

# Evaluating the Potential for Biological Control of Garlic Mustard in Michigan

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Michigan Department of Natural Resources, Wildlife Division  
Michigan Department of Military and Veterans Affairs, Environmental Division  
USDA-National Research Initiative, Biology of Weedy and Invasive Plants Program  
Michigan Department of Agriculture  
The Nature Conservancy, Michigan Chapter  
Michigan Agricultural Experiment Station  
Michigan State University Extension

## EXECUTIVE SUMMARY

### OVERVIEW

Garlic mustard (*Alliaria petiolata*) is a globally distributed, invasive weed that is problematic in natural communities across North America. Several research projects carried out by our group are focused on understanding the patterns and processes of its invasions in Michigan forests and will contribute to the design and implementation of new control strategies.

### PRIMARY CONCLUSIONS

*Alliaria petiolata* populations are expanding within invaded forests in Michigan. This trend is significant across seven locations where measurement of spread was possible.

We found that *A. petiolata* plants are almost universally fed upon by herbivores across southern Michigan. However, damage to plants rarely exceeded 2% of the total leaf area in a quadrat. Although widespread, this feeding appears to have no impact on *A. petiolata* survival or fecundity.

Initial matrix population models simulating the impacts of herbivore-induced mortality to *A. petiolata* populations indicate that control of some Michigan populations may be possible using insect biocontrol agents that are currently being tested in quarantine. Further, the simulation suggests that control may be feasible by release of a single biocontrol agent species, which may carry lower risk of causing non-target impacts than releases of multiple biocontrol agent species.

The data presented here paint a portrait of an invasive weed that is spreading rapidly into new habitats and is unchecked by natural enemies. These data show that, in Michigan, damage to *A. petiolata* from herbivores is not biologically significant. Our initial modeling exercises indicate that increasing mortality at key stages in *A. petiolata*'s lifecycle with introduced natural enemy insects may present a new opportunity to slow or reverse its spread. Given the potential for *A. petiolata* to cause harm to the communities that it invades as others have shown (e.g. Stinson and Klironomos 2005, Stinson et al. 2006) and the ineffectiveness of conventional controls, classical biological control agents may be recommended for *A. petiolata* in Michigan if agents are approved for release in the future. If natural enemy agents are released, these studies will provide a useful benchmark for evaluating their performance.

## INTRODUCTION

Garlic mustard (*Alliaria petiolata* (M.Bieb.) Cavara and Grande) (Brassicaceae) is an exotic invasive weed of European origin that is widespread in North America. In Michigan, *A. petiolata* is widely distributed throughout the southern four to five tiers of counties and in isolated areas north of the core invasion (Voss 1985, Blossey et al. 2001b). In 1998 a consortium of partners in North America and Europe initiated a search for suitable biocontrol agents to address the threat that *A. petiolata* poses to native communities.

We are currently involved in three projects addressing various aspects of *A. petiolata* invasions and control in Michigan. (1) We are developing *A. petiolata* population models built using data from Michigan populations to help guide the selection of the most appropriate biocontrol agents for use in Michigan if multiple agents are approved for release. (2) In preparation for potential biocontrol agent releases in Michigan in the future and to better understand the biology of Michigan *A. petiolata* populations, we established potential biocontrol agent release sites across southern Michigan where we have monitored the spread of *A. petiolata* and plant community composition since spring of 2003. Finally, (3) a study of the independent and combined effects of *A. petiolata* invasions and overabundant deer herds on native communities addresses more fundamental questions about invasion processes. Data from this third research area is will be discussed in future reports.

## BIOLOGICAL CONTROL SUMMARY AND OUTLOOK

A search for suitable biological control agents for *A. petiolata* was initiated in 1998 (Hinz and Gerber 1998, Blossey et al. 2001b) with efforts now focused on four weevils in the genus *Ceutorhynchus* (Coleoptera: Curculionidae) that target varied stages in *A. petiolata*'s life cycle (Hinz and Gerber 2000, 2001, Gerber et al. 2002, Gerber et al. 2003, Gerber et al. 2004).

*Ceutorhynchus scrobicollis* and *C. alliariae* are currently the furthest along in host specificity testing. Of these *C. scrobicollis* has had the greatest impacts on *A. petiolata* performance and is predicted to be the most effective of the four weevils if released (see Demographic Modeling section below). Both of these two as well as *C. roberti* have been imported into the United States to the quarantine facility at the University of Minnesota since 2003 for further host-range testing on native North American plant species (Gerber et al. 2004, 2005, Katovich et al. 2005). While work with *C. scrobicollis* has progressed in quarantine in Minnesota, no tests have been conducted using *C. alliariae* or *C. roberti* because of difficulties encountered in getting them to lay eggs (L.C. Skinner personal communication 01/23/2006).

Of the plant species most frequently and commonly accepted for oviposition, feeding, and development by the group of potential biocontrol agents, *Thlaspi arvense* (field pennycress) and *Peltaria alliacea* (garlic cress) are both native to Europe and considered by some to be invasive in North America. Various sources list *Rorippa nasturtium-aquaticum* (water cress) in North America as either native (USDA-NRCS

2006) or exotic (Gerber et al. 2004 and references therein). The assertion that *C. roberti* and *C. alliariae* are unlikely to encounter these species under natural field conditions is plausible for *T. arvense* and *P. alliacea*, but *A. petiolata* and *Rorippa spp.* are sympatric at one known location in Michigan where *A. petiolata* is being studied (J. Evans personal observation). The consistent acceptance of *Rorippa spp.* by multiple *Ceutorhynchus* species in host-specificity trials is of concern to some, but no conclusions have been reached yet regarding the potential for future agent releases to impact these plant species in natural communities and whether those risks are acceptable (L.C. Skinner personal communication 01/23/2006).

Petitions must be submitted to and approved by the USDA Technical Advisory Group (TAG) on weed biological control before any proposed biological control agent can be released in the United States. No petition for approval to release any of the potential agents in North America has been submitted yet, although a proposal to release *C. scrobicollis* seems a likely next step in the *A. petiolata* biocontrol program followed by proposals for the leaf miners (*C. alliariae* and *C. roberti*) and finally the seed feeder (*C. constrictus*) (Gerber and Hinz 2005). Gerber and Hinz (2005) have indicated that the first three species are predicted to be compatible with each other and could potentially be released together. However, Hinz and Gerber (2005) propose that further testing of native North American *Thlaspi* and *Rorippa* species and investigation of the phylogenetic relationship of *T. arvense*, *R. nasturtium-aquaticum*, and *P. alliacea* be conducted prior to submission of a release proposal to the USDA TAG as these questions are likely to be raised by any review board. An expanded version of this summary including details on the biology and host-specificity testing of each species is available in chapter 2 of Evans (2006, available on request as pdf file).

## **DEMOGRAPHIC MODELING STUDY**

### **OBJECTIVES**

The goal of this research is to use population models to guide the selection of the most effective biological control agent(s) of North American *A. petiolata* populations (Davis et al. *in press*). Demographic analysis of plant populations utilizes measurements of the probability that individual plants survive from one life stage to the next (i.e. from seedling to overwintering rosette) to calculate the growth rate of the population as a whole. Landis et al. (2004a) proposed to analyze *A. petiolata* demographic data and use prospective modeling to make predictions about the outcome of *A. petiolata* biocontrol across the range of habitat types and landscapes invaded by *A. petiolata* in Michigan.

“Specific objectives are to: 1) Characterize variation in *A. petiolata* demography at plot and landscape scales and in different habitats in Michigan, 2) Assess the feasibility of *A. petiolata* biocontrol using matrix population models (demographic models) of the impact of seed and rosette mortality on *A. petiolata* population dynamics, and 3) Compare *A. petiolata* demography in the exotic (Michigan) and native (Switzerland) range to determine the relative effects of growing environment and natural enemies on population expansion in the two areas.” (Landis et al. 2004a)

This research is the first to use both empirical and modeling studies to guide the selection of natural enemies. It may help improve the overall safety of biological control by preventing introductions of natural enemies predicted to be ineffective and by preventing the non-target impact risks associated with such introductions.

## METHODS

### Study Sites

Sites for this study are located in the four quadrants of *A. petiolata*'s core distribution in Michigan (Figure 1, Table 1). Two sites each are located in Cass and Lenawee Counties, and one site each is located in Clinton, Kent, Ottawa and Shiawassee Counties. Within each site we marked four permanent sampling areas in which data on *A. petiolata* germination rate, seedling survival, overwintering survival, and fecundity are being recorded in separate quadrats. Two sampling areas at each site are located at or near the habitat edge, while two are located in the habitat interior.

Survival data from each site are then assembled into a matrix (Figure 2) that summarizes the life cycle of the plant and the probability of an individual plant at that particular site surviving from one life stage to the next. The dominant eigenvalue calculated from each matrix is an estimate of the population's growth rate and is referred to as  $\lambda$  (lambda). Populations whose  $\lambda$  values exceed one are expanding (each individual more than replaces itself), while those with  $\lambda$  values below one are declining (individuals fail to replace themselves). When  $\lambda$  equals one, the population is stable.

The goal of any weed biocontrol effort is to reduce the value of  $\lambda$  for the population to less than one. We can use these models to ask which life stage transitions in *A. petiolata*'s life cycle contribute the most to  $\lambda$  and how much damage to those transitions will be required to reduce  $\lambda$  below one in any give population or assemblage of populations. Potential biocontrol agents which inflict the necessary amount of damage to those target life stages are thus predicted to have the greatest probability of successfully reducing  $\lambda$  below one. Those which are predicted to be effective and are shown to be host specific would be the best choices for release. We can also use the model to ask whether single or multiple-agent biocontrol is necessary to control the spread of *A. petiolata*. By including combinations of different types simulated feeding mortality in the model we can asses what single agents or combinations of agents will likely reduce  $\lambda$  below one. If single agent management is predicted to be successful, releases of potentially ineffective agents and the risks of non-target impacts associated with their introduction could thus be avoided.

## PRELIMINARY RESULTS

Preliminary models of *A. petiolata* biocontrol parameterized from the eight Michigan populations suggest that agents which reduce survival from the rosette to the mature adult stage and which reduce fecundity should be considered as primary choices. Those which reduce seedling survival to the rosette stage should be considered

secondarily. Of the four *Ceutorhynchus* weevils currently under consideration for release one, *C. scrobicollis* impacts both overwintering survival and fecundity, and the others affect fecundity either directly through seed feeding behavior or indirectly through leaf feeding.

These initial evaluations indicate that *A. petiolata* spread at seven (RF, RL, ELF, GF, HSP, IR and SH ) of the eight sites could be controlled by combined releases of *C. scrobicollis* and *C. alliariae* (Figure 3) if the damage inflicted by them is at the high range of the what has been observed in Europe (Davis et al. *in press*). *Ceutorhynchus scrobicollis* is predicted to control *A. petiolata* at five (RF, RL, ELF, GF, HSP) of the eight study sites if released alone.

#### MODELING CONCLUSIONS AND FUTURE MODELING WORK

The analysis presented here was built using data from the first complete cohort of *A. petiolata* plants in the study. Eventually the model will include data from at least three separate cohorts. Further development of these preliminary models will incorporate variability in growth between cohorts, the differential growth of edge versus interior populations of *A. petiolata* as well as both spatial and temporal variation in population growth. We will incorporate more of the biocontrol agent biology into the model as more detailed data on the impacts of the *Ceutorhynchus* weevils becomes available. While these models are still early in their development and their predictions are preliminary, they suggest that successful biological control of some *A. petiolata* populations may be feasible in some locations.

#### PRE-RELEASE STUDY

If agents are approved, the first releases will be conducted by members of the Cornell based consortium. A similar group of state and federal collaborators carried out the highly effective purple loosestrife biocontrol program across North America (Katovich et al. 1999, Blossey et al. 2001a, Blossey et al. 2001c, Katovich et al. 2001, Albright et al. 2004) and in Michigan (Kaufman and Landis 2000, Blossey et al. 2001a, Sebolt and Landis 2002, Landis et al. 2003). If approved, biocontrol agents for *A. petiolata* will be made available to states with a demonstrated need, baseline *A. petiolata* population data and the capability to execute successful biocontrol projects (Landis et al. 2004a).

#### OBJECTIVES

In 2003 permanent sampling quadrats were established at eight forests in southern Michigan where *A. petiolata* occurred. Our objectives were to (1) describe the study sites and invaded communities prior to any biocontrol agents releases, (2) determine whether Michigan *A. petiolata* populations are spreading within infested sites, and (3) measure the degree to which existing herbivores are impacting *A. petiolata* populations. These baseline data will contribute to any future assessments of natural enemy performance. If biological control agents for *A. petiolata* are approved for release in the future, initial test releases may be made at a subset of these sites to

allow comparisons of pre and post-release community dynamics and to evaluate the effectiveness of the agents.

## METHODS

### Site Selection

We established eight study sites within *A. petiolata*'s primary range in Michigan's southern Lower Peninsula (Landis et al. 2004b). Criteria for site selection included (1) forested lands > 2 ha in extent, (2) under state, federal, or other long-term conservation management, (3) on which *A. petiolata* populations have been established for at least four years, and (4) with protection from future disturbance or *A. petiolata* management for at least ten years. In spring of 2003 we recorded GPS coordinates for each site. We then marked 10 permanent 0.5 m<sup>2</sup> sampling quadrats (0.5 x 1 m) along each of two parallel, 100 m long transects spaced 10 m apart at seven sites and a single 200 m transect with quadrats spaced 10 m apart at the eighth site (Russ Forest) for a total of 20 quadrats per site. Site inventories included data on forest type (MNFI 2003), maturity (diameter at breast height of principal overstory trees), and understory composition. Because accurate records of species composition were not kept at these sites before the initiation of this study, it is not possible to determine exactly how long *A. petiolata* had been present at any of them prior to 2003, although the extent of the invasions and anecdotal evidence from managers indicated that they met the criteria listed above.

### *Alliaria petiolata* Evaluations

We collected data on *A. petiolata* distribution and abundance in accordance with a nationally standardized protocol (Nuzzo and Blossey unpublished). In spring (June) and fall (Sept. – Nov.) of 2003 – 2005 we visited each site and recorded data from each quadrat including: vegetation cover (*A. petiolata* total, *A. petiolata* by adult, seedling, and rosette stage plants, total non-*A. petiolata* vegetation and non *A. petiolata* vegetation by species), counts of *A. petiolata* adults, seedlings and rosettes, percent cover of substrate (bare soil, leaf litter, woody debris, and rock sum to 100%), and litter depth (cm). We recorded damage to *A. petiolata* plants as the estimated percent of leaf area removed and identified nine categories of damage to *A. petiolata* as either present or absent in each quadrat (leaf mining, windowpaning, edge feeding, holes, spittle bug, scale damage, browse, disease, and other). Finally, we recorded the height of and the number of siliques (seed pods) on each mature second year plant during the spring sampling period.

In contrast to the methods outlined by Nuzzo and Blossey (unpublished), not all sampling quadrats at each site contained *A. petiolata* at the initiation of the study. Rather, the transects traversed the *A. petiolata* invasion front where possible. This was done to allow us to measure spatial spread of *A. petiolata* populations within sites. At one site (Fernwood) this was not possible as all 20 quadrats there contained *A. petiolata* from the outset of the study.

## Site Descriptions

The Michigan Natural Features Inventory (MNFI) has identified 74 community-types that occur in Michigan (MNFI 2003). We used data on the identities, sizes, and abundances of the principal canopy trees as well as physical features of the sites and the inventories of all ground-layer vascular plant species that occurred in the sampling quadrats from June 2003 to October 2005 to describe each site in terms of the MNFI community types. The General Land Office (GLO), which was established by the United States federal government in 1785, systematically surveyed Michigan from 1816 through 1856 and made detailed records of soils, water resources, forests, and other natural features (MNFI 2005). The MNFI has interpreted the GLO data and created maps of early nineteenth century Michigan vegetation (MNFI 2005) with which we compared the current communities. In the site descriptions we have included an overview of the site topography, any important known or probable disturbances, important overstory and understory plant species, and the native species and total species richness that we observed in the sampling quadrats.

The eight sites selected are distributed across the southern four tiers of Michigan counties and represent a diverse assortment of *A. petiolata*-invaded forest types ranging from Southern Floodplain Forest to Dry Southern Forest (Figure 1, Table 2). Detailed site descriptions are contained in Appendix 1 of this document. Summaries of the data used in the analyses that follow are presented in chapter 2 and Appendices 1 and 2 of Evans (2006).

## Analyses of Data

### *Spread of Alliaria petiolata within Sites*

A portion of the sampling quadrats at seven of the eight sites had not yet been invaded when the study was initiated in 2003. We coded each quadrat as either invaded or uninvaded for each sampling period based on the presence or absence of live *A. petiolata* plants. We tested for changes in the number of invaded quadrats per site over time using a repeated measures general linear model in SAS version 8.2 (SAS Institute 2001) after checking that the data met the assumptions of the procedure. We tested the significance of changes in the mean number of invaded quadrats within-sites using Dunn-Sidak adjusted (Gotelli and Ellison 2004) pairwise comparisons in SYSTAT version 11.0 (SYSTAT Inc. 2004). Both first and second year *A. petiolata* plants were present during spring sampling, but second year plants senesced each year prior to fall sampling. Because first and second year plants were often spatially segregated, the fall data do not reflect the full distribution of *A. petiolata* within each site. We used only spring data in the spatial-spread analysis for this reason, although we present the fall data graphically.

### *Estimation of Alliaria petiolata Fecundity*

We estimated fecundity by multiplying the number of siliques per plant by the mean number of seeds per silique using an established ratio of 14.3 seeds per silique (Evans et al. 2005).

### *Calculation of Survival Probabilities*

We calculated survival probabilities for seedling to rosette (“seedling survival”) and rosette to adult plant (“rosette survival”) transitions for *A. petiolata* plants in each sampling quadrat at each site. Seedling survival is expressed as the number of seedlings observed during the spring sampling period divided into the number of rosettes observed during the fall sampling period of the same year, giving the proportion of seedlings that survived the summer. Rosette survival was similarly calculated by dividing the number of rosettes observed during the fall sampling period into the number of flowering adult plants observed during the spring of the following year.

### *Sampling Error*

We detected two forms of observational error in the data. There were 16 cases where fewer seedlings were recorded in spring than the number of rosettes observed in fall and nine similar cases where fewer rosettes were observed in fall than flowering plants the following spring, which generated survival probabilities greater than one. Also there were 20 cases where rosettes were recorded where no seedling had been recorded in the spring and nine cases where flowering plants were observed where no rosettes had been recorded the previous fall (divide by zero error). These errors most often occurred where *A. petiolata* density was lowest and the overlooked plant(s) represented a greater proportion of the quadrat total. These 54 observations were omitted from analyses. Future estimation of sampling error may allow correction of these observations and allow accounting for future errors.

### *Herbivore Impacts on Alliaria petiolata*

We tested for impacts of herbivore damage on *A. petiolata* per capita fecundity and on both seedling and rosette survival using Spearman rank correlations. Spearman correlation coefficients range from -1 to 1 where the sign of the coefficient indicates the direction of the relationship between damage and survival or fecundity.

We calculated correlations between each of the three measures of *A. petiolata* performance listed above and estimated percent leaf damage to *A. petiolata*. All analyses were performed on site mean values across the three years of sampling. We first calculated the mean for each parameter at each site for spring and fall of each year. We then calculated values for each site in spring and fall by taking the mean for each parameter across the three years. We correlated spring leaf damage data with fecundity and seedling survival. Where fall data were used to predict overwintering survival and fecundity we paired estimates of survival and fecundity with fall damage data from the previous year which allowed for two winters’ data to be included (fall 2003 – spring 2004 and fall 2004 – spring 2005).

## RESULTS AND DISCUSSION

### Spread of *Alliaria petiolata* within Sites

The spatial distribution of *A. petiolata* increased at seven of the eight sites from 2003 to 2005 (Figure 4). At the Fernwood site all 20 quadrats were originally invaded, and detection of spread was not possible. All 20 quadrats remained invaded for the duration of the study at this site, and Fernwood was therefore excluded from analyses of spread. In spring of 2003, the number of sampling quadrats ( $n = 20$ ) that contained *A. petiolata* at the seven other sites ranged from 7 – 18 (mean = 11.9) (Table 3). By spring of 2004, this range had shifted to 11 – 18 (mean = 15.9) quadrats invaded per site and to 11 – 20 (mean = 16.4) by spring of 2005. Across these seven sites, the mean percent increase in the number of quadrats invaded from spring of 2003 to spring of 2005 was  $45.9 \pm 12.1\%$  (range 5.6 – 100%). An average of  $59.0 \pm 9.0\%$  (range 30.8 – 100%) of initially uninvaded quadrats became invaded over this same period (Table 3).

The change in the number of invaded quadrats per site over time was significant in a repeated measures analysis (Table 4). The main effect of year on the number of invaded quadrats was significant indicating a change in the distribution of *A. petiolata* within sites over time ( $F_{2,12} = 11.8575$ ,  $P = 0.0014$ ). Although change in the number of invaded quadrats per site was not significant during either one-year time step, over the two year period the 45.9% increase from spring 2003 to spring 2005 was significant (Table 5, *D-S* adjusted  $P = 0.0154$ ). While it would be desirable to estimate the rate of *A. petiolata* spread either within sites or across the landscape, these data are not suited to that purpose. Nuzzo's (1999) study of *A. petiolata* spread in Illinois concluded that populations expanded at a mean rate of approximately 5.4 m/year, which may be similar to the rate of spread at some of these sites.

Our findings offer quantitative support for the frequent observation that *A. petiolata* populations almost invariably expand within sites once established. Populations do fluctuate in density from year to year and from spring to fall (Figure 5) which may result from density dependent effects, competition between first and second year plants (Winterer et al. 2005), or response to variable environmental conditions and interactions with the receiving community. The sharp decline in *A. petiolata* abundance at Shiawassee in fall of 2004 resulted from the drowning of most seedlings during the flood that spring. This was offset by the large emergence of seedlings the following year. Seasonal variation in abundance (Figure 5) is primarily an artifact of *A. petiolata*'s biennial life cycle. Both seedlings and adults are present during the spring sampling period, but adults senesce in mid-summer leaving just rosettes in the fall counts. The increasing number of invaded quadrats coupled with lower percent cover in newly invaded quadrats partly explains the apparent overall decline in *A. petiolata* cover over time (Figure 6), although the decreases in mean *A. petiolata* cover from 2004 to 2005 may be due in part to environmental conditions such as reduced precipitation in 2005. Over time, we expect that newly invaded quadrats should increase in *A. petiolata* cover to the same levels as quadrats that were initially invaded.

### *Alliaria petiolata* Damage by Herbivores

We observed damage to *A. petiolata* plants 536 out of the 631 times (84.9%) that sampling quadrats contained *A. petiolata* across all sites and years (of 960 total quadrat observations). However, the mean proportion of *A. petiolata* leaf area damaged or consumed per quadrat was estimated to be only  $2.9 \pm 2.2\%$  across all sampling dates, and incidence of more substantial damage was infrequent (Figure 7).

### *Spring Damage*

Within the subset of quadrats that contained *A. petiolata* plants across all sites and years, we observed leaf edge feeding damage in an average of 41.6% (range 13.0 – 62.5%) quadrats sampling<sup>-1</sup>, leaf hole damage in 79.4% (range by site 48.1 – 98.2%), and windowpaning in 7.1% (range 0 – 35.0%) of sampling quadrats. We recorded browse by larger herbivores (i.e. deer, woodchucks) at four sites with damage occurring in 2.8 – 5% of quadrats. The majority of sampling quadrats at the Shiawassee site are located on the Shiawassee River floodplain, which was substantially flooded during the spring of 2004. This accounts for the high *A. petiolata* seedling mortality observed during that season, which was recorded as “other” damage.

*Diseases on A. petiolata in Michigan:* We observed diseased plants at one site in spring 2003 and at three sites in spring 2005 with 1.7 – 8% of quadrats containing diseased plants within those sites. Plants from Ives Road in spring of 2005 had virus-like symptoms but tested negative for cucumber mosaic virus (CMV). Diseased plants were stunted with unusual growth patterns that included highly convoluted leaf surfaces and siliques. Plants with these symptoms were typically grouped close together within a site and were seen at Russ Forest and at the Kellogg Biological Station Bird Sanctuary in Hickory Corners, MI. Wilted plants at the Gasinski Farm demography site in Springville, MI (approximately 20 km west-northwest of the Ives Road site) tested positive for *Pythium sp.* (personal communication Jan Byrne, Mich. State Univ. Plant Disease Diagnostician, Diagnostic Services May 18, 2005), and fungal growths that caused weakening of *A. petiolata* stems at a site approximately 6 km south of Russ Forest were identified as *Sclerotinia sclerotiorum* (white mold) by Dr. Patrick Hart (personal communication. Mich. State Univ. Department of Plant Pathology, May, 2004).

### *Fall Damage*

The damage types we observed in the spring were also most common in the fall. Edge feeding damage occurred in an average of 65.0% (range = 47.8 – 80.0%) quadrats site<sup>-1</sup> sampling<sup>-1</sup>, leaf hole damage in 75.7% (range 44.1 – 97.4%), and windowpaning in 22.6% (range 0 – 32.1%) of quadrats site<sup>-1</sup> sampling<sup>-1</sup>. We saw evidence of browse only once during fall sampling at one site and disease only twice. Diseased plants at Lux Arbor appeared to be virally infected as described above, but those at Shiawassee were only yellowed and not wilted.

### *Extensively Damaged Quadrats*

In most quadrats *A. petiolata* was not accepted for sustained feeding by herbivores, and feeding damage was therefore limited to “tasting” followed by rejection. However, the few quadrats in which *A. petiolata* was more extensively damaged are of special interest because they suggest the possible existence of local populations of herbivores that are more accepting of *A. petiolata*. With the exception of flood damage at Shiawassee in spring 2004, there were only 33 quadrats with greater than 10% leaf area damaged, 28 of which were observed during fall sampling. Most of these represented feeding in quadrats containing a small number of *A. petiolata* plants which may give a false impression of extensive damage. Nearly all quadrats with high damage estimates had holes and edge-feeding damage.

The most interesting cases were in four quadrats: two each from Fernwood in fall 2003 and Lux Arbor in spring 2004 with higher *A. petiolata* cover (10 – 45%) which sustained 10 – 20% leaf area damage. Each of these four quadrats had damage from edge feeding insects and holes from other herbivorous invertebrates, and one at Lux Arbor had been browsed by deer. The extensive edge and hole damage in one quadrat at Lux Arbor (20% damage in a quadrat with 45% *A. petiolata* cover) may be worth monitoring in the future. If local populations of herbivores at some locations are capable of feeding on *A. petiolata* and taking advantage of it as an abundant food source, it is possible that they could multiply and spread to other locations.

Despite the widespread presence of herbivore damage, total leaf area removed averaged 2.1% (range 0.3 – 9.5%) across all sites and years in spring and 4% (range 0.9 – 8.9%) in fall. The highest damage estimate represents the effects of the flood at Shiawassee.

### Impacts of Damage

Correlations between damage to *A. petiolata* and plant performance were insignificant in most analyses (Table 6). The one exception was a significant positive relationship between percent leaf damage and per capita fecundity using spring damage estimates ( $P = 0.0208$ ). This positive association appears to be driven by the Shiawassee site where flooding in spring 2004 caused extensive damage to some plants after they had already produced seed. Thus some plots with high damage still had high fecundity estimates. Dropping this site from the analysis reduces the strength and significance of the association ( $r_s = 0.7143$ ,  $P = 0.0713$ ). It is also possible that moderately damaged plants overcompensate with increased growth or that sites where *A. petiolata* fecundity is highest also harbor larger herbivore populations where spillover feeding is most likely to occur.

These analyses show that the impacts of existing herbivore communities and other forms of damage to *A. petiolata* are not significantly correlated with *A. petiolata* survival or fecundity. Although *A. petiolata* plants were minimally fed upon in the majority of quadrats, this feeding had positive impact on *A. petiolata* performance if any.

## CONCLUSIONS

*Alliaria petiolata* populations are expanding within invaded forests in Michigan. This trend is significant across seven locations where measurement of spread was possible. At an eighth sampling location the population had completely invaded the study area from the initiation of sampling in spring of 2003. Although we were not able to detect increase in the spatial distribution of *A. petiolata* at this site, we were able to show that the distribution has not decreased over the course of the study.

Surprisingly, we found that *A. petiolata* plants are almost universally fed upon by herbivores across southern Michigan. However, damage to plants rarely exceeded 2% of the total leaf area in a quadrat. Although widespread, this feeding appears to have no impact on *A. petiolata* survival or fecundity as we measured it. Because we only sampled each site twice annually, the measures of survival that we used are simplified and do not represent the true demographic rates of these transitions as those in the demography study do. However, because all sampling was done in a short time period each year, using these rates for comparisons between sites is appropriate.

## SUMMARY

The data presented here paint a portrait of an invasive weed that is spreading rapidly into new habitats and is unchecked by natural enemies. These data show that, in Michigan, damage to *A. petiolata* from herbivores is not biologically significant. Our initial modeling exercises indicate that increasing mortality at key stages in *A. petiolata*'s lifecycle with introduced natural enemy insects may present a new opportunity to slow or reverse its spread. Given the potential for *A. petiolata* to cause harm to the communities that it invades as others have shown (e.g. Stinson and Klironomos 2005, Stinson et al. 2006) and the ineffectiveness of conventional controls, classical biological control agents may be recommended for *A. petiolata* in Michigan if agents are approved for release in the future. If natural enemy agents are released, these data will provide a useful benchmark for evaluating their performance.

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**Table 1.** *Alliaria petiolata* demography study sites

<b>Site</b>	<b>Abbreviation</b>	<b>Quadrant</b>	<b>County</b>	<b>Owner/Manager</b>	<b>Characteristics</b>
Shiawassee	SH	NE	Shiawassee	YMCA	upland black locust fragment
Rose Lake	RL	NE	Clinton	Michigan DNR	old-field edge to lowland interior, soft maple overstory
Holland State Park	HSP	NW	Ottawa	Michigan DNR	Lake Michigan back-dune community
Johnson Park	JP	NW	Kent	Kent CO. Parks	hilly urban park, mature hardwood forest
Ives Rd. Fen	IR	SE	Lenawee	The Nature Conservancy	prairie edge to riparian lowland deciduous forest
Gasinski Farm	GF	SE	Lenawee	Gasinski Family	second growth oak forest
ELF	ELF	SW	Cass	Edward Lowe Foundation	high quality upland deciduous forest
Russ Forest	RF	SW	Cass	Michigan State University	mature oak forest

**Table 2.** Michigan sites selected for long-term monitoring of garlic mustard

<b>Site Name</b>	<b>County</b>	<b>Latitude</b>	<b>Longitude</b>	<b>Dominant Canopy Trees (DBH cm)</b>	<b>MNFI Community Type</b>
Box Woodlot	Ingham	42.689479°	-84.489951°	sugar maple (67, 74), silver maple (82, 80), bur oak (69, 67), sycamore (74), green ash (46, 35)	Southern Mesic Forest
Fernwood	Berrien	41.867417°	-86.346351°	White oak (44), red oak (80), tulip tree (51, 60), black walnut (33, 56, 64), hackberry (12), American elm (54), redbud (25), black oak, black cherry	Dry-Mesic Southern Forest
Ft. Custer	Kalamazoo	42.305018°	-85.325651°	Black oak (81), white oak (77, 78), shagbark hickory (76), sugar maple (76), black walnut (43, 46)	Dry-Mesic Southern Forest
Ives Road	Lenawee	41.980206°	-83.932771°	White oak (91), red oak, shagbark hickory	Dry-Mesic Southern Forest
Lux Arbor	Barry	42.492880°	-85.466543°	Red oak (66, 89), white oak (46, 63), black cherry (46)	Dry-Mesic/Dry Southern Forest
Pinckney	Livingston	42.440907°	-84.005645°	White oak (105), black walnut (17), black cherry (51), sugar maple (18), red oak (40)	Dry-Mesic Southern Forest
Russ Forest	Cass	42.011616°	-85.970255°	Black oak (83), white oak (79, 83), black cherry (30, 49), tulip tree (84)	Dry Southern Forest
Shiawassee	Shiawassee	42.885813°	-84.046135°	Silver maple (28), cottonwood (256, 81), black walnut (92), red ash (54), black cherry (43), basswood (39), hackberry (29)	Southern Floodplain Forest

**Table 3.** Number of sampling quadrats at each site where live *A. petiolata* was observed during each spring sampling period and percent change over time. Mean values are  $\pm 1$  SE. Means for percent change and relative percent change do not include data from Fernwood which was fully invaded during all years.

Year	Box	Woodlot	Fernwood	Ft. Custer	Ives Rd.	Lux Arbor	Pinckney	Russ Forest	Shiawassee	Mean
<b>Invaded Quadrats</b>										
2003	16	20	20	7	18	9	10	9	14	13 $\pm$ 1.7
2004	18	20	20	11	17	16	16	14	15	16 $\pm$ 1.0
2005	19	20	20	11	19	15	20	13	18	17 $\pm$ 1.2
<b>Relative Change (%)<sup>a</sup></b>										
2003 $\rightarrow$ 2004	12.5	0.0	0.0	57.1	-5.6	77.8	60.0	55.6	7.1	37.8 $\pm$ 12.2
2004 $\rightarrow$ 2005	5.6	0.0	0.0	0.0	11.8	-6.3	25.0	-7.1	20.0	7.0 $\pm$ 4.7
2003 $\rightarrow$ 2005	18.8	0.0	0.0	57.1	5.6	66.7	100.0	44.4	28.6	45.9 $\pm$ 12.1
<b>Change (%)<sup>b</sup></b>										
2003 $\rightarrow$ 2004	50.0	0.0	0.0	30.8	-50.0	63.6	60.0	45.5	16.7	30.9 $\pm$ 14.8
2004 $\rightarrow$ 2005	50.0	0.0	0.0	0.0	66.7	-25.0	100.0	-16.7	60.0	33.6 $\pm$ 18.0
2003 $\rightarrow$ 2005	75.0	0.0	0.0	30.8	50.0	54.5	100.0	36.4	66.7	59.0 $\pm$ 9.0

<sup>a</sup> Relative percent change indicates the change in the number of invaded quadrats during the time interval indicated relative to the number invaded at the start of the interval.

<sup>b</sup> Percent change is the percent of initially uninvaded quadrats that were invaded during the indicated time interval.

**Table 4.** Univariate repeated measures ANOVA of the number of quadrats invaded by *A. petiolata* over time within sites. Test excludes the Fernwood site where initial conditions prevented estimation of spread.

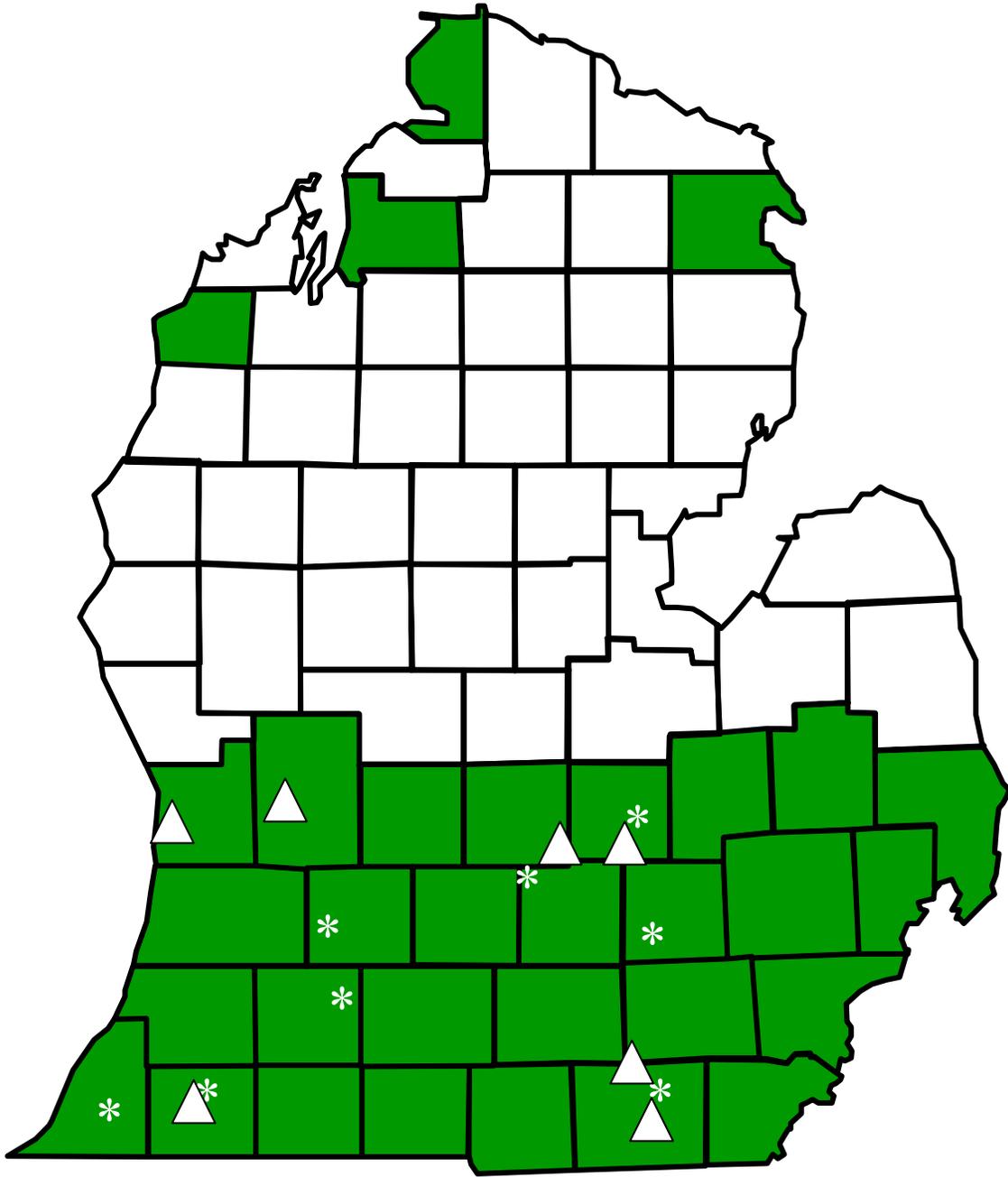
Source	SS	df	MS	F	P
Year	79.2381	2	39.6190	11.8575	0.0014
Error	40.0952	12	3.3413		

**Table 5.** Dunn-Sidak adjusted comparisons of the number of invaded quadrats per site between years.

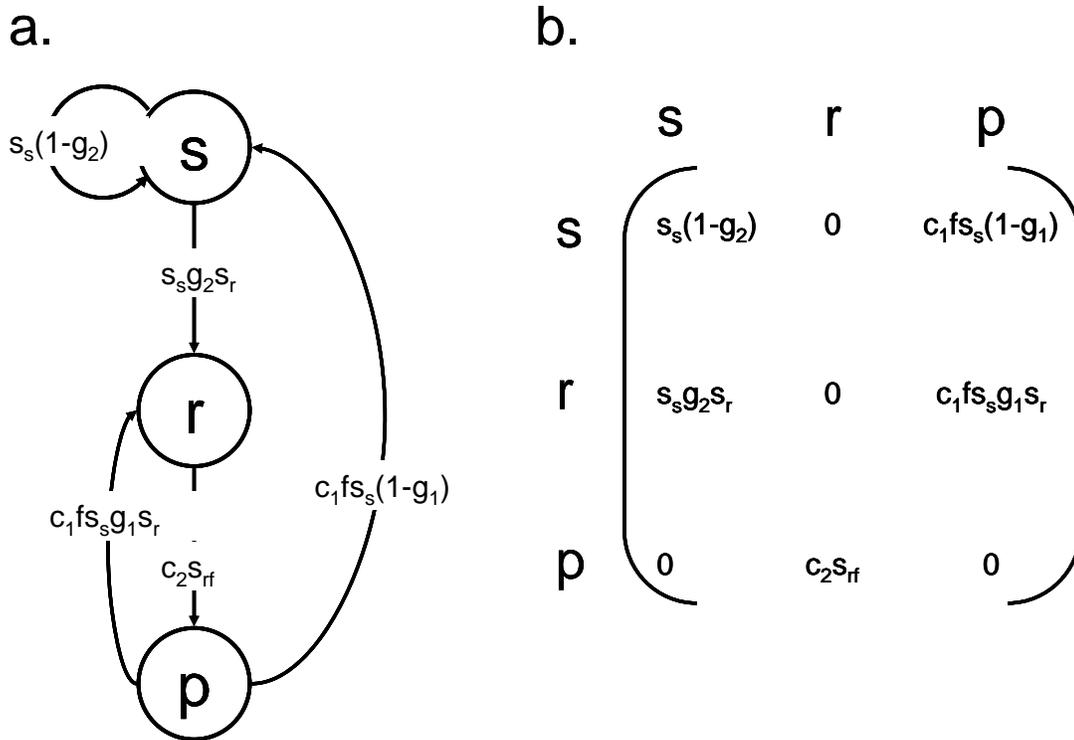
Within Subject Factor Comparing:	Mean Difference Between Levels	Std Error Of Difference	P	Lower 95% CI	Upper 95% CI
2003 ↔ 2004	-3.4286	1.088	0.0582	-6.9904	0.1333
2004 ↔ 2005	-1.1429	0.7377	0.4330	-3.558	1.2723
2003 ↔ 2005	-4.5714	1.0659	0.0154	-8.0609	-1.082

**Table 6.** Spearman rank correlations between percent damage to *A. petiolata* and overwintering survival, seedling survival, and per capita fecundity. Spring and fall indicate the season during which damage estimates were made. *P* values are uncorrected for multiple comparisons.

Season	Overwintering Survival		Seedling Survival		Fecundity	
	$r_s$	P	$r_s$	P	$r_s$	P
Spring	-	-	0.1191	0.7789	0.7857	0.0208
Fall	-0.2190	0.5309	0.0714	0.8665	0.2619	0.5309



**Figure 1.** Approximate known distribution of *A. petiolata* within Michigan's lower peninsula (shaded counties) (Voss 1985, J. Evans and D. Landis pers. obs ) and locations of demography study sites (triangles) and pre-release study sites (stars).

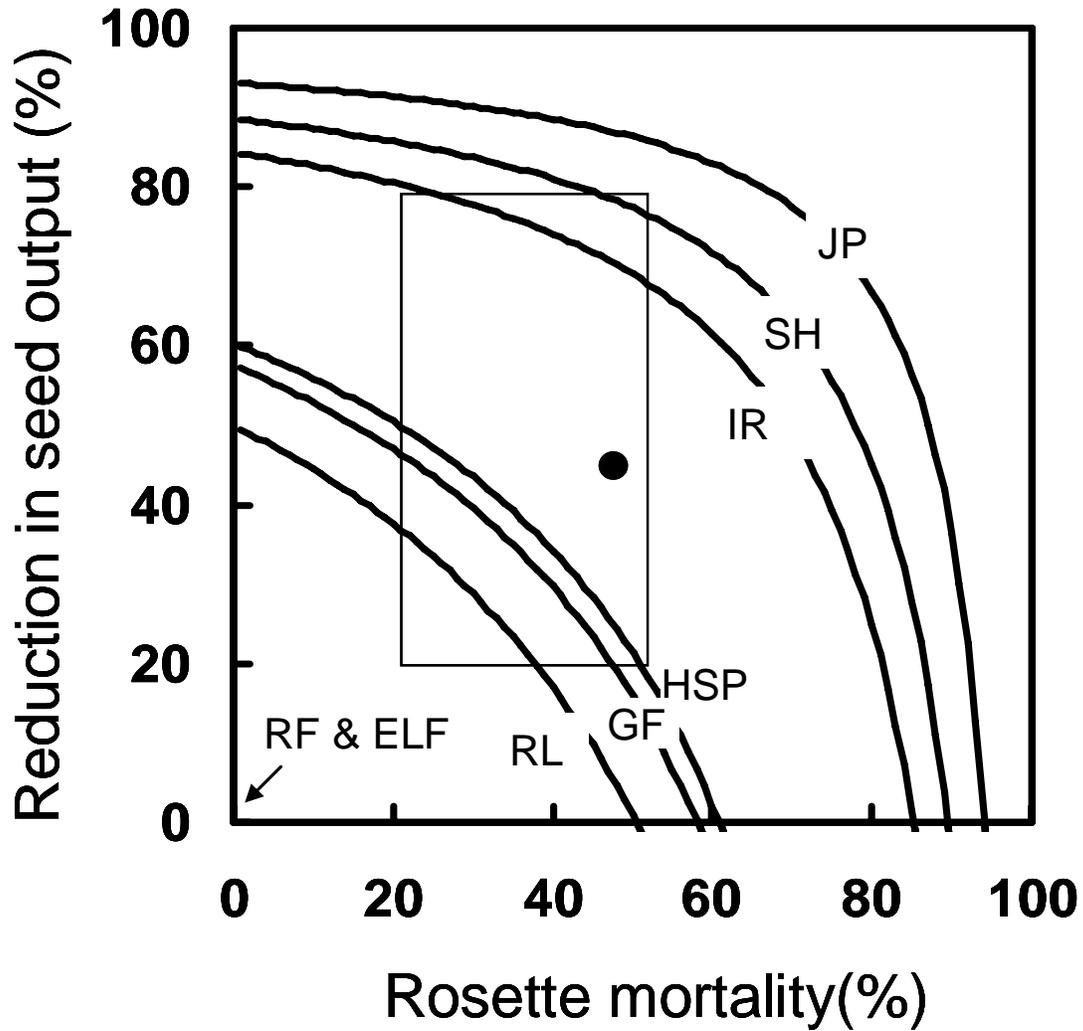


**Figure 2.** Life cycle of *A. petiolata* in a) graphical and b) **A** matrix format. Reproduced from Davis et al. (2005).

Explanation of abbreviations

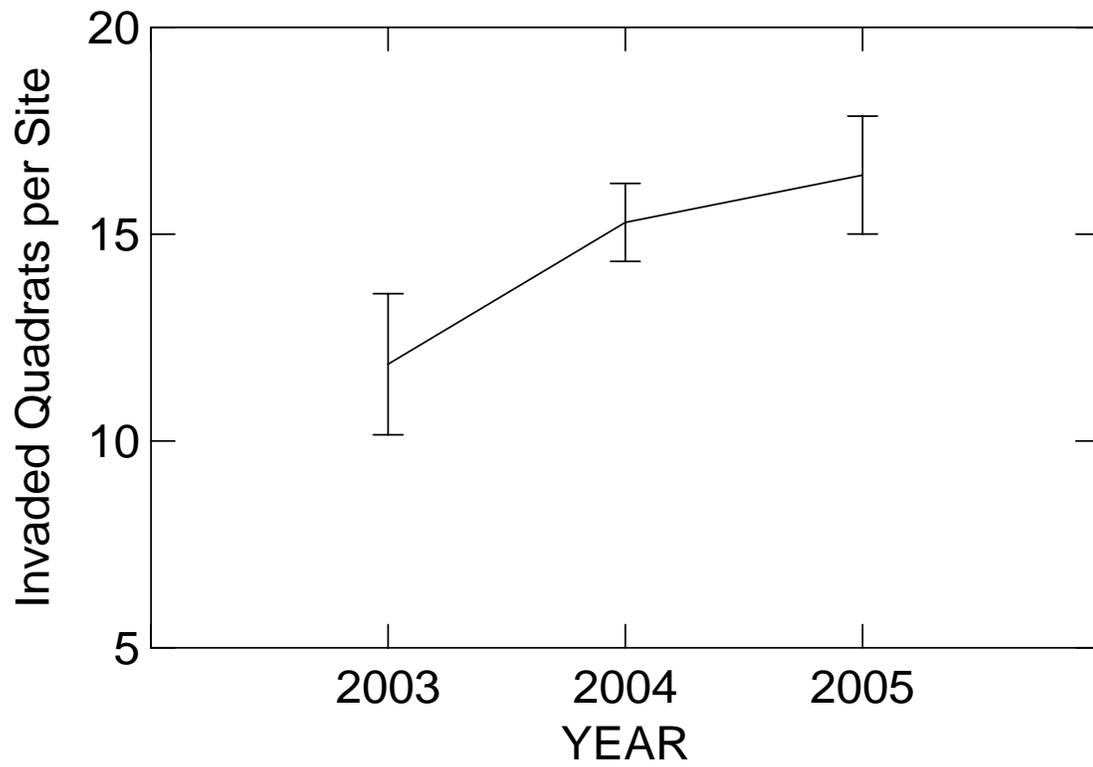
*Life stages:* s = seeds, r = rosettes, and p = adult (second year) plants.

*Lower level demographic parameters:*  $s_s$  = survival of seeds in the soil seedbank,  $g_1$  = germination of seeds in the first year following seed rain,  $g_2$  = germination of seeds from the soil seedbank in the second year following seed rain,  $s_r$  = survival of seedlings to the rosette stage,  $s_{rf}$  = survival of rosettes to the flowering stage, f = fecundity,  $c_1$  = biocontrol by agent affecting seed inputs to seedbank,  $c_2$  = biocontrol by agent affecting rosette survival to flowering stage. All parameters expressed as proportions, with the exception of f, which is expressed in seeds plant<sup>-1</sup>.

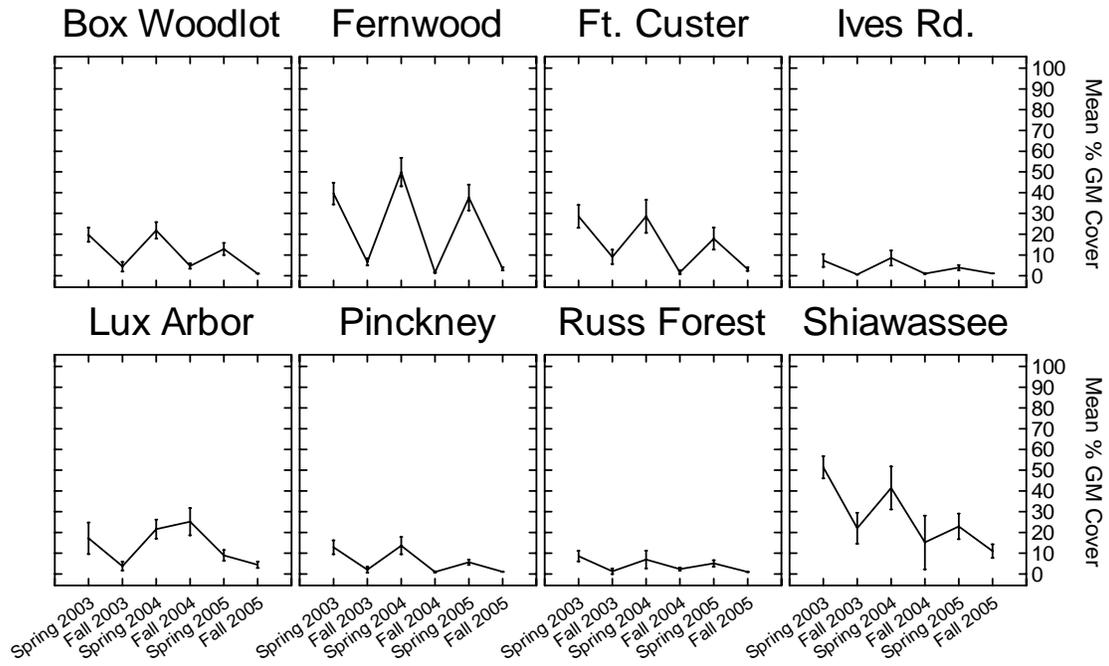


**Figure 3.** Simulated contours of  $\lambda = 1$  for *A. petiolata* at 8 study sites in MI, with overlay (gray box) of pre-release observations of the combined impact of *C. scrobicollis* and *C. alliariae* on seed and rosette survival. Black dot shows impact of *C. scrobicollis* alone.

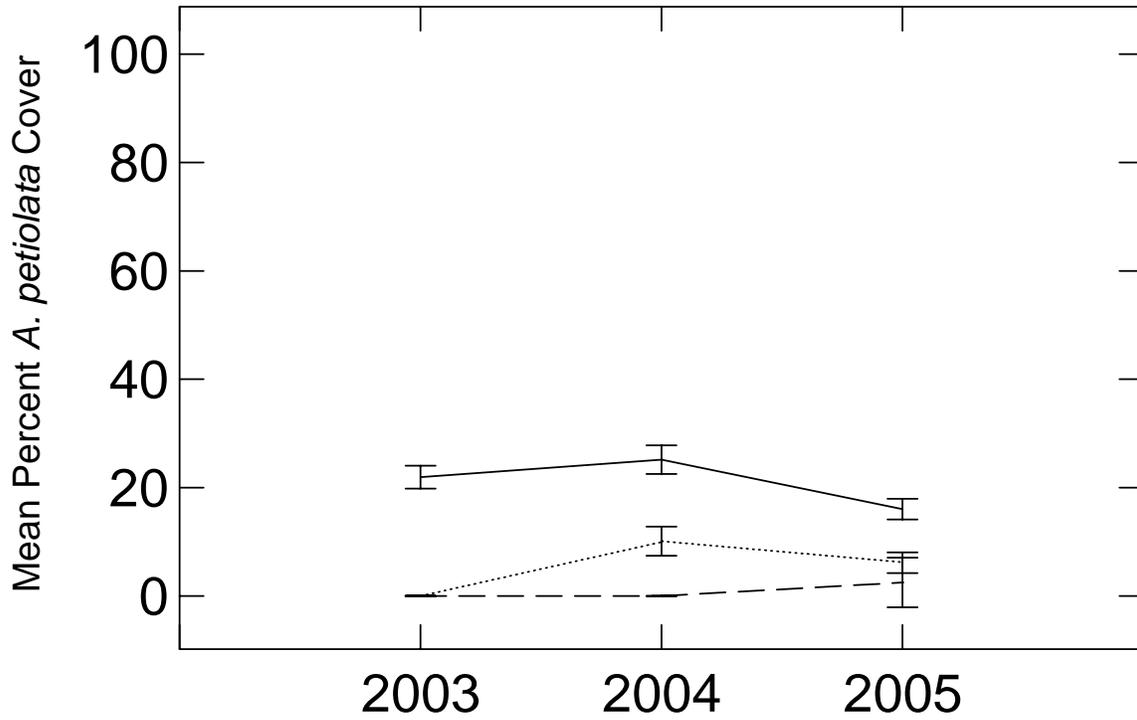
Notes: Contour lines are labeled with abbreviations of site names (see Figure 2 for explanation of abbreviations and map of site locations). The region between each contour line and the x- and y- axes represents all values of seed and rosette survival that result in a declining *A. petiolata* population for a given site.



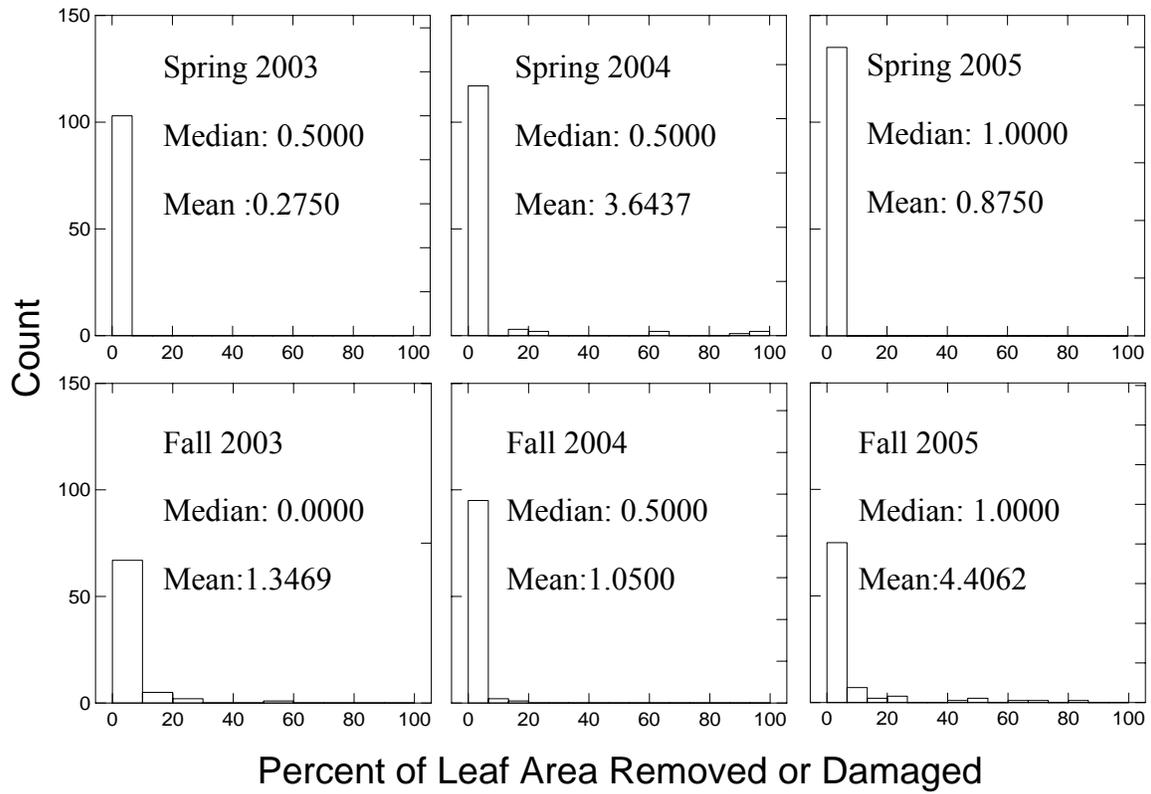
**Figure 4.** Mean number of sampling quadrats per site ( $\pm 1$  SE,  $n = 20$ ) where live *A. petiolata* plants were observed. Fernwood data are not included because all quadrats were invaded there during all three years.



**Figure 5.** The mean percent *A. petiolata* cover ( $\pm 1$  SE) within invaded sampling quadrats across the first six sampling periods has fluctuated seasonally.



**Figure 6.** Mean percent *A. petiolata* cover per quadrat ( $\pm 1$  SE) from all quadrats during each sampling period. Solid line shows quadrats that were invaded in 2003, dotted line shows quadrats that were not invaded in 2003 but became invaded in 2004, and the dashed line shows quadrats that became invaded in 2005. Cover estimates are from spring only.



**Figure 7.** Frequency distribution of damage to *A. petiolata* foliage during each sampling season. Damage was frequent but was rarely extensive.

## Appendix 1. Study site detailed descriptions.

*Box Woodlot:* Box Woodlot is an isolated mesic southern forest (MNFI 2003) surrounded by crop fields with a gravel road along one edge. The overstory is dominated by large *Acer saccharum* (sugar maple) and *A. saccharinum* (silver maple) with *Fagus grandifolia* (American beech) and *A. rubrum* (red maple) occurring less frequently. Vegetation circa 1800 data shows the site as shrub swamp/emergent marsh and mesic southern forest (MNFI 2005). Anthropogenic influences such as isolation, selective cutting and drainage have affected changes in community structure. *Alliaria petiolata* is present throughout the site. Box Woodlot has the lowest plant species richness of the eight study sites with 17 species documented in the sampling quadrats, 16 of which are native.

*Fernwood:* The Fernwood Botanic Garden site is a mature dry-mesic southern forest (MNFI 2003) adjacent to an open community of old fields and restored native prairie. The overstory is dominated by *Quercus alba* (white oak), *Q. rubra* (red oak), *Q. velutina* (black oak), and *Prunus serotina* (black cherry). Prior to settlement the site was broadly classified as mesic southern forest (MNFI 2005). The sampling transects traverse several steep, minor drainages. The transects are approximately perpendicular to the primary slope of the hill and parallel to the forest edge 10 to 20 meters away. *Alliaria petiolata* abundance is greatest along the forest boundary but dense populations persist throughout the interior as well. Frequent deer trails, foot paths, and down-slope drainage are likely means of *A. petiolata* seed dispersal into the forest interior. This site has intermediate species richness with 43 species occurring in the quadrats, 41 of which are native. *Alliaria petiolata* had the largest spatial distribution at this site over the whole study period and occurred in 20/20 sampling quadrats.

*Fort Custer:* Fort Custer is a gently sloping dry-mesic southern to dry southern forest (MNFI 2003) whose canopy is dominated by large *Q. velutina*, *Q. alba* and *Carya ovata* (shagbark hickory) and borders previously disturbed areas along a two-track military access road. Pre-settlement vegetation surveys indicate the site as former mixed oak savanna (MNFI 2005) the largest oaks still showing an open-grown canopy structure. Suppression of fire has transformed the site to closed-canopy forest and led to loss of understory prairie species, although infrequent savanna-like openings persist at the site. *Alliaria petiolata* abundance is heaviest along the forest edge near the access road and in the openings but penetrates the entire forest. Military vehicle and foot traffic along the road and deer trails through the forest interior appear to be the primary means of *A. petiolata* dispersal. Fort Custer had the second highest species richness of the eight study sites with 58 species recorded in the quadrats, 52 of which are native. Invasion by *Berberis thunbergii* (Japanese barberry), *Rosa multiflora* (multiflora rose), and *Lonicera spp.* (bush honeysuckles) is also occurring at this site.

*Ives Road:* The Ives Road Fen Preserve is a 267 hectare property owned and managed by The Nature Conservancy that contains a mix of fen, restored native prairie, southern floodplain forest, and dry-mesic southern forest habitats (MNFI 2003). The study transects quarter a steeply sloping ecotone of mature dry-mesic southern forest that separates the upland restored prairie from the southern floodplain forest. Vegetation circa 1800 data show the lowlands as mixed hardwood swamp bordered by black oak barrens

(MNFI 2005) The ecotone is too narrow to be resolved on the circa 1800 vegetation maps. However, the dominant canopy trees include *Q. alba*, *Q. rubra* and *C. ovata* indicating its coarse soil structure.

*Alliaria petiolata* stands appear most robust along the forest/prairie interface and decline in stature and density as the transects descend towards the bottomlands. *Alliaria petiolata* populations in the bottomlands are characterized by large, robust plants at medium to high densities. The population on the floodplain is addressed in a separate study (Davis et al. 2005). We recorded 48 species in the sampling quadrats at this site, 44 of which are native. *Alliaria petiolata* is the most abundant non-native invasive plant species at the Ives Road site, but *Lonicera spp.*, *R. multiflora*, *Hesperis matronalis* (dame's rocket), *Euonymus alata* (winged burning bush), and *Ligustrum spp.* (privet) also occur.

*Lux Arbor*: Lux Arbor is characterized as a mature dry-mesic southern forest in a bottomland grading up a hill into dry southern forest (MNFI 2003). The canopy is dominated by mature *Quercus velutina* and *Q. rubra* with an understory of modest species richness including several *Rubus* species (brambles) and *Phytolacca americana* (pokeweed). Circa 1800 vegetation data shows the site classified as mixed oak savanna (MNFI 2005). In spring 2005 logging activities led to major changes in canopy density and woody debris at ground level. Most large trees were cleared resulting in greatly increased light availability and substantial soil disturbance. In late spring 2005 we located and re-marked quadrats damaged by logging equipment and continued with normal sampling. *Alliaria petiolata* occurs throughout this site but is most abundant in the more mesic lowland and at the crest of the hill than along the hillside. At Lux Arbor 38 species have been recorded in the sampling quadrats, 34 of which are native. Continued monitoring at this site may reveal information on *A. petiolata*'s response to disturbance and changes in light availability at the population level.

*Pinckney*: The sampling area at Pinckney State Recreation Area is located in a well-drained, mature, dry-mesic southern forest on a gently sloping hillside. Canopy dominants in this system are large *Quercus rubra*, *Q. alba*, and *Carya ovata*, with a diverse understory community including *Cornus florida* and *C. foemina* (flowering and gray dogwoods), *Amelanchier spp.* (serviceberry), and *Sassafras albidus* (sassafras). The two transects are aligned transverse to the slope of the hill. *Alliaria petiolata* is present throughout the site, although abundance is heterogeneous and appears to track animal and foot trails which likely serve as dispersal corridors. Human activities at Pinckney include mountain biking and hiking along a trail approximately 10 – 30 m from the study site and hunting which draws limited foot traffic directly through the sampling area. At the Pinckney site 39 species occur in the quadrats, 38 of which are native.

*Russ Forest*: Russ Forest is an old growth dry southern forest (MNFI 2003) dominated by *Quercus alba* and *Q. velutina*. Large *Acer saccharum*, *Prunus serotina*, and *Liriodendron tulipifera* (tulip tree) trees are also present and *A. saccharum* constitutes the majority of sub-canopy trees. Circa 1800 vegetation maps show the site as mixed oak savanna and mesic southern forest (MNFI 2005). The site topography is flat and level. Two roads border Russ Forest along its northern and western edges. *Alliaria* populations are well established and robust along the forest border to the north and diminish in evenness and

density towards the forest interior. This site has a single, 200 m long transect consisting of 20 evenly spaced sampling quadrats that run parallel to the road which is approximately 15 – 20 m to the north. Russ Forest has lower species richness with 32 species observed in the sampling quadrats, 31 of which are native.

High winds produced during a storm event in the spring of 2004 caused a major blow-down in the northwest corner of the forest. The core blow-down area was completely deforested and is approximately 2 ha in size. Six quadrats at the western end of the transect are either in or near large treefall gaps created by the storm. Subsequent salvage logging operations conducted with horse teams and conventional skidders resulted in soil disturbance. Forest managers instructed logging crews to avoid the *A. petiolata* study area and established a no-entry perimeter that extended approximately 20 m from the sampling areas for this and a separate study in the same forest.

*Shiawasse*: The Shiawasse YMCA Camp site is classified as southern floodplain forest (MNFI 2003) and is located on the floodplain of the Shiawasse River. Two parallel transects run from the first bottom of the river plain, which is dominated by *Acer saccharinum* and *Fraxinus pennsylvanica* and has a relatively open canopy, up a small rise to the second bottom of the river valley (Tepley et al. 2004), which is dominated by *Juglans nigra* (black walnut) and adjoins a two-track service road/foot path and *Pinus sylvestris* (scotch pine) plantation. Prior to settlement the site was classified as mesic southern forest (MNFI 2005), although it is doubtful that the actual floodplain would have supported that community type. *Alliaria petiolata* density is high throughout the site. Plant densities and adult plant sizes are exceptionally high in the second and first bottom floodplain areas, respectively. Second year *A. petiolata* plants on the first bottom were typically multi-stemmed and produced high numbers of seeds. However, the lowest areas, in which greater than 50% of the quadrats are located, are subject to periodic flooding. Flooding eliminated all seedlings and new rosettes from the first bottom areas in the late spring of 2004. Second year plants had already flowered and produced seeds, although they had all been knocked down by the flood. We were able to measure heights and estimate fecundity of the downed second year plants, although this required handling plants to separate and measure matted stems. Shiawasse had the highest species richness of all eight sites. We identified 59 species in the sampling quadrats at Shiawasse, 53 of which were native.