber 1998).

**Allelopathy**

Current studies have started looking at allelopathic effects created by *A. petiolata* which are also believed to be a factor in its invasiveness. Vaughn and Berhow (1999) were the first to really look into the allelopathy of *A. petiolata* by finding and isolating phytotoxic glucosinolate hydrolysis products from root tissues which saved the hypothesis from previous researchers who had discredited allelopathy. *A. petiolata* does have direct allelopathic effects on particular plants regardless of mycorrhizae and these chemicals disrupt the formation of mycorrhizal interactions (Callaway *et al.* 2008; Roberts and Anderson 2001; Stinson *et al.* 2006; Vaughn and Berhow 1999, Wolfe *et al.* 2008). Additionally, *A. petiolata* affects growth of specific plants differently. Since plants have different dependencies on mycorrhizae, these plants also vary in their responses to changes in mycorrhizal symbiosis caused by *A. petiolata*. All plants which form mycorrhizal associations see heavily reduced colonization rates in the presence of *A. petiolata*, but those which are more dependent on mycorrhizae are the ones which
suffer more from the presence of *A. petiolata* (Stinson *et al.* 2006). Woody species tend to have an increased dependency on mycorrhizal symbiosis meaning that *A. petiolata* poses a serious threat to many forest canopy species. When trees die off and leave openings in the canopy, there may not be the typical canopy tree seedlings left to fill that gap if the forest is inhabited by *A. petiolata*. Species which are less-dependent on mycorrhizae may become an increased canopy species since they may be released from competition with the more mycorrhizal dependent tree species (Callaway *et al.* 2008). This interaction could change forests as we know them. Timing is another issue when it comes to mycorrhizal associations. In a study of *Impatiens pallida* grown in soils injected with *A. petiolata* root and leaf extracts, plants which had not formed mycorrhizal associations followed previous trends of inhibited seed germination and seedling growth. However, *Impatiens pallida* which had formed arbuscular mycorrhizae relationships seem to be freed from detrimental growth effects (Barto *et al.* 2010).

To really understand if all of these effects are all due to novel weapons of *A. petiolata* we need to look at them biogeographically. Looking at European vs. North American *A. petiolata* we begin to see some interesting results. North American *A. petiolata* does not compete with European plant neighbors as well as the native European GM (Prati and Bosdorf 2004). Another study conditioned soils with *A. petiolata* by growing *A. petiolata* in the soil for some time and then removing the *A. petiolata* and planting a target plant in that same soil. This allowed them to look at allelopathic effects without direct competition. North American soils conditioned with *A. petiolata* show a reduction in mycorrhizal diversity and overall quantity. However European soils conditioned with *A. petiolata* show no detrimental effects on the mycorrhizal
communities (Callaway et al. 2008). This suggests that European soils have been able to co-evolve with A. petiolata and have become resistant to the harmful allelochemicals produced by them. Conversely, North American soils have only been in contact with these allelochemicals for 140 years or less which has not been adequate time to adjust (Hallett 2006).

**Powdery Mildew**

*Erysiphe cruciferarum* (*E. cruciferarum*) is a fungal plant pathogen which infects plants of the Brassicaceae family causing powdery mildew disease. It occurs naturally worldwide and has been observed infecting A. petiolata in the Wright State Biological Preserve for at least 10 years (Cipollini, personal observation) as well as Indiana (Blossey et al. 2001), the British Isles (Ellis and Ellis 1997), Germany (2006), and Armenia (2006) (Enright and Cipollini 2007). *E. cruciferarum* is dispersed through windblown conidia. Currently it is unknown how far these conidia may travel by wind, however it could be possible for them to be carried anywhere with the right winds. *E. cruciferarum* may infect any aboveground plant tissue however the temperature and humidity must be just right. Generally this climate occurs in late June to early July for the Dayton area (Cipollini and Enright, personal observation). When infection is successful, it reduces both target host’s plant growth as well as reproductive success based on the degree of disease. Infection also reduces cold hardiness in host plants making them more prone to frost damage and winter mortality (Paul and Ayres 1986). Severely infected A. *petiolata* can show reduced growth at two weeks of age and only produce 50% of the seeds in the field relative to undiseased plants (Enright and Cipollini 2007).
Additionally, *E. cruciferarum* can release neighbors from belowground affects of *A. petiolata*. Infection of *A. petiolata* allows for neighboring *Impatiens pallida* to increase its reproductive output to levels at or above its output with no neighbors present (Cipollini and Enright 2009). These results therefore suggest that *E. cruciferarum* infection of *A. petiolata* reduce the harmful allelopathic or other competitive effects on neighboring plants.

**Hypotheses and Predicted Results**

We conducted a greenhouse study to investigate the aspects of the novel weapons hypothesis in *A. petiolata* and how its allelopathic and competitive effects would affect growth and mycorrhizal colonization rates in three native species (*Acer saccharum* (Sugar Maple), *Elymus canadensis* (Canada Wild Rye) and *Impatiens capensis* (Common Jewelweed)), each with varying degrees of mycorrhizal dependence as well as an invasive species, *Lonicera maackii* (Amur Honeysuckle) (Brundrett and Kendrick 1988). We used a target-neighbor design in which single target plants were grown either with or without competition by *A. petiolata* plants in pots. In addition, we had two soil treatments (sterilized and non-sterilized) which either allowed target plants access to mycorrhizae before introduction to *A. petiolata* or denied access to mycorrhizae prior to introduction to *A. petiolata*. Sterilized soil contained no mycorrhizae and no microbes other than those able to withstand 121°C and higher. We also included a soil fungicide treatment to only the *I. capensis* experiment to see how closely *A. petiolata* invaded soils were to sterilized soils with no microbes. Additionally, we wanted to see how close *A. petiolata* invaded soils were to non-sterilized soils with fungicide (has microbes) and also
if these microbes made a difference in the growth of *I. capensis*. Finally, we included a treatment in which the competing *A. petiolata* was either infected with *E. cruciferarum* or protected from infection to investigate how *E. cruciferarum* affected allelopathic and competitive effects of *A. petiolata* on its neighbors.

Results of this experiment will answer many questions raised by numerous papers cited above. We will be able to provide insight on the competitive and allelochemical effects *A. petiolata* has on its neighbors and which of these is more detrimental. Additionally, we will be able to answer questions as to how allelochemicals affect *A. petiolata*’s neighbors. Are they affected by a “legacy effect” in which the mycorrhizae are reduced by *A. petiolata* prior to germination or are mycorrhizae affected by allelochemicals much faster? Growing these plants in the greenhouse in individual pots with individual treatments will force competition and allelochemical effects will be more natural compared to studies which have utilized extracts of allelochemicals. The greenhouse will also facilitate optimal conditions for the *E. cruciferarum* which gives an advantage over the changing conditions of the field.

For all of the experiments, we expect neighbors of *A. petiolata* infected with *E. cruciferarum* to grow fitter than their uninfected counterparts because we expect *E. cruciferarum* to diminish *A. petiolata*’s allelopathy. We believe this will occur with all target plants, but to varying degrees and for different reasons. For the mycorrhizal species, we believe that they will be spared the mycorrhizae they need to develop, which is the most important allelopathic effect *A. petiolata* has over these plants. For the non-mycorrhizal species we believe they will still be subjected to the effects of allelopathy
from *A. petiolata*, but these too will be diminished with infection of *A. petiolata* neighbors with *E. cruciferarum*.

We hypothesize that the fitness of *I. capensis* and *A. saccharum* will be greatest grown by itself. *I. capensis* and *A. saccharum* grown with an *A. petiolata* infected with *E. cruciferarum* neighbor will rank the second fittest over plants grown with uninfected *A. petiolata* neighbor. We also predict that *I. capensis* grown in sterilized soils will be less fit than the *I. capensis* grown in non-sterilized soils other than the one treatment of uninfected *A. petiolata* neighbor which I believe will be similar to its sterilized counterpart.

*E. canadensis* we hypothesize will grow the same in sterilized soil and non-sterilized soil since it is a non-mycorrhizal species. However, we still predict that the *E. canadensis* grown alone will grow the tallest in both sterile and non-sterile soil since there is no competition for any resources or light.

Finally we hypothesize that *L. maackii* will be affected similarly to *I. capensis* and *A. saccharum* since it is a mycorrhizal species, but the effects should be much more diminished with *L. maackii*’s rapid growth and other invasive qualities. We predict that *L. maackii* will grow the best when grown alone in sterile soil over non-sterile soil.

Assessments of mycorrhizal colonization rates of all of the above experiments were a goal of our study, but did not work out because of various factors so it will not be discussed further.
MATERIALS AND METHODS

Soil and Conditions

Soil used for all pots in all experiments was Promix BX with mycorrhizae. Sterile soil was created by autoclaving batches of soil at 121°C for 30 minutes then allowed to cool to ambient room temperature and then autoclaved a second time at 121°C for 30 minutes. Fungicide used in the *I. capensis* experiment contained 200mg/L chlorothalonil which is found in Daconil Fungicide Concentrate™. This fungicide mixture was used to water the plants from the surface every 4-5 days based on their need of water and was used to eliminate arbuscular mycorrhizae.

All pots were grown in the Wright State University greenhouse in random positions under ambient light supplemented with fluorescent light on a 14 hour light/10 hour dark cycle and were haphazardly moved around the greenhouse every week. Testing pots used in all experiments were 2.42L circular pots filled with soil and watered with DI water every 2-3 days as needed. All plants were treated periodically for spider mite infestation, using AVID® (Syngenta) miticide per manufacturer’s instruction.

*A. petiolata* seeds for all experiments were collected from the Wright State Biological Preserve and stored dry until moist stratification. *A. petiolata* were moist stratified in 9-cm Petri dishes lined with filter paper with 5-mL double distilled water at 4°C for approximately 3 months until germination and then immediately transplanted in sets of 2 into opposite sides of 2.42L testing pots containing approximately 2L of soil. Infecting *A. petiolata* with *E. cruciferarum* was accomplished by brushing *E.*
*cruciferarum* conidia directly onto the leaves of the *A. petiolata* with a paint brush and then placing them in plastic containers with a mesh-covered windowed top for three days to increase humidity for higher infection success. Spraying *A. petiolata* with Daconil fungicide concentrate (active ingredient: 29.6% chlorothalonil) diluted to 2.929ml/L prevented unintended infection with *E. cruciferarum*.

**Experiment 1: Impatiens capensis**

In 2010, we used three-week-old *I. capensis* plants collected in the Wright State Biological preserve. These plants were transplanted into either 250 ml sterilized (48 pots) or non-sterilized soil (48 pots) in 18-cell, 304 ml starting pots and watered as needed every 2-3 days. *I. capensis* plants were left in their starting pots until it was assured that they had survived the transplantation (approx. 1 wk). Cells containing *I. capensis* were then transplanted into the center of the pots containing *A. petiolata* allowing them to be surrounded. Thirty two pots (16 sterile/16 non-sterile soil) did not contain *A. petiolata* and only contained *I. capensis* plants while the other 64 had *A. petiolata* neighbors. Half of the pots with neighbors (16 sterile/16 non-sterile soil) were then infected with *E. cruciferarum* and the other half (16 sterile/16 non-sterile soil) was sprayed with Daconil. Half of the six treatments above were then watered regularly with the fungicide mixture to create 12 individual treatment combinations with eight replicates each (Figure 1).

The following season in 2011, we replicated this experiment with a total of 120 *I. capensis* plants allowing for 10 plants for each treatment to be measured instead of eight the previous year. In 2011, we also reared our *I. capensis* from seed found at the Glen
Helen Preserve in Yellow Springs, OH. These seeds were soaked in a 10% bleach solution for 10 minutes and then soaked in double DI water three separate times for 10 minutes each to rid them of any surface fungi or bacteria. The seeds were then moist stratified in 9-cm Petri dishes lined with sterile sand at 4°C for approximately 3 months until germination when they were transplanted to their treated pots.

Stem height and basal stem diameter BSD were measured every two weeks until week 13 for the transplanted *I. capensis* in 2010 and harvested at 7 weeks in 2011 due to infestation with spider mites. Harvesting consisted of cutting the stem at the base just at ground level and placing the above ground biomass in individually marked paper bags. The pot, remaining soil and below ground biomass were then carefully washed in a plastic tub with DI water and slightly agitated until the pot would come off and almost all of the soil was removed from the roots. The below ground biomass was also then placed into individually marked paper bags and then both above and below ground bags were placed into a drying oven at 60°C for 48 hours before weighing individually without the paper bags. In 2010, biomasses were not recorded, but seed pods were recorded every two weeks when they started to form. We have omitted the data from the 2011 season due to the overwhelming effects of the spider mites on the *I. capensis*.

**Experiment 2: Acer saccharum**

*A. saccharum* seedlings were bought from Porcupine Hollow Farm and Nursery in Central Lake, MI. All seedlings were the same age and had a starting height between 7.7cm-15.1cm and a basal stem diameter between 1.63mm-3.59mm. There were 30 seedlings split into three treatments of 10 seedlings each. One treatment grown alone,
one treatment with three *A. petiolata* neighbors and one treatment with three *A. petiolata* neighbors infected with *E. cruciferarum*. All were grown in the same pots as noted above in non-sterile soil (Figure 2).

Initial height and BSD were recorded at the time of planting and was measured every two weeks after. Number of leaves and condition/color of leaves was also noted every two weeks. After 18 weeks, the leaves and stem were harvested while the remaining pots with soil and below ground biomass were separated just like the *I. capensis*. Leaves, stems and below ground biomass were all placed in individually marked paper bags and dried at 60°C for 48 hours before weighing individually without the paper bags.

**Experiment 3: *Elymus canadensis***

*E. canadensis* seeds were bought from an online seed supplier and planted in groups of three directly into pots of either sterile (30 pots) or non-sterile soil (30 pots). Twenty pots of each soil type were also planted with two *A. petiolata* plants each. Ten of each of those *A. petiolata* pots then had their *A. petiolata* infected with *E. cruciferarum* according to the same procedure above. The remaining ten pots of sterile soil and non-sterile soil were left as controls with no neighbors (Figure 3). When the *E. canadensis* germinated all but one was removed from all pots.

Height of the stem and total number of tillers were recorded one week after planting and every two weeks thereafter. After 23 weeks, the stem and tiller for each plant was harvested right at the soil level and placed into individually marked paper bags. They were then dried in an oven at 60°C for 48 hours before weighing individually.
without the paper bags. *E. canadensis* belowground masses were thrown out because they had become root bound to the pot and there was no chance of removing all of the soil to get an accurate weight of the root mass.

**Experiment 4: Lonicera maackii**

*L. maackii* plants were two weeks old when planted according to the same experimental design as the *E. canadensis* (Figure 3). Initial height and BSD were recorded one week after being planted in their various treatments and then continued to be measured every two weeks throughout the experiment. Beginning week 10, we noticed the emergence of the stem branching and began recording the total lengths of all branches per plant every two weeks. After 25 weeks, the leaves were removed and placed in individually marked paper bags. The stem was harvested at the base and placed in bags with the branches and the remaining pots with soil and below ground biomasses were treated like the other experiments to recover the below ground biomass without soil. These were all dried in an oven at 60°C for 48 hours before weighing individually without the paper bags.

**Statistics**

For *I. capensis*, final height, BSD and seed pods in 2010 and final height, BSD and total biomass in 2011 were compared among soil treatments, neighbor treatments, fungicide treatments and their interactions with two-way ANOVA. Means within neighbor treatment, sterilization and fungicide treatment were compared using Tukey’s tests. Height and BSD were analyzed with repeated measures MANOVA. Correlations between all end of experiment measurements were made using Pearson correlations.
For *A. saccharum*, final height, BSD, total leaves and total biomass were compared among the three neighbor treatments with ANOVA. Means were compared using Tukey’s tests and height and BSD were analyzed with repeated measures MANOVA. Correlations between all end of experiment measurements were made using Pearson correlations.

For *E. canadensis*, number of tillers, leaf biomass and final height were compared among neighbor treatments, sterilization treatments and their interactions with two-way ANOVA. Means within neighbor and sterilization treatment were compared using Tukey’s tests. Height and number of tillers were analyzed with repeated measures MANOVA. Correlations between all end of experiment measurements were made using Pearson correlations.

For *L. maackii*, branch length, total leaves, total biomass, final height and BSD were compared among neighbor treatments, sterilization treatments and their interactions with two-way ANOVA. Means within neighbor and sterilization treatment were compared using Tukey’s tests. Height and BSD were analyzed with repeated measures MANOVA. Correlations between all end of experiment measurements were made using Pearson correlations. All of the above statistical analyses were performed using SAS Version 9.2., and Figures were made with Sigma Plot Version 10.0 and 12.3.
RESULTS

Effects of soil type, neighbor and fungicide treatments on Impatiens capensis growth

In 2010, height of *I. capensis* was significantly impacted by the neighbor treatment (Table 1). Plants were 47% smaller when grown with a neighbor compared to no neighbor, but plants grew 16% larger if their neighbor was infected (Figure 4). Sterilization and fungicide had no significant effects upon height, but the neighbor sterilization interaction approached significance while the remaining interactive treatments effects had no significance (Table 1). Time also had a significant effect on plant height along with the time*neighbor, time*sterilization and time*neighbor*sterilization interactions, while the remaining interactions were not significant (Table 2). Plants with a neighbor started the experiment 17% smaller than plants with no neighbor and 1% smaller than plants with infected neighbors, but ended the experiment 47% smaller than plants with no neighbor and 14% smaller than plants with infected neighbors (Figure 5). Plants grown in sterile soil started out 20% smaller than plants grown in non-sterile soil, but at the end of the experiment were 3% larger (Figure 5).

Basal stem diameter was significantly affected by the neighbor treatment and the effect of sterilization approached significance (Table 1). Plants were 21% smaller when grown with a neighbor compared to no neighbor and were 6% smaller when the neighbor was infected compared to uninfected (Figure 4). Time impacted basal stem diameter significantly as well as the time*sterilization interaction (Table 2). Plants were 29%
smaller when grown in sterile soil at the beginning of the experiment, but were only 14% smaller at the end compared to non-sterile soil (Figure 5).

The final number of seed pods followed the same patterns as above by being significantly affected by the neighbor treatment, but it was also significantly affected by the neighbor*sterilization interaction (Table 1). Plants produced more seeds in non-sterile soil compared to sterile soil within every neighbor treatment. Plants with no neighbor in sterile soil produced 36% less seeds than non-sterile soil, plants with a neighbor in sterile soil produced 33% less seeds than non-sterile soil and plants with an infected neighbor in sterile soil produced 41% less seeds than its non-sterile soil (Figure 4).

**Effects of neighbor treatment on Acer saccharum growth**

None of the growth measurements of *A. saccharum* were significantly affected by the neighbor treatment or even approached significance (Table 3 and Figure 6). However, time did have a significant effect on height and basal stem diameter while the time*neighbor interaction was significant for basal stem diameter, but not for height (Table 4). At the beginning of the experiment, *A. saccharum* grown with a neighbor are the same height and BSD regardless of whether the neighbor is infected or not and are 2% smaller in these measurements than *A. saccharum* with no neighbor (Figure 7). At the end of the experiment, *A. saccharum* grown with an uninfected neighbor had a BSD 13% smaller than no neighbor and 6% smaller than those grown with an infected neighbor while they had a height 6% larger than no neighbor and 3% smaller than infected neighbors (Figure 7).
Effects of soil type and neighbor treatment on Elymus canadensis growth

Height of *E. canadensis* was significantly impacted by the neighbor treatment and soil type (Table 5). Plants were 19% smaller when grown next to a neighbor compared to no neighbor, no difference in height when the neighbor was infected or not infected and 16% smaller when grown in sterilized soil compared to non-sterilized soil (Figure 8). Neighbor and sterilization had no significant interactive effect on height (Table 5). Time and the time*sterilization interaction had a significant effect on plant height while the time*neighbor and time*neighbor*sterilization interactions had no significant effects (Table 6). For the first seven weeks of the experiment all of the plants grew at the same rate regardless of treatments. At week nine we can start to see the effects of time for all treatments growing at different rates and we see the time*sterilization interaction effect with the plants grown in sterile soil growing at a slower rate than plants with no neighbor and plants with an infected neighbor both grown in non-sterile soil (Figure 9). At week seven the sterile plants are 19% smaller than the non-sterile plants with no neighbor and with an infected neighbor compared 21% smaller at the conclusion of the experiment (Figure 9).

The number of tillers was significantly affected by soil type, neighbor treatment and the neighbor*sterilization interaction (Table 5). Patterns of statistical significance and effects on the number of tillers followed all of those on height as well as others not found in height (Table 5, Figure 8, and Figure 9). The neighbor*sterilization interaction is easily found when looking at the sterile soil *E. canadensis* with an infected neighbor or the non-sterile no neighbor *E. canadensis* which is more than three times the size of the former (Figure 8). Over time the effects of the time*sterilization interaction on the
number of tillers was more than height. At week one of the experiment, plants grown in sterile soil were 19% smaller than non-sterile plants compared to 38% smaller at the conclusion (Figure 9). The time*neighbor interaction for the number of tillers was also significant (Table 6). Plants grown with a neighbor started out 15% larger than no neighbor, but ended 43% smaller, while plants with infected neighbors started 10% smaller than uninfected neighbors, but ended up having the same amount of tillers at the conclusion of the experiment (Figure 9).

Above ground biomass also followed the pattern of being significantly affected by the neighbor and sterilization treatment, but the neighbor*sterilization interaction had no significant effects (Table 5). Above ground biomass of plants grown in non-sterile soil were almost twice that sterile soil plants, plants with no neighbor were more than twice the biomass of plants grown with a neighbor and there was no difference in biomass with plants with an infected or uninfected neighbor (Figure 8).

**Effects of soil type and neighbor treatment on Lonicera maackii growth**

Height of *L. maackii* was significantly impacted by soil type and by neighbor treatment (Table 7). Plants were 20% smaller when grown in non-sterilized soil compared to sterilized soil, 15% smaller when grown with a neighbor compared to with no neighbor and 25% smaller when grown with an infected neighbor compared to no neighbor (Figure 10). Neighbor and sterilization had no significant interactive effect on height (Table 7). Time also had a significant effect on plant height while the time*neighbor*sterilization interaction approached significance (Table 9). The time*neighbor and time*sterilization interactions had no significant effects upon height
(Table 9). Over time, all of the plants increased in size at a steady rate until week nine, after which plants in each of the treatments grew at different rates (Figure 11). Plants with no neighbor in sterile soil grew the tallest of all treatments, while plants with an infected neighbor grown in non-sterile soil grew the least (Figure 11).

Basal stem diameter was significantly affected by the neighbor treatment and the effect of sterilization approached significance (Figure 10). Patterns of statistical significance and effects on basal stem diameter followed many of those on height (Table 7, Table 8, Figure 10, and Figure 11). Basal stem diameter was also impacted significantly by the time and time*neighbor interactions (Table 9). Over time, plants grown with a neighbor started out 17% larger than no neighbor, but ended 9% smaller, while plants with infected neighbors started 10% smaller than uninfected neighbors, but ended up 21% smaller at the conclusion of the experiment (Figure 11).

Total number of leaves and total biomass also followed the pattern of being significantly affected by the neighbor treatment, while the effect of neighbor treatment on branch length approached significance (Table 7). The total amount of leaves were 21% less when L. maackii was grown next to a neighbor compared to no neighbor and 49% less when that neighbor was infected (Figure 10). Total biomass for a L. maackii with no neighbor was more than twice that of a L. maackii grown next to an infected neighbor which was 33% smaller than a L. maackii with a neighbor (Figure 10).
DISCUSSION

Allelopathic effects vs. Competition effects

Separating allelopathic effects from effects of competition can be very tricky since the two produce similar effects upon neighbors. Some studies use activated carbon (AC) mixed into soil to absorb allelopathic volatiles in order to alleviate the allelopathic effects to view purely competitive effects for resources (Barto et al. 2010, Cipollini, K.A. et al. 2008, Nilsson 1994, Ridenour and Calloway 2001, Wixted and McGraw 2010). Others have used allelopathic plant extracts such as glucosinolate and flavonoid extracts to use as a soil treatment to create allelopathic effects without physical resource competition (Barto et al. 2010, Calloway et al. 2008, Cipollini, D. et al. 2008, Roberts and Anderson 2001, Stinson et al. 2006). In our experiment we separated effects by using a combination of neighbor, sterilization and soil fungicide treatments. This does not purely separate competitive effects or allelopathic effects as above, but it does give us very specific results which we have compared to other studies which used the above methods. The three neighbor treatments coupled with the sterilization treatments we utilize also show whether allelopathy is present since E. cruciferarum inhibits an infected neighbor and we can compare this to an uninfected neighbor and no neighbor. This allows us to still make fairly accurate predictions about what occurred due to allelopathy and what occurred due to competition for resources.
Competitive Effects

Our results show that most of our target plants experienced significant competitive effects with *A. petiolata*, *A. saccharum* being the only exception to this. We saw many trends which show *E. cruciferarum*’s ability to inhibit *A. petiolata*’s allelopathic and competitive effects, but none of these were found to be significant. A possible reason for this could be that we needed to increase our frequency of watering since *A. petiolata* has been found to accumulate plant defense proteins while under even intermediate drought conditions which were found to diminish the effects of *E. cruciferarum* infection (Enright and Cipollini 2011). Another reason could have been that we inadvertantly increased plant defense proteins another way, for example by limiting the soil environment by pot size which would have the same effect as drought. Another possibility could have been that the *A. petiolata* seeds we collected from an *E. cruciferarum* susceptible population have begun showing phenotypic plasticity due to prolonged selection for powdery mildew disease (Byers and Quinn 1998). This however is probably not the case since *A. petiolata* infection by *E. cruciferarum* is still a relatively new and isolated occurrence within Ohio (Ciola, and Cipollini 2008). Despite treating *A. petiolata* with preventative fungicide to shield it from *E. cruciferarum*, the spray fungicide can also only prevent infection to a certain degree for so long which can cloud interactive results (Cipollini and Enright 2009, Enright and Cipollini 2011). This speaks well for *E. cruciferarum* as a successful bio-control, but makes it harder to control unwanted infections. Daconil Fungicide Concentrate™ (diluted to 200mg/L chlorothalonil) used as a fungicide soil treatment has previously been found as an
affective inhibitor of mycorrhizae (Barto et al. 2010), but in our experiments of *I. capensis* we found no significant effects or even trends from its use in the soil.

**Powdery Mildew**

Powdery mildew infection of the *A. petiolata* neighbors caused no significant effects on the growth parameters of any of the studied species, but did follow many patterns which have been found significant in other publications (Cipollini and Enright 2008, Enright and Cipollini 2007). In *E. canadensis* and *I. capensis*, we saw that plants with infected neighbors in non-sterile soil had larger heights, weights, basal stem diameters and total number of tillers than plants with uninfected neighbor counterparts, but these effects again were not significant.

**Impatiens capensis**

In the *I. capensis* experiments we found that competition was a significant factor in which plants with no neighbor grew significantly taller than those with a neighbor, as expected. *I. capensis* grown with infected neighbors in non-sterile soil with no fungicide treatments grew taller and produced more total seed pods than those grown with a fungicide treatment because they were allowed access to mycorrhizal colonization while the latter was not. Since the same plants grew taller and produced more total seed pods than their uninfected counterparts we can say we found that infection of *A. petiolata* by *E. cruciferarum* did inhibit *A. petiolata*’s allelopathic effects over its *I. capensis* neighbors. We also saw that *I. capensis* with infected neighbors grown in sterile soil produced more seeds than their uninfected neighbor counterparts regardless of fungicide
treatment which also showed that infection of *A. petiolata* by *E. cruciferarum* also
inhibited *A. petiolata*'s competitive effects over its *I. capensis* neighbors. Other research
have also found similar results whereby *E. cruciferarum* inhibited *A. petiolata* allowing
for more seed pods to be produced, but they did not find above ground differences
(Cipollini and Enright 2009). At the same time *I. capensis* grown in sterile soil grew the
same height whether it was grown with an infected or uninfected neighbor, which
allowed us to believe that *E. cruciferarum* plays a much stronger role by inhibiting
allelopathic effects rather than direct competitive effects. Other research has found that
above-ground competition and allelopathy have nearly equivalent effects on *I. capensis*
(Cipollini, K.A. *et al.* 2008). We then saw plants grown with uninfected neighbors in no
soil fungicide treatments grow smaller and produce less seed pods than their fungicide
treatment counterparts. This indicated that *A. petiolata* was inhibiting mycorrhizal
colonization of *I. capensis* and indirectly affecting it with allelopathy opposed to directly
affecting it. Another study which investigated similar themes found that *A. petiolata*
glucosinolate and flavonoid enriched extracts inhibited growth of *Impatiens* pallida up to
presymbiosis of mycorrhizae and beyond if exposed prior to mycorrhizal symbiosis
(Barto *et al.* 2010). Also they found that arbuscular mycorrhizae were able to shield
effects of allelopathy if exposed after symbiosis occurred. Also to a very small degree it
seemed that the fungicide treatments protected *I. capensis* from the pathogenic effects of
a fungus while leaving valuable beneficial microbes. We did not find the same above-
ground differences in basal stem diameter as we did in height, but again others have also
found similar results yet still found effects upon seed production as we did (Cipollini and
Enright 2009). Sterilization had significant effects on basal stem diameter with non-
sterile plants growing larger than their sterile counterparts as predicted due to the absence of mycorrhizae and most other microbes in the sterile soil. We also see that sterilization affected the height and final number of seed pods of the no neighbor treatment positively in sterile soil compared to non-sterile soil. A possible explanation for this is that when the *I. capensis* became root bound within the pot, it stopped utilizing mycorrhizae because of the lack of space and resources (Barto *et al* 2010, Smith and Read 2008). This in turn made the plants more susceptible to the pathogenic effects of microbes found within non-sterile soil.

At the conclusion of the experiment on week 13, we can extrapolate our lines to see some continuing trends in that the sterile soil plants continue to grow smaller in basal stem diameter than non-sterile soil counterparts (Fig. 5). We also saw that the plants with infected neighbors in non-sterile soil with no fungicide begin to approach their no neighbor counterparts in basal stem diameter and exceed their counterpart’s height which strengthens the argument for *E. cruciferarum* to be a significant allelopathic suppressor of *A. petiolata*.

*Acer saccharum*

*A. saccharum* seedlings were unaffected by any treatment in any measured parameter throughout the 19 weeks we measured them. We did notice a somewhat inverse relationship between height and basal stem diameter. We also noticed that competition seems to encourage seedlings to grow taller at an increased rate than those without direct competition which instead grow more in basal stem diameter. This was found to be a common strategy among shade-intolerant species referred to as the shade
avoidance strategy, in which a plant develops resources to put into stem elongation at the cost of other effects (Ballare et al. 1990, Cipollini and Schultz 1999, Ricard et al. 2003). Utilizing the shade avoidance strategy reduced expression of plant defenses which left them susceptible to increased herbivore damage (Cipollini and Bergelson 2002). Others have also found in short-term studies, where the abundance of *A. saccharum* seedlings benefited from the presence of *A. petiolata* in sites with reduced density as opposed to full eradication (Stinson et al. 2007). This is possibly due to the fact that the green rosettes increase decomposition of leaf litter resulting in greater N and P availability (Rodgers et al. 2008). Since *A. saccharum* is a slow growing tree species, we believe that *A. petiolata* still allelopathically affects it, but it is hard to view significant results in just one growing season. There is also the possibility that *A. petiolata* will not affect *A. saccharum*’s growth visibly, but will affect the total amount of seeds produced which is still a major fitness effect such as seen in other species (Cipollini and Enright 2009).

This however may be hard to determine if allelopathy or trade-off effects of the shade avoidance strategy are causing this since both are known to have this effect. Other researchers found that *A. petiolata* did not affect arbuscular mycorrhizae richness, but did suppress colonization of the mycorrhizae (Barto et al. 2011), which again may not be evident for years. Our experiment indicates possible allelopathic effects in basal stem diameter with plants with no neighbor being the largest followed by those with infected neighbors and uninfected neighbor respectively. If continued throughout many seasons, we believe that we would find a significant difference in fitness due to competition and also inhibition of allelopathic effects of *A. petiolata* via *E. cruciferarum*. 

28
**Elymus canadensis**

*E. canadensis* is a largely non-mycorrhizal plant which seemed to show allelopathy from *A. petiolata* the best of all of our target plants since it demonstrated allelopathic effects that are independent of indirect allelopathic effects on mycorrhizae. Another study using *Arabidopsis thaliana* (another non-mycorrhizal species) did not find any of these independent effects using extracts of *A. petiolata* (Cipollini et al. 2008). However, we seem to have found multiple examples of *A. petiolata* affecting the growth of *E. Canadensis* in leaf biomass, height and abundance of tillers via both competition for resources and allelopathy. We found competition significantly lowered growth rates compared within sterilization treatments. We also found a significant difference between the non-sterile treatments and sterile treatments within the infected neighbor and no neighbor group which meant that there must be a microbe that is beneficial to *E. canadensis* in non-sterile soil that is removed with sterilization. This microbe is so beneficial to *E. canadensis* that when it was suppressed from the soil, *E. canadensis* grew the same as if it were under competition with a neighbor with access to the microbe. This may also indicate that *E. canadensis* is not affected through competition of resources with *A. petiolata*, but only by allelopathic effects which seem to inhibit the same microbe which is inhibited via sterilization.

In the infected neighbor group we saw that the sterile soil treatment grew the least in each parameter among all treatments. We think this may be due to allelopathic effects from *A. petiolata*. The uninfected *A. petiolata* neighbors in sterile soil were unaffected by *E. cruciferarum* so they were possibly expressing allelopathy which in turn suppressed a microbe which was pathogenic to *E. canadensis* and also survived sterilization. When
under those same soil conditions, but with an infected neighbor, *A. petiolata* was not exhibiting allelopathy and therefore the pathogenic effects of the microbe affected the *E. canadensis* which caused it to grow the least. Another possible explanation for this result could be that the *E. cruciferarum* infection did not successfully affect *A. petiolata*. However, we do see an increase in fitness for all parameters for the *E. canadensis* grown in non-sterile soil with an infected neighbor compared to its uninfected counterpart which means that its infected neighbors were in fact inhibited by the infection.

The repeated measures analyses also suggest that allelopathic effects were found since all of the treatments grew at nearly identical rates until week seven. Before week seven, we saw no differences in any of the treatments meaning competition was not a factor, nor was sterilization. At week seven the buildup of allelopathic compounds most likely became too strong as the roots were forced into very close quarters within the pot which created the affects described above. Extrapolating the repeated measures figures (Fig. 8) also shows *E. canadensis* grown in non-sterile soil with an infected neighbor surpassing plants with no neighbor grown in sterile soil in both height and number of tillers and *E. canadensis* in non-sterile soil with an uninfected neighbor also approaching the same plants. This again suggests that the sterilization destroys a microbe very valuable to *E. canadensis* and *A. petiolata*’s allelopathy closely mimics this effect.

*Lonicera maackii*

*L. maackii* was the opposite of *E. canadensis* in its interaction with allelopathic effects of *A. petiolata*. *L. maackii* grew significantly taller in sterilized soil compared to non-sterilized soil within the no neighbor and infected neighbor treatment. *L. maackii*
also seemed to benefit from possible allelopathic effects of *A. petiolata* because plants with an uninfected neighbor in non-sterile soils grew taller, wider and heavier than their infected neighbor counterparts. Since there was a significant difference between the other two neighbor treatments and also between each of their soil treatments, then this indicated that allelopathic effects of *A. petiolata* inhibited pathogenic effects of microbes in the soil in the uninfected neighbor treatment to the same degree that sterilization had made. Others have also found where sterilization has benefited plants by destroying pathogenic microbes (Klironomos, 2002; Beckstead and Parker, 2003). Another recent study, which also found *L. maackii* grew better in sterilized soil, found that *L. maackii* displayed plasticity in response to soil conditioning and sterilization of different soils (Scharadin and Cipollini 2012). We found that in non-sterile soils, allelopathy of *A. petiolata* can negate the impact of itself as a neighbor while unininfected by *E. cruciferarum*. When *A. petiolata* is infected, its allelopathy is inhibited and the neighboring *L. maackii* suffers effects from pathogenic effects of microbes.

Total number of leaves was the only parameter that did not follow the trends in which *L. maackii* in sterile soil grew better than non-sterile soil. Instead, we saw the opposite trend in the total number of leaves which indicated that *L. maackii* in sterile soils changed its architecture and put more resources into increasing the size of their stem rather than increasing their abundance of leaves. This again makes sense because a larger plant will have more opportunity to find light resources, while a smaller plant will need to compensate by building more leaves in order to catch all available light at their size.

The repeated measures analysis of height and basal stem diameter of *L. maackii* showed results similar to *E. canadensis* in which the effects of the neighbor treatments
and sterilization were not affected until week 7. This again strengthened that allelopathic effects of \textit{A. petiolata} were seen since the \textit{L. maackii} with no neighbor in sterile soil and non-sterile soil began divergence here showing that at this point in \textit{L. maackii}’s development they become sensitive to microbial differences. This again is possibly due to the roots filling the pot approximately at this time, or it could be due to the plants age. When we extrapolate our repeated measures graphs (Fig. 11) we see where the infected neighbor treatments begin to level off in height and basal stem diameter while the other treatments continue on with positive growth in both measurements. This means that if extended, our experiment may have eventually had three distinct neighbor groups again strengthening the hypothesis that \textit{A. petiolata}’s allelopathy saves \textit{L. maackii} from the pathogenic effects of microbes.

\textbf{Conclusions}

We expected to see strong evidence that \textit{E. cruciferarum} would release neighbors from allelopathic effects of \textit{A. petiolata}. While we did not find strong evidence, we did find evidence that it does benefit some species (\textit{I. capensis} and \textit{E. canadensis}), possibly by allowing access to mycorrhizal associations to occur or by inhibiting the destruction of other beneficial effects from soil microbes. In other cases, infected \textit{A. petiolata} did not benefit neighbor species (\textit{L. maackii}) and to a certain degree could hurt neighbor growth where we saw allelopathic effects of \textit{A. petiolata} benefiting neighbor species by inhibiting pathogenic effects of microbes in the soil. This all indicated that \textit{A. petiolata} not only affects plants by disrupting mycorrhizal associations, but that it also affected soil communities by disrupting other mutualisms and parasitisms.
Sterilization treatments had variable effects on target plants as well, many of which mirror the effects that allelopathic plants (A. petiolata) that disrupt soil microbes had as described above. We saw sterilization inhibit growth of E. canadensis through the destruction of beneficial effects from microbes. Then we saw sterilization increase growth of L. maackii by inhibiting pathogenic effects of microbes that would have otherwise been found in the soil. When looking at I. capensis we had variable effects of sterilization indicating there were possible tradeoffs between being allowed access to beneficial mycorrhizae in non-sterile soil and also the pathogenic effects of microbes found there. This caused variable growths with sterilization for different parameters.


Schaffner, J.H. 1934. Additions to the revised catalog of Ohio vascular plants. II. The Ohio journal of science. Vol. XXXIV: 165-174


**Table 1:** Results of two-way ANOVA of neighbor, sterilization and fungicide on height, basal stem diameter and total number of seed pods on *Impatiens capensis*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
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<th>Factor</th>
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<th>Total # of Seed Pods</th>
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<td>12.93</td>
<td>6.063</td>
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<tr>
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<td>11.67</td>
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<tr>
<td>Fungicide</td>
<td>1</td>
<td>0.0873</td>
<td>0.135</td>
<td>0.0052</td>
</tr>
<tr>
<td>Neighbor*Sterilization</td>
<td>2</td>
<td>2.488</td>
<td>0.737</td>
<td>0.780</td>
</tr>
<tr>
<td>Neighbor*Fungicide</td>
<td>2</td>
<td>0.365</td>
<td>0.259</td>
<td>0.330</td>
</tr>
<tr>
<td>Sterilization*Fungicide</td>
<td>1</td>
<td>1.022</td>
<td>0.302</td>
<td>0.296</td>
</tr>
</tbody>
</table>

**Table 2:** Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with neighbor, sterilization and fungicide treatments on height and basal stem diameter on *Impatiens capensis*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Height</th>
<th>Basal Stem Diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>6</td>
<td>0.12607295</td>
<td>0.19369798</td>
</tr>
<tr>
<td>Time*Neighbor</td>
<td>12</td>
<td>0.64882202</td>
<td>0.82435483</td>
</tr>
<tr>
<td>Time*Sterilization</td>
<td>6</td>
<td>0.71680211</td>
<td>0.67356891</td>
</tr>
<tr>
<td>Time<em>Neighbor</em>Sterilization</td>
<td>12</td>
<td>0.66344048</td>
<td>0.84558025</td>
</tr>
<tr>
<td>Time*Fungicide</td>
<td>6</td>
<td>0.86294901</td>
<td>0.87696082</td>
</tr>
<tr>
<td>Time<em>Neighbor</em>Fungicide</td>
<td>12</td>
<td>0.81509701</td>
<td>0.93952292</td>
</tr>
<tr>
<td>Time<em>Sterilization</em>Fungicide</td>
<td>6</td>
<td>0.87555435</td>
<td>0.87416247</td>
</tr>
<tr>
<td>Time<em>Neighbor</em>Sterilization*Fungicide</td>
<td>12</td>
<td>0.76998977</td>
<td>0.82102065</td>
</tr>
</tbody>
</table>
Table 3: Results an ANOVA on neighbor on total leaves, basal stem diameter, height, and total biomass on *Acer saccharum*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Height</th>
<th>Basal Stem Diameter</th>
<th>Total Leaves</th>
<th>Total Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neighbor</td>
<td>2</td>
<td>0.32</td>
<td>(0.7298)</td>
<td>0.73</td>
<td>(0.4909)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.05</td>
<td>(0.9527)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.58</td>
<td>(0.6804)</td>
</tr>
</tbody>
</table>

Table 4: Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with the neighbor treatment on height and basal stem diameter on *Acer saccharum*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Height</th>
<th>Basal Stem Diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>9</td>
<td>0.07863805</td>
<td>0.09584608</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt;.0001)</td>
<td>(&lt;.0001)</td>
</tr>
<tr>
<td>Time*Neighbor</td>
<td>18</td>
<td>0.45998150</td>
<td>0.22189386</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.5324)</td>
<td>(0.0191)</td>
</tr>
</tbody>
</table>

Table 5: Results of two-way ANOVA of neighbor and sterilization on number of tillers, leaf biomass and height on *Elymus canadensis*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Height</th>
<th>Above Ground Biomass</th>
<th>Number of Tillers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neighbor</td>
<td>2</td>
<td>9.506</td>
<td>15.52</td>
<td>22.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.0003)</td>
<td>(&lt;.0001)</td>
<td>(&lt;.0001)</td>
</tr>
<tr>
<td>Sterilization</td>
<td>1</td>
<td>9.285</td>
<td>25.45</td>
<td>29.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.0036)</td>
<td>(&lt;.0001)</td>
<td>(&lt;.0001)</td>
</tr>
<tr>
<td>Neighbor*Sterilization</td>
<td>2</td>
<td>2.542</td>
<td>1.221</td>
<td>3.613</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.0885)</td>
<td>(0.3035)</td>
<td>(0.0341)</td>
</tr>
</tbody>
</table>
Table 6: Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with neighbor and sterilization treatments on height and number of tillers on *Elymus canadensis*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Height</th>
<th>Number of Tillers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>11</td>
<td>0.01050893</td>
<td>0.08321631</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(&lt;.0001)</td>
<td>(&lt;.0001)</td>
</tr>
<tr>
<td>Time*Neighbor</td>
<td>22</td>
<td>0.54005101</td>
<td>0.29494572</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.1693)</td>
<td>(0.0001)</td>
</tr>
<tr>
<td>Time*Sterilization</td>
<td>11</td>
<td>0.48645116</td>
<td>0.44257008</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.0006)</td>
<td>(0.0001)</td>
</tr>
<tr>
<td>Time<em>Neighbor</em>Sterilization</td>
<td>22</td>
<td>0.65545276</td>
<td>0.65846507</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.6237)</td>
<td>(0.4986)</td>
</tr>
</tbody>
</table>

Table 7: Results of two-way ANOVA of neighbor and sterilization on branch length, total leaves, basal stem diameter, height, and total biomass on *Lonicera maackii*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Branch Length</th>
<th>Total Leaves</th>
<th>Basal Stem Diameter</th>
<th>Height</th>
<th>Total Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neighbor</td>
<td>2</td>
<td>2.749</td>
<td>6.291</td>
<td>4.941</td>
<td>3.539</td>
<td>4.612</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.0768)</td>
<td>(0.0036)</td>
<td>(0.0109)</td>
<td>(0.0362)</td>
<td>(0.0142)</td>
</tr>
<tr>
<td>Sterilization</td>
<td>1</td>
<td>0.207</td>
<td>1.784</td>
<td>2.854</td>
<td>5.898</td>
<td>1.141</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.6520)</td>
<td>(0.1875)</td>
<td>(0.0971)</td>
<td>(0.0187)</td>
<td>(0.2903)</td>
</tr>
<tr>
<td>Neighbor*Sterilization</td>
<td>2</td>
<td>0.541</td>
<td>0.472</td>
<td>1.085</td>
<td>0.864</td>
<td>1.021</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.5865)</td>
<td>(0.6262)</td>
<td>(0.3455)</td>
<td>(0.4275)</td>
<td>(0.3671)</td>
</tr>
</tbody>
</table>
Table 8: Correlation matrix of *Lonicera maackii* end of season measures. Numbers represent Pearson Coefficients and P-values

<table>
<thead>
<tr>
<th>End of season measures</th>
<th>Number of Leaves</th>
<th>Total Biomass</th>
<th>Basal Stem Diameter</th>
<th>Height</th>
<th>Stem Biomass</th>
<th>Above-ground Biomass</th>
<th>Root Biomass</th>
<th>Leaf Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Leaves</td>
<td>0.69752</td>
<td>0.58265</td>
<td>0.61795</td>
<td>0.63172</td>
<td>0.74409</td>
<td>0.60740</td>
<td>0.79373</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td></td>
</tr>
<tr>
<td>Total Biomass</td>
<td>0.94906</td>
<td>0.88743</td>
<td>0.95690</td>
<td>0.99127</td>
<td>0.97410</td>
<td>0.97221</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal Stem Diameter</td>
<td>0.85477</td>
<td>0.91019</td>
<td>0.92093</td>
<td>0.96072</td>
<td>0.88778</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;.0001</td>
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<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>0.86763</td>
<td>0.88475</td>
<td>0.86412</td>
<td>0.86046</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stem Biomass</td>
<td>0.96261</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.90715</td>
<td>0.89590</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td></td>
</tr>
<tr>
<td>Aboveground Biomass</td>
<td>0.93666</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.98182</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>&lt;.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Root Biomass</td>
<td>0.91889</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>&lt;.0001</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf Biomass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 9: Results of repeated measures MANOVA with Wilks’ Lambda test for the effect of time and its interactions with neighbor and sterilization treatments on height and basal stem diameter on *Lonicera maackii*. F-values (P-values) shown. P-values <0.05 are considered significant.

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>Height</th>
<th>Basal Stem Diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>11</td>
<td>0.20888773</td>
<td>0.09397709</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.001)</td>
<td>(&lt;.0001)</td>
</tr>
<tr>
<td>Time*Neighbor</td>
<td>22</td>
<td>0.37437828</td>
<td>0.21970904</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.3387)</td>
<td>(&lt;.0001)</td>
</tr>
<tr>
<td>Time*Sterilization</td>
<td>11</td>
<td>0.50863655</td>
<td>0.55009364</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.1319)</td>
<td>(0.2450)</td>
</tr>
<tr>
<td>Time<em>Neighbor</em>Sterilization</td>
<td>22</td>
<td>0.27264547</td>
<td>0.27529597</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.0795)</td>
<td>(0.1104)</td>
</tr>
</tbody>
</table>

42
**Figure 1.** Experimental design layout for the *Impatiens capensis* experiment utilizing the neighbor, sterilization and fungicide treatments

![Diagram showing experimental design layout for *Impatiens capensis* experiment utilizing the neighbor, sterilization and fungicide treatments.](image-url)
Figure 2. Experimental design layout for the *Acer saccharum* experiment utilizing the neighbor treatment.
Figure 3. Experimental design layout for the *Elymus canadensis* and *Lonicera maackii* experiments which utilize the neighbor and sterilization treatments.
Figure 4. Mean (+1SE): (A) Final Height, (B) Final Basal Stem Diameter (BSD) and (C) Final Number of Seed Pods of *Impatiens capensis* in response to soil sterilization, fungicide and neighbor treatments. Upper case letters above bars represent significantly different neighbor groups while lower case letters represent significantly different sterilization treatments within neighbor groups. (NS-Non-Sterile, S-Sterile)
Figure 5. Mean change (+1SE) in (A) Height and (B) Basal Stem Diameter (BSD) in Impatiens capensis over time in response to soil sterilization, fungicide and neighbor treatments. (NN-No Neighbor, N-Neighbor, IN-Infected Neighbor, NS-Non-Sterile, S-Sterile, NF-Non-Fungicide, F-Fungicide)
Figure 6. Mean (+1SE) (A) Final Height, (B) Final Basal Stem Diameter (BSD), (C) Total Number of Leaves and (D) Final Biomass of *Acer saccharum* in response to the neighbor treatment.
Figure 7. Mean change (+1SE) in (A) Height and (B) Basal Stem Diameter (BSD) in *Acer saccharum* over time in response to the neighbor treatment.
Figure 8. Mean (+1SE) (A) Final Height, (B) Number of Tillers, and (C) Total Leaf Weight of *Elymus canadensis* in response to soil sterilization and neighbor treatments. Upper case letters above bars represent significantly different neighbor groups while lower case letters represent significantly different sterilization treatments within neighbor groups.
Figure 9. Mean change (+1SE) in (A) Height and (B) Number of Tillers in *Elymus canadensis* over time in response to sterilization and neighbor treatments. (NN-No Neighbor, N-Neighbor, IN-Infected Neighbor, NS-Non-Sterile, S-Sterile).
Figure 10. Mean (+1SE) (A) Final Height, (B) Final Basal Stem Diameter (BSD), (C) Total Number of Leaves and (D) Total Biomass of *Lonicera maackii* in response to soil sterilization and neighbor treatments. Upper case letters above bars represent significantly different neighbor groups while lower case letters represent significantly different sterilization treatments within neighbor groups.
Figure 11. Mean change (+1SE) in (A) Height and (B) Basal Stem Diameter (BSD) in Lonicera maackii over time in response to sterilization and neighbor treatments. (NN-No Neighbor, N-Neighbor, IN-Infected Neighbor, NS-Non-Sterile, S-Sterile).