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Competition and Allelopathic Effects of Native and Invasive Populations of *Lonicera Maackii*: A Comparative Analysis

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COMPETITION AND ALLELOPATHIC EFFECTS OF NATIVE AND INVASIVE POPULATIONS OF *LONICERA MAACKII*: A COMPARATIVE ANALYSIS

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By

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Daniel M. Romanek ENTITLED Competition and Allelopathic Effects of Native and Invasive Populations of *Lonicera maackii*: A Comparative Analysis BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science

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ABSTRACT

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Competition and Allelopathic Effects of Native and Invasive Populations of *Lonicera maackii*: A Comparative Analysis.

It is unknown if the novel weapons or evolution of increased competitive ability hypotheses explain the invasiveness of *L. maackii* in eastern United States woodlands. I tested if *L. maackii*'s allelopathic properties have a significant impact on the fitness of native *Pilea pumila* in addition to below ground competition as well as if *L. maackii* populations vary in allelopathic and/ or competitive ability within the invasive range and between native and invasive ranges. Addition of activate carbon to potting soil increased the ability of *L. maackii* to inhibit the fitness of *P. pumila* in addition to competition. *L. maackii* from Ohio had a greater effect on its competitors and responded less to competition than *L. maackii* from a population in China. Results indicate that *L. maackii* can alter soil chemistry resulting in inhibition of its neighbors and *L. maackii* from Ohio is a better competitor both inter- and intra-specifically.

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INTRODUCTION

Exotic invasive species are globally threatening both economically and environmentally (Mack *et al.* 2000). Typically, the underlying causes of these invasions are poorly understood. The seemingly overwhelming question still remains: why do certain species function as minor community members in their native ranges while aggressively dominating communities within introduced ranges? While it is unlikely that a single factor is capable of explaining this phenomenon on a global scale, several generalized hypotheses have been proposed to address this question.

Hypotheses of particular interest to this study include the evolution of invasiveness and the novel weapons hypothesis. The evolution of invasiveness hypothesis proposes that introduction into a new range causes rapid genetic changes by altering selection pressures on the species (Hierro *et al.* 2005; Mack *et al.* 2000). This selection may result from natural differences between native and invasive ranges but also from anthropogenic cultivation (Ellstrand and Schierenbeck, 2006). The evolution of increased competitive ability hypothesis specifically states that the release from natural enemies in introduced ranges creates selection pressure for genotypes with increased competitive traits such as increased growth and fecundity (Blossey and Nötzold 1995). The novel weapons hypothesis states that an invasive species may dominate in its introduced range due to the exudation of harmful allelochemicals for which native species lack coevolved defenses (Callaway and Aschehoug 2000; Callaway and Ridenour 2004). The novel

weapons and evolution of invasiveness hypotheses are particularly interesting as they are not exclusive of one another.

Other hypotheses proposed to explain the success of certain exotic species are the propagule pressure and empty niche hypotheses (Bossdorf *et al.* 2005; Callaway and Ridenour 2004; Colautti *et al.* 2006; Hierro *et al.* 2005; Mack *et al.* 2000). However, one of the most widely studied hypotheses is the enemy release hypothesis which states that the absence of specialized enemies in introduced ranges provides a species with a competitive advantage by allowing plants to reallocate recourses away from defense from specialized herbivores. (Hierro *et al.* 2005; Keane and Crawley 2002; Mack *et al.* 2000).

Goals

The purpose of this study was to investigate mechanisms contributing to the invasive success of *Lonicera maackii* with regards to the novel weapons and evolution of increased competitive ability hypotheses. The goal was to determine if allelopathy and differences in growth and competitive ability between invasive and native populations could increase the ability of *L. maackii* to compete against plants native to its introduced range. I examined whether allelopathy by *L. maackii* had a significant negative impact on target species fitness in addition to below ground competition. Also, I investigated whether *L. maackii* populations varied in allelopathic and/ or competitive ability between its native and invasive ranges. To my knowledge, this is the first study to separate effects of belowground competition and allelopathy by *L. maackii* on a co-occurring native, to examine population variation in effects, and to directly compare the competitive ability of native and invasive populations of *L. maackii*.

Evolution of invasive plants

Biogeographic studies of invasive species are particularly important in identifying the characteristics and events that contribute to species invasiveness. Cross continental comparisons of exotic and native genotypes of an invader can indentify evolutionary differences in certain physiological and life history traits important to the species invasiveness (Hierro *et al.* 2005). For example, Dlugosch and Parker (2008a) conducted a biogeographic comparison of the shrubby invasive *Hypericum canariense* and showed that in spite of a large genetic bottleneck, invasive populations had evolved increased growth and locally favorable flowering date. Similarly, Ridenour *et al.* (2008) conducted study in which they investigated the enemy release hypothesis with regard to the evolution of increased competitive ability hypothesis. They were able to demonstrate that *Centaurea maculosa* from its invasive range had increased size, greater competitive effects and responded less to competition. Despite the increase in competitive ability the invasive genotype had increased defenses against herbivores. This suggests defensive compounds were also selected for in its invasive ranges and selective pressures did not require tradeoffs between these traits and competitive ones. With respect to the novel weapons hypothesis, if allelopathy was of significant importance in an invaders invasive range then invasive genotypes should show more allelopathic properties than native genotypes. However, the novel weapons hypothesis alone does not require evolution of increased allelopathic potential as long as the presumed allelopathic compounds are novel to the invaded ranges. Prati and Bossdorf (2004) found that allelopathic effects of *Alliaria petiolata* on *Geum laciniatum* were independent of whether the *A. petiolata* genotype was

from its invasive or native ranges. To my knowledge no study has investigated intrapopulation variation in allelopathic effects of a woody invader.

Collectively, biogeographic studies of invasive species allow for specific traits within invaded ranges to be assessed for local selection or variability of success within different environments and community assemblages. These comparisons can evaluate the importance of community structure to invasibility and specific mechanisms utilized by an invader.

Novel weapons: Allelopathy

Allelopathy has received increased attention recently with the rise in understanding of its implications in plant invasions (Hierro and Callaway 2003). Currently there is strong support for the role of allelopathy in the invasions of *Alliaria petiolata*, *Centaurea diffusa* and *Centaurea maculosa*. Compounds exuded by these plants have been shown to have negative effects on biomass accumulation, seed germination and mycorrhizal mutualisms of species native to invaded ranges (Callaway and Aschehoug, 2000; Callaway *et al.* 2008; Prati and Bossdorf, 2004; Ridenour and Callaway, 2001). However, identifying allelopathy as an important mechanism aiding a plants invasive ability is a daunting task and there is no single experiment that can prove its significance (Inderjit and Callaway, 2003). In order for allelopathy to be considered to facilitate invasion several aspects of its allelopathic properties must be examined. First, production and release of potentially allelopathic compounds must be identified. Second, it must be shown that concentrations from the method of release seen in field conditions (e.g. continuous release by root exudates or seasonal release of leachates from leaf litter)

must be enough to inhibit the fitness of targeted natives in natural conditions (this includes: soil types, micro-biota, nutrient and water availability). Finally, the allelopathic effects on the target species must be significant relative to the effect of competition (Inderjit and Callaway, 2003). It is important to stress that evidence of allelopathy within an invasive system is unlikely to be adequate evidence for the cause of invasion nor is it exclusive to other factors that facilitate invasion. Reductions in specialist herbivore attack as well as gained competitive ability by selective pressures are still likely factors contributing to a plant's invasive ability.

While support exists for several herbaceous invaders, determining the allelopathic effects of woody species is slightly more complicated because of certain life history traits which may influence the ability to study allelopathy. Such traits may include longevity of certain developmental stages and/ or the plant's size. Despite this daunting task, allelopathy is gaining support for several woody invaders as a significant mechanism facilitating their invasion.*Ailanthus altissima* (tree of heaven) is one of the best studied woody invaders with regards to allelopathy. Laboratory or greenhouse experiments have shown that potentially allelopathic compounds (mostly quassinoids and alkaloids) are produced by *A. altissima* and extracts from various plant parts have negative effects on the fitness of several plant species (Gomez-Aparicio and Canham 2008). Gomez-Aparicio and Canham (2008) conducted a field study using activated carbon to reduce effects of potential allelopathic compounds produced by *A. altissima* in the soil. They were able to demonstrate that the introduction of activated carbon to the soil in the presence of *A. altissima* increased seedling growth of *Acer rubrum* and *A. saccharum.* Investigation of the allelopathic potential of other woody invaders has gained support for

allelopathy being an important factor in invasion by woody species. Thus far extracts from other woody invaders such as *Elaeagnus umbellate* (autumn olive) and *Sapium sebiferum* (Chinese tallow tree) have also been shown to inhibit germination and size of target plant species (Conway and Smith, 2002; Orr *et al.* 2005;).

Lonicera maackii

Lonicera maackii is a woody invasive of North American eastern forests and early succession areas that is native to northeastern China and Korea (Luken and Thieret, 1996). *Lonicera maackii* (hereafter referred to as "LM") was introduced to the United States by 1898 and has been reintroduced multiple times from different origins. Following introduction, it has been cultivated in the United States and distributed commercially, mainly as an ornamental. One of the more successful cultivars (available commercially as late as 1996) is Rem-Red. However, it was not until the 1950's that naturalized populations were recognized as invasive (Luken and Thieret, 1996). The lag-time between introduction and invasion, coupled with multiple introductions and anthropogenic selection, sets the stage for LM to have evolved in its invasive ranges (Bossdorf *et al.* 2005; Dlugosch and Parker, 2008b). Yet, to my knowledge, no study has made direct comparisons between LM from North America and China.

Introduction of LM to Ohio occurred around 1960 near Oxford and it has now spread throughout much of southwestern Ohio (Hutchinson and Vankat, 1997). Here, LM is associated with disturbance and is common in fragmented landscape features, forest edge habitats, riparian areas, old field habitats, and forest interiors lacking heavy canopy (Bartuszevige *et al.* 2006; Hutchinson and Vankat, 1997). Establishment in these habitats

is favorable for LM because of high light availability, limited competition from native shrubs and high propagule pressure from birds that distribute LM seeds (Bartuszevige and Gorchov, 2006; Hutchinson and Vankat, 1997; Luken and Thieret, 1996).

Once established, LM can have devastating effects on species growth, abundance and community structure. It is capable of reaching high densities and is associated with lower native diversity and abundance of herbaceous and woody species' seedlings and saplings (Collier *et al.* 2002). Much of LM's ability to create near monocultures in invaded areas has been attributed to its ability to compete for above ground resources. *Lonicera maackii* casts very dense shade and is one of the first shrubs to expand its leaves in the spring and one of the last to lose leaves in the fall (Trisel, 1997). This phenological advantage can be attributed to its superior cold tolerance compared to native shrubs (McEwan *et al.* 2009). Likewise above ground competition of mature LM shrubs has been demonstrated to be more important than below ground competition on *Impatiens capensis* (Cipollini *et al.* 2008). However, these findings were limited by low sample size and the methods used to limit above ground effects was cutting, which undoubtedly also affected below ground processes. Ultimately, not much is known about the nature of *L. maackii's* below ground effects on natives with respect to competition or allelopathy.

Recently, LM has been shown to produce potentially allelopathic compounds supporting the possibility for allelopathy to be a significant to LM's invasiveness. Phenolic compounds such as chlorogenic acid, luteolin and apigenin were identified in methanol leaf extracts of LM by Cipollini *et al.* (2008a). In the same study the leaf extracts were shown to have anti-herbivore effects and to reduce germination of *Arabidopsis thaliana* seeds. A number of other studies have shown that extracts prepared

from LM parts can inhibit the fitness of native herbs and woody plants (Trisel, 1997; Dorning and Cipollini 2006; Cipollini *et al.* 2008; Cipollini *et al.* 2008a; Cipollini *et al.* 2008b). However, all of these extract studies have yet to demonstrate the ability of these compounds to inhibit natives in field conditions. This is largely because concentrations of these compounds and methods of releases in natural settings are unknown or difficult to duplicate. Yet evidence exists for LM's ability to alter soil in a way that inhibits fitness of target plants. Cipollini and Dorning (2008) used soils conditioned by LM and showed delayed phenology and reduced survival of *Arabidopsis thaliana* grown in LM conditioned soils in comparison to those grown in soils not conditioned by LM. However, plants that survived the conditioned soil treatment eventually grew larger and produced more seed than those grown in unconditioned soil. One explanation of this result is that soil biota may have broken down allelochemical making it possible for the target plants to recover and thrive in the ansence of continual inputs. This underlines the importance of designing experiments in which the target plants are exposed to allelochemicals in the same fashion as field conditions (Inderjit 2001).

The importance of allelopathy in relation to competition has yet to be demonstrated with LM. Cipollini *et al.* (2008) conducted a field study where activated carbon was used to limit the effects of potential allelopathic compounds on the target plant *Impatiens capensis*. In this study activated carbon had no effect on the fitness of *I. capensis* but results were somewhat inconclusive due to small sample sizes.

Hypotheses:

I investigated of the Evolution of Increased Competitive Ability (here on referred to as EICA) and Novel Weapons hypotheses in the common eastern United States forest invader *Lonicera maackii*. In accordance to the EICA hypothesis I predicted LM individuals from an invasive population in Ohio will have greater intra- and interspecific competitive ability than individuals from a native population in China. I tested this first by comparing the competitive effect of both populations on a native North American forest annual, *Pilea pumila.* Then intraspecific competitive ability was assessed by testing the response of individuals from both populations when growth with either Chinese or Ohio LM.

Lonicera maackii is thought to be potentially allelopathic. The novel weapons hypothesis predicts that the allelopathic compounds produced by LM reduce the fitness of plants native in its invasive ranges thus giving it a competitive advantage. Although it has been shown that compounds produced by LM are capable of reducing the fitness of *Impatiens capensis*, it remains unknown if the production of these compounds is a significant contributor to its invasive ability. I tested to see if LM's allelopathic properties have a significant negative impact on *Pilea pumila* fitness in addition to below ground resource competition. In order to separate allelopathic and competitive effects, activated carbon will be introduced into the soil to diminish the effects of the allelochemicals. Specifically, I hypothesized that LM reduction of *P. pumila* fitness should be greater in soils not treated with activated carbon.

As stated earlier the novel weapons and evolution of increased competitive ability hypotheses are not exclusive to one another. In order to see if LM has evolved within its

invaded range in both competition and allelopathy, individuals from China and Ohio will be used in the activated carbon experiments. If allelopathy is indeed significantly contributing to the invasive ability of LM; I predict that LM individuals from Ohio would have been increasingly selected to be allelopathic and therefore have a greater allelopathic ability than individuals from China. However, this prediction is not necessary for either EICA or Novel Weapons hypothesis to be supported. Lastly, to establish the extent of variation in allelopathic and competitive ability within LM*'s* invasive Ohio population, multiple areas were sampled and their allelopathic and competitive effects on *Pilea pumila* were compared. I hypothesized that populations of LM within Ohio would vary in their allelopathic and competitive ability. The idea being that if evolution of this invasive occurred by natural selection some variation would have to be present within its invasive region.

MATERIALS AND METHODS

The following experiments took place during two seasons, one from May to October of 2008 and the other from May to September, 2009. All plants were grown in the Wright State University green house in 1-L pots filled with commercial potting soil (Promix BX with mycorrhizae, Premier Horticulture INC., Quakertown PA. USA). Plants were watered with deionized water as needed and fertilized twice a month (details given for each experiment), at which time the plants were also moved within and among the green house benches in order to deter any micro-habitat effects. In experiments where *Pilea pumila* was the target, treatments consisted of the presence or absence of LM collected from one of several populations, as well as the presence or absence of finely ground activated carbon (activated carbon). For this a full factorial design was used (Figure 1). In the experiment on intraspecific competition of LM; target plants were either from within its native region (China) or its invasive region (Ohio, USA) and the treatment was the origin of the competitor. LM from each location grown alone served as a control.

In this study the herbaceous woodland annual *Pilea pumila* (L.) Gray (clearweed, Urticaceae) was used as the native competitor and target plant of allelopathy. *Pilea pumila* (hereafter referred to as "*Pilea*") is a common resident in eastern North American floodplain forests and is shade tolerant with seed germination co-occurring with canopy closure (Cid-Benevento, 1987). *Pilea* and LM often occur in proximity of one another (personal observation). One would anticipate that *Pilea* with shade-tolerant phenology

would be somewhat resistant to light competition from LM. However, a study by Gould and Gorchov (2000) demonstrated that *Pilea* fitness and fecundity were both negatively affected by the presence of LM. Yet, *Pilea* has not been used in allelopathic studies so its potential sensitivity to allelopathic compounds remains unknown.

In order to separate competition from allelopathy, activated carbon treatments of the soil were used in which activated carbon was mixed into the soil at a concentration of 20 ml activated carbon/1L soil (Prati and Bossdorf, 2004). In other studies, activated carbon has been successfully used to isolate allelopathic effects (Callaway and Ashehoug, 2000; Hierro and Callaway, 2003; Prati and Bossdorf, 2004; Ridenour and Callaway, 2001). Activated carbon was chosen in allelopathic studies for its high affinity and adsorptive properties of organic compounds (Inderjit and Callaway, 2003; Lau *et al.* 2008). The rationale for using activated carbon is that the potentially allelopathic organic molecules being excreted by the focal plant are rendered inactive in the soil while having limited effects on nutrient uptake by both the focal and test plants (Inderjit and Callaway, 2003; Lau *et al.* 2008). However, there is evidence to suggest that addition of activated carbon to soil could affect plant growth in the absence of allelopathy (Lau *et al.* 2008). The importance of the factorial design is the ability to detect independent and interactive effects between activated carbon and the focus plant on the fitness of the target species (Lau *et al.* 2008). Typically, allelopathic effects are observed if the target plant fitness is greater when grown with the focus plant and activated carbon compared to the focus plant alone.

For all plants, measurements were taken periodically throughout the growing season and consisted of basal stem diameter (basal stem diameter) and primary stem

length (primary stem length). At the end of the season below and above ground biomass (root and shoot biomass respectively) was collected and dried to consistent weight. In pots where plants were competing, roots were separated by soaking tangled roots (already rinsed of soil) in warm water and hair conditioner (~1tbsp conditioner/L; Suave Naturals Hair Conditioner, Unilever INC. Trumbull CT, USA). Roots were then gently separated by hand and rinsed thoroughly to remove any conditioner residue. All statistical analyses were performed using SAS 9.2.

Effects of *Lonicera maackii* on *Pilea pumila*:

Experiment one: Effects of *Lonicera maackii* within Ohio

Lonicera maackii populations collected from several areas within Ohio were compared in terms of their competitive and allelopathic effects on *Pilea* to see if variation of these characteristics exists within a portion of the invasive range of this plant.

LM from six Ohio populations were collected and transplanted to the Wright State green house in May of 2008. Populations of LM were chosen based on availability of plants of desired size/ age as well as proximity to other populations. While it was preferred that most populations be several miles away from one another, a range of distributions was collected. Some populations were relatively close to each other (Cedar Falls and Yellow Springs population), while one was relatively distant from all others (Athens population) (Figure 2). All saplings were located in edge habitats and were removed from the soil by hand shovel while preventing as much root loss as possible. Individuals were transplanted into pots within six days of collection and allowed at least four days to establish before *Pilea* was transplanted into experimental pots. Time of

collection, planting and sample size can be found on table 1. Individual LM collected were 2-3 yrs old (basal stem diameter ~2.0-5.0mm). This size/ age was selected because growth rates of LM in greenhouse conditions were unknown and it was assumed that this size would have been a viable competitor to an annual of *Pilea*'s size. Populations of LM were chosen based on availability of plants within desired size/ age as well as proximity to other populations (Figure 2).

On May 26th 2007 *Pilea* was collected from a single population in the Wright State University woods and immediately transplanted into experimental pots. *Lonicera maackii* was absent from the immediate area where *Pilea* was collected but individual LM plants existed within ~30m. After *Pilea* was transplanted, they were allowed to establish for six days. After this period, all plants still alive were considered established and first measurements were taken June 1, 2008. Primary stem length and basal stem diameter were recorded bi-weekly throughout the experiment. All pots for this experiment were fertilized every once a month with 221 ml of *Peter's Professional Grade* all purpose plant food (20-20-20 N-P-K plus micronutrients, Grace-Sierra, Milpitas, CA), diluted to 0.564g/L in distilled water.

All plants were harvested during the first week of October 2008. Shoots of all plants were collected and placed in unsealed paper bags. The materials were then left to dry at room temperature in our laboratory until they reached constant weight (about two weeks). Roots of both *Pilea* and LM were randomly sub-sampled from each of the LM and activated carbon treatments (3 pots per treatment, 12 treatments, for a total of 36 pots). Root biomass from all pots in the *Pilea* controls (activated carbon+ and activated carbon-) was sampled. Shoot and root biomass of *Pilea* were highly significantly

correlated and thus it was decided to subsample roots from each treatment due to the time consuming nature of root cleaning and separation (Table 2).

Flower production of *Pilea* was estimated by counting all of the axils that contained flowers after the plant had been dried to constant weight. Flower production was sub-sampled due to time constraints and dried stem biomass was shown to be significantly correlated with this estimate of flower production (Table 2). A similar method was used in Cid-Benevento (1987). Sub-sampling for flower production was done by selecting two *Pilea* per treatment (including controls). Random sampling per treatment was done by using a random number generator and selecting plants with the corresponding identification number.

Data analysis:

Variation in effects on *Pilea*'s end of season biomass between invasive LM populations within Ohio was analyzed by two-way ANCOVA. Treatment variables consisted of collection site as well as the presence or absence of activated carbon. Transplanted LM from the field varied somewhat in size. In order to account for the potential effect of these size differences on *Pilea* biomass, initial basal stem diameter of LM was used as a covariate. It was also shown that location of LM collection was a non-significant predictor of all *Pilea* measures. For the remaining analysis, LM treatment was defined as either present or absent after all populations were combined. The effect of activated carbon on LM total biomass was analyzed using ANOVA to see if activated carbon affected the size of LM. This was done to ensure that the lack of effect on *Pilea* biomass by activated carbon was not due to differences in LM biomass between those treatments. The effect of LM, activated carbon and their interactions on *Pilea* biomass

was analyzed by two-way ANOVA. Means within LM and activated carbon treatments were compared using Tukey's means comparison test. Repeated measures ANOVA was used to see how direct and interactive effects of activated carbon and LM influenced growth of *Pilea* basal stem diameter and primary stem length throughout the growing season.

Experiment 2: Effects of *Lonicera maackii* from native and invasive ranges

Variation between populations from LM's invasive and native ranges was examined by comparing their competitive and allelopathic effects on *Pilea*. Two populations of LM were used, one from each range. Typically, it is best to use multiple populations from both regions to make sure that results are indicative of the entire region and not simply one population. However, when multiple populations of LM from within Ohio where compared there was no significant variation in their ability to inhibit the fitness of *Pilea*. This implies that LM populations within Ohio were similar in terms competitive and allelopathic potential. All efforts to collect seeds from areas outside of Ohio where LM is invasive failed as well as attempts to receive seeds from multiple locations within its native range.

For this experiment all plants were grown from seed. This was done to eliminate any possible maternal effect of the environment the plants were from. Native LM seeds were collected in March of 2008 from Dong Ling hills at Shenyang Agricultural University in Shenyang, China. Invasive LM seeds were collected in October of 2008 from the Wright State University Biological Preserve, Dayton Ohio, USA. Warm stratification of the LM seeds began in February 2, 2009. *Lonicera maackii* seeds were

placed on moist filter paper in covered Petri dishes. Dishes were then placed in an incubator (22.0°C, lighted: 16hr on, 8hr off) until seeds germinated. It was noticed, but not quantified, that some LM seeds from Ohio started geminating sooner than Chinese seeds. When seedlings were selected for transplant, individuals were selected from both groups that germinated near the same time. Seedlings were then transplanted into trays of potting soil until May when they were transplanted into experimental pots.

Pilea seeds were collected from WSU woods during October of 2008 and stored dry. Seeds were cold stratified starting on December 16, 2008. Seeds were placed in covered Petri dishes with moist filter paper at 4°C for four months, then placed in an incubator (22.0°C, lighted:16hr on 8hr off) to break dormancy (Carmen Cid, personal communication). Multiple *Pilea* seedlings were planted into experimental pots one week after LM were planted. The *Pilea* were given two weeks to establish then thinned to one plant per pot.

The first measurement of primary stem length for both LM and *Pilea* was taken May 27, 2009. Measurements of both species were taken once a month throughout the entire experiment. During the first two months basal stem diameter was not recorded for fear of damaging the seedlings with the calipers while measuring. Given that the basal stem diameter of both species at this age is about one millimeter, very little variability between plants could be accurately measured. Measurements from day 58 to the end of the experiment included both basal stem diameter and PLS. Plants were fertilized twice a month with 10 ml of *Peter's professional grade* all purpose plant food (20-20-20 N-P-K plus micronutrients, Grace-Sierra, Milpitas, CA) at a concentration of 12.46g plant food/

L of distilled water. Note that the change in concentration of fertilizer between experiments one and two is relative to the volume given (1.24g of fertilizer per pot).

Shoot and root biomass for all plants was collected during the last week of September 2009. *Pilea* flower production was estimated by collecting all of the infructescences by hand before shoot biomass was dried. All plant material was dried in a drying oven at 100°C for 1hr then at 70°C to constant weight (~36 hr total) (Chiarello *et al*. 1989).

Data analysis:

Pearson's correlation test was used to examine correlations between all *Pilea* end of season measures. Primary stem length at the end of the experiment was not significantly correlated with the other end of season measures. To see if primary stem length was valid measure throughout the experiment, *Pilea* primary stem length at day 58 of the experiment was added to the correlation analysis. Direct and interactive effects of LM and activated carbon on average root, shoot, and infructescence biomass of were analyzed using a two-way ANOVA and Tukey means comparison test. The square root transformation of infructescence biomass was used to meet normality assumptions of ANOVA. *Lonicera maackii* treatments consisted of its collection site (China or Ohio) and absence. Activated carbon treatments were simply present or absent. A three-way ANOVA was used to see if activated carbon affected the size of LM from either Ohio or China and if this effect was dependent on the presence of *Pilea*. It is important to note that this analysis depended on using LM grown in activated carbon without *Pilea*. Since no such treatment was incorporated into this study, plants were used from a parallel experiment (germinated and grown in the same fashion) but there were only five of these

plants and they were not harvested at the same time. As a result the basal stem diameter at day 59 of the experiment was used as a measure of LM size. Another analysis was performed analyzing the effect of activated carbon on LM biomass from China and Ohio but only in the presence of *Pilea,* as well as an ANOVA of the effect of LM origin and *Pilea* competition on LM basal stem diameter at day 59. The direct and interactive effects of LM and activated carbon on primary stem length growth of *Pilea* were analyzed by repeated measures ANOVA. *Pilea* primary stem length growth consisted of measurements taken on day 1, 35, 58, and 124 of the experiment.

Intraspecific competition of native and invasive *Lonicera maackii*

This experiment tested the hypothesis that LM individuals from Ohio are less sensitive to intraspecific competition than LM from China. For this experiment LM individuals were germinated, planted, and measured as in experiment two "Effects of *Lonicera maackii* on target plant *Pilea pumila.*" Fifteen LM from China and Ohio were used as target plants per treatment. Treatments consisted of one Ohio or Chinese competitor grown in the same pot. All plants were identified with a small tag located near the side of the pot. Fifteen individuals from each location were grown alone as controls.

Data analysis:

Pearson correlations of all end of season measures were performed for both Chinese and Ohio LM. The effect of target plant origin (Chinese and Ohio) and competition treatment (None, Chinese and Ohio) on LM biomass was analyzed using two-way ANOVA. Means were compared using Tukey's means comparisons test. The response to competition in LM was measured as the difference between the target plant

biomass and the average biomass of the control group. The effect of target plant origin as well as competition treatment on LM response was analyzed using two-way ANOVA and Tukey's means comparison test. Repeated measures ANOVA was used to determine the effect of competitor treatment on LM primary stem length through time. Ohio and Chinese LM were analyzed separately.

RESULTS

Effects of *Lonicera maackii* on *Pilea pumila*:

Experiment one: Effects of *Lonicera maackii* within Ohio

Nearly all end of season measures of *Pilea* were significantly positively correlated. Infructescence biomass was not significantly correlated with primary stem length and basal stem diameter, but it showed a marginally significant correlation with root biomass (Table 2). However, total and shoot biomass were significantly correlated with infructescence mass suggesting that root biomass would have greater correlation values with increased sample sizes.

When grown in competition with LM, *Pilea* biomass was independent of the population origin of the LM competitor, after accounting for the size of LM at the beginning of the experiment (Table 3). The presence of LM significantly affected all biomass measures of *Pilea* (Table 4). Overall, *Pilea* grown in the presence of LM had significantly lower biomass than plants grown alone (Figure 3A). Activated carbon significantly affected stem and root biomass of *Pilea*, but the effect on total biomass only approached significance (Table 4). The mean root biomass of *Pilea* grown in activated carbon was significantly higher than plants grown without activated carbon, but shoot and total biomass did not significantly differ between activated carbon treatments (Figure 3). However, there was a significant interactive effect of activated carbon and LM on *Pilea* biomass (Table 4). Activated carbon had a strong positive effect on *Pilea* when

grown alone, but LM inhibited this effect (Figure 4). LM was not affected by the presence of activated carbon when in competition with *Pilea* (Table5).

Pilea size changed through time (Table 6; Figures 5). Activated carbon significantly affected primary stem length of *Pilea* through time, but LM did not. Basal stem diameter was just the opposite, with LM significantly affecting changes in basal stem diameter through time while activated carbon had only a marginal impact. There was no significant interactive effect of LM and activated carbon on either basal stem diameter or primary stem length (Table 6). Within subjects, *Pilea* size was significantly affected by both LM and activated carbon. Interactions between these factors were only significant on primary stem length while having suggestive impacts on basal stem diameter (Table 7). In general, activated carbon increased the primary stem length and basal stem diameter of *Pilea.* However, activated carbon had little effect on the size of *Pilea* in the presence of LM (Figure 5).

Experiment 2: Effects of *Lonicera maackii* from native and invasive ranges

All end of season measures of *Pilea* were significantly correlated with one another with the exception of end of season primary stem length. However, stem length at day 58 of the experiment was significantly correlated to all end of season measures except final stem length (Table 8). This suggests that primary stem length taken during the midpoint of the experiment was a better indicator of *Pilea* fitness than final stem length.

Competition type significantly affected all *Pilea* biomass measures (Table 9). Shoot and total biomass of *Pilea* were significantly affected by activated carbon, which

had no effect on root and infructescence biomass. Only root biomass was significantly affected by the interaction of LM competitor treatments and activated carbon (Table 9). All biomass measures were significantly lower in LM present treatments than in controls. *Pilea* shoot, root and total biomass were significantly lower when grown with Ohio LM than with Chinese LM, but infructescence biomass did not differ between these groups. Only total and shoot biomass of *Pilea* were significantly reduced by activated carbon (Figure 6B and 6C). Root biomass of *Pilea* was lower in the presence of LM but this effect was dependent on activated carbon and the origin of LM (Table 9). In the presence of activated carbon, both LM populations decreased root biomass of *Pilea*. In the absence of activated carbon, the root biomass decrease of *Pilea* was greater with Ohio LM than with Chinese LM (Figure 7).

Lonicera maackii biomass was independent of activated carbon treatment (Table 10 and 11). The interaction of LM origin and *Pilea* competition significantly affected LM size, as both populations were the same size in controls, but LM from Ohio were larger in competition and LM from China were smaller in competition (Table12, Figure 8).

Lonicera maackii significantly reduced the size of *Pilea* primary stem length throughout the experiment. Activated carbon alone did not significantly alter the size of *Pilea* through time or overall, but it did have a significant interactive effect with competitor treatment (Tables 13 and 14). *Pilea pumila* grown with Ohio LM had the slowest growth from days 58 to 101. However, this difference was not as apparent when activated carbon was absent (Figure 9).

Intraspecific competition of native and invasive *Lonicera maackii*

All end of season measures for both Chinese and Ohio LM were significantly and positively correlated with each other (Tables 15 and 16). The origin of the target plant had a significant effect on the shoot and total biomass of LM while the effect on root biomass approached significance. Competition treatment had a significant impact on both shoot and total biomass but the effect on root biomass was not significant (Table 17). Overall Chinese LM was smaller than Ohio LM (Figure 10). Shoot biomass of LM was significantly smaller when grown with an Ohio competitor than when grown by itself or with Chinese LM (Figure 10A). However, total biomass of LM was not significantly different between Ohio and Chinese competitor treatments and root biomass was independent of competition treatments (Figure 10B and 10C).

The interactive effect between target plant origin and competitor treatment on LM shoot and total biomass was only suggestive while root biomass was unaffected (Table 17). It appears that Ohio LM was less responsive to competition than Chinese LM. Specifically, when Ohio LM was grown with Chinese LM, it was larger than when it was grown with another Ohio LM, but neither of these treatments differed greatly from the control group. Chinese LM grown alone was larger than plants grown in competition with either Ohio or Chinese LM. (Figure 11)

The origin of the target and competitor LM had a significant effect on the response of shoot and total biomass of LM to competition, but root biomass response was only affected by the origin of the target plant (Table 18). *Lonicera maackii* from Ohio responded less to competition than Chinese LM for all measures of biomass (Figure 12).

Shoot and total biomass of LM showed greater reduction when competing with LM from Ohio than with LM from China (Figure 12A and 12C).

Competitor treatments significantly affected the primary stem length of Chinese LM through time and overall (Tables 19 and 20). Although Ohio LM was not significantly affected, the influence of competitor treatment through time approached significance (Tables 19 and 20). Chinese LM grown alone had the highest primary stem length followed by those grown with Chinese and Ohio competitors, respectively (Figure 13).

DISCUSSION

Our results indicate that the allelopathic effects of LM on *Pilea* were a significant contributor to its competitive ability, and that LM from Ohio was more competitive than LM from a population in China. While previous studies have indicated that LM has allelopathic properties, this is the first to demonstrate the ability of LM to negatively affect a target plant by altering soil properties relative to its competitive effects. While our exact hypothesis that activated carbon should decrease the overall impact of LM on *Pilea* was falsified, the effect of LM was significantly different between activated carbon treatments indicating an alteration of soil chemistry. However, the exact mechanism by which this happens is unknown and likely indirect. *Lonicera maackii* from Ohio had a greater effect on its competitors and responded less to competition than LM from a population in China suggesting that invasive populations of LM in Ohio are a more competitive genotype which likely contributes to its invasive success.

Pilea **as a target plant**

Given the phenology and nature of *Pilea*'s reproductive structures; acquiring quantitative measures of its fitness was difficult to do directly. *Pilea* is wind pollinated and even though previous studies have recorded pollination in greenhouse conditions (Cid-Benevento 1986, 1987), pollination and seed development was inconsistent in this study. As a result, we used female flower production as a metric of fitness. Other studies

have shown significant correlations between female flower production, biomass and seed production (Cid-Benevento 1986, Gould and Gorchov 2000). Our study showed a positive correlation between total biomass and female flower production as well as infructescence biomass, suggesting that changes in *Pilea* biomass do reflect changes in its fitness. The fact that biomass measures were correlated with flower production helps reduce error in estimating the fitness of *Pilea* as biomass was much simpler to record accurately. However, end of season basal stem diameter and primary stem length were not significantly correlated with female flower production in experiment 1. For experiment 2, end of season primary stem length was not correlated with any other measure of fitness. This was likely caused by plants reaching maximal primary stem length and basal stem diameter while still increasing biomass and flower production. For both experiments primary stem length and basal stem diameter measured halfway through the experiments were significantly correlated with end of season fitness measures of *Pilea*. This implies that growing conditions throughout the experiment as reflected in midseason stem length can weigh heavily on the final fitness of *Pilea*. While seemingly obvious, this highlights the importance of how and when allelochemicals can affect a target plant's fitness. *Lonicera maackii* could expose *Pilea* to allelochemicals in different ways and cause a reduction of *Pilea* fitness. Typically, allelochemical response is thought of as ongoing continuous exposure to allelochemicals by the target plant. However, it is also likely that short term exposure to allelochemicals by LM, say, in response to stress, could significantly reduce the overall fitness of *Pilea*.

Effects of *Lonicera maackii* on *Pilea pumila*

Experiment one: Effects of *Lonicera maackii* within Ohio

When collected from the field, the response of *Pilea* to LM did not differ between Ohio LM populations. However, the size of LM at the beginning of the experiment (indicated by basal stem diameter) did affect *Pilea* biomass meaning that as the size of LM increases so does its ability to affect competitor fitness. Even though LM was collected from the field in the first experiment it is unlikely that maternal effects of the environment could have affected a given population's performance. *Lonicera maackii* was collected from different populations but in similar habitats (edges of old-field and wood lots). Also, any affect of environment would be short lived due to the high plasticity of LM to environmental changes (Luken 1988, 1997). While the amount of genetic variation in Ohio LM is unknown, the fact that *Pilea* fitness was not related to the origin of LM suggests that variation within Ohio is low for the competitive abilities I examined.

In this study LM had a significant impact on *Pilea* fitness. Most of the overall effects on *Pilea* in these experiments were due to belowground interactions as above ground competition was limited in the greenhouse. Activated carbon increased the size and biomass of *Pilea* at the end of the season as well as during the experiment, but the presence of LM eliminated this effect. The fact that LM had a disproportionately negative effect on *Pilea* when activated carbon was present suggests that below ground chemical interactions were likely occurring. I hypothesized that activated carbon would limit the ability of LM to inhibit *Pilea* fitness by adsorbing allelochemicals leached in to the soil. In our experiment activated carbon increased the ability of LM to affect *Pilea*, even early

on in the experiment when resource competition would likely be less limiting. Given that activated carbon alone had a positive effect on *Pilea* biomass, it seems that LM has a greater effect in more beneficial environment. A similar pattern in the effects of LM on a target plant has been observed by Cipollini and Dorning (2008) and Cipollini *et al.* (2008b). They found that soils that were conditioned by LM, or had been treated with LM extracts had a greater impact on the fitness of *Arabidopsis thaliana* at higher nutrient levels than at low nutrient levels. In our study it was not likely that the addition of activated carbon to soil was associated with an addition of nutrients, because LM was not affected by activated carbon. If activated carbon did not alter the biomass of LM then it was unlikely the differences in effect of LM on *Pilea* were caused by changes in direct resource competition by LM. It is not known how activated carbon benefited *Pilea* grown alone. It is apparent that LM has a greater impact on target plants in a beneficial environment and this effect seemed to happen early on in the experiment and without benefit to LM fitness.

Experiment 2: Effects of *Lonicera maackii* from native and invasive ranges

Lonicera maackii from its native range (China) had a weaker competitive effect than invasive LM from Ohio. It was shown in experiment one that the effect of LM on *Pilea* was related to its size, and in experiment two LM from China was smaller and responded negatively to competition. Differences in the effect of LM on *Pilea* likely reflect size and competitive response differences between invasive and native ecotypes of LM. Thus invasive LM is more competitive against *Pilea*, which is native to Ohio, than LM from the population in China. It is also important to note that neither LM population

was affected by activated carbon. However, the treatment of LM alone in the presence of activated carbon had a small sample size of just five individuals per LM population.

Studies that have compared competitive ability of an invader from its native and non-native regions by interspecific competition have led to mixed results (Bossdorf *et al*. 2005). The mixture of results may be due to the specific competitors chosen in those studies (Bossdorf *et al* 2005). In this study we used a co-occurring native plant from the invasive range. More importantly *Pilea* has been show to be negatively affected LM in field conditions and this effect was similar compared to other co-occurring natives (Gorchov and Trisel, 2003; Gould and Gorchov, 2000). This suggest that LM from Ohio is likely more competitive than Chinese LM for a variety of co-occurring natives.

Root biomass of *Pilea* was the only end of season measure that activated carbon and LM affected interactively. The difference in effect of activated carbon between Chinese and Ohio LM was likely caused by the size and competitive response difference between the two. Chinese LM was smaller and likely less capable of directly affecting *Pilea* root biomass but was capable of affecting *Pilea* in the presence of activated carbon.

The repeated measurers ANOVA gives perhaps the clearest picture of interaction between activated carbon and LM. *Lonicera maackii* had a greater effect on *Pilea* in the presence of activated carbon even though *Pilea* did not benefit from activated carbon alone. Ohio LM had a greater impact on the growth of *Pilea* than Chinese LM but only in the presence of activated carbon, indicating that Ohio may have greater chemical effects on *Pilea*. However due to size differences between Ohio and Chinese LM, the allelopathic effect should be compared relative to size.While LM from Ohio is more allelopathic per individual, indicated by the greater effect of Ohio LM on growth of

Pilea, Chinese LM may be have more allelopathic effects relative to its size. However, little can be said about the relationship between size and allelopathic effect. Gomez-aparicio and Canham. (2008) demonstrated that higher densities were correlated with increased allelopathic effects in *Ailanthus altissima,* but found no relation to size.

The EICA hypothesis states that allocation of resources to herbivore defense compounds may be lost due to reduced specialized herbivores and selection for increased growth in introduced areas (Blossey and Nötzold 1995). However, the EICA makes no assertions about the production of allelochemicals. In order for allelochemical production to be selected against, allelochemical activity would have to either be nonfunctional in introduced habitats or the use resources for production of allelochemicals would decrease growth.

Intraspecific competition of native and invasive *Lonicera maackii*

Lonicera maackii from Ohio had a greater impact on its competitor than Chinese LM except when comparing root biomass. Not only did LM from Ohio respond less to competition from itself, it may actually respond by increasing its growth when competing with an inferior competitor. Increased growth in the presence of competition has been documented in multiple invasive species (e.g. Pattison *et al*. 1998; Smith and Knapp 2001, Grotkopp *et al*. 2002; Zou 2007). When in competition with Chinese LM, the competitive effect of Ohio LM on primary stem length throughout the experiment was greater than Chinese LM, suggesting that Ohio LM has a greater ability to inhibit growth early in its life. It is notable that this trend is apparent in interspecific as well as intraspecific competition.

One of the more obvious reasons that LM from China had a weaker competitive effect than LM from Ohio was that Chinese LM was simply smaller in size. Across all competitive treatments Ohio LM was larger than LM from China. While this may be caused by Chinese LM"s greater response to competition, comparison of size within control treatments suggests that Ohio stem and total biomass was greater than Chinese LM, while root biomass was equal between the two populations.

A difference in the size of shoot biomass but not root biomass suggest that Chinese LM may be allocating resources to growth differently than Ohio LM, causing proportionately larger roots than shoots. However, root biomass of Chinese LM was shown to respond more to competition than Ohio LM. This could be a crucial difference between Ohio and Chinese LM. Lower root to shoot ratios of invasive plants may account for their increased growth (Ehrenfeld 2003). *Sapium sebiferum* from invasive populations were demonstrated to have lower root to shot ratios and increased growth compared to *Sapium sebiferum* from native populations in China (Zou 2007). Plasticity of resource allocation is also a feature common to invasive and weedy plants (Baker 1974). Resource allocation patterns of invasive LM have been shown to be plastic (Luken 1988, Luken 1997). The ability to alter resource allocation for increased growth would likely benefit LM in its invasive regions.

Implications for allelopathy in *Lonicera maackii*

The novel weapons hypothesis states that the allelopathic impact of LM on a target plant should be a significant contributor to its overall competitive ability. In both experiments LM had a greater ability to inhibit the growth and biomass of *Pilea* in

activated carbon. While this was seen in experiment one as a decrease in the beneficial effect activated carbon, in experiment two activated carbon did not benefit *Pilea* growth, yet the effect of LM on *Pilea* was still greater in that treatment. However this was the opposite of our hypotheses. Lau *et al*. (2008) showed that activated carbon has the ability to alter nutrient availability in potting soil and emphasized the importance of accounting for effects of activated carbon on both target and focus plant species. By accounting for the effects of activated carbon on *Pilea* I assumed that differences seen between LM and activated carbon treatments were independent of the effect of activated carbon alone. We hypothesized that activated carbon would decrease the ability of LM to inhibit the fitness of *Pilea* because activated carbon should absorb allelochemicals limiting their ability to directly inhibit the fitness of *Pilea*. Our results do not necessarily mean that LM is not allelopathic. *Lonicera maackii* clearly modified the effect of activated carbon, and this mechanism was likely chemical. It may be possible that the chemicals potentially released by LM were indirectly affecting *Pilea* and that this indirect effect by LM was somehow enhanced by activated carbon. However the mechanism by which this would happen is unclear.

Maternal effects of the environment and soil micro-biota were both factors likely to affect the response of *Pilea* to activated carbon treatments in these experiments. *Pilea* did not respond positively to activated carbon in the second experiment. The positive overall effect of activated carbon on *Pilea* in experiment one may be a result of maternal effects, soil-biota or both. The difference between these two experiments was not likely genetic as the same collection site was used for both experiments. When *Pilea* was grown from seed it was not affected by activated carbon alone indicating that the benefit of

activated carbon in experiment one might be linked to collection from the field. One factor that may contribute to varying effects of activated carbon is that microorganisms were transplanted along with *Pilea* into experimental pots in Experiment 1 but not Experiment 2. Microorganisms in soil are known to alter soil chemistry (Inderjit, 2005; Inderjit and Callaway, 2003; Lankau 2009) making it possible for an interaction with activated carbon to affect *Pilea* fitness. However, this does not fully explain the difference in effect of LM on *Pilea* between activated carbon treatments. The positive effect of activated carbon on the competitive ability of LM does not fit the typical activated carbon model for separation of competitive and allelopathic effects; but it is apparent that LM was altering soil chemistry in a way that may indirectly affect the fitness of target plant.

Implications to the evolution of increased competitive ability hypothesis

Our results support our hypothesis that LM from its invasive ranges were more competitive both inter- and intraspecificly. *Lonicera maackii* from Ohio was larger, had a greater competitive effect and responded less to competition than the population of LM from China. The use of only one population from the native region of LM limits the ability to state whether our results reflect large scale differences between native and invasive populations of LM. However, it was demonstrated that young LM exhibit little variation in competitive ability within a reasonable portion of its invasive range, and the use of individuals grown from seeds of multiple plants suggests differences seen between populations in this study were genetic. Yet the possibility exists that no evolution has

actually occurred but that larger and more aggressive genotypes from the native range were the ones established in North America.

The increased competitive ability of LM is likely the result of plasticity and resource allocation differences between ecotypes as LM's effect on plants was associated with its size. Whether differences in competitive ability relate to alterations in selection pressure by enemy release remains unknown, but LM has been observed to have less herbivory than native shrubs (Trisel and Gorchov, 1994). Changes in compensatory growth and root to shoot biomass allocation may have greater effects on invasiveness in field conditions due to increased herbivore tolerance and increased competitive effects aboveground (Zou 2007).

It was noted that Ohio LM seemed to germinate sooner than Chinese LM. The effect of this in our experiment was avoided by selecting seeds from each group that germinated at the same time, but in the field, delayed germination would likely further limit their long term competitive ability (Ross and Harper 1972, Miller 1987). In experiment one, the size of *Pilea* at the end of the experiment was dependent on the staring size of LM. Earlier seed germination would likely make Ohio LM larger when they start competing thereby increasing its overall effect on target plant fitness

Multiple studies have examined the effect of LM on plant communities at mature stages and have found that above ground resource competition is partly responsible for the effects of LM on native communities (e.g., Cipollini *et al.* 2008b, Gorchov and Trisel 2003, Gould and Gorchov 2000). Our study focused on small shrubs unlikely to be able to compete well for above ground resources. One of the key differences of LM between native and invasive ecotypes was their response to competition at this size. Reduced

response to intraspecific completion likely increases its ability to reach high densities. This would help facilitate its own invasion as the shrub grows by making it a formidable competitor for above ground resources. Intraspecific competitive ability resulting in the ability to reach high densities is associated with the success of multiple invaders such as *Alliaria petiolata, Solidago gigantean* and *Phalaris arundinacea* (Bossdorf *et al*. 2004, Lavergne and Molofsky 2004, Weber and Jakobs 2004).

Few studies have tested the ECIA hypothesis by intraspecific competition between individuals from native and invasive regions. Most recently *Sapium sebiferum* from native and invasive populations were competed against one another by Zou (2007). Their study found that *Sapium sebiferum* from invasive populations grew to be larger in size than native in spite of having greater herbivore damage. Bossdorf *et al.* (2004) tested the ECIA hypothesis on the herbaceous invader *Alliaria petiolata* by competing individuals from native and invasive populations. Interestingly, they found that *Alliaria petiolata* from its invasive range was less competitive in intraspecific competition, suggesting that that competitive ability for resources does not limit *A. petiolata*'s invasive success. The results of our study suggest that resource competition is a contributing factor to the ability of LM to invade communities. However, interspecific competition alone is unlikely to be responsible for invasion; highlighting the importance of studies which compare both inter and intra-specific competition between native and invasive genotypes.

Further research

Further study on the allelopathic potential of LM should strongly consider interactive effects of soil type and chemistry on the competitive ability of LM. A key

limitation to this study was not knowing if compounds identified in LM leaf extracts by Cipollini *et al.* (2008a) were present in the soil. In the future any such assay should demonstrate the existence of compounds in the soil. While this can be a difficult, several methods are available for quantifying potential allelochemicals in soil (Weidenhamer, 2005). Future studies on LM should use soil gathered from the field to ensure substrate allows for normal movement of allelochemicals as well as making sure that micro-organisms are represented. I suggest a three way full-factorial design which alters the nutrient levels, micro-biota along with LM. Ideally sterilized soil would be used to eliminate effects of micro-biota and fertilizer additions could be used to see how LM affects competitors in positive environments.

Further study is needed to gather a more comprehensive perspective on how differences between native and invasive ecotypes could explain the invasive ability of LM. Studies should include multiple populations from both native and invasive regions and make comparisons across variety of life history traits. Differences between the early life history stages of LM ecotypes could affect its ability to impact communities as it ages.

Conclusions

Lonicera maackii's invasive ability may be dependent on both its allelopathic and competitive properties. It is not know if the allelopathic impact observed in this study would transcribe to field conditions so that native plant populations would be effected in the long term. It is likely that young *L. maackii* in may affect target plants such as *Pilea* in close proximity via allelopathy. Invasive *L. maackii* in Ohio is likely a representative

of a more competitive genotype than those from the native population. It is unknown if the competitive difference seen in this study was the result of evolution by natural or anthropogenic selection or if *L. maackii* in Ohio is from a more competitive population in its native range. Regardless, it is likely that the increased competitive ability of *L. maackii* is contributing to the successful establishment of *L. maackii* in newly invaded areas.

TABLES

Table 1: Population collection and planting information for experiment 1. N= #individuals on date of first measurements (6/1/08).

Population	Lat and Long (deg/ min/ sec)	Collection Date (s)	Planting Date (s)	N per treatment	
				C+	C-
Athens	39°18'17.85"N 82°11'1.99"W	1. 5/4/08 2. 5/17/08	1. 5/10/08 2. 5/20/08	13	12
Cedar Cliff Park	39°44'35.38"N 83°49'37.29"W	5/8/08	5/10/08	12	11
Caesar Creek State Park	39° 30’ 46.03”N 84° 1’ 22.14”W	5/17/08	1. 5/18/08 2. 5/20/08	15	14
Englewood Metro Park	39° 51’ 43.17”N 84° 16’ 4.81” W	5/16/08	5/18/08	15	14
Winton Woods (Cincinnati)	39° 15’ 29.76” N 84° 32’ 04.89”W	5/20/08	5/22/08	9	10
Yellow Springs	39° 47’ 13.65” N 83° 53’ 22.72 W	5/8/08	5/10/08	13	10

Table 2: Correlation matrix of *Pilea pumila* end of season measures for experiment 1. Numbers represent: Pearson Coefficients, P-value and sample size.

End of season measures	Primary stem length	Basal stem diameter	Root biomass	Shoot biomass	total biomass	Flower production
Primary stem length	1	0.41962	0.48826	0.53637	0.48946	0.38594
	NA	<0.001	<0.0001	<0.0002	<0.0003	0.2411
	162	162	64	162	64	12
Basal stem diameter		1	0.56954	0.57889	0.66661	0.50135
		NA	<0.0001	<0.0002	<0.0003	0.1162
		162	64	162	64	12
Root biomass			1	0.80945	0.85768	0.58748
			NA	<0.0001	<0.0001	0.0574
			64	64	64	12
Shoot biomass				1	0.99617	0.88742
				NA	<0.0001	0.0003
				162	64	12
total biomass					1	0.87877
					NA	0.0004
					64	12
Flower production						1
						NA
						12

Table 3: Experiment 1ANCOVA. Effect of LM population treatments (LM POP) and activated carbon on *Pilea* biomass using starting basal stem diameter of LM as a covariate (LM basal stem diameter).

Factors		Root biomass		Stem biomass		Total biomass	
	DF	F	P	F	P	F	P
Model	12	1.43	0.22	2.5	0.005	1.24	0.31
LM basal stem diameter	1	6.13	0.0207	13.33	0.0004	2.79	0.1081
activated carbon	1	2.83	0.1053	0.59	0.4431	0.31	0.5822
LM POP	5	0.41	0.8381	1.63	0.1579	0.25	0.937
LM POP*activated carbon	5	0.93	0.4767	1.11	0.359	0.81	0.552
		Error DF=36		Error DF=122		Error DF=36	

Table 4: Experiment 1 ANOVA. Effect of LM and activated carbon on *Pilea* root, shoot and total biomass.

		Root biomass		Shoot biomass		Total biomass	
Factors	DF	F	P	F	P	F	P
activated carbon	1	11.69	0.0011	5.56	0.0196	3.11	0.0829
LM	1	42.53	<0.0001	34.16	<0.0001	16.46	<0.0001
LM*activated carbon	1	6.5	0.0134	10.33	0.0134	9.55	0.003
		Error DF=60		Error DF= 158		Error DF= 60	

Table 5: Experiment 1 ANOVA of effects of activated carbon on LM biomass within *Pilea* treatments.

		Root biomass		Shoot biomass		Total biomass	
Factors	DF	F	P	F	P	F	P
activated carbon	1	0.69	0.41	0.96	0.32	0.93	0.34
		Error DF=35		Error DF= 133		Error DF= 35	

Table 6: Experiment 1, Repeated measures MANOVA with Wilks' lambda test (W) for the effect of time and its interactions with LM, activated carbon on the growth of *Pilea*.

		Primary stem length			Basal stem diameter		
subjects	DF	W	F	P	W	F	P
Time	8	0.044	406.81	<0.001	0.048	373.83	<0.001
Time x LM	8	0.921	1.6	0.1292	0.8464	2.95	0.0043
Time x activated carbon	8	0.857	3.14	0.0026	0.912	1.82	0.0767
Time x LM x activated carbon	8	0.943	1.14	0.337	0.972	0.53	0.834

Table 7: Experiment 1, ANOVA for between subject effects of LM, activated carbon and their interactions on the growth of *Pilea*

		Primary stem length		Basal stem diameter	
Factors	DF	F	P	F	P
LM	1	9.9	0.002	12.16	<0.001
activated carbon	1	5.16	0.0245	13	<0.001
LM x activated carbon	1	4.31	0.0395	2.6	0.109
		Error DF=158		Error DF= 158	

Table 8: Experiment 2, Correlation matrix of *Pilea* end of season measures and stem length at day 58 of the experiment. Numbers represent: Pearson Correlation Coefficients, P-value, and sample size.

	Primary stem length	basal stem diameter	Root biomass	Shoot biomass	Total biomass	Infructescence biomass	day 58 stem length
Primary stem length	1	0.20059	0.02924	0.13885	0.12815	-0.0467	0.03649
	NA	0.058	0.7844	0.1918	0.2274	0.6713	0.7327
	90	90	90	90	90	85	90
basal stem diameter		1	0.49219	0.58468	0.6021	0.35027	74
		NA	<0.001	<0.001	<0.001	0.001	<0.001
		90	90	90	90	85	90
Root biomass			1	0.6093	0.70789	0.49908	0.42972
			NA	<.001	<0.001	<0.001	<0.001
			90	90	90	85	90
Shoot biomass				1	0.99139	0.61583	0.59999
				NA	<0.001	<0.001	<0.001
				90	90	85	90
Total biomass					1	0.63393	0.60542
					NA	0.001	<0.001
					90	85	90
Infructescence BM						1	0.57701
						NA	<0.001
						85	90
Day 58 primary stem length							1
							NA
							90

Table 9: Experiment 2 ANOVA. Effect of competition treatment (Comp) and activated carbon on *Pilea* root, shoot and total biomass as well as square root of Infructescence (sqrt (IF)) biomass.

		Root biomass		Shoot biomass		Total biomass		sqrt(IF) biomass	
Factors	DF	F	P	F	P	F	P	F	P
Comp	2	28.37	<0.001	52.46	<0.001	58.57	<0.001	12.51	<0.001
activated carbon	1	0.95	0.3336	12.89	<0.001	9.47	0.0028	2.04	0.1306
Comp*activated carbon	2	3.37	0.0391	1.08	0.3431	1.37	0.2603	1.4	0.1511
		Error DF=84		Error DF= 84		Error DF= 84		Error DF=79	

Table 10: Experiment 2 ANOVA. The effect of activated carbon and LM origin on mean LM biomass within *Pilea* treatments.

		Root biomass		Shoot biomass		Total biomass	
Factors	DF	F	P	F	P	F	P
activated carbon	1	0.61	0.44	0.08	0.77	0.21	0.65
LM	1	13.81	<0.0005	50.96	<0.0001	43.86	<0.0001
		Error DF=57		Error DF= 57		Error DF= 57	

Table 11: Experiment 2 ANOVA. The effect of activated carbon, LM origin and *Pilea* competition on mean basal stem diameter of LM at day 59.

Factors	DF	SS	F	P
activated carbon	1	0.2191	1.56	0.2153
Pilea	1	0.4825	3.43	0.0672
activated carbon x *Pilea*	1	0.1632	1.16	0.2843
LM	1	0.7093	5.04	0.0271
activated carbon x LM	1	0.0309	0.22	0.6402
LM x *Pilea*	1	0.6384	4.54	0.0358
activated carbon x LM x *Pilea*	1	0.0245	0.17	0.6775
		Error DF=92		

Table 12: Experiment 2 ANOVA. The effect of LM origin and *Pilea* competition on mean basal stem diameter of LM at day 59.

Factors	DF	SS	F	P
Pilea	1	0.5526	3.91	0.0508
LM	1	0.6915	4.9	0.0293
LM x *Pilea*	1	0.9337	6.61	0.0117
		Error DF=96		

Table 13: Experiment 2, repeated measures MANOVA with Wilks' lambda test for the effect of time and its interactions with competition treatment (Comp) and activated carbon on the growth of *Pilea*.

		Primary stem length		
Subjects	DF	W	F	P
Time	3	0.0082	3287.36	<0.001
Time x Comp	3	0.7257	4.75	<0.001
Time x activated carbon	3	0.9765	0.66	0.5805
Time x Comp x activated carbon	3	0.7702	3.81	0.0014

Table 14: Experiment 2, ANOVA for between subject effects of Competition treatment, activated carbon and their interactions on the growth of *Pilea*

		Primary stem length	
Factors	DF	F	P
Comp	2	15.63	<0.001
activated carbon	2	1.04	0.3112
Comp x activated carbon	2	5.18	0.0076
		Error DF=158	

Table 15: Correlation matrix for Chinese LM end of season measures in intraspecific competition experiment. Values are correlation coefficients, p-value, and sample size.

	Primary stem length	Basal stem diameter	Root biomass	Shoot biomass	Total biomass
Primary stem length	1	0.78082	0.65632	0.8287	0.81235
	NA	<0.001	<0.001	<0.001	<0.001
	39	39	39	39	39
Basal stem diameter		1	0.71227	0.7978	0.80274
		NA	<0.001	<0.001	<0.001
		39	39	39	39
Root biomass			1	0.78202	0.8639
			NA	<0.001	<0.001
			39	39	39
Shoot biomass				1	0.98949
				NA	<0.001
				39	39
Total biomass					1
					NA
					39

Table 16: Correlation matrix for Ohio LM end of season measures in intraspecific competition experiment. Values are correlation coefficients, p-value, and sample size.

	Primary stem length	Basal stem diameter	Root biomass	Shoot biomass	Total biomass
Primary stem length	1 NA 40	0.56388 <0.001 40	0.55924 <0.001 40	0.44892 0.0037 40	0.50753 <0.001 40
Basal stem diameter		1 NA 40	8.4624 <0.001 40	0.73542 <0.001 40	0.81245 <0.001 40
Root biomass			1 NA 40	0.70847 <0.001 40	0.81395 <0.001 40
Shoot biomass				1 NA 40	0.98665 <0.001 40
Total biomass					1 NA 40

Table 17: Intraspecific competition experiment: ANOVA for the effect of target plant origin and competition treatment on LM Biomass.

		Root biomass		Shoot biomass		Total biomass	
Factors	DF	F	P	F	P	F	P
Target	1	3.79	0.0555	36.62	<0.001	27.69	<0.001
Competitor	2	1.57	0.2142	4.92	0.0099	4.31	0.0169
Target x Competitor	2	1.55	0.2195	2.27	0.1101	2.30	0.1069
		Error DF=74		Error DF= 74		Error DF= 74	

Table 18: Intraspecific competition experiment: ANOVA for the effect of the target plant origin and competition treatment on the response of LM Biomass to competition.

		Root biomass		Shoot biomass		Total biomass	
Factors	DF	F	P	F	P	F	P
Target	1	11.09	0.0015	12.00	<0.001	13.37	<0.001
Competitor	1	2.52	0.1177	5.96	0.0178	5.64	0.0210
Target x Competitor	1	0.76	0.3879	1.66	0.2025	1.59	0.2121
		Error DF=56		Error DF= 56		Error DF= 56	

Table 19: Intraspecific competition experiment: repeated measures MANOVA with Wilks' lambda test (W) for the effect of time and its interactions with LM competitor origin on Chinese and Ohio LM primary stem length.

		Chinese LM			Ohio LM		
subjects	DF	W	F	P	W	F	P
Time	3	0.0497	216.62	<0.001	0.0259	437.85	<0.001
Time x competitor treatment	6	0.6145	3.12	0.0092	0.7470	1.83	0.1054

Table 20: ANOVA for between subject effects of LM competition treatments on target LM primary stem length.

		Chinese		Ohio	
Factors	DF	F	P	F	P
Competitor treatment	2	5.13	0.011	1.67	0.2029
		Error DF=36		Error DF= 37	

FIGURES

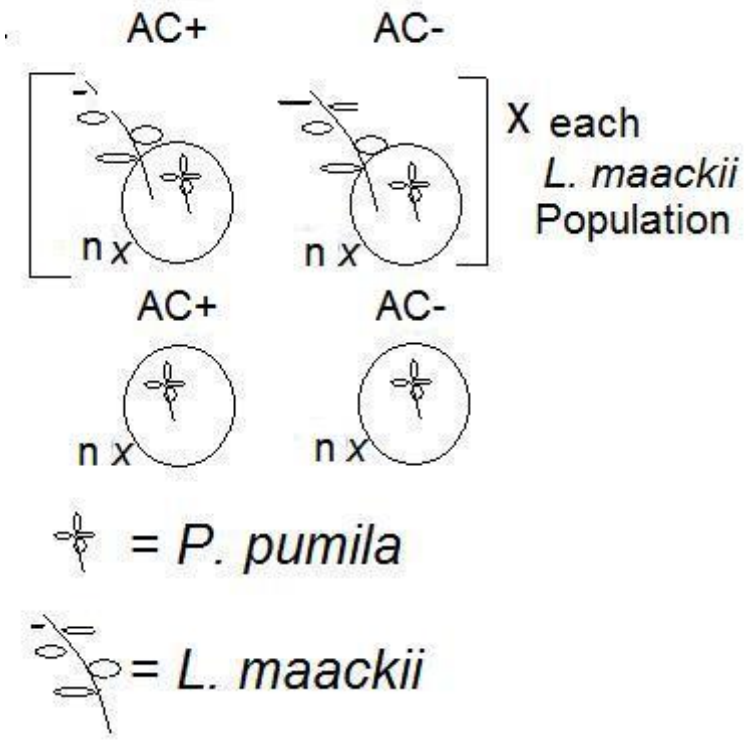

Figure 1: Full factorial design for effects of *Lonicera maackii* on the target plant *Pilea pumila*.

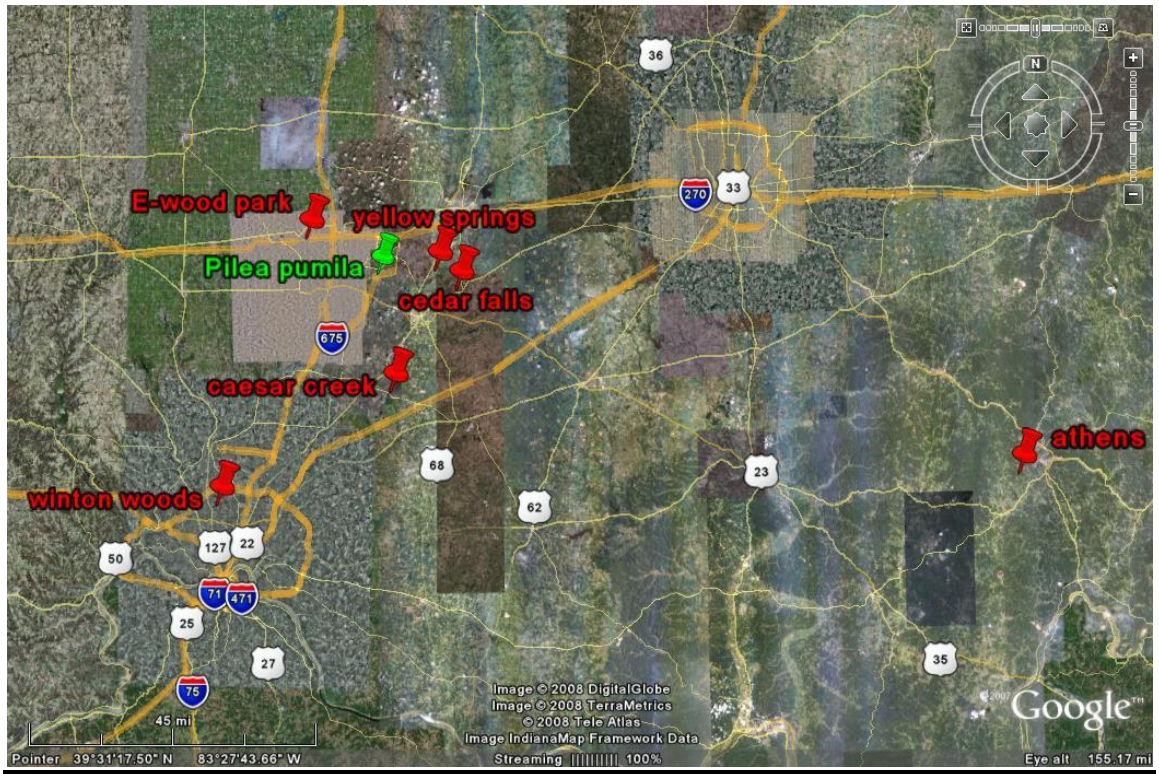

Figure 2: Map showing *L. maackii* sampling locations for experiment 1.

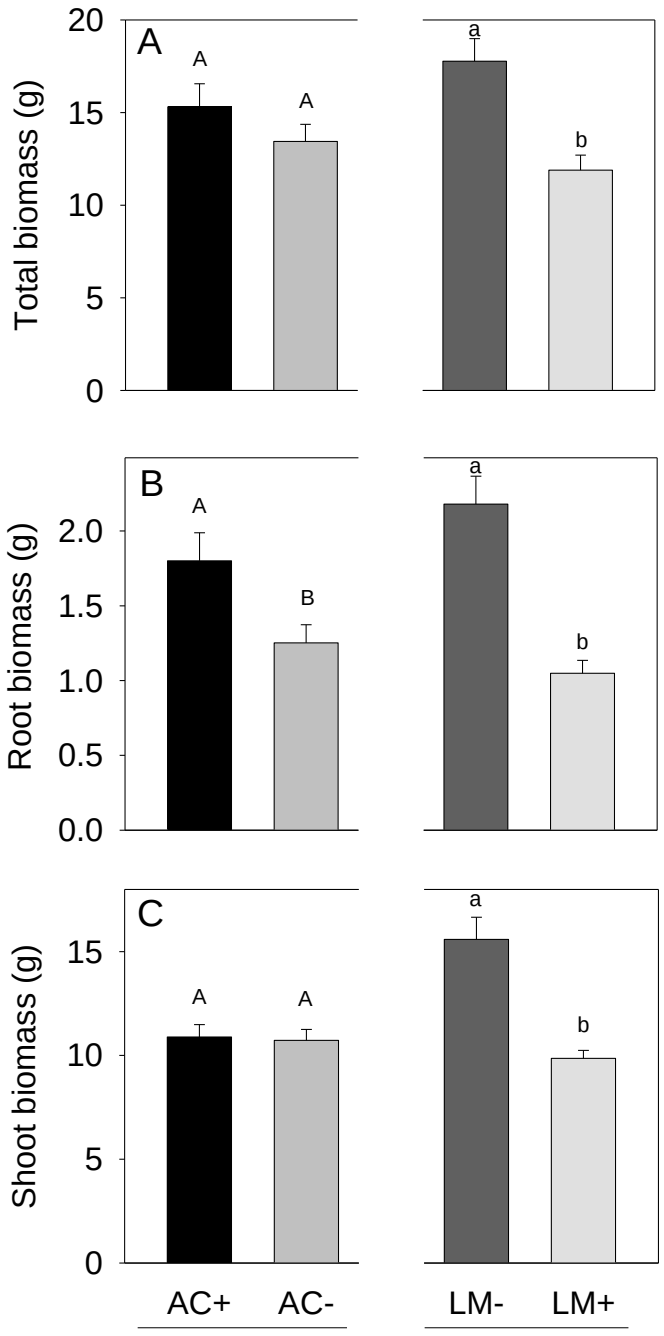

Figure 3: Mean (+ 1SE) dry Total biomass (A), Root biomass (B) and Shoot biomass (C) of *Pilea* in response to the presence or absence of activated carbon (AC+ and AC- respectively) and *Lonicera maackii* (LM +or -) treatments for experiment 1. Bars with different letters are significantly different at α=0.05. Bars with letters of different case size cannot be compared.

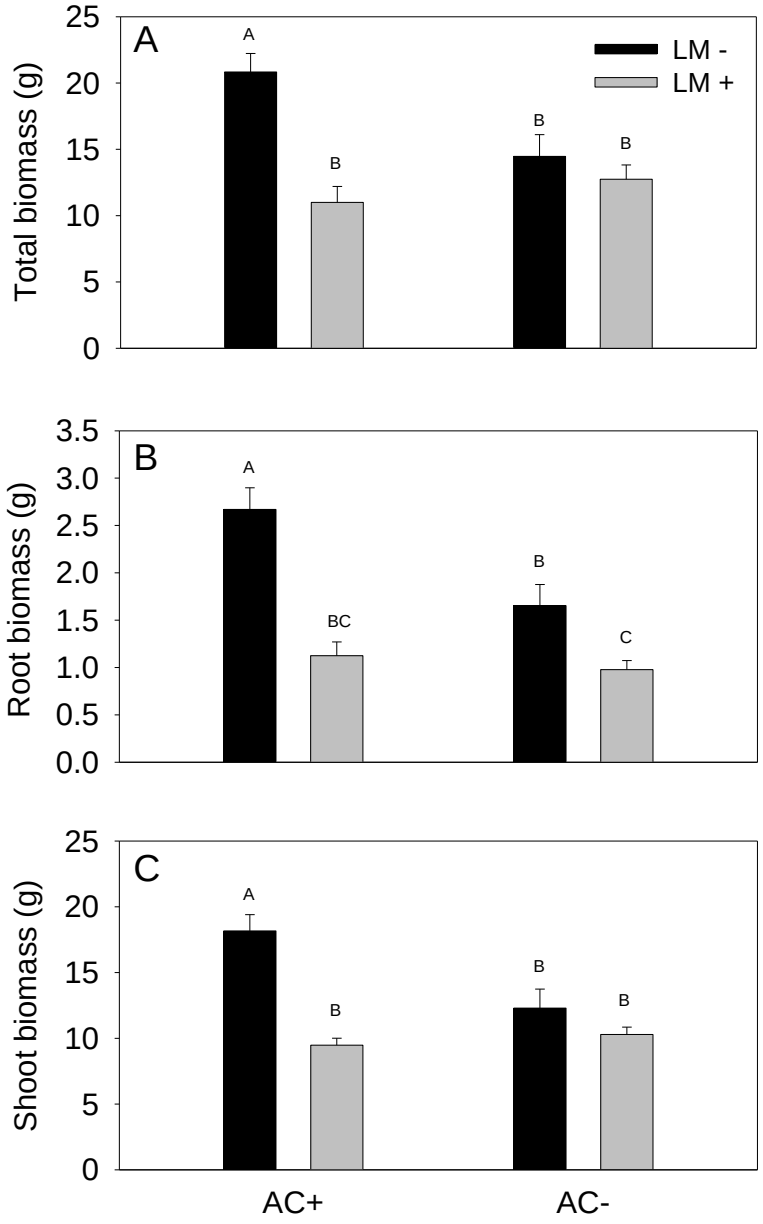

Figure 4: Mean (+1SE) dry Total biomass (A), root biomass (B) and shoot biomass (C) of *Pilea* in response to activated carbon and LM treatment interactions for experiment 1. Bars not sharing letters are significantly different at $p<0.05$.

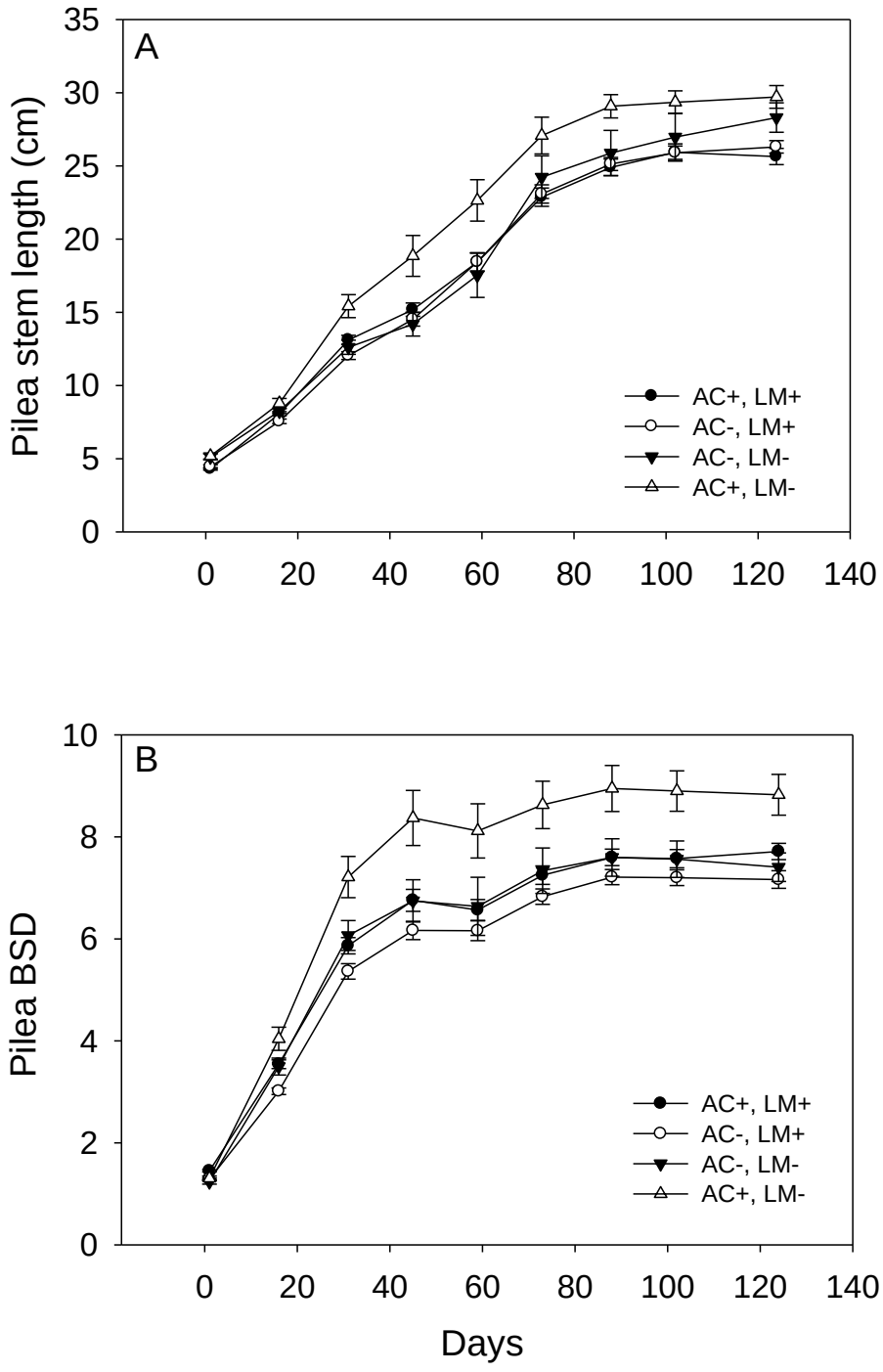

Figure 5: Change in the primary stem length (A) and basal stem diameter (B, BSD) (mean ± 1SE) of *Pilea* in response to LM and activated carbon treatments throughout the experiment.

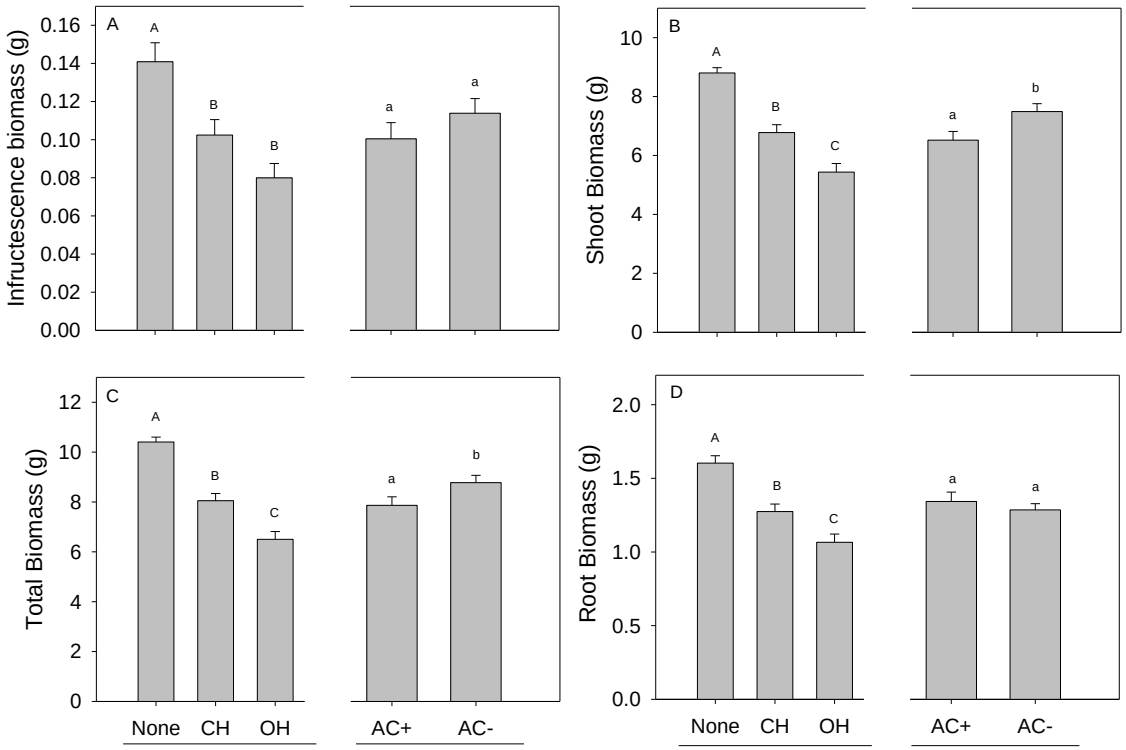

Figure 6: Mean *Pilea* biomass (+1SE) from experiment 2 by treatment factors. A. Infructescence biomass. B. Above ground biomass. C. Total biomass. D. Root biomass. Competition treatments consist of None, Chinese origin (CH) and Ohio origin (OH) LM. Bars not sharing letters with in their treatment type are significantly different. (α=0.05)

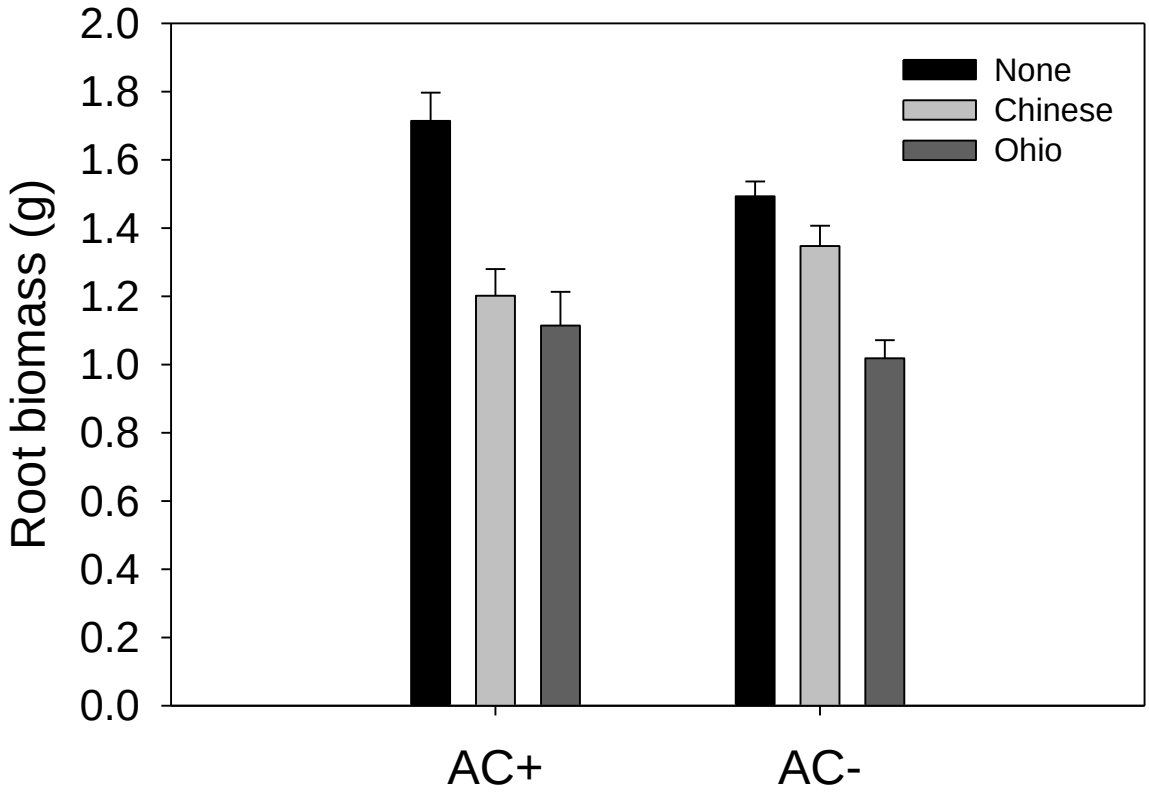

Figure 7: Dry root biomass (mean +1SE) of *Pilea* in response to LM and activated carbon treatment interactions for experiment 2.

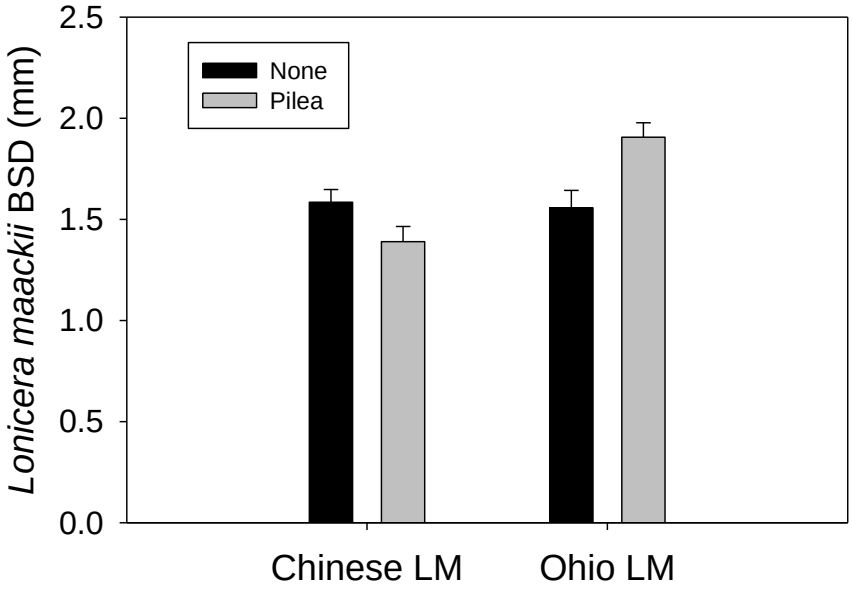

Figure 8: Bars represent mean (+1SE) basal stem diameter (mm) of LM from its two origins with and without *Pilea*.

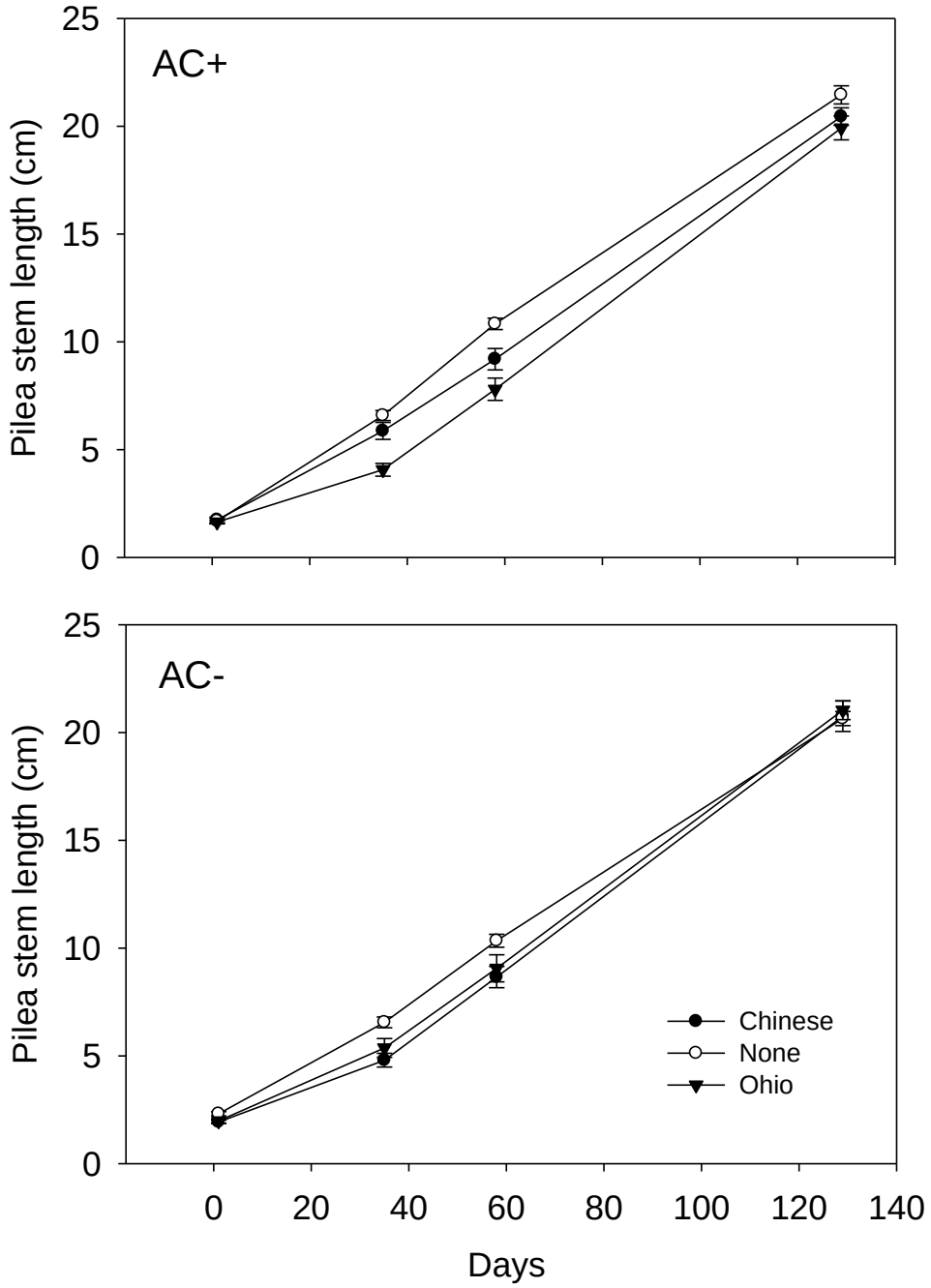

Figure 9: Mean (±1SE) primary stem length of *Pilea* throughout experiment 2. Graphs are separated by activated carbon treatment (AC+ or AC-) for easer interpretation of interactive effects and symbols correspond to different LM treatments.

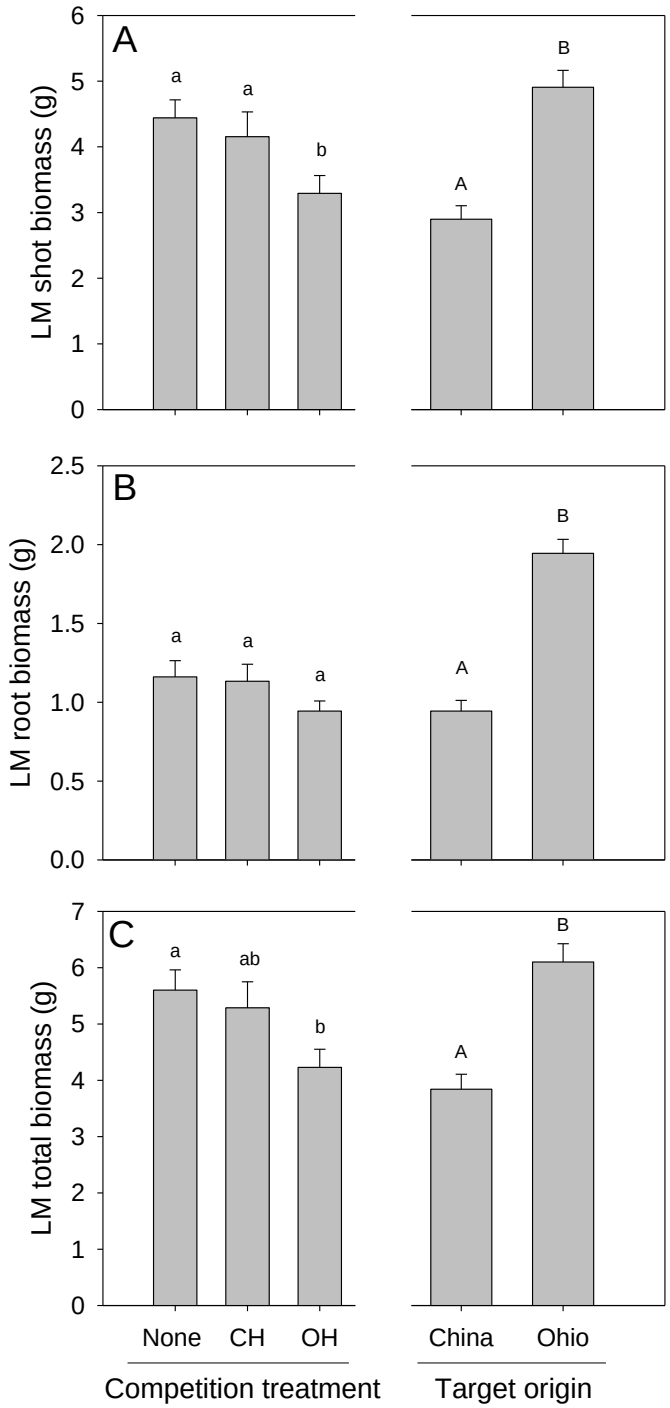

Figure 10: The mean (+1SE) LM dry shoot biomass (A), root biomass (B) and total biomass (C) categorized by competitor treatments and target LM origin. Bars not sharing letters are significantly different at $\alpha=0.05$ and letters of different case size are not comparable.

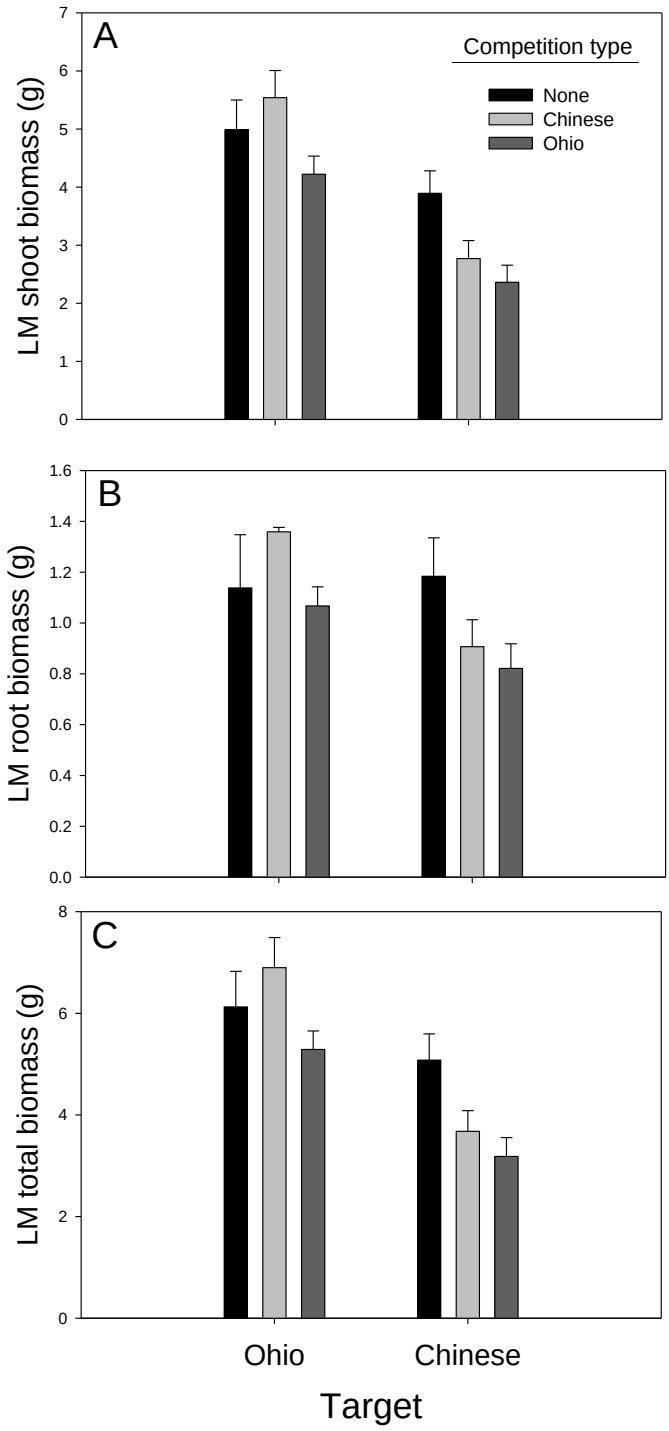

Figure11: Mean (+1SE) LM shoot biomass (A), root biomass (B) and total biomass (C) based on target origin and competitor treatment interactions.

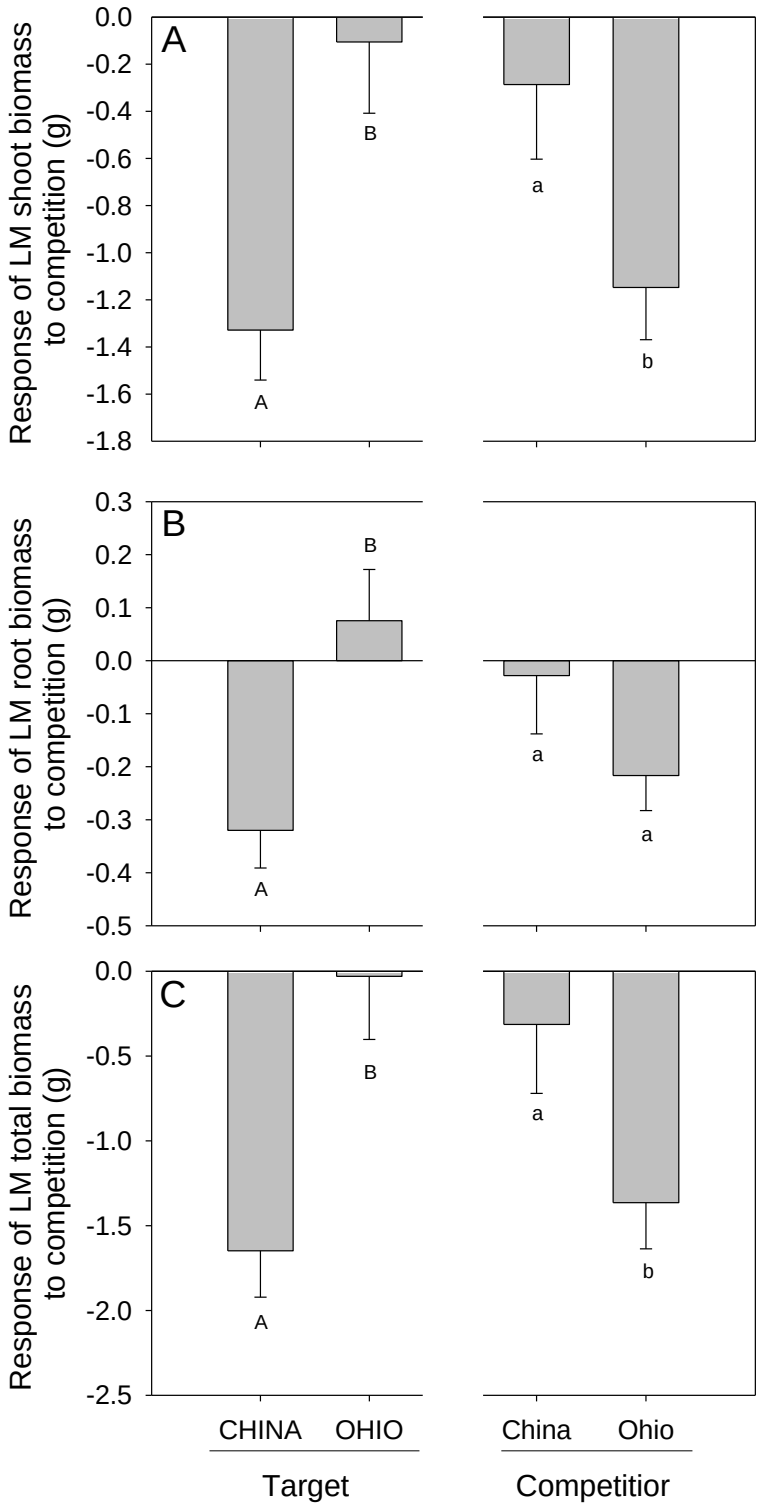

Figure12: Mean (+ or -, 1SE) response of LM shoot biomass (A), root biomass (B) and total biomass (C) to competition based on the origin of the target and competitor LM. Bars not sharing letters are significantly different but letters of different case size are not comparable.

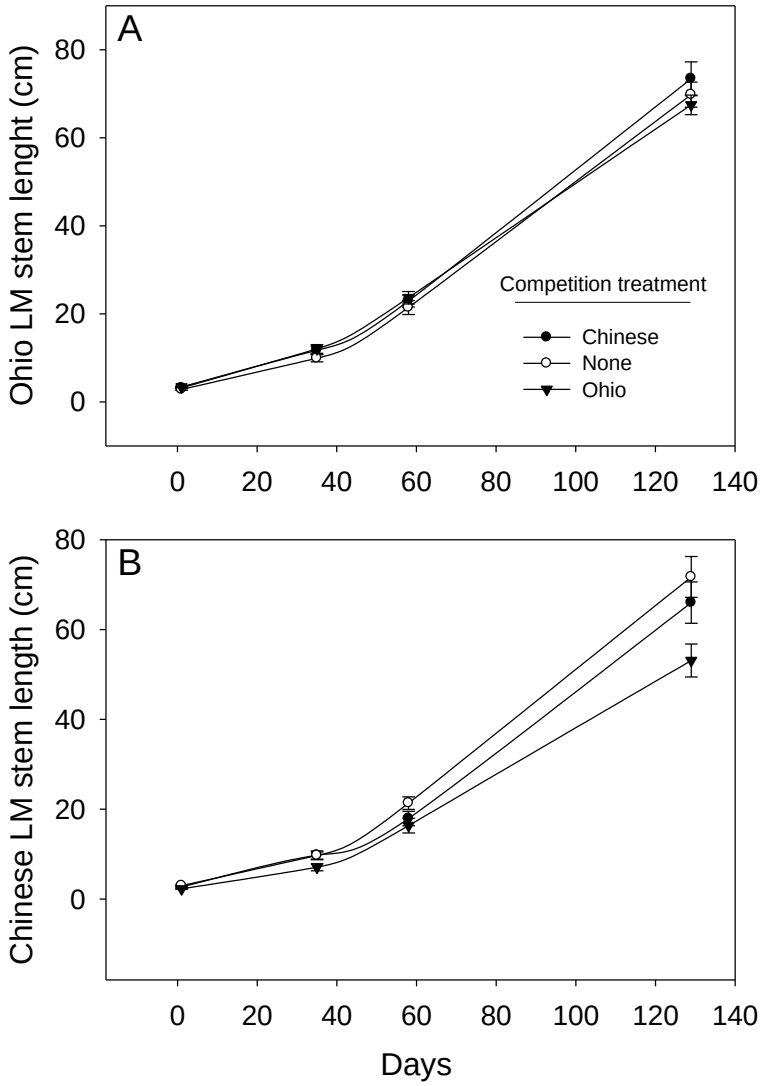

Figure 13: Mean primary stem length (± 1SE) of Ohio (A) and Chinese (B) LM through time between LM competitor treatments.

LITERATURE CITED

Baker, H.G. 1974. The evolution of weeds. Annual Review of Ecology and Systematics 5: 1-24

Bartuszevige, A.M., and D.L. Gorchov. 2006. Avian seed dispersal of an invasive shrub. Biological Invasions 8: 1013-1022.

Bartuszevige, A.M., D.L. Gorchov, and L. Raab. 2006. The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. Ecography 29: 213-222.

Blossey, B. and R. Notzold. 1995. Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants: A Hypothesis. Journal of Ecology 83 (5): 887-889

Bossdorf, O., D. Prati, H. Auge1 and B. Schmid. 2004. Reduced competitive ability in an invasive plant. Ecology Letters 7: 346–353

Bossdorf, O., H. Auge, L. lafuma, W.E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia 144: 1-11.

Callaway, R.M., and E.T. Aschenhoug. 2000. Invasive Plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290: 521-523.

Callaway. R.M., and W.M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2(8): 436-443.

Callaway, R.M., D. Cipollini, K. Barto, G.C. Thelen, S.G. Hallett, D. Prati, K. Stinson, and L. Klironomos. 2008. Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89(4): 1043-1055

Chiarello, N.R., H.A. Mooney, and K. Willions. 1989. Growth, carbon allocation and cost of plant tissues. Pg 327-365 in W. Pearca, J. Ehlearinge, H.A. Money and P.W. Rudel, eds Plant Physiological Ecology: Filed methods and instrumentation. Chapmen & Hull New York, NY.

Cid-Benevento, C.R. 1987. Relative effects of light, soil moisture availability and vegetative size on sex ratio of two monecious woodland annual herbs: *Acalypha rhomboidea* (Euphorbiaceae) and *Pilea pumila* (Urticaceae). Bulletin of the Torrey Botanical club 114(3): 293-306.

Cid-Benevento, C.R., and P.A. Werner. 1986. Local distributions of old-field and woodland annual plant species: demography, physiological tolerances and allocation of biomass of five species grown in experimental light and soil-moisture gradients. The Journal of Ecology 74(3): 857-880.

*a*Cipollini, D., R. Stevenson, S. Enright, A. Eyles, and P. Bonello. 2008. Phenolic metabolites in leaves of the invasive shrub *Lonicera maackii* and their potential phyotoxic and anti-herbivore effects. Journal of Chemical Ecology 24: 144-152.

*b*Cipollini, D., R. Stevenson, and K. Cipollini. 2008. Contrasting effects of allelochemical from two invasive plants on the performance of a nonmycorrhizal plant. International Journal of Plant Sciences 16993): 371-375.

Cipollini, D., and M. Dorning. 2008. Direct and indirect effects of conditioned soils and tissue extracts of the invasive shrub, *Lonicera maackii*, on target plant performance. Castanea 73(3): in press.

Cipollini, K.A., G.Y. McClain, and D. Cipollini. 2008. Separating above- and belowground effects of *Alliaria petiolata* and *Lonicera maackii* on the performance of *Impatiens capensis*. American Midland Naturalist 160: 117-128.

Colautti, R.I., I.A. Grigorovich, and H.J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037.

Collier, M.H., J.I. Vankat, and M.R. Hughes. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. American Midland Naturalist 147: 60-71.

Conway, W.C., L.M. Smith, and J.F. Bergan. 2002. Potential allelopathic interference by the exotic Chinese tallow tree (*Sapium sebiferum*). American Midland Naturalist 148: 43-53.

Dorning, M. and D. Cipollini. 2006. Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. Plant Ecology 184: 287-296.

Dlugosch, K.M., and I.M. Parker. 2008. Founding events in species invasions: genetic variation adaptive evolution and the role of multiple introductions. Molecular Ecology 17: 431-449.

Ellstrand, N.C. and K.A. Schierenbeck. 2006. Hybridization as a stimulus for the evolution of invasiveness in plants?. Euphytica 148: 35–46

Ehrenfeld, J.G. (2003) Effect of exotic plant invasion on soil nutrient cycling processes. Ecosystems 6: 503-523.

Gomez-aparicio, L., and C.D. Canham. 2008. Neighborhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. Journal of Ecology 96: 447-458.

Gorchov, D.L., and D.E. Trisel. 2003. Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. Plant Ecology 166: 13–24.

Gould, A.M., and D.L. Gorchov. 2000. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of annuals. American Midland Naturalist 144: 36-50.

Grotkopp, E., M. Rejmanek, and T.L. Rost. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. American naturalist 159: 396-419.

Hierro, J.L., and R.M. Callaway. 2003. Allelopathy and the exotic plant invasion. Plant and Soil 256: 29-39.

Hierro, J.L., J.L. Maron and R.M. Callaway. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. Journal of ecology 93: 5-15.

Hutchinson T.F., and J.L. Vankat. 1997. Invasibility and effect of Amur honeysuckle in southwestern Ohio. Conservation Biology 11(5): 1117-1124.

Inderjit. 2005. Soil microorganisms: An important determinant of allelopathic activity. Plant and Soil 274:227–236

Inderjit. 2001. Soil: environmental effects on allelochemical activity. Agronomy Journal 93: 79-84.

Inderjit, and R.M. Callaway. 2003. Experimental designs for the study of allelopathy. Plant and Soil 256: 1-11.

Kean, R.M., and M.J. Crawley. 2002. Exotic plant invasions and enemy release hypothesis. Trends in Ecology and Evolution 17(4):164-170.

Lankau, R. 2009. Soil microbial communities alter allelopathic competition between *Alliaria petiolata* and a native species. Biological Invasions DOI 10.1007/s10530-009-9608-z

Lau, J.A., K.P. Puliafico, J.A. Kopshever, H. Steltzer, E.P. Jarvis, M. Schwarzländer, and R.A. Hufbauner. 2008. Inference of allelopathy is complicated by the effects of activated carbon on plant growth. New Phytologist 178: 412-423.

Lavergne, S. and J. Molofsky. 2004. Reed Canary Grass (*Phalaris arundinacea*) as a Biological Model in the Study of Plant Invasions. Critical Reviews in Plant Sciences 23(5): 415–429.

Luken, J.O., L.M. Kuddes, T.C. Tholemeier and D.M. Haller. 1997. Comparative responses of *Lonicera maackii* (Amur Honeysuckle) and *Lindera benzoin* (Spicebush) to increased light. American Midland Naturalist 138(2): 331-343

Luken, L.O., and W. Thieret. 1996. Amur honeysuckle, its fall from grace. BioScience 46(1): 18-24.

Luken, J.O. 1988. Population structure and biomass allocation of naturalized shrub *Lonicera maacki*i (Rupr.) Maxim. in forest and open habitats. American midland naturalist 119(2): 258-267.

Mack, R.N., D. Siberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10(3): 689-710.

McEwan, R.W., M.K. Birchfield, A. Schoergendorfer, and M.A. Arthur. 2009. Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors The Journal of the Torrey Botanical Society 136(2):212-220

Miller, T.E. 1987. Effects of emergence time on survival and growth in an early old-field plant community Oecologia 72:272-278.

Orr, S.P., J.A. Rudgers, and K. Clay. 2005. Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. Plant Ecology 181: 153-165.

Pattison, R.R., G. Goldstein and A. Ares. 1998. Growth, biomass allocation and Photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117: 449-459.

Prati, D., and O. Bossdorf. 2004. Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). American Journal of Botany 91: 285-288.

Ridenour W.M., and R.M. Callaway. 2001. The relative importance of allelopathic interference: the effects of an invasive weed on native bunchgrass. Oecologia 126: 444-450.

Ridenour, W.M., J.M. Vivanco, Y. Feng, J. Horiuchi, and R.M. Callaway. 2008. No evidence for trade-offs: *Centaurea* Plants from America are better competitors and defenders. Ecological Monographs 78(3): 369-386.

Ross, M.A., and J.L. Harper. 1972. Occupation of Biological Space During Seedling Establishment. Journal of Ecology 60(1): 77-88.

Singh, S., and M. Pal. 2003. Growth yield and phonological response of wheat cultivars to delayed sowing. Indian Journal of Plant Physiology 8: 227-286.

Smith, M.D., and A.K. Knapp. 2001. Physiological and morphological traits of exotic, invasive exotic, and native plant species in tall grass prairie. International Journal of Plant Science 162: 785-792.

Trisel, D.E., DL Gorchov. 1994. Regional distribution, ecological impact, and leaf phenology of the invasive shrub Lonicera maackii. Bulletin of the Ecological Society of America 75: 231.

Trisel, D.E. 1997. The invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifocliaceae): factors contributing to its success and its effect on native species. Dissertation. Miami University. Oxford, OH.

Weber, E. and G. Jakobs. 2005. Biological flora of central Europe: *Solidago gigantea* Aiton. Flora 200: 109–118

Weidenhamer, J.D. 2005. Biomimetic measurement of allelochemical dynamics in the rhizosphere. Journal of Chemical Ecology 31(2): 221-236.

Zou, J. 2007. Shifts in traits of the Invasive Plant Sapium Sebiferum and rheir Effects on Ecosystem Carbon and Nitrogen Processes. Dissertation. Rice University. Houston, TX.