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ScienceDirect
Biological Control 42 (2007) 300–307
Biological Control
www.elsevier.com/locate/ybcon

Pre-release monitoring of *Alliaria petiolata* (garlic mustard) invasions and the impacts of extant natural enemies in southern Michigan forests

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Received 17 January 2007; accepted 30 May 2007
Available online 9 June 2007

Abstract

Monitoring of populations of a target weed species prior to releasing natural enemies has the potential to improve the rigor and safety of biological control and to determine the invader's impacts on native communities while creating a reference point for evaluating the efficacy of subsequent biocontrol agent releases. Eight populations of garlic mustard, *Alliaria petiolata* (M. Bieb) Cavara and Grande (Brassicaceae), an invasive weed in southern Michigan, were monitored in anticipation of releases of classical biological control agents. The *A. petiolata* populations were shown to be expanding with 44.4% of initially uninvaded sampling quadrats becoming invaded after four years. While 88.2% of quadrats with *A. petiolata* showed evidence of foliar damage from pathogens and browsing by mammals, insects and other invertebrates, levels of damage were low and had little impact on rosette or seedling survival. Contrary to expectations, damage was positively correlated with *A. petiolata* fecundity ($P = 0.0465$). Given the continued expansion of *A. petiolata* and the lack of significant herbivore damage by acquired natural enemies, a biological control program should be considered against this invasive plant. If biological control agents are released, the results of this study will provide a benchmark for evaluating their performance.

Keywords: Pre-release monitoring; Herbivore damage; Invasiveness; Before–After, Control–Impacts (BACI); Agent impacts; *Alliaria petiolata*; *Ceutorhynchus*

1. Introduction

As many as 5000 non-indigenous plant species are naturalized in the United States (Pimentel et al., 2000) and present a variety of management challenges (Wilcove et al., 1998; Pimentel et al., 2000; Pimentel, 2005). Practitioners of classical weed biological control consider introductions of natural enemies to be a potentially effective and environmentally safe management option. Waterhouse (1998) found that of over 350 introductions of weed biocontrol agents, only eight showed signs of non-target damage. Although this safety record is impressive, some authors have identified areas in which the practice of biological control could be improved. Calls have been made for increased evaluation of risks to non-target native species (e.g. Simberloff and Stiling, 1996), selection of agents with strong impacts on target weeds (e.g. McEvoy and Coombs, 1999; Pearson and Callaway, 2003), and follow-up monitoring of weed biocontrol (Howarth, 1991).

Weed biocontrol practitioners are responding to these calls through greater focus on native non-target plant species in host specificity trials (McFadyen, 1998; Delfosse, 2005), *a priori* evaluation of target weed susceptibility to particular biocontrol agents (Briese, 2006; Davis et al., 2006), and regulation and implementation of post-release monitoring (Delfosse, 2005). Pre-release monitoring could further improve the quality and scope of post-release evaluation of agent efficacy (Blossey, 1999) and facilitate understanding of weed interactions within invaded communities by establishing benchmark data suitable for Before

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doi:10.1016/j.biocontrol.2007.05.018

and After, Control and Impact (BACI) studies (Gotelli and Ellison, 2004). BACI studies use a type of repeated measures experimental design that allows comparison of a response variable within experimental units before and after a treatment (e.g. a biocontrol agent release). Additionally, pre-release studies of potential target weeds can be used to rationalize target and agent selection processes (Davis et al., 2006).

Alliaria petiolata (M. Bieb) Cavara and Grande (garlic mustard) (Brassicaceae) is a biennial invasive weed of European origin that is now widely distributed across North America (Nuzzo, 1993, 2000; USDA-NRCS, 2007). It is notable for its ability to establish in high quality forest understories as well as disturbed areas and edge habitats. Allelochemicals produced by *A. petiolata* disrupt the development of mycorrhizal associations that are essential to many later successional species (Wolfe and Klironomos, 2005; Stinson et al., 2006) and may also directly suppress the germination and growth of some competitors (Prati and Bossdorf, 2004). Exotic earthworms that increase litter cycling rates are also postulated to facilitate *A. petiolata*'s spread and dominance in some systems (Bohlen et al., 2004; Hale et al., 2005).

Alliaria petiolata seedlings emerge at high densities in early spring and grow over the summer to form low rosettes of petiolate leaves. Seedling mortality during summer is high, with fewer than 20% of seedlings surviving to the rosette stage in southern Michigan (J. Evans, unpublished data). Rosettes overwinter as green plants, then bolt, flower, set seed and senesce in summer of the second year. Overwintering rosette survival in southern Michigan ranged from 52% to 89% from fall of 2004 to spring of 2005 (J. Evans, unpublished data). Seeds are produced in siliques along the upper stem and are released from mid summer though mid autumn. Seeds can remain viable in the soil for at least 10 years (V. Nuzzo and B. Blossey, unpublished data). The longevity of the seedbank dictates that any effective control efforts will have to be sustained over many years until the seed supply is exhausted (Drayton and Primack, 1999). This requirement is impractical for managers using conventional methods in all but the smallest infestations.

A search for suitable biological control agents for *A. petiolata* was initiated in 1998 (Hinz and Gerber, 1998; Blossey et al., 2001) with efforts now focused on four weevils in the genus *Ceutorhynchus* (Coleoptera: Curculionidae) that target different stages in *A. petiolata*'s life cycle (Hinz and Gerber, 1998, 2000, 2001; Gerber et al., 2002, 2003, 2004, 2005, but see Blossey et al., 2001). In order to evaluate the impacts and effectiveness of future biocontrol efforts, *A. petiolata*-invaded communities were monitored in advance of the anticipated natural enemy releases. Our objectives were to (1) describe the study sites and invaded communities, (2) determine whether Michigan *A. petiolata* populations were spreading within infested sites, and (3) measure the degree to which existing herbivores were affecting *A. petiolata* populations. If biological control is to be used against *A. petiolata* in the future, initial releases in Michigan 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.

2. Materials and methods

2.1. Site selection

Eight study sites were set up across the southern four tiers of counties in Michigan's Lower Peninsula where *A. petiolata* is established (Table 1). 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 had been established for at least four years, and (4) with protection from future disturbance or *A. petiolata* management for at least 10 years. In spring of 2003, 10 permanent 0.5 m^2 sampling quadrats (0.5×1 m) were marked 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 an 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. It was not possible to determine exactly how long *A. petiolata* had been established at each site prior to 2003, although the extent of the invasions and anecdotal evidence from managers indicated that they equaled or exceeded four years in all cases.

2.2. Alliaria petiolata evaluations

Data were collected on *A. petiolata* distribution and abundance in accordance with a standardized protocol (Nuzzo and Blossey, 2003). In spring (June) and fall (Sept.–Nov.) of 2003–2006 we visited each site and recorded data from each quadrat ($n = 1280$ total quadrat observations over eight sampling periods from 2003 to 2006) including: percent vegetation cover (*A. petiolata* total, *A. petiolata* by mature, seedling, and rosette stage plants, total non-*A. petiolata* vegetation and non-A. *petiolata* vegetation by species), counts of *A. petiolata* mature plants, seedlings and rosettes, percent cover of substrate (bare soil, leaf litter, woody debris, and rock sum to 100%), and litter depth (cm). Damage to *A. petiolata* plants was recorded as the estimated percent of leaf area removed, and nine categories of damage to *A. petiolata* were identified as either present or absent in each quadrat [leaf mining, windowpaning, edge feeding, holes, spittle bug or scale damage (noted as leaf-chlorosis from sap-sucking), browse, disease, and other]. The number of siliques on each mature second-year plant was recorded during the spring sampling period to allow estimation of fecundity.

In contrast to the methods outlined by Nuzzo and Blossey (2003), not all sampling quadrats at each site contained

Table 1
Michigan sites selected for long-term monitoring of *Alliaria petiolata* and possible future biocontrol agent releases

Site name	County	Latitude	Longitude	Dominant canopy trees[a] (DBH[b] cm)	Community type[c]	SR[d]
Box Woodlot	Ingham	42.6894°	−84.4899°	ACSA2 (82), ACSAS (74), PLOC (74), QUMA2 (69), FRPE (46)	Southern mesic forest	17
Fernwood	Berrien	41.8674°	−86.3463°	QURU (80), JUNI (64), LITU (60), ULAM (54), QUAL (44), CECA4 (25), CEOC (12), PRSE2, QUVE	Dry-mesic southern forest	49
Fort Custer	Kalamazoo	42.3050°	−85.3256°	QUVE (81), QUAL (78), CAOV2 (76), ACSAS (76), JUNI (46)	Dry-mesic southern forest	58
Ives Road	Lenawee	41.9802°	−83.9327°	CAOV2 (91), QUAL (91), QURU	Dry-mesic southern forest	48
Lux Arbor	Barry	42.4928°	−85.4665°	QURU (89), QUAL (63), PRSE2 (46)	Dry-mesic/dry southern forest	38
Pinckney	Livingston	42.4409°	−84.0056°	QUAL (105), PRSE2 (51), QURU (40), ACSAS (18), JUNI (17)	Dry-mesic southern forest	39
Russ Forest	Cass	42.0116°	−85.9702°	LITU (84), QUAL (83), QUVE (83), PRSE2 (49)	Dry southern forest	32
Shiawassee	Shiawassee	42.8858°	−84.0461°	PODE3 (256), JUNI (92), FRPE (54), PRSE2 (43), TIAM (39), CEOC (29), ACSA2 (28)	Southern floodplain forest	59

[a] Tree Species (after USDA-NRCS, 2007): ACSA2, Silver Maple (*Acer saccharinum* L.); ACSAS, Sugar Maple (*Acer saccharum* Marsh.); CECA4, Redbud (*Cercis canadensis* L.); CEOC, Hackberry (*Celtis occidentalis* L.); CAOV2, Shagbark Hickory (*Carya ovata* (Miller) K. Koch); FRPE, Green Ash (*Fraxinus pennsylvanica* Marsh.); JUNI, Black Walnut (*Juglans nigra* L.); LITU, Tulip Tree (*Liriodendron tulipifera* L.); PLOC, Sycamore (*Platanus occidentalis* L.); PODE3, Cottonwood (*Populus deltoides* Marsh.); PRSE2, Black Cherry (*Prunus serotina* Ehrh.); QUAL, White Oak (*Quercus alba* L.); QUMA2, (*Quercus macrocarpa* Michaux); QURU, Red Oak (*Quercus rubra* L.); QUVE, Black Oak (*Quercus velutina* Lam.); TIAM, Bass Basswood (*Tillia americana* L.); ULAM, American Elm (*Ulmus americanum* L.).
[b] Diameter at breast height of largest specimen of each dominant tree species. DBH not available for three small trees at Fernwood and Ives Road.
[c] Based on Michigan Natural Features Inventory (2003). See Evans (2006) for details.
[d] Species richness = the number of ground layer species identified in the sampling quadrats from 2003 to 2005.

A. petiolata at the initiation of our study. Rather, transects were laid across what was perceived as the ''invasion front'' at each site such that they passed through both invaded and uninvaded areas where possible. This was done to allow measurement of *A. petiolata* population spread within sites. All 20 quadrats at one site (Fernwood) contained *A. petiolata* from the outset of the study. This site was therefore not included in analyses of population spread.

2.3. Site descriptions

The Michigan Natural Features Inventory (MNFI) has identified 74 plant community-types that occur in Michigan (MNFI, 2003). Sites were qualitatively described in terms of standard MNFI community types using the identities, sizes, and abundances of the principal canopy trees, physical site features and the inventories of all ground-layer vascular plant species that occurred in the sampling quadrats from June 2003 to October 2005 (Table 1). Detailed site descriptions are presented in Evans (2006).

2.4. Spread of Alliaria petiolata within sites

Each quadrat was coded as either invaded or uninvaded during each sampling period based on the presence of absence of live *A. petiolata* plants. Linear trends in the number of invaded quadrats per site over time were tested with a repeated measures general linear model using the REPEATED command in SAS version 8.2 PROC GLM (SAS Institute, 2001). The assumption of sphericity for within-subjects effects in univariate repeated measures analysis was evaluated with Mauchly's test (Scheiner and Gurevitch, 2001). Between-year differences in the number of invaded quadrats per site were tested using GLM contrasts (GLM command, SYSTAT Inc., 2004).

2.5. Estimation of Alliaria petiolata fecundity

Fecundity was estimated non-destructively in the field by counting the number of siliques $plant^{-1}$ and multiplying by the number of seeds $silique^{-1}$. This ratio was calculated using a linear regression (SYSTAT Inc., 2004) of number of seeds $plant^{-1}$ on number of siliques $plant^{-1}$ from 132 mature plants collected from six locations in southern Michigan: Edward Lowe Foundation ($n = 30$), Cassopolis; Gasinski Farm ($n = 30$), Springville; Holland State Park ($n = 24$), Holland; Johnson State Park ($n = 12$), Wyoming; Rose Lake Wildlife Management Area ($n = 29$), East Lansing; Shiawassee YMCA Camp ($n = 7$), Bancroft). The number of siliques was counted on each plant. Seeds were then dissected out and counted using an automated seed counter (SeedBuro model 801 Count-A-Pac Seed Counter®, SeedBuro Equipment Co., Chicago, IL).

2.6. Calculation of survival probabilities

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

Seedling mortality extends from the beginning of the germination period in March into the summer. Our sampling method captured the number of seedlings present during a single visit but did not account for seedling mortality prior to spring sampling or the germination and mortality of additional seeds between spring and fall sampling.

2.7. Herbivore impacts on Alliaria petiolata

Spearman rank correlations between estimated percent leaf damage to *A. petiolata* and per capita fecundity, seedling survival, and rosette survival were used to test the potential impacts of herbivore damage on *A. petiolata*. All analyses were performed on site mean values in invaded quadrats across the four years of sampling. The mean for each parameter at each site was first calculated for each year or transition period. Site mean values were then calculated by averaging across the four years for each parameter. Spring leaf damage estimates were correlated with seedling survival and fecundity and with overwintering survival of rosettes from the previous fall. Correlations were also calculated between fall leaf damage and survival of seedlings from the preceding spring, between fall damage and fecundity during the following spring (previous fall damage) and between fall damage and overwintering rosette survival to spring of the following year (previous fall damage). The study included four summers (beginning in spring 2003) and three overwintering periods (beginning in fall 2003). Thus, there were four estimates of seeding survival and fecundity but only three estimates of overwintering survival. Statistical significance was interpreted using $\alpha = 0.05$ and variability is shown as ±one standard error.

2.8. Sampling error

Two forms of observational error were detected in the data. These errors most often occurred during the first year of the study when we chose not to move the leaf litter to search for obscured *A. petiolata* individuals or in quadrats where *A. petiolata* density was lowest and any overlooked plants represented a greater proportion of the quadrat total. Out of 1280 total observations there were 19 cases where fewer seedlings were recorded in spring than the number of rosettes observed in fall and 13 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 10 cases where flowering plants were observed where no rosettes had been recorded the previous fall (divide by zero error). A survival rate of 100% was conservatively estimated for all of these 62 observations in analyses of herbivore impacts. In the repeated measures analysis corrected invasion status of these quadrats was inferred by assuming that if rosettes were present in a quadrat in the fall, that the quadrat had contained seedlings in the spring. Similarly, if a quadrat had contained mature plants in the spring, it was assumed to have contained rosettes the previous year.

3. Results and discussion

3.1. Spread of Alliaria petiolata within sites

The number of *A. petiolata*-invaded quadrats site^{-1} ($n = 20$ site^{-1}) increased an average of 44.4 ± 20.7% from 2003 to 2006 (repeated measures ANOVA $F_{3,18} = 5.2822$, $P = 0.0086$, Table 2), and the assumption of sphericity was satisfied (Mauchly's $W = 0.5468$, df = 5, $\chi^2 = 2.8511$, $P = 0.7229$). Between-year contrasts of the number of invaded quadrats per site revealed insignificant change from 2003 to 2004 ($F_{1,6} = 2.7500$, $P = 0.1483$). However, over the two year period from 2003 to 2005 and the three year period from 2003 to 2006 the changes were significant and positive ($F_{1,6} = 8.2373$, $P = 0.0284$ and $F_{1,6} = 7.7279$, $P = 0.0323$, respectively).

This analysis offers quantitative support for the frequent, qualitative observation that *A. petiolata* populations almost invariably expand within sites once established. The spread reported here is from a combination of new quadrat invasion events and "reinvasions" from either new seed dispersal into the quadrats or germination from the seedbank, which buffers populations against stochastic mortality. In 16 instances live *A. petiolata* were not observed in quadrats that had been invaded the previous year. In 11 of these cases *A. petiolata* reappeared in the quadrat a year later. At one site *A. petiolata*'s overall distribution decreased in 2004 but rebounded during the following year. These interannual fluctuations in population density may result from density dependent mortality, competition between first and second-year plants (Winterer et al., 2005), or response to environmental variability and interactions with the invaded community. Identifying these stochastic changes required pre-release monitoring over at least three generations and will give us a valuable opportunity to evaluate the impact of future biocontrol efforts on *A. petiolata*. While it would be desirable to estimate the rate of *A. petiolata* spread either within sites or across the landscape, the data are not suited to that purpose.

Table 2
Number of sampling quadrats at each site (of 20 site^{-1}) in which living *Alliaria petiolata* was observed and percent change over time by year

Year/interval	Box woodlot	Fernwood	Fort Custer	Ives Road	Lux Arbor	Pinckney	Russ Forest	Shiawassee	Mean
Invaded quadrats									
2003	17	20	9	18	14	13	9	18	14.0 ± 1.5
2004	19	20	11	18	16	16	14	15	15.6 ± 1.0
2005	19	20	12	19	15	20	13	18	16.6 ± 1.2
2006	18	20	16	17	20	20	16	18	17.9 ± 0.6
Relative change[a] (%)									
2003 → 2004	66.7	n/a	18.2	0.0	33.3	42.9	45.5	−150.0	34.4[b] ± 8.8
2003 → 2005	66.7	n/a	27.3	50.0	16.7	100.0	36.4	0.0	42.4 ± 12.6
2003 → 2006	33.3	n/a	63.6	−50.0	100.0	100.0	63.6	0.0	44.4 ± 20.7

Mean values are ±1 SE and do not include data from Fernwood which was fully invaded during all years.
[a] Relative change is the percent of initially uninvaded quadrats that were invaded during the indicated time interval.
[b] Calculated without Shiawassee. Flooding at Shiawassee in spring 2004 affected plants in nine of 20 quadrats. Value with Shiawassee included is 8.1 ± 27.5.

3.2. Estimation of Alliaria petiolata fecundity

The ratio of seeds per plant to siliques per plant was consistent across sites. Plants ranged in number of siliques from 0 to 266. The linear regression of the number of seeds versus siliques had a slope of 14.2996 ($R^2 = 0.9805$), meaning that each silique contained an average of 14.3 seeds. Mean per capita fecundity by site ranged from 0 to 446 across all years with a mean per capita fecundity across all sites and years of 207. The maximum estimated fecundity of any individual plant was 6177 seeds.

3.3. Alliaria petiolata damage by herbivores

Damage to *A. petiolata* plants was frequent but rarely extensive. Leaf damage was observed 785 out of the 890 times (88.2%) that sampling quadrats contained *A. petiolata* across all sites and years. However, the mean proportion of *A. petiolata* leaf area damaged or consumed per quadrat was estimated to be only 3.3 ± 0.3% across all sampling dates, and incidence of more substantial damage was infrequent (Fig. 1).

Within the subset of quadrats that contained *A. petiolata* plants during spring sampling across all sites and years, leaf-edge feeding damage occurred in an average of 54.9% (range 28.2–75.0%) of the quadrats sampled, leaf-hole damage in 78.6% (range 45.1–95.0%), and windowpaning in 27.6% (range 15.4–56.6%) of sampling quadrats. Browse by larger herbivores [e.g. white-tailed deer (*Odocoileus virginianus*) Boddaert, woodchuck (*Marmota monax*) L.] occurred at four sites with damage occurring in 3.7% 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 probably accounts for the high *A. petiolata* seedling mortality observed during that season, which was recorded as "other" damage.

Diseased plants were observed at one site in spring of 2003, three sites in spring of 2005 and one site in spring of 2006 with 1.4–6.2% of invaded quadrats containing diseased plants. Plants from Ives Road in the spring of 2005 had virus-like symptoms resembling cucumber mosaic virus (CMV) but tested negative for this pathogen. These plants were stunted with unusual growth patterns that included highly convoluted leaf surfaces and siliques. Plants with similar 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 (not a study site). Wilted plants in Springville, MI (approximately 20 km west-northwest of the Ives Road site) tested positive for *Pythium* sp. (pers. comm. 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 (pers. comm. Mich. State Univ. Department of Plant Pathology, May, 2004). Chen (1998) has previously identified *S. sclerotiorum* from *A. petiolata* in Illinois. None of the observed pathogens spread or occurred consistently across years within populations. Thus, they seem unlikely to present a viable biocontrol opportunity.

The types of damage observed in the spring were also most common in the fall. Edge feeding damage occurred in an average of 72.1% (range 52.3–83.7%) of invaded quadrats site^{-1} sampling^{-1}, leaf-holes in 74.7% (range 48.0–99.1%), and windowpaning in 34.2% (range 20.9–46.4%) of quadrats site^{-1} sampling^{-1}. Evidence of browse was observed 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.

In most quadrats there was no evidence of sustained feeding on *A. petiolata* by herbivores, and feeding damage was generally limited. 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 38 quadrats with

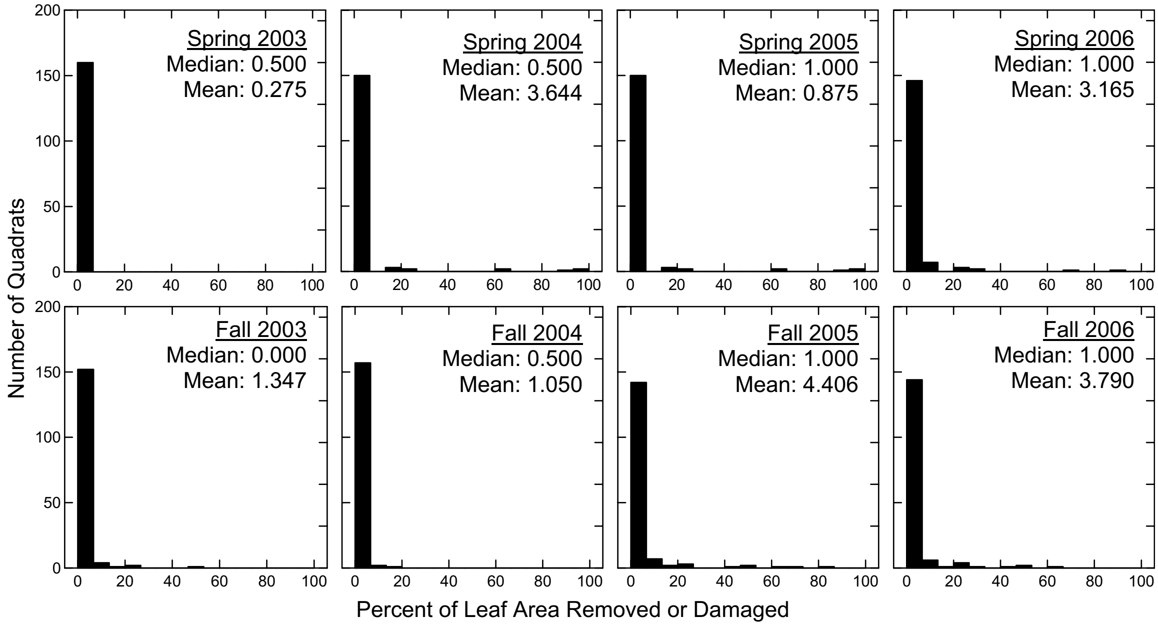

Fig. 1. Frequency distribution of damage to *Alliaria petiolata* foliage during each sampling season.

greater than 10% leaf area damaged, 27 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: one each from Fernwood in fall 2003 and Lux Arbor in fall 2005 and two in Lux Arbor in spring 2004 with higher *A. petiolata* cover (8–45%) which sustained 15–20% leaf area damage. Each of these four quadrats had damage from edge-feeding insects and holes from other herbivorous invertebrates (possibly slugs), 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) will be monitored in the future.

The herbivore species responsible for the feeding damage were not observed. Some caterpillars (Lepidoptera: Pieridae) are known to feed on *A. petiolata* in North America, but not all are able to complete development on it (Porter, 1994b,a; Renwick et al., 2001). The only animals observed actively feeding on *A. petiolata* were small slugs that were frequently present on foliage of senescing second-year plants, though these were not successfully preserved for identification. Despite the widespread presence of herbivore damage, total leaf area removed averaged 2.3% (range 0.6–9.8%) across all sites and years in spring and 4.5% (range 1.8–6.7%) in fall, and the highest damage estimates represented the impacts of flooding.

3.4. Herbivore impacts on Alliaria petiolata

Correlations between damage to *A. petiolata* and plant performance were insignificant in all but one analysis (Table 3). The exception was a barely significant but positive relationship between percent leaf damage and per capita fecundity using spring damage estimates ($r_s = 0.7143$, $P = 0.0465$). It is possible that moderately damaged plants overcompensated with increased growth (sensu Agrawal, 2000; Guillet and Bergstrom, 2006) or that sites where *A. petiolata* fecundity is greatest 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* did not significantly affect the weed's

Table 3
Spearman rank correlations (r_s) between percent damage to *Alliaria petiolata* and overwintering survival, seedling survival, and per capita fecundity

Damage estimated	Overwintering survival		Seedling survival		Fecundity	
	r_s	P	r_s	P	r_s	P
Spring	0.0714	0.8665	0.3333	0.4198	0.7143	0.0465
Fall	—	—	0.0714	0.8665	—	—
Previous fall	−0.5238	0.1827	—	—	0.57143	0.1390

Spring, fall, and previous fall indicate the season during which foliar damage estimates were made relative to when survival or fecundity estimates were made.

survival or fecundity. Although *A. petiolata* plants were minimally fed upon in the majority of quadrats, this feeding had a positive impact on *A. petiolata* performance if any.

4. Conclusions

The ability of a pre-release study to facilitate post-release agent evaluation will depend on its capacity to characterize natural spatiotemporal variability in the target species' rates of spread and survival. Our four-year record of *A. petiolata* has followed three full cohorts from seedling to seed, and we are just now beginning to resolve the effects of annual variation in environmental conditions and various stochastic population behaviors. For longer-lived target species or those with less predictable life histories, longer pre-release studies might be necessary to later discern the subtle impacts of natural enemies from natural population variability. Additionally, it is crucial to identify *a priori* measurements of target performance that will later aid in agent evaluation. For example, if a seed-feeding insect is being considered as a weed biocontrol agent, collecting pre-release fecundity or seedbank data would be rewarding. Finally, we would advise future investigators conducting similar studies to place their sampling quadrats randomly or haphazardly, rather than linearly, which effectively limited our ability to perceive spatial spread to a single, linear dimension.

The results of this study paint a portrait of an invasive weed that is spreading rapidly into new habitats and is unchecked by extant natural enemies. Preliminary demographic models of Michigan *A. petiolata* populations indicate that increasing herbivore damage with introduced natural enemies may present a new opportunity to slow or reverse its spread (Davis et al., 2006). Given the potential for *A. petiolata* to cause harm to the communities that it invades and the ineffectiveness of conventional controls, classical biological control may be considered for *A. petiolata* in Michigan if agents are approved for release in the future. If natural enemy agents are released, these data will provide useful benchmarks for evaluating their performance.

Acknowledgments

We thank Adam Davis, Anna Fiedler, Mary Gardiner, John Hoffmann and two anonymous reviewers for helpful comments that improved this manuscript and R. Johnston, T. Lehman, R. McDonald, M. Murphy, K. Newhouse, D. Sebolt, C. Stahlman, N. Vuljaj, and M. Wood for assistance with data collection and management. We thank Fernwood Botanic Garden, Michigan State University, Michigan DNR, Michigan DMVA, The Nature Conservancy, and the Shiawassee YMCA Camp for access to field sites. These studies were supported in part by the Michigan Department of Natural Resources, the Michigan Department of Military and Veteran's Affairs, The Michigan Agricultural Experiment Station, US Department of Agriculture, under agreement number 2005-35320-15312, and by fellowships to J. Evans: the Michigan State University Plant Sciences Fellowship and EPA STAR Graduate Fellowship FP-91650101.

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